Riparian vegetation response to clearcutting along small streams of boreal forest

by

Shekhar R. Biswas

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for the degree of Master of Science in Biology

Department of Biology

Lakehead University
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Abstract

In this thesis I examined three important ecological questions to understand the role of forest management disturbance on unmapped small stream riparian plant communities: i) how do small stream riparian plant communities respond to forest harvesting and site preparations? ii) How do species diversity – functional diversity relationships vary in disturbed riparian and disturbed upland habitats? and iii) Do riparian buffer reserves act as plant refuges in the clearcut boreal forests?

In chapter 1, I answer the first question by reviewing and synthesizing published (searching ISI Web of Knowledge^{TM} database) and grey literature. I found that small stream riparian plant communities are very poorly studied. Forest harvesting and scarification significantly reduce riparian plant species richness and diversity causing a shift from herbaceous to shrub dominance. I suggest that disturbance along small streams may facilitate the spread of invasive species into the streams that are protected by buffer reserve. I argue that the distribution patterns of plant functional traits might be useful as a predictor in developing an early warning system against habitat degradation.

In chapter 2, I answer the second question by sampling naturally colonized plants along small streams in clearcut, clearcut plus soil scarification, riparian buffer reserve near clearcut, riparian buffer near clearcut plus soil scarification and uncut reference sites. Using 36 sets of functional traits as a surrogate of functional diversity, I test the effects of disturbance on species diversity – functional diversity relationships in two habitats: riparian and upland. I found that both species diversity and functional diversities reach their peak under moderate intensity of disturbance, producing a bell shaped disturbance-diversity curve. The disturbance-habitat sensitivity coupling has very little effect on overall diversity although the effect on particular life forms and functions may be significant. The novel finding in this study is that in natural communities, species-functional diversity relationships are linear in low intensity disturbance but this relationship shifts to curvilinear (quadratic) with moderate to high intensity of disturbance, due to uneven functional redundancy. This finding invokes that the current approach of conservation that predominantly relies on species richness needs to be reevaluated by considering plant functional traits.

In chapter 3, I answer the third question by sampling plant communities around small streams in the clearcuts, the riparian buffer reserves around clearcut and in the uncut reference forests. I used a combination of trait based functional dichotomy and plant cover to predict plant colonization from the clearcuts to riparian buffer reserves. I found that riparian buffer reserves support more species than the clearcuts and the reference forests. In the trait display I was able to show that additional species in riparian buffer reserves were coming from adjacent clearcuts. This finding suggests that in the boreal forest, riparian buffer reserves act as refuges for plants, especially in the early stages after clearcutting. This finding invokes that careful management of riparian buffers may help in reducing the local extinction risk of many disturbance-sensitive plants.

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Introduction

Loss of biodiversity and the proportional loss of ecosystem functions has likely been the most dramatic change humans have imposed on ecosystems in the past century (Chapin et al. 2000). Natural resource managers and ecologists have been trying to understand the effects of disturbance on biodiversity and ecosystem functions. Most of these studies are conducted in biodiversity rich areas (Lamb et al. 2003). Riparian ecosystems, located at the land-water interface, are one of the most biologically diverse and functionally active ecosystems in the boreal forest (Naiman et al. 2005). Riparian habitats are considered to be biodiversity hotspots and are attributed high conservation value (Naiman and Decamps 1997, Malanson 1993, Naiman et al. 2005, Sabo et al. 2005). Current understanding of riparian ecology is largely based on larger stream riparian ecosystems. Riparian ecosystems of small streams receive very little attention (Hupp 1986, Wipfli et al. 2007), although small streams occupy almost 80% of the total stream length in a watershed (MacDonald and Coe 2007). Studies on small stream riparian plants constitute only 5% of the total published riparian literature. Few studies have been conducted on the response of small stream riparian plants to habitat disturbance; although small stream riparian plant community experiences frequent anthropogenic disturbance from forest management as well as natural disturbance. Natural disturbances include fires, flooding, beaver activities and insect infestations whereas anthropogenic disturbances include forest management by clearcutting and site preparation by soil scarifications.

Ecologists are interested in understanding the responses of ecosystems to anthropogenic disturbance so that negative impacts can be minimized. Lamb (2002) found that anthropogenic disturbances, especially clearcutting, do not affect the species composition of riparian plant communities of relatively larger streams that are protected by riparian buffer reserves. However, how riparian plant communities vary along unmapped small streams that are not protected by riparian buffer reserves respond to the forest management disturbances remains unknown. This knowledge is critical for developing an ecologically sound management plan for forest harvesting around small streams because small streams are connected with larger streams both structurally and functionally (Gomi et al. 1991). In this thesis I review the existing riparian literature and synthesize the possible impacts of, and responses by, small stream riparian plant communities to the forest management disturbances of clearcut harvesting and soil scarification.

One of the main objectives of biodiversity conservation is to conserve functional diversity so that diverse ecosystem functions are sustained. Hence, a clear understanding of the relationship between species diversity and functional diversity is essential, and critical for conservation planning. So far this understanding is mostly based on theoretical study (Naeem 2002). A predominant understanding in conservation ecology is higher the number of species conserved more and more ecosystem functions would be maintained (Loreau et al. 2001, 2002). Very recently Danovaro et al. (2008) challenged this concept. Using deep sea benthic diversity, they provided evidence of an exponential relationship between species diversity and functional diversity. Findings of Danovaro et al. (2008) is a warning for the conservation ecologist since exponential relationship implies that rare species play an important role in sustaining ecosystem functions. Therefore, it is urgent to test this relationship in natural plant communities that are affected by anthropogenic disturbances such as forest harvesting and scarification. To my knowledge no field study evaluated this relationship in naturally colonized plant communities, let alone riparian plant communities, especially in a gradient of habitat disturbances. In this thesis, using plant communities around small streams I evaluate the relationship between species diversity and functional diversity in a gradient of disturbance severity (i.e. varied intensity of forest management disturbances). I also test this in two habitat conditions that differ in their sensitivity to disturbances: riparian and upland habitats.

An important part of riparian management and conservation is the management of riparian buffer reserves. Ecological theory predicts that in the human dominated forest landscape, remnant forest patches play an important role in maintaining biodiversity (Fahrig 2003). In managed North American boreal forests, riparian buffer reserves constitute protected forest patches adjacent to the clearcut forests. It is likely that the riparian buffer reserves may help maintain biodiversity by providing temporary habitat for plants colonizing from the adjacent clearcut forest. In other words riparian buffer reserves may act as refuges for plants. This potential role of riparian buffer reserves as refuges for plants has never been evaluated, although this understanding could help in effective planning for riparian plant conservation.

This thesis consists of three chapters covering three important ecological aspects of small stream riparian plants in the context of habitat disturbance. These are i) a review and synthesis on how small stream riparian plant communities respond to forest management, ii) an empirical study on the effects of disturbance on species diversity – functional diversity relationships in small stream riparian plant communities and iii) a study on the potential of riparian buffer reserves as a plant refuge in the clearcut boreal forests. Specific questions addressed in the three chapters are:

Chapter 1:

- i) What is the current state of knowledge on small stream riparian vegetation?
- ii) What are the effects of forest harvesting and site preparations on riparian plant communities along unmapped small streams?
- iii) What are the functional responses of riparian plant communities to forest management disturbance?

Chapter 2:

- i) Does moderate disturbance intensity favour high species and functional diversity?
- ii) Does habitat sensitivity influence the relationship between species diversity and functional diversity?
- iii) Does species diversity-functional diversity relationship shift from linear to curvilinear in disturbed natural communities?

Chapter 3:

- i) Do the riparian buffer reserves support more plant species than a clearcut and an uncut forest?
- ii) Is the prevalence of colonization traits higher in the riparian buffer reserves than the nearby clearcuts and the uncut forests?

The three chapters are standalone manuscripts preceded by an introduction and a general methods section. The three chapters are followed by a general discussion. In the general discussion, I synthesize the findings of these chapters, discuss the implications for these findings in a broader context and highlight future research needs.

General methods

In this chapter I provide an overview of my study sites and the general sampling protocol. Specifics of the study sites and sampling protocol relating to particular questions are also described in the following chapters that were written as standalone manuscripts.

1. Site description

I conducted this study in the Current River and Mackenzie River Watershed 30 km east of Thunder Bay, Ontario, Canada (Fig.1). Geologically, this area is characterized by Precambrian rocks of the Lake Superior and glacial tills. In some areas Phanerozoic sedimentary rocks overlie the bedrock. The bedrock is chiefly shales of low porosity and permeability resulting in marginal groundwater supply. This area enjoys a boreal temperate (modified continental) climate. Mean temperatures between of January and July range from -26 to -22 ^{0}C and from 21 to 25 ^{0}C, respectively. Total annual precipitation ranges from 700 to 850 mm (Baldwin et al. 2000). The region is marked by a pattern of low winter and high summer precipitation. In summer, a succession of cyclonic storms passes through the area. This area lies in the Boreal forest region and is dominated by black spruce (*Picea mariana* (Mill.) BSP.), jack pine (*Pinus banksiana* Lamb.) and balsam fir (*Abies balsamea* (L.) Mill.) as well as mixed wood communities of conifers and northern deciduous species such as trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.) (Baldwin et al. 1997). In the study sites, the dominant overstory vegetation includes black spruce, white spruce, balsam fir and trembling aspen, whereas the dominant understory vegetation includes large-leaved aster (*Aster macrophyllus* L.), bunchberry (*Cornus canadensis* L.) and blue bead lily (*Clintonia borealis* (Ait.) Raf.). In Table 1, I describe the site specific dominant vegetation and habitat parameters of my sampled sites.

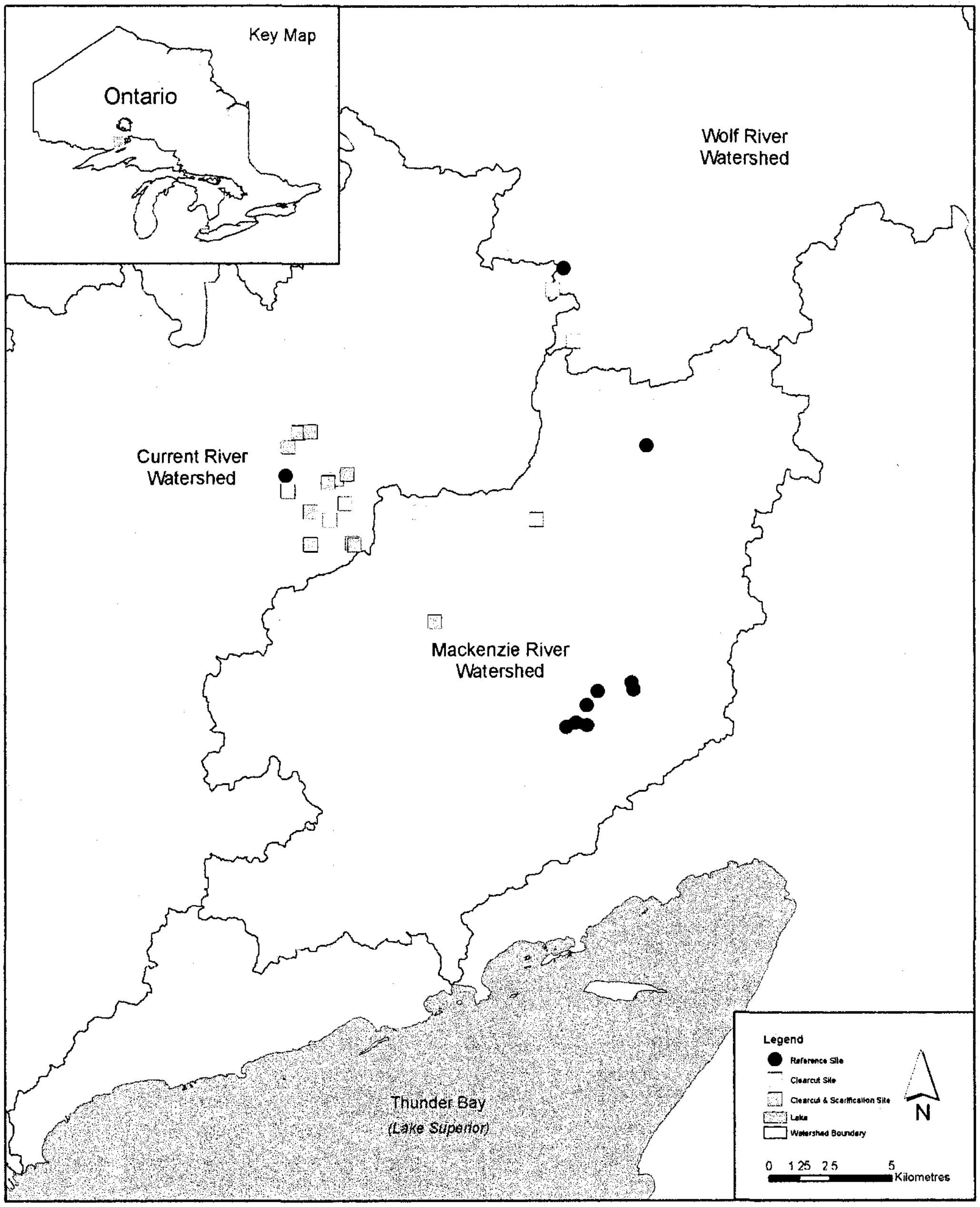

Fig.1 Distribution of study sites in northwestern Ontario

Table 1

Dominant vegetation and habitat parameters (± standard deviations) of the sampling sites

	Vegetation	*Exposed mineral soil*	*Canopy exposure (%)*	*Ground exposure (%)*	*Soil moisture content*	*Soil temperature (^{0}c)*	*Upland slope*
C1	BP, PB, PT, AI	0.61±0.27	14.81±4.27	1.23±0.33	15.05±2.27	11.30±0.09	1.84±0.30
C2	PM, PB,SD	0.50±0.37	12.39±4.05	7.64±2.09	13.83±3.08	11.26±0.28	2.61±0.40
C3	AB, PM, AI	0.44±0.23	8.88±1.21	6.72±1.95	6.60±2.26	11.09±0.27	12.60±0.51
C4	PM, SD, AI	-	34.73±7.44	0.64±0.44	17.37±2.99	11.21±0.15	1.20±0.21
C5	BP, PM, SD, AI	1.23±0.39	1.57±0.48	12.20±2.20	16.17±2.18	11.28±0.18	0.59±0.18
C6	BP, PM, PT,AI	2.07±0.80	7.24±2.27	8.48±2.30	5.90±1.70	11.60±0.21	7.93±0.99
C7	BP, PM, AS	-	15.57±3.02	9.95±2.10	8.82±1.70	11.39±0.31	3.62±0.50
C8	BP, PM, AS	0.17±0.16	1.00±0.43	12.03±2.07	2.87±0.46	11.65±0.18	4.10±1.46
C9	BP, PT, PM, AS	0.47±0.46	9.59±3.51	13.13±1.50	4.12±0.49	11.41±0.17	3.44±0.81
C10	FN, AB, PM	0.74±0.30	5.53±1.00	12.12±1.41	7.56±1.12	11.60±0.26	3.60±1.60
CC1	PM, PB, AI	1.78±0.80	100.00	12.50±5.32	19.25±1.36	11.32±0.18	2.72±0.52
CC2	PM, PG, PB, AI	2.00±0.78	100.00	4.55±3.08	22.87±2.12	11.40±0.26	0.25±0.12
CC3	PB, PB, AI	3.00±0.43	100.00	3.75±1.51	14.18±2.97	11.29±0.29	15.63±7.09
CC4	PM, AI	1.41±0.44	79.18±8.30	8.45±3.33	8.741±1.12	11.84±0.33	1.06±0.24
CC5	PG, PB	0.25±0.21	100.00	19.10±5.82	7.55±5.23	11.61±1.04	2.00±0.02
CC6	PT, AI	0.70±0.37	100.00	2.48±0.78	24.63±1.45	11.78±0.25	1.70±0.85
CC7	PM, BP, LL	1.96±0.68	78.26±7.76	3.35±0.85	35.14±2.76	11.69±0.39	2.75±0.75
CC8	PM, AI	2.39±1.74	100.00	4.83±2.11	19.72±2.04	11.54±0.31	0.43±0.22
CC9	PM, PT, AS	1.60±0.63	100.00	2.85±0.78	26.98±6.21	11.44±0.07	4.25±0.75
CC10	PM, PG, PB	1.30±0.56	91.30±6.01	10.00±2.74	8.88±1.64	11.64±0.34	4.60±1.92
SC1	PM, AI, CS	7.86±3.18	100.00	16.24±5.51	16.92±3.91	11.79±0.42	4.24±1.45
SC2	PT, AI	4.47±2.02	100.00	2.50±0.61	22.93±1.58	11.52±0.20	14.00±6.14
SC3	PT, AI, CS	4.56±3.32	100.00	6.06±4.41	27.92±4.21	11.73±0.41	0.67±0.30
SC4	PB, PT, AI	1.50±0.86	100.00	2.25±0.98	20.67±1.69	11.86±0.45	5.96±1.15
SC5	BP, PM, AB	0.52±0.44	100.00	0.30±0.23	16.59±2.46	11.84±0.42	0.52±0.18
SC6	PT, AI	10.20±3.86	95.00	14.40±5.03	18.47±3.43	11.53±0.29	4.20±1.21
SC7	AB, PM, PT	6.43±2.4	98.57±1.04	11.29±3.87	26.77±1.07	11.35±1.10	3.20±0.81
SC8	PM, PT, AI	2.53±1.07	90.00	7.42±3.12	28.03±2.01	11.44±0.17	1.25±0.41
SC9	PM, PT, AI	7.09±2.36	100.00	9.36±3.63	26.68±1.76	11.89±0.31	-.12±0.53
SC10	PM, BP,	1.96±0.78	100.00	3.12±1.07	21.68±1.79	11.87±0.20	2.00

Where: C = reference sites, CC = clearcut sites and SC = clearcut plus soil scarification. In vegetation, PM = *Picea mariana*, PG = *Picea glauca*, PT = *Populus tremuloides*, PB = *Pinus banksiana*, LL = *Larix lariciana*, AB = *Abies balsamea*, PB = *Populus balsamifera*, BP = *Betula papyrifera*, AI = *Alnus incana*. NB. Soil temperature, soil moisture are instant measurement (using HH2 moisture meter, Delta-T, Devices, Cambridge, UK). All sites are measured within a week with no noticed significant weather change. The continuous measurement of soil temperature [using HOBO Temperature Logger (H08-001-02), Onset Computer Corporation; USA] for the study period is reported in Appendix 1.

2. Experimental design

2.1 Small stream: definition and their identification in the field

In the literature the terms *small, headwater, first order and narrow stream* are often used interchangeably to describe small streams. I use the term *small stream*. In the boreal forest, small streams are characterized by missing channel features (Hupp, 1986), channels on the bed rock and subsurface or below ground flow. As such, it is a challenge to identify small streams in the field, especially in harvested sites. For field sampling, first, I used a GIS map derived from a digital elevation model (i.e. flow accumulation) to locate potential small streams on the map. Secondly, I verified those streams in the field using the following five criteria:

1. Connection with a larger stream
2. Flowing water to the downstream
3. Width between ~0.25 -1 m
4. Presence of a stream bed and upward slope on either side and
5. Catchment area less than 1 km^2

2.2 Sampling design

I sampled 30 small streams in total; 10 of which received a clearcut treatment, 10 clearcut plus soil scarification and the remaining 10 streams were from the reference sites. In Ontario, all streams receive Area of Concern (AOC) prescriptions which usually mean retention of riparian buffer reserves along streams. My selected streams were not in the topographic map so there was no riparian buffer reserve retained along those streams during harvesting. After forest harvesting the elevated water table and surface runoff create temporary channels that can be confused with a small stream. To ensure that my study streams were indeed small streams, I selected streams that were connected with larger streams which typically had riparian buffer reserves. These buffer reserves also served as sites for intermediate disturbance. Therefore, each of my selected small streams in clearcut and clearcut plus soil scarified sites had received two types of treatments: i) disturbance (i.e. either clearcut or clearcut plus soil scarification – no protection) and ii) adjacent riparian buffer reserves (these are riparian buffer reserves of larger streams not the sampled small stream). On each stream, I laid six transects. Four of those transects were in the respective disturbance treatments (i.e.

either in clearcut or in clearcut plus scarified) and the remaining two transects were in the nearby riparian buffer reserves (i.e. riparian buffer reserve of large stream) (Fig.2). I considered two habitat types across the stream: i) riparian habitat and ii) upland habitat, situated adjacent to the riparian zone.

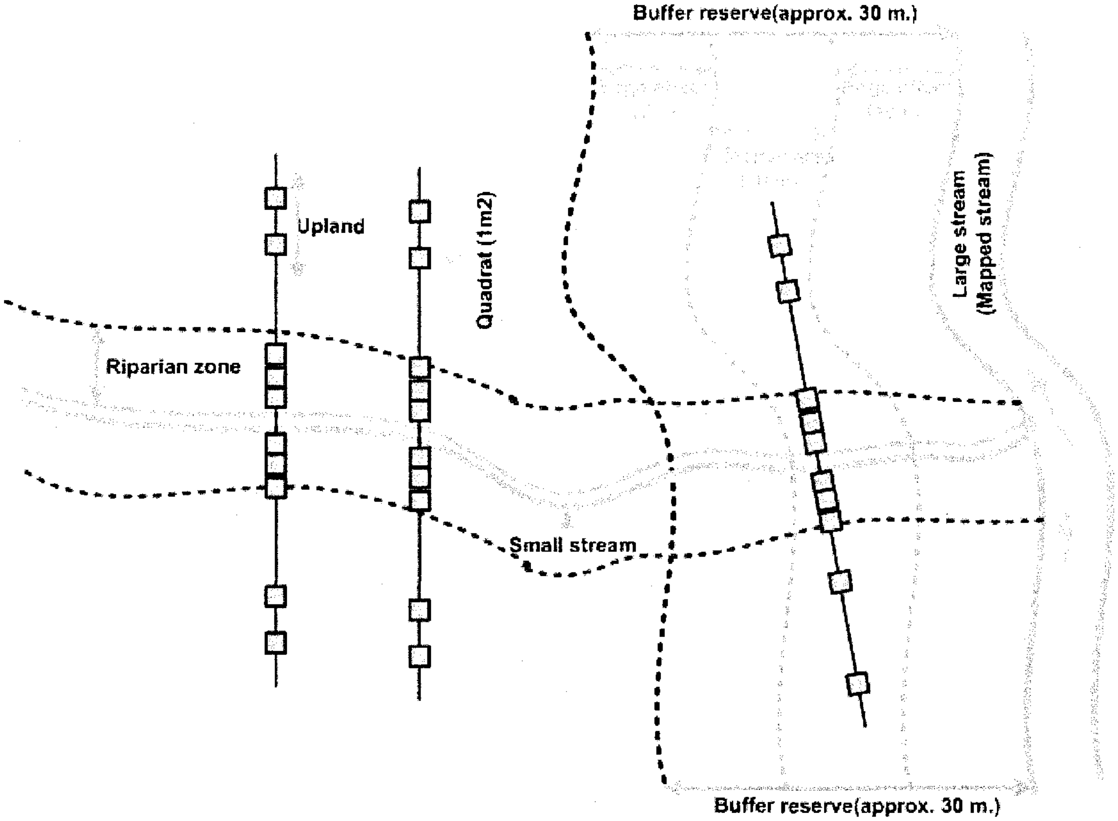

Fig. 2 Schematics of sampling design for the study

On each study stream, I selected a 50 m section 10 m from the cut edge towards the upstream (i.e. towards either clearcut or clearcut plus scarification area) and divided it into five 10 m sections. From these five sections, I randomly selected two sections for sampling and placed four transects perpendicular to the stream bank towards the upland (see Fig.2). I placed two such transects in the adjacent riparian buffer reserve using the same protocol.

On each side of the stream, each transect was divided into approximately ten 1x1 m consecutive quadrats. The numbers of quadrats were not fixed because the width of riparian zones is not constant. However, I placed at least two consecutive quadrats for riparian zone and two random quadrats in the uplands.

2.3 Field data

I collected field data on two broad categories: i) habitat and ii) vegetation. Habitat conditions were characterized by recording: stream width (in meters), channel morphology (single or multiple channel), flow type, ground slope to the upland forest (in degrees), degree of harvesting ruts (percent estimation in a 1 m^2 quadrat) and exposed mineral soil (percent estimation in a 1 m^2 quadrat) and depth of organic matter (in meters using soil Auger). I also measured soil moisture, and soil temperature using a HH2 moisture meter, Delta-T, Devices, Cambridge, UK.

Under the vegetation head, I recorded the name of species encountered and visually estimated their percent cover in the 1 m^2 quadrates.

2.4 Data analyses

Data analyses and statistical protocols are described in the following chapters as they relate to the individual research questions.

Chapter 1

Response of riparian plant communities of boreal small streams to forest management – A review and synthesis*

Abstract

Small headwater streams are numerous and occupy a large portion (60 - 80%) of a watershed. With hydrologic connections, they influence higher order streams that are protected by riparian buffer reserves. Adversely affected riparian plant communities affect vertebrate, invertebrate and microbial diversity. However, forest harvesting and silvicultural impacts around less protected small streams, especially on the plant communities, have received very little attention. In this review and synthesis, I address three specific questions: i) what is the current state of knowledge on small stream riparian vegetation? ii) how do riparian habitat and plant communities of small streams respond to forest harvesting and site preparations? and iii) can I identify a set of functional responses of riparian plant communities to disturbances with respect to species traits? I searched the ISI Web of Science™ (Expanded) data base and consulted citations therein. I also reviewed the available grey literature and communicated with contemporary researchers working on small streams. I found that of all the forest stream riparian studies, only 5% are studies on small stream riparian vegetation. Forest harvesting and scarification significantly reduce riparian plant species richness, diversity and shift the herbaceous dominance to shrubs. Disturbance along small streams may facilitate the spread of invasive species into the streams protected by riparian buffer reserve. I hypothesize that functionally, riparian plant communities respond to forest harvesting and scarification by converging disturbance-responsive and invasive traits. I argue that the distribution pattern of plant functional traits might be useful as a predictor in developing an early warning system against habitat degradation and biological invasion.

Keywords: riparian plant community; clearcutting; invasive species; trait dispersion; community assembly

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1. Introduction

Naiman et al. (2005) defines riparian systems as "transitional semi terrestrial areas regularly influenced by fresh water, usually extending from the edge of water bodies to the edges of upland communities". Riparian ecosystems support a disproportionately large number of plants, vertebrate, invertebrate and microbial communities in comparison to either of the adjacent aquatic or terrestrial environments. Riparian ecosystems provide a wide range of ecological services to streams (Malanson 1993) including i) input of organic matter, ii) filtering and buffering of sediment, nutrient, agricultural contaminants and runoff, iii) maintaining water quality (Triska et al. 1993, McClain et al. 1994, Molles et al. 1995, Sabo et al. 2005), iv) protection of stream banks from erosion, v) contribution of energy to the ecosystem energy budget, and vi) provide propagule dispersal corridors for plants and animals (Gregory et al. 1991, Gould and Walker 1999; Hannon et al. 2002, NRC 2002, Allan et al. 2003, Melody and Richardson 2004, Shirley 2004, Sabo et al. 2005). The quality and quantity of these ecological services are highly influenced by the ecological setting of a riparian ecosystem and its plant community. Ecological condition of the riparian ecosystems is determined by the complex interactions of geomorphological, hydrological and biological processes. These processes vary depending on stream size, flow patterns (e.g. surface and subsurface flow), upland slope and aspect (Dodds and Oakes 2007, Hack and Goodlett 1960) and riparian vegetation. Small headwater streams differ from larger streams in many ways. For example, in the North American boreal forests small streams may have subsurface flow that often lack externally visible channel morphology (e.g. riffles) and continuous flows (some flows are either discontinuous or intermittent) (Lamb 2002). Therefore, the ecological characteristics of small stream riparian areas are presumably different from those of larger streams (Richardson et al. 2005). However, small streams are structurally and functionally connected with larger streams (see Fig. 1.1 for small stream – large stream connectivity), and provide some unique ecological services (see Wipfli et al. 2007 and references therein). For example, small stream riparian ecosystems provide a predator-free environment as large predators usually do not move on the small streams because of space constraint (see the reviews of Richardson and Danehy 2007, Olson et al. 2007).

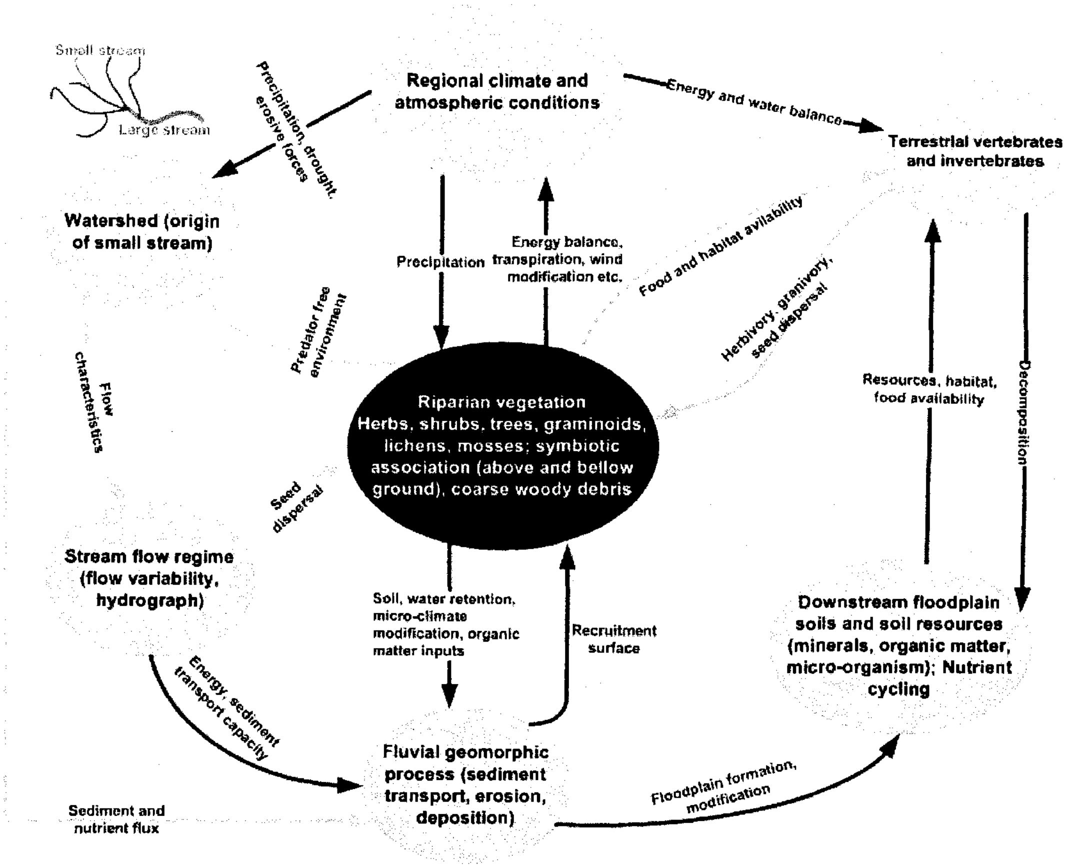

Fig. 1.1 Conceptual model depicting the structure and functioning of riparian ecosystem. Grey lines indicate direct relationship of small streams with large stream and dotted arrow indicates the importance of plant community to vertebrates and invertebrates (modified and redrawn from Scot et al. 2005).

Disturbance is a common phenomenon in natural ecosystems, and riparian ecosystems are no exception. Natural disturbance includes flooding, beaver (*Castor canadensis*) activity, insect/pathogen infestation and fire (Gregory et al. 1991, Pollock et al. 1998, Naiman et al. 2000). These disturbances are normal processes and they influence ecosystem functioning (Bendix 1994). For example, flooding assists seed dispersal, forest fire facilitates conifer regeneration, etc. Anthropogenic disturbances primarily originating from forest harvesting and site preparation by scarification cause additional disturbance in riparian habitat and biota. For example, forest harvesting alters the macro and micro-environment;

scarifications displace top soil and redistribute soil nutrients (de Chantal et al. 2006), logging road construction and slash accumulation modify stream channels etc.

High biodiversity and associated ecological services of riparian ecosystems prompted ecologists, conservationists and forest managers to protect riparian habitats and their biota from adverse effects of forest management (Lamb et al. 2003). Riparian buffer reserves (also called RMAs; riparian management areas) are often used as a management tool to protect stream water quality and associated riparian values from the adverse effects of land use activities (Lee et al. 2004). A riparian buffer reserve is a belt of forested vegetation that is kept intact along the streams. Topographic maps are used to locate the forest streams and the riparian management areas. Therefore, streams that appear on the topographic maps receive buffer reserve protection (Hupp 1986). However, a watershed contains both relatively large and small headwater streams. Small streams are numerous and occupy a major portion, between 60 and 80 % of the total stream length in a watershed (MacDonald and Coe 2007). For the protection of wetlands and small streams, additional management protocols such as Best Management Practices (BMP) and Area of Concern (AOC) are used with situation specific management planning during forest harvesting. These protocols suggest that care should be taken during harvesting of any wetlands with emphasis on water quality (Phillips et al. 2000). Although AOC and BMP are obligatory management protocols, often small streams and their riparian plant communities are affected by forestry activities.

Responses of a plant community to disturbance can be determined in several ways including change in species richness, composition and abundance. These are also related to the abundance of species functional trait(s). Plant functional traits have evolved in response to the habitat, thus identification and quantification of plant functional traits is very useful to determine their response to disturbance and environmental change (see Menges and Waller 1983, Lamb and Mallik 2003, McIntyre et al. 1999, Weiher et al. 1999). Analysis of functional traits is often used as a proxy measure of ecosystem functions. This approach has received significant attention in recent years because of its universality in interpretation of ecological change beyond taxonomic identity of species.

Current understanding on the effects of forest harvesting and silviculture on riparian ecosystems has so far been focused on the effectiveness of buffers to prevent changes in riparian ecosystems including water quality and biota (specifically fauna) due to forest management (e.g. Nilsson and Homstrom 1985, Nilsson 1987, Buttle and Metcalfe 2000, Macdonald et al. 2003a, 2003b, Story et al. 2003, England and Rosemond 2004, Melody and Richardson 2004, Price et al. 2004, De Groot et al. 2007, Melody and Richardson 2007). Very few studies were conducted on riparian vegetation responses to forest harvesting along buffer-protected streams (e.g. Lamb et al. 2003). However, small unmapped streams are largely ignored. To my knowledge no field study demonstrated the effects of forest management and silvicultural site preparation around small headwater streams that are not protected by buffer reserves.

The specific objectives of this paper are to review and synthesize i) the current state of knowledge on small stream riparian vegetation, ii) identify the effects of forest harvesting and site preparations on riparian plant communities along unmapped small streams, and iii) discuss functional responses of riparian plant community to disturbance .

2. Methods

2.1 Literature review

I searched the ISI Web of Knowledge ™ (Science Citation Index - EXPANDED) database for relevant articles published in English from 1975 to April 2007 by using the word riparian in the title, abstract, or keywords. First, I categorized the studies into large and small streams by using the i) advanced search and analyzing options of the ISI Web of Knowledge ™ and ii) reading the abstract and methods of these papers. I restricted the literature search to plant ecology of small headwater streams. Secondly, I categorized the small stream studies into i) type of streams ii) study aspects (such as habitat and biota, plants, animals) and iii) geographical area where the study was conducted. I reviewed the available literature and citations relating to the questions that I asked. Following these reviews I developed some hypotheses that are based on research results on higher order streams, common ecological knowledge, discussion with persons involved in riparian plants research and personal field observations. The results of a preliminary field survey of 11 unmapped small streams conducted by Mallik et al. (2007) to determine the response of riparian plant communities to i) clearcut, ii) clearcut with soil scarification and iii) unharvested sites provided empirical support to my arguments and hypotheses.

2.2 Definition of key terms

(a) *Small streams*: The term small streams is defined as channel width between 0.5 and 3 m (at high water mark), have continuous or intermittent water flow above ground, below ground or a combination of the two. All unmapped streams are considered small streams.

(b) *Small streams riparian ecosystems*: I define small stream riparian ecosystem as the dynamic ecosystem at the land - water interface shaped and reshaped by the lateral and longitudinal influence of a small stream.

(c) *Forest management disturbance*: I consider forest harvesting through clear cutting and silvicultural site preparation by soil scarification to be the major forest management disturbance.

(d) *Plant functional traits*: I consider plant functional traits as defined by Violle et al. (2007) 'any morphological, physiological or phenological feature measurable at individual level, from cell to the whole-organism level, without reference to the organism or any other level of organization.'

(e) *Invasive traits vs disturbance responsive traits*: Invasive traits are the plant functional traits that help a plant to invade and gradually expand in a newly colonized habitat. These traits include rapid colonization, competitive ability (Seabloom et al. 2003), enhanced resource capture ability (Davis et al. 2000), stress tolerance and chemical defense (Callaway and Ridenour 2004). The difference between disturbance responsive traits and invasive traits is that disturbance responsive traits help a plant to survive and grow in a disturbed habitat whereas at a later stage the invasive traits not only help the plant to survive and grow well but also dominate the habitat by out-competing the local inhabitants including disturbance specialists that do not possess invasive traits. Examples of invasive traits include rapid and profuse regeneration by seeds and vegetative means, extensive root formation, high ecological amplitude and high competitive ability.

(f) *Trait convergence*: I define trait convergence as having a lower value of a particular trait, or group of traits, or abundance of traits, along a single or multiple disturbance gradients in a temporal scale.

3. Results and discussion

3.1 Limited knowledge on small stream riparian plant community

With the growing emphasis on land management and biodiversity conservation, riparian ecosystems have received increasing attention since the early 1990s. This is reflected in the increasing number of peer reviewed papers focused on riparian ecology (Fig.1.2). However, the study of riparian ecosystem along small streams remains almost unaddressed. To date, limited research has been conducted on small streams. Research on small streams accounts for only 5% of the total riparian studies (Fig. 1.2). Within the 5% of small stream riparian research, review and synthesis lies a large proportion. Secondly, irrespective of stream size, studies on riparian plant communities are extremely few and limited to the boreal

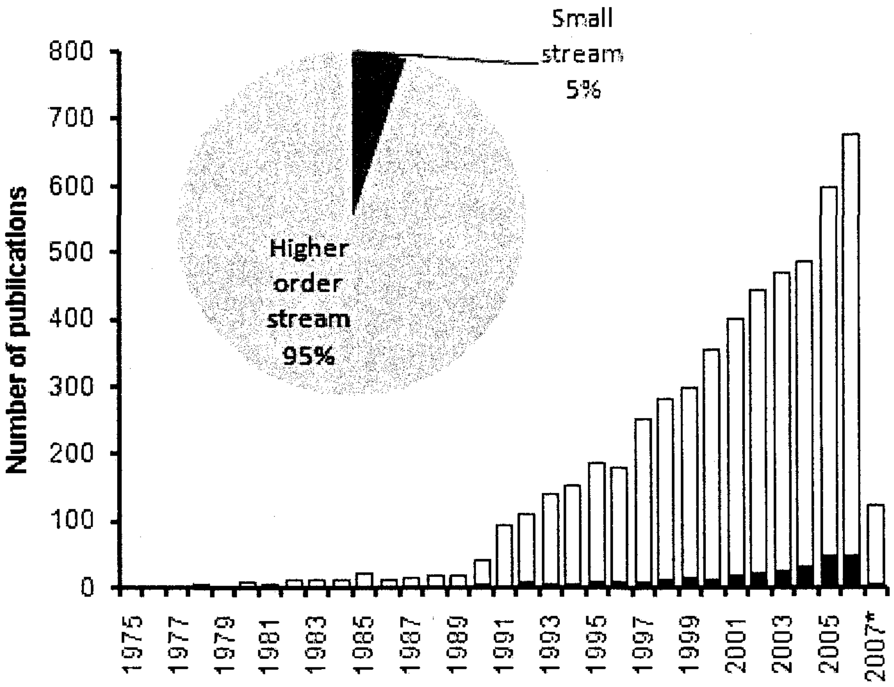

Fig. 1.2 Publication rate of papers on small streams riparian ecosystem. The total length of a bar illustrates the total number of paper published per year with the word "riparian" in the title, abstract, or keywords, that occurred in ISI's Web of Knowledge ^{TM}. Dark coloured bars within a bar and pie chart illustrate the total number of studies on small streams riparian ecosystem. *The result is updated as of April, 2007.

forest. Hagan et al. (2006) studied riparian plant communities along small headwater streams in Maine. It was the first study that provides empirical evidence on the existence of riparian vegetation along unprotected small streams. Plant community studies in the riparian areas of higher order streams of the boreal region have mainly focused on species richness along the Arctic-boreal rivers (Gomi et al. 2001), lakeside riparian vegetation distribution in Quebec (Danneler et al. 1999), stream flow responses to disturbances in northeastern Ontario (Buttle and Metcalfe 2000), and ecological attributes including trait structure (Lamb and Mallik 2003) and early impact of adjacent clearcutting and forest fire on riparian zone vegetation along small coldwater streams in northwestern Ontario (Lamb 2002, Lamb et al. 2003). Table 1.1 provides an account of existing research on small stream riparian vegetation with the geographic location of the studies.

3.2 Forest management impacts on riparian habitat and vegetation

Forest harvesting activities have both direct and indirect effects on riparian habitats and their biota. Physical damage of habitat, removal of plants and, displacement and compaction of soil by heavy machineries are direct impacts. The canopy removal by forest harvesting changes the light regime at the forest floor (Fedoroff et al. 2005). Furthermore, forest harvesting is normally followed by site preparation by scarification and tree planting. Scarification causes five major ecological disturbances: i) removal of the humus layer from the top soil, ii) stream channel blocking/displacement, iii) frost heaving, iv) alteration and often damage to soil-microbial associations, and v) displacement of the soil seed bank as buried seeds can be exposed by scarification while seeds on the soil surface get buried. Logging roads built prior to harvesting can cause significant damage to small streams as they are not mapped and easily overlooked during road building process. These effects on the habitat can be mirrored in the plant community.

3.2.1 Impact on plant species richness and dominance

Mallik et al. (2007), following a preliminary study in NW Ontario, reported that species diversity was lower in sites subjected to clearcut harvesting and scarification compared to

Table 1.1

Small streams riparian vegetation: how much we know?

Type of stream	*Ecological field*	*Study location*	*Advancement of knowledge*	*References*
First-order	Vascular plant communities	Western Maine, USA	A narrow riparian zone exists along the small headwater stream that is reflected by the presence of herbaceous plant community.	Hagan et al. 2006
First and second order	Ground-flora species (herbaceous and woody species <1 m tall)	Wisconsin, USA	Ground-flora is strongly related to hierarchical landscape properties, including valley type and the transverse geomorphic structure of the stream valley.	Goebel et al. 2006
Small streams	Plant communities	NW Ontario, Canada	There is no significant difference in the overall abundance and distribution of species in the riparian vegetation of undisturbed sites, adjacent clearcut sites and sites burned by forest fire. However, abundance of few species increased in burned sites.	Lamb et al. 2003
Small streams	Trait structure of plant communities	NW Ontario, Canada	Identified specific trait patterns and change in the prevalence of trait patterns that may indicate functional responses of vegetation to change in the environmental factors from stream bank, riparian zone, transition zone and uplands.	Lamb and Mallik 2003
Small streams	Liverworts and mosses	Sweden	Species richness and composition for mosses and liverworts are highly correlated with pH index than other habitat properties.	Hylander and Dynesius 2006
Small streams	Bryophytes	Sweden	Clearcut negatively affects bryophyte cover and species composition in riparian zone. Less than half as many bryophyte species disappeared after from clearcuts as compared to adjacent buffer strips.	Hylander et al. 2005

Type of stream	*Ecological field*	*Study location*	*Advancement of knowledge*	*References*
Small streams	Herbaceous riparian vegetation	Oregon, USA	Determined the impact of stubble height, time of clipping and soil water status on production and regrowth of herbaceous riparian vegetation.	Boyd and Svejcar 2004
Small to moderate sized streams	Indigenous vegetation or mixed indigenous and introduced flora	Coromandel Peninsula, North Island, New Zealand.	Riparian vegetation composition and maturity can influence the physical characteristics of afforested and harvested streams.	Boothroyd et al. 2004
First, second, third order streams	Algae, restoration of forested riparian habitats	Mid-Atlantic Piedmont region of the eastern U.S.A	Developed an empirical model that provides a spatially explicit, quantitative framework for predicting the effects of changes in catchments land cover composition and spatial configuration on specific characteristics of stream ecosystems.	Johnson et al. 2007
Small- to medium-sized lowland streams	Macrophytes	Denmark	The dispersal and retention of macrophyte stem fragments declined exponentially with distance below the point of release.	Riis and Sand-Jensen 2006
Secondary channel	-woody vegetation (*Pinus nigra*) and its effect on bar formation in rivers	River Loire (France)	Woody vegetation responds morphologically to fast-flowing waters and sediment deposition.	Rodrigues et al. 2007
Second-order streams	Understory vegetation	Adirondack park, New York	Herbaceous plants dominate the preserved site, however, abundance and richness both decrease with distance from the stream.	Dieterich et al. 2006
New river channel cut into flood plain	Floristic vegetation/seeds	River Cole, West Midlands, United Kingdom	Seed remobilization and hydrochorous transport from the upstream catchments are important for colonization.	Gurnell et al. 2007

Type of stream	*Ecological field*	*Study location*	*Advancement of knowledge*	*References*
Various	Woody plants	Southeastern Australia	Correlations between load and stream characteristics are complex and have not been demonstrated to be predictive.	Lester et al. 2006
Various	Alien vegetal riparian species and other vegetation	Portuguese	After disturbance only 12 % of the studied areas retain normal riparian functions and remaining vegetation changed.	Chaves et al. 2006
Small catchments	Shrubs	Texas, USA	Provided a shrub–streamflow framework	Wilcox et al. 2006
Not specified	Bryophytes	Thunder Bay, Canada	Bryophytes can be used as a phytometer. The extents of edge effects are approximately 10 meter on both edges.	Stewart and Mallik 20
Not stated	*Salix* spp.	Southeastern Oregon	Covering small willow shrubs (< 2 m tall) with felled western juniper is an effective deterrent to browsing.	Matney et al. 2005
Variable	Old growth forest	Canada	Regardless of the criteria for buffers, the accumulation of old growth is rapid in the first 40–60 years and it dropped (2–4%) till100 years and the primary location of old growth shifts from the harvest to the riparian land base.	Lee and Barker 2005
Large watersheds	Herbaceous ground-flora richness in valleys	The Northern lake States, USA	The environmental heterogeneity associated with a variety of individual reaches can be responsible for greater species richness provided by riparian areas at the watershed level.	Goebel et al. 2003
Not stated	Woody species (*Quercus, Betula,*	Maryland, USA	There is no significant difference in growth and survivorship of few riparian species (Quercus and Acer) between bare root and	Sweeney et al. 2002

Type of stream	*Ecological field*	*Study location*	*Advancement of knowledge*	*References*
	Acer)		containerized seedlings.	
Alluvial plains	*Ulmus, Quercus,*	Japan	Spatial distributions of tree populations and subpopulations reflect past disturbances.	Sakai et al. 1999
Wetlands, coastal island	Plant species richness	Coastal islands in southeast Alaska, USA	Small-scale spatial variation can dramatically alter the impact of disturbances in riparian ecosystem. This study support Michael Huston's dynamic-equilibrium model of species diversity.	Pollock et al. 1998
Not stated	Forest and grass areas	Central Illinois, USA	Riparian zones link the stream with its terrestrial catchments; they can modify, dilute or concentrate substances before they enter a lotic system. In small to medium sized streams forested riparian zones can moderate temperature, reduce sediment inputs, provide important sources of organic matter and stabilize stream banks.	Osborne and Kovacic 1993
Small watersheds	Streamside forests	Eastern North America	Actual or potential effects of streamside forest on availability of habitat, nutrient chemistry and the quantitative and qualitative nature of primary food base has been identified in this study.	Sweeney 1992

unharvested control. Harvesting and scarification along small streams alters and often impair stream flow. Alteration of stream flow regimes can cause a shift in dominant species (Stromberg et al. 2007). In undisturbed conditions, riparian ecosystems are dominated by herbaceous species (see Fig. 1.3A) whereas clearcut followed by soil scarification facilitates the shift in species dominance from herbs to graminoids, ferns, and in some instances shrubs (Fig. 1.3B,C). Mallik et al. (2007) in the same study reported a significant increase of grasses and mosses but a significant decrease of trees, herbs and ferns in both clearcut and clearcut followed by scarified sites (Fig. 1.4). They found that shrub abundance and diversity increase following clearcutting but with clearcut followed by scarification both abundance and diversity of shrubs decrease.

3.2.2 Shift in dominant plant's regeneration strategy

Riparian plants have regeneration strategies (e.g. ruderal, competitive, and stress tolerant; *sensu* Grime 1979) to cope with frequent disturbance such as frequent flooding by acquiring certain life history traits (McIntyre et al. 1999). In an undisturbed or naturally disturbed riparian ecosystem plants with competitive, stress tolerant and ruderal strategies might co-exist and the dominance is ultimately governed by the competitive exclusion principle. On the other hand, disturbance in the riparian ecosystem facilitates colonization and persistence of species with ruderal strategies. Tabacchi and Planty-Tabacchi (2001) provided empirical evidence in support of ruderal dominance along large stream riparian ecosystems experiencing frequent natural flooding. In their study they didn't notice any significant change in the dominant plant strategy even over a ten year period (Fig. 1.5). Although Tabacchi and Planty-Tabacchi (2001) did not include an anthropogenic disturbance in their study, it is likely that there would be a rapid shift from competitive to ruderal dominance in riparian vegetation along an added disturbance gradient i.e. forest management disturbance. Second, this vegetation shift might be more prominent along the small streams since small streams are more sensitive to environmental change than larger streams (Richardson and Danehy 2007).

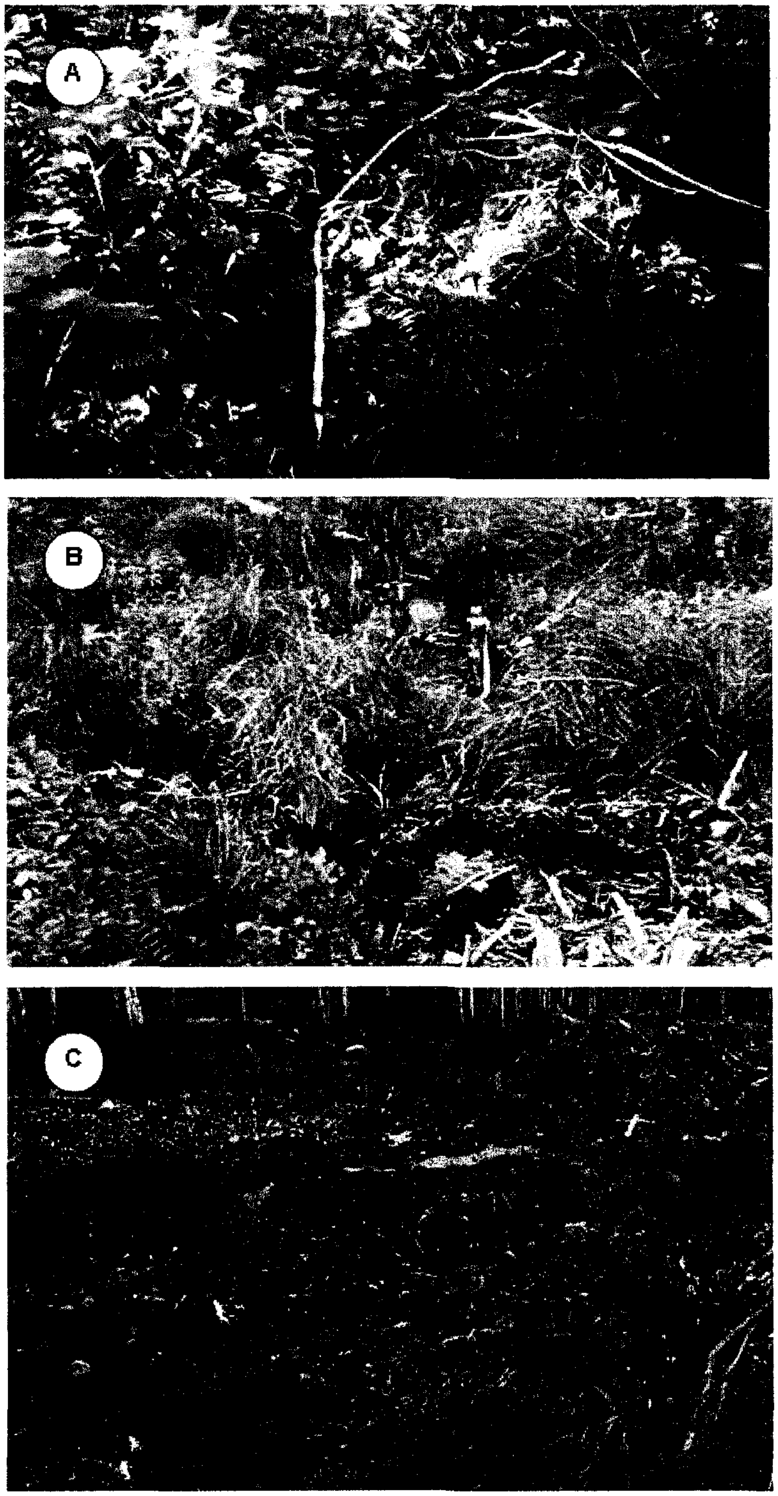

Fig. 1.3 Effect of disturbance on small stream riparian plant community. (A) Undisturbed streams are dominated by herbs and shrubs. (B) The disturbed riparian area is often colonized by grasses and mosses after clearcutting and scarification. (C) Extensive ground disturbance during and after harvesting, slash piling and puddling results in destruction of small streams.

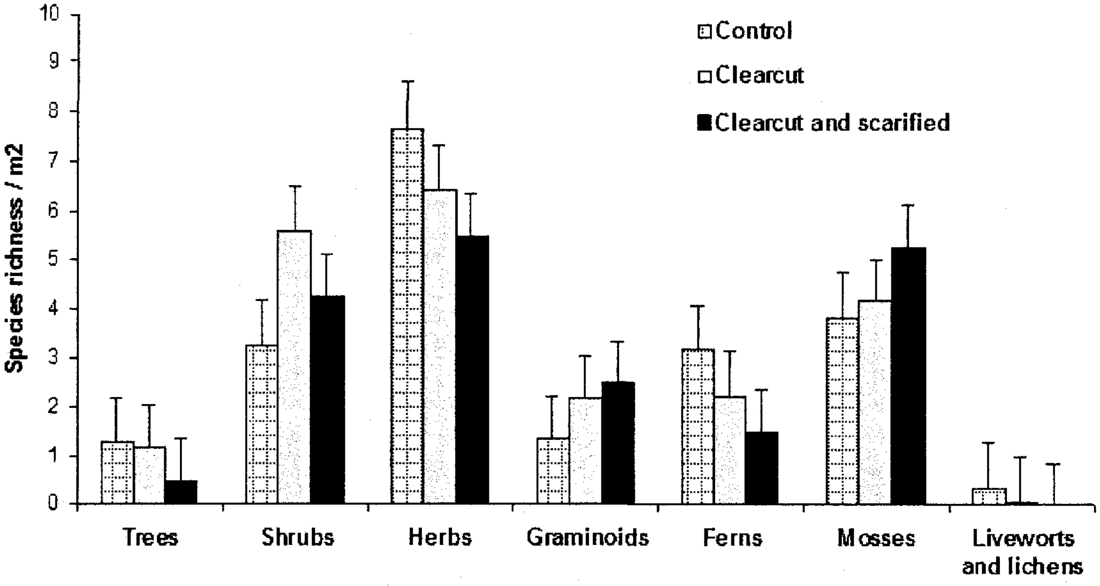

Fig. 1.4 Mean richness (+1S.E) of plant functional groups in clearcut and clearcut with scarified sites as compared with control (data from Mallik et al. 2007).

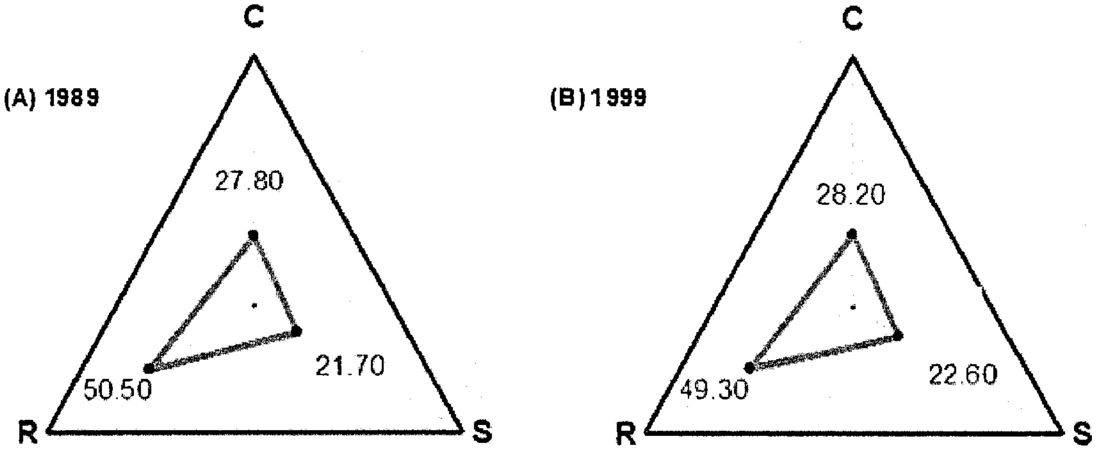

Fig. 1.5 Riparian vegetation is subjected to frequent disturbance and dominated by species with ruderal strategy. The two triangles are the results successive survey in the same location in 10 years (data from Tabacchi and Planty-Tabacchi 2001). C, S and R indicate species with competitive, stress tolerant and ruderal strategy as per Grime (1979).

3.2.3 Disturbed riparian ecosystem and exotic invasion

Disturbances encourage invasive species colonization and persistence (Burke and Grime 1996, Rajmanek 1989). Forest harvesting and scarification creates added stress on the unprotected riparian ecosystems over and above the natural disturbance regime and make them more prone to invasion. The main reasons behind the susceptibility of riparian zones to invasion are their diverse habitats and repeated hydrological disturbance (Planty-Tabacchi et al. 1996). Stohlgren et al. (1998), after an extensive study in Colorado, South Dakota, Wyoming and Montana stated that 'riparian corridors are heaven for invasive species'. Of the total exotic species encountered in these areas, 85% were present in the riparian zone. Following a field study in the Gros Morne National Park, Newfoundland, Rose and Hermutez (2004) concluded that boreal ecosystems are susceptible to alien invasion. In light of the findings of Stohlgren et al. (1998) and Rose and Hermutez (2004) it is obvious that disturbances, such as trampling, frequent flooding and animal movement can increase plant invasion in the riparian ecosystems of boreal forests. Specific reproductive strategies of invasive plants allow them to colonize, persist and out-compete native species in highly disturbed habitats (Grime 1979).The investigation of invasive species so far has focused on exotics. There is a strong possibility that native species can also become invasive, since many native aggressive species possess similar functional traits as the exotic invasive species (Thompson et al. 1995). To my knowledge, the invasion pattern in small stream riparian ecosystems of boreal forests has not been investigated. However, it is likely that small stream riparian zones are highly susceptible to exotic invasion since they experience frequent anthropogenic disturbances in addition to natural disturbances. If small streams are colonized by invasive species they can quickly expand their range into the protected streams and throughout the watershed through flow facilitated dispersal (see Nilsson 1987, Deferrai and Naiman 1994 for circumstantial examples).

3.3 Disturbance mediated riparian plant assembly- a functional perspective

From the late 1990s ecologists and land managers have been concerned with the distribution of plants' functional traits to understand how habitat disturbance affects ecosystems. This is a major shift from the understanding of species richness or species diversity response to disturbance. Empirical studies in other ecosystems (e.g. grassland) showed that plant response to disturbance is clearly reflected by the changes in their functional traits even though species level response often fails to capture this change (e.g. Fukami et al. 2005).

Disturbance acts as a filter for trait structuring that eventually assembles riparian plant communities. Grime (2006) opined that in herbaceous vegetation disturbance leads to convergence of species with disturbance responsive functional traits. Although empirically untested in the riparian context, this statement is a concern for riparian managers since riparian ecosystems are dominated by herbaceous species and experience frequent disturbance such as flooding, beaver activities, clearcut harvesting, soil scarification and forest fire. Numerous findings of ruderal dominance in riparian plant assemblage bolster this concern (Fig. 1.5). In small stream riparian ecosystem, these changes may be conspicuous shortly after disturbance because of high habitat sensitivity (Richardson and Danehy 2007).

Hypothetically, plants' functional traits converge at a very slow rate (i.e. a forest will approach climax in a successional gradient) and we assume that repeated disturbance accelerates the rate of trait convergence even though overall species richness remains high. For example, immediately after disturbance, trait diversity would be higher because of co-occurrence of generalist and disturbance specialists. Empirically, the degree of trait divergence in naturally disturbed riparian plant communities will be similar to that of riparian buffer reserves – where only natural disturbance enriches species richness as well as trait diversity. However, with added disturbance, certain disturbance responsive traits will converge. Among the disturbance responsive traits, invasive traits can become dominant at the later successional stage provided the disturbance is chronic (see Fig. 1.6). The underlying mechanisms can be explained as: i) at natural disturbance (of low to intermediate level) three groups of plants can co-occur - generalist, disturbance specialist and invasive. ii) with an added disturbance such as clearcutting (i.e. natural disturbance + clearcut), the habitat starts to become unsuitable for generalist species but favourable for the disturbance specialists possessing disturbance-responsive traits; these plants will gradually out compete the generalists, iii) if another disturbance is added such as scarification (natural disturbance + clearcut + scarification), the habitat may not be suitable for all the disturbance specialists and plants with severe disturbance tolerance traits (i.e. invasive plants) might occupy the habitat (Fig. 1.6).

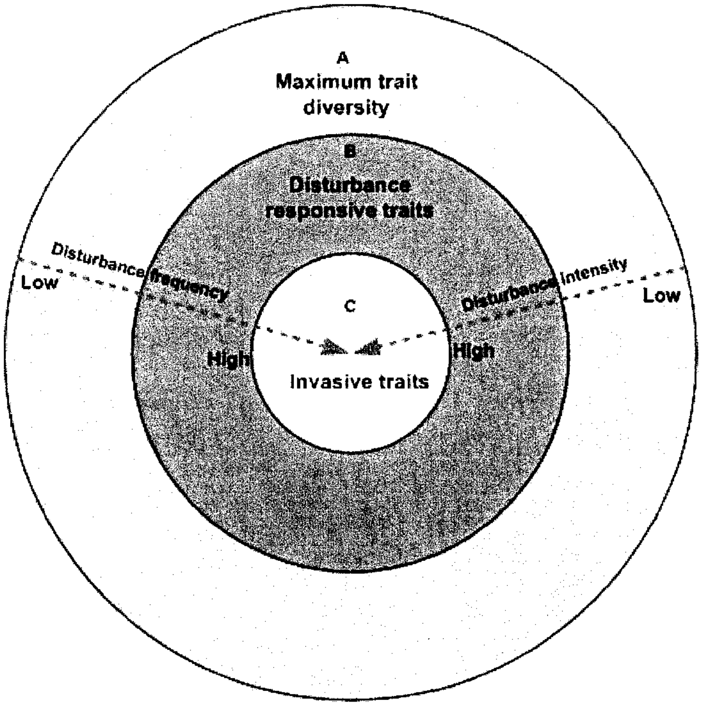

Fig. 1.6 A hypothesis on successive filtering of plant traits based on disturbance intensity and frequency. Outer circle (A) is characterized by low to intermediate level of disturbance; disturbance filter permits all traits here, consequently supporting the highest species diversity. The second circle (B) indicates frequent/severe disturbance and plants (from circle A) that can tolerate such disturbance with their disturbance responsive traits will occupy here. The inner small circle (C) represents most severe disturbance and plants with only invasive traits.

Fukami et al. (2005), after nine years of manipulative experiments with varying degrees of disturbance, concluded that species diverge temporally but traits converge, and occupancy by dominant traits depends on the ecological memory in the nature of the vegetation that occupied the site prior to disturbance. We can expect that after natural disturbance there will be a lesser degree of trait convergence in riparian areas. Natural disturbances are less frequent and less severe allowing a quicker recovery of riparian vegetation. Forest management activities (harvesting and scarification) on the other hand increase disturbance intensity to small stream riparian zones that does not allow sufficient time for vegetation to recover and may result in a rapid convergence of disturbance responsive and invasive traits. For example, the natural fire cycle in the North American forest varies depending on geographic location, ranging from 60 – 2000 years in Atlantic Canada (Wein and Moore 1979) while in the Rockies it is roughly 60-70 years (Wanger et al. 2006). These time frames provide ample opportunity for riparian vegetation to recover. This contrasts with harvesting disturbance in these areas, which usually rotates on a 60-80 year cycle. This does not allow sufficient time for a full recovery of the riparian zone vegetation (Lecomte et al. 2005).

4. Conclusion and management implications

Limited knowledge on small stream riparian plant community response to disturbance (Fig. 1.2) forces us to rely on large stream riparian and even non riparian literature to predict forest management impacts on riparian community. Two factors might contribute to the lack of research in this field: i) small streams are ignored as they are inconspicuous and often not in the forest inventory maps, and ii) it is assumed that small streams behave more or less similarly to larger streams. Towards the end of the last century, riparian ecologists have become interested in small streams (see Richardson and Danehy 2007, Wipfli et al. 2007). For example, the University of British Columbia recently organized a conference exclusively on the ecology of small headwater stream riparian ecosystems, and the journal Forest Science (April 2007) published a special issue on headwater streams. Nonetheless, there remains a serious concern that riparian vegetation receives little attention. With poor understanding of riparian plant communities we run the risk of making poor judgments on the protection of biodiversity and ecosystem services of small headwater streams.

Inadequate knowledge on ecological functions of small streams and their associated riparian plants communities raises a controversy on the effectiveness of the protective functions of riparian buffer reserves along the mapped streams. By the same token considering their large numbers and extensive networks in a watershed, it is also not practical to provide buffer protection along all small streams. Nonetheless, certain negative impacts must be and can be minimized by informed management. For example, soil scarification can be avoided close to small streams (De Groot et al. 2007). Specific conservation and management steps can be taken only after a thorough understanding of the impacts and functional responses of riparian plants to disturbance. It is only the proper 'Best Management Guidelines' in the protection of small streams can be developed and practiced.

In this paper I showed how the species and functional traits of relatively less protected small stream riparian vegetation can be affected by forest management activities. Distribution patterns of plant functional traits along a disturbance gradient will serve as a useful indicator of riparian ecosystem integrity and this might be a good predictor for the amount of vegetation required to protect riparian functions.

Biological invasion is a threat to the global biodiversity. In a riparian ecosystem, small streams can act as a point of introduction for invasive species which could gradually expand to the larger streams and even into the entire watershed. A thorough understanding of the trait dispersion (with and without disturbance over time) and monitoring of small streams riparian vegetation can provide an early warning system against plant invasion. For example, in disturbed riparian habitats if invasive traits become dominant then steps can be taken to eradicate them or stop further expansion in the downstream.

Like other watersheds, the North American boreal forest watersheds are characterized by the presence of large streams, small streams and ephemeral streams; all these form a complex network in the whole watershed. Ecological impacts of forestry operation on the riparian zone are different from those of upland areas and the response of riparian plant communities to forestry operations would most likely differ from the upland plant community response. We must understand these differences and incorporate the knowledge into forest management guidelines for the conservation of riparian habitats and biodiversity.

Chapter 2

Disturbance effects on species diversity– functional diversity relationship in small stream riparian plant communities*

Abstract

Understanding the relationship between species diversity–functional diversity is of fundamental importance in conservation ecology. Here I tested the relationships between species diversity and functional diversity in small stream riparian plant communities along a gradient of forest management disturbance. I further tested if the degree of species and functional diversity responses to disturbances vary depending on habitat sensitivity. I studied natural plant assemblages around stream banks (considered fragile habitats) and uplands (stable habitats) of 30 small streams (width < 1 m) in the boreal forest of north-western Ontario, Canada. The forests were harvested and sites prepared by soil scarification 2-4 years previously. I conducted habitat and vegetation surveys along stream banks in clearcuts, clearcuts plus scarified and riparian buffer reserves and compared these with unharvested reference sites. I used 36 plant functional traits as a surrogate of dominant functions: life history, morphology, productivity, potential of supporting other biodiversity, site stability, reproduction, and adaptation to disturbance. Using nested ANOVAs I analyzed how species diversity and ecosystem function react to disturbance and habitat sensitivity. I tested the linearity assumption of species diversity and functional diversity relation using curvi-linear regression. I found bell shaped diversity curves in a disturbance gradient. I explained the bell shaped diversity curves in light of species composition and trait dispersions. Species diversity response to disturbance was similar in both fragile and stable habitats with an insignificant interaction effect. However, the relationships between species diversity and functional diversity shifted from linear to a quadratic function with increasing disturbance intensity. The curvilinear relationships between species diversity and functional diversity appeared to be due to low and uneven functional redundancy. My results highlight the need for considering species richness and functional traits simultaneously instead of just species richness and diversity as a conservation priority.

Key-words: Forest harvesting, functional redundancy, headwater stream, intermediate disturbance hypothesis, plant functional trait, riparian buffer, soil scarification

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1. Introduction

Although ecologists have tried for decades to understand the processes and mechanisms of disturbance, diversity and ecosystem functions, the conceptual linkages are not clear (Diaz et al. 2007). These linkages are even more puzzling in disturbed habitats, especially in natural, multi-species assemblages. Here I tested the species diversity and functional diversity response to disturbance and the relationships between these two in naturally colonizing small stream riparian plant communities along a gradient of forest management disturbance. I also tested whether this response differs depending on habitat sensitivity to disturbances.

First, to explain species diversity in a disturbed habitat, the intermediate disturbance hypothesis (IDH) (Grime 1973, Connell 1978, Huston 1979) is a prominent and widely debated theory (Collins and Glenn 1997, Mackey and Currie 2001, Roxburgh et al. 2004). The IDH predicts that species diversity would be at a maximum at a moderate intensity of disturbance. Although counter evidence is available (Arim and Barbosa 2002, Shea et al. 2004, Haddad et al. 2008), generally both control (Gaedeke and Sommer 1986, Weider 1992, Buckling et al. 2000) and manipulative field experiments (Sousa 1979, Folder and Sommer 1999) support the assertion of IDH. High species diversity is considered to be synonymous with high functional diversity, as supported by rigorous experimentation (Tilman et al. 1994, Hooper and Vitousek 1997). Presumably, peak functional diversity can be expected at moderate intensity of disturbance. Although this assumption held true for natural plankton communities (Willby et al. 2001, Weithoff 2003) it remains unclear in natural plant communities. Surprisingly few studies focused on functional diversity response to disturbance (e.g. Mayfield et al. 2005).

Second, the current approach to understanding the relationship between disturbance, species diversity and ecosystem function is highly monotonic with ecologists treating environmental variability as background noise and focusing on independent mechanisms to explain patterns (Shea et al. 2004). Bypassing the environmental variability in dynamic natural systems introduces the risk of ignoring habitat sensitivity even though that might affect plant community reactions to disturbance. Habitat sensitivity can be defined as the ease by which a habitat absorbs a particular disturbance (*sensu* Levitt 1980). Although this is highly context dependent, in a forest ecosystem, soil moisture, soil particle size (a combination of these can act as a surrogate of soil strength) and depth of organic matter can be a good surrogate of habitat sensitivity. I predict that depending on habitat sensitivity, disturbance effects on species and functional diversity will differ. For example, in a riparian habitat that has low soil strength due to high soil moisture and organic content, the impact of small scale disturbance on species diversity may be abrupt, whereas in the less sensitive upland habitat, this reaction might be gradual. Here, I test if species and functional diversity response to disturbance varies depending on habitat sensitivity (i.e. between two habitats: riparian and uplands).

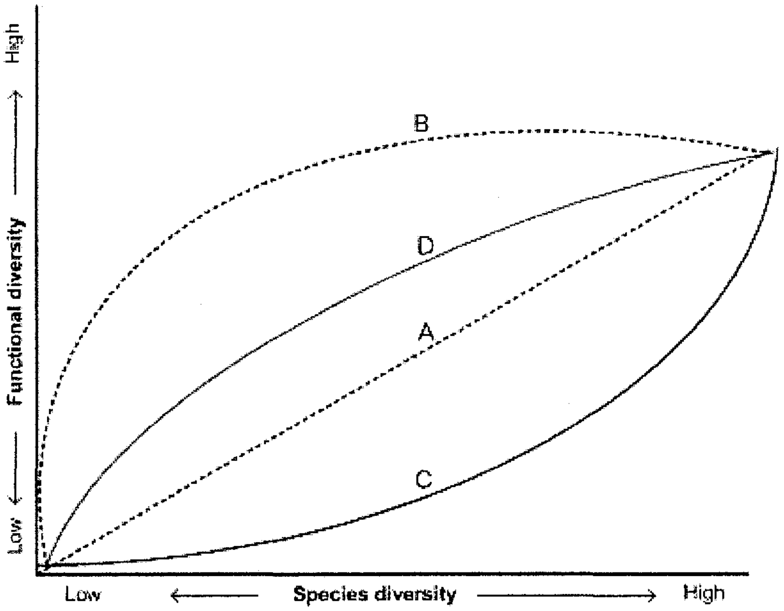

Fig. 2.1 Possible relationships between species diversity and functional diversity. A. linear, B. logarithmic, C. exponential, D. quadratic/cubic relationships (see text for explanations)

Third, a common assumption in conservation ecology is that the relationship between species diversity and functional diversity is linear or log-linear (reviewed by Srivastava and Vellend 2005). Linear relationships signify unique functions for each species (Fig. 2.1 line A) whereas a log-linear relationship implies that a small number of species could provide most of the functions (Fig. 2.1 line B). This type of curve is expected in moderately disturbed habitats where diversity of life form is at its peak (minimum stress). Theory predicts that in highly disturbed habitat, species with similar disturbance-related traits can co-occur, i.e. they can provide similar functions (Grime 1973). In a disturbed habitat, initially many species would contribute little to the total ecosystem functions followed by an increase in functions with increasing species diversity. This would produce an exponential curve (Fig. 2.1 line C). Danovaro et al. (2008) recently provided evidence of this pattern from deep sea benthic diversity. However, in a disturbed habitat, another possible pattern is a quadratic curve where few but not too many species provide similar functions (*sensu* rivet hypothesis of Ehrlich and Ehrlich 1981, Ehrlich and Walker 1998) (Fig. 2.1 line D).

Explanations in the literature, exploring the relationship between species diversity and functional diversity, do exist, however, often as a secondary focus (Fukami et al. 2005, Mayfield et. al. 2005) and many of them are in other ecological systems (e.g. Micheli et al. 2005, Danovaro et al. 2008). In the context of plant communities, studies that provide evidence for linearity are predominantly theoretical and manipulative (reviewed by Schwartz et al. 2000, Srivastava and Vellend 2005) and in most cases their primary focus was to test the effects of species diversity (addition and/or removal) on ecosystem stability. Although it is commonly assumed that disturbance leads to changes in species diversity which in turn leads to changes in functional diversity, in most ecosystems these links are unclear (Naeem 2002). To my knowledge no field study tested the relationships between species diversity and functional diversity in natural plant communities along a disturbance gradient. Although field experiments are often criticized because study variables are affected by abiotic factors (Lawton et al. 1998), a careful consideration can often provide valuable insights and can be complementary to theoretical and controlled experiments.

In North American boreal forests small streams that do not appear on the forest management map (i.e. topographic map) remains mostly unprotected from forest management activities that create a range of disturbance from severe in riparian areas to less severe in upland area (Richardson et al. 2005). Such streams provide ideal locations to test i) the relationship between species diversity and functional diversity following disturbance and ii) how this relationship differs between sensitive and stable habitats.

The objective of this study is to gain an insight into the disturbance–diversity-ecosystem function linkages in natural communities. I test three hypotheses: i) moderate disturbance favours high species and functional diversity, ii) habitat sensitivity influences the response of diversity to disturbance, and iii) species-functional diversity relationship shifts from linear to curvilinear in disturbed natural communities.

2. Methods

2.1 Study system and natural history

I conducted my study in the Mackenzie River and Current River watersheds, on the north side of Lake Superior and about 30 km northwest of Thunder Bay, Canada ($48^0 22^/$ N, $89^0 19^/$ W; 199 m above sea level). While ground slope of the larger area varies from 0 – 50^0, slopes of my selected study sites ranged from 5 - 15^0. This area has low rolling relief with underlying bedrock composed of primarily Precambrian granite and gneiss. This area has a boreal temperate climate with minimum and maximum temperature ranges from -45^0C to + 40^0C (mean 2.5^0C). Mean temperatures for the months of January and July range from -26 to -22^0C and from 21 to 25^0C, respectively. Total annual rainfall varies from 700 – 850 mm (Baldwin et al. 2000).

Vegetation in the boreal forest is dominated by fire-adapted conifers. Pre-harvested and existing (for control sites) dominant overstory species were *Picea mariana, Picea glauca, Abies balsamea* and *Poplus tremuloides. Alnus incana, Aster macrophylus, Cornus canadensis* and *Clintonia borealis* dominated the understory (Stewart and Mallik 2006). All the reference sites, and presumably the riparian buffers, were 80-100 years old whereas the harvested sites were 3-5 years old. Detail habitat and vegetation of the sampled sites are described in section 1 and Table 1 in general methods.

In North American boreal forests, many small streams are on bedrock, on subsurface and often have a discontinuous flow (Lamb 2002); ruts created by harvesting machines at times give a false impression of small streams. Therefore, it is a real challenge to correctly identify small streams in the field in harvested areas. I used a digital elevation model to identify potential streams on maps and followed by field verification with three specific criteria: i) flowing water to the downstream, ii) small streams connected to a large stream and iii) the presence of a stream bed, e.g., indication of water movement, gravel movement etc. The width of our study streams was between 0.5 -1 m.

2.2 Disturbance regimes and habitat sensitivity

I selected my sites based on similar vegetation, ground slope, aspect, and drainage. Three types of sites were selected, i) unharvested (control), ii) clearcut harvested (3-5 yrs old) and iii) clearcutting plus scarification, creating a gradient of disturbance intensity. I also included two more treatments with moderate disturbance intensity between control and clearcut. These were riparian buffer reserves (width 30 m) adjacent to clearcut sites and buffer reserves adjacent to clearcut plus scarified sites. Biologically, disturbances (compared to control) in a riparian buffer reserve originate from increased canopy openings with higher susceptibility to wind throw and interrupted water flow in small streams due to adjacent clearcut and soil scarification (Stewart and Mallik 2006). Thus, altogether I had five treatments in a disturbance gradient from low to high. In order to validate this disturbance gradient, I combined field data on canopy exposure, ground exposure, exposed mineral soil and ruts into a quantitative index of disturbance severity (IDS). The IDS differed significantly between the five disturbance categories in the hypothesized direction (Kruskal Wallis $\chi^2_{df=4} = 68.967$; $p<0.0001$), and IDS was positively correlated to ruderal species abundance (Spearman's correlation $r = +0.39$, $p<0.001$).

I followed Levitt's (1980) mechanistic concept of sensitivity and translated that into our contextual definition of habitat sensitivity as the ease (mechanical strength) with which a habitat absorbs disturbance. My previous data (*unpublished data*) and that of Lamb (2002) revealed that riparian habitats have significantly higher moisture content, finer soil particles and higher organic matter content in comparison to adjacent uplands (also supported by N. Braithwaite, *personal communication*), rendering them more sensitive (hereafter referred as fragile habitats) than the adjacent uplands (hereafter referred as stable habitats).

2.3 Sampling protocol and sample size

I studied 30 small streams where we sampled 174 transects and 1044 quadrats. On each study stream I selected a 50 m section 10 m from the cut edge towards the upstream and divided it into five 10 m sections. From these five sections I randomly selected two sections for sampling by placing transects perpendicular to the stream bank towards the upland (see Fig.2 in General methods). I placed one such transect in the adjacent riparian buffer reserve using the same protocol. On each side of the stream, each transect was divided into approximately ten 1x1 m consecutive quadrats. Since the widths of riparian zones vary, I placed at least two consecutive quadrates for riparian zone and two in the uplands.

2.4 Floristic survey and diversity indices

I determined percent cover of vascular and non-vascular plants in 1x1 m^2 quadrats by visual estimate. Reference specimens were collected and subsequently identified by consulting identification keys and comparing pressed samples in the Claude Garton Herbarium of Lakehead University. For species diversity, I used richness (number of species) and Shannon's $H'_{SD,}$ defined as - $\Sigma p_i \ln p_{i,}$ where p_i is the relative cover of species *i* in the community.

For functional diversity, I used functional richness (analogous to phylogenetic richness) and Shannon's H'_{FD}. Although recent literature shows several functional diversity indices (e.g. FD of Petchy and Gaston 2006, FAD of Walker et al. 1999, FD_{var} of Mason et al. 2005, and Rao's Quadratic entropy), I used Shannon's index to make our study comparable to the majority of published articles in the area. Several authors (e.g. Stevens et al. 2003; Fukami et al. 2005; Danovaro 2008) found that Shannon's H'_{FD} is sufficient to capture variation in functional diversity.

Many authors (e.g. Lavorel and Garnier 2002, Diaz et al. 2007, Lavorel et al. 2008) are of the opinion that until we clearly know the specific ecological role of individual species and their interaction effects, plants functional traits can be used as a good surrogate of ecosystem functions. Therefore, I used diversity of plant functional traits as a synonym of functional diversity. I followed Viole et al. (2007) for the definition of plant functional traits as "any morphological, physiological or phenological feature measurable at an individual level, from cell to the whole organism, without reference to the organism or any other level of organization". I included 36 functional traits related to life history, morphology, productivity, phenology, potential of supporting other biodiversity, site stability, reproduction and adaptation (see Appendix 2.1A and B for the list of traits and surrogate functions). My trait selection was constrained by the availability of information and functions of interests. Many traits are sensitive to disturbance (i.e. plastic traits Fukami et al. 2005) and therefore, I included only static traits in our study and give equal weight for each traits. I developed my trait database from published literature and the USDA plant data base (www.usda.org).

For functional trait analysis I followed Garnier et al. (2007). I constructed a species-abundance matrix and a species-trait matrix. By multiplying these two matrices I developed a trait-abundance matrix. I used the abundance weighted trait matrix for testing treatment effects as $trait_i = \sum_{i=1}^{n} P_i \times trait_i$ where p_i is the relative contribution of species i to the community and $trait_i$ is the trait value of species i. The relative contribution of each particular attribute was calculated as the sum of the relative abundance of a species within that attribute.

2.5 Data analyses and statistical protocol

To test the effects of disturbance on the richness and diversity of species and functional traits, I conducted four nested model of ANOVAs with type III sum of squares. I used disturbance and habitat type (riparian and upland) as fixed factors, sites as random factors and species richness, functional richness, species diversity and functional diversity as responses. The model was expressed as

$$Y_{ijk} = \mu + D_i + S_{(i)j} + H_k + DH_{ik} + SH_{(i)jk} + \varepsilon_{(ijk)}$$

Where, Y_{ijkl} is the species richness, species diversity, functional richness and functional diversity, μ is the overall sample mean, D_i is the disturbance effect (i= 1, 2, .., 5), $S_{(i)j}$ is the effects of site j (j=1, 2, .. ,30) nested within disturbance i, H_k is the effects of habitat type k (k= 1,2), DH_{ik} is the interactions between disturbance i and habitat type k, $SH_{(i)jk}$ is the interactions between habitat type k and site j nested within disturbance i, $\varepsilon_{(ijk)}$ is the error term. To identify significant differences between disturbances, I used Tukey's Honest Significant Difference (HSD) *post-hoc* test. To estimate the proportion of the total variance that attributed to an effect, I calculated the effect size (η^2) of each factor as the ratio of the effect variance (SS_{factor}) to the total variance (SS_{total}) i.e. $\eta^2 = (SS_{factor}) / (SS_{total})$, where SS is the sum of squares (Tabachnick and Fidell 1989).

To meet the assumptions of ANOVA, I checked the residuals for normality (Kolmogrov-Smirnov test; p = 0.05) and homogeneity of the variances (Levene test; p = 0.05). Species richness and functional richness data were transformed to $\log_e$.

To test for differences in species composition and functional trait composition, I conducted a series of nested ANOVAs, using the number of species for each life form (e.g. trees, shrubs, herbs, ferns, grass, mosses and lichens) or trait state as response variables and disturbance category and habitat type as fixed factors and site as random factors. I calculated the effect size (η^2) as in previous tests. Treatment effects were tested using Tukey's Honest Significant Difference (HSD) *post-hoc* test.

To identify the relationship between species diversity (H'_{SD}) and functional diversity (H'_{FD}), I used curvi-linear regression analyses using least squares (SPSS 1999). I compared five models i.e. linear, logarithmic, quadratic, cubic and exponential models. I used species diversity as independent variable and functional diversity as the dependent variable. I selected the final model based on lowest Akaike's Information Criterion (AIC) and distribution of residuals. I calculated AIC value as

$$AIC = -2*\ln(RSS/n)+2*k,$$

where, RSS is the residual sum of squares, *n* the number of observations and *k* the number of parameters in the model. I selected a cut off value of $n/K<40$ for bias adjustment and corrected as

$$AIC_{corrected} = -2*\ln(RSS/n)+2*k +(2*k*(k+1))/(n-k-1).$$

To identify a second possible model, we calculated the distance from observed (Δ_i) for the models as

$$\Delta_i = AIC_i - AIC_{min,}$$

Where, AIC_i is the AIC value of model i and AIC_{min} the model with the lowest AIC (best fit). We performed all the analysis in SPSS version 16 released in 2007 (SPSS 1999).

3. Results

3.1 Diversity response to disturbance and habitat sensitivity

I found significant differences in species richness (Nested ANOVA, $p<0.0001$), species diversity (Nested ANOVA, $p<0.0001$), functional richness (Nested ANOVA, $p<0.0001$) and functional diversity (Nested ANOVA, $p<0.05$) for different disturbance treatments (Table 2.1). Tukey's *post- hoc* HSD (at $\alpha = 0.05$) identified two homogeneous subsets for species richness and three homogeneous subsets for functional richness. Both extremes of disturbances were found in one subset and moderate disturbances were in other subset.

Table 2.1

Results of nested ANOVAs with species richness, functional richness, species diversity and functional diversity as dependent variables and disturbance and habitat type as fixed factors, sites nested within disturbance as random factor.

Response variable	*Source of variation*	*Df*	*F – ratio**	*p value*	*Estimated effect size (η^2)*	*Post-hoc$*
A. Species richness	Disturbance (D_i)	4	11.769	**<0.0001**	0.41	($T_1T_4T_5$), (T_2T_3)
	Site($S_{(i)j}$)	45				
	Habitat type (H_k)	1	15.563	**0.0003**	0.05	
	Disturbance X Habitat type (DH_{ik})	4	0.832	0.5117	0.01	
	Site X Habitat type ($SH_{(i)jk}$)	45				
	Error ($\varepsilon_{(ijkl)}$)	0				
B. Functional richness	Disturbance (D_i)	4	7.620	**<0.0001**	0.30	
	Site($S_{(i)j}$)	45				($T_1T_4T_5$), (T_1T_2), (T_2T_3)
	Habitat type (H_k)	1	7.070	0.753	0.03	
	Disturbance X Habitat type (DH_{ik})	4	0.736	0.572	0.01	
	Site X Habitat type ($SH_{(i)jk}$)	45				
	Error ($\varepsilon_{(ijkl)}$)	0				
C. Species diversity	Disturbance (D_i)	4	13.703	**<0.0001**	0.44	($T_1T_4T_5$), (T_2T_4), (T_2T_3)
	Site($S_{(i)j}$)	45				
	Habitat type (H_k)	1	3.834	**0.0564**	0.02	
	Disturbance X Habitat type (DH_{ik})	4	0.670	0.6163	0.01	
	Site X Habitat type ($SH_{(i)jk}$)	45				
	Error ($\varepsilon_{(ijkl)}$)	0				
D. Functional diversity	Disturbance (D_i)	4	2.571	**<0.0505**	0.12	($T_1T_4T_5$), (T_2T_3) ($T_2T_4T_5$)
	Site($S_{(i)j}$)	45				
	Habitat type (H_k)	1	1.865	0.1788	0.02	
	Disturbance X Habitat type (DH_{ik})	4	2.32	0.0712	0.07	
	Site X Habitat type ($SH_{(i)jk}$)	45				
	Error ($\varepsilon_{(ijkl)}$)	0				

*EMS algorithm: $D_i = \sigma^2 + 2\sigma^2_S + 20\Phi(D)$, $H_k = \sigma^2 + \sigma^2_{HS} + 50\Phi(H)$, $DH_{ik} = \sigma^2 + \sigma^2_{HS} + 10\Phi(DH)$, $S_{j(i)} = \sigma^2 + 2\sigma^2_S$, $HS_{jk(i)} = \sigma^2 + \sigma^2_{HS}$, $\varepsilon_{(ijk)} = \sigma^2$; where, $\Phi(D_i)$ = MS (D) / MS (S); $\Phi(H_j)$ = MS (H) / MS (HS); $\Phi(DH_j)$ = MS (TH) / MS (HS). σ^2Stands for variance and corresponding letter(s) indicate factors in the model.

$ Symbols correspond to Fig. 2.2.

This resulted in bell shaped curves (Fig. 2.2A,B). For species diversity, low to extreme disturbances were found in one set and moderate disturbances in another set, resulting in a bell curve (Fig. 2.2C). The functional diversity curve was idiosyncratic (Nested ANOVA, $p<0.05$) with higher functional diversity in moderate disturbed habitats than the other two extremes (Fig. 2.2D). All of four diversity indices (diversity and richness) were higher in moderately disturbed habitats (T2,T3) than in other habitats. Compositionally, at the species level we found a significant increase in graminoides (Nested ANOVA, $p<0.0001$) and a significant decrease in lichens (Nested ANOVA, $p<0.0001$) while other life forms (trees, herbs and ferns) showed a unimodal response to disturbance (see Appendix 2.2 for *post-hoc* comparisons). At the functional level, disturbed habitats were dominated mostly by plants with functional traits of a low C: N ratio (Nested ANOVA, $p<0.0001$), low rooting depth (Nested ANOVA, $p<0.0001$), annual (Nested ANOVA, $p<0.0001$), evergreen leaf (Nested ANOVA, $p<0.0001$), a persistent soil seed bank (Nested ANOVA, $p<0.0001$) and seed dispersal by water (Nested ANOVA, $p<0.0001$), whereas the undisturbed habitats were dominated by a high C: N ratio (Nested ANOVA, $p<0.0001$), high rooting depth (Nested ANOVA, $p<0.0001$), vegetative reproduction (Nested ANOVA, $p<0.0001$) and colourful flowers (Nested ANOVA, $p<0.0001$) (see appendix 2.5 for *post- hoc* comparisons).

Species richness (Nested ANOVA, $p<0.0003$) differed significantly between two habitat types but species diversity (Nested ANOVA, $p=0.0564$), functional richness (Nested ANOVA, $p=0.753$) and functional diversity (Nested ANOVA, $p=0.1788$) did not significantly differ. The disturbance-habitat coupling (interactions) was non-significant for all diversity measures, with a very low effect size (Table 2.1, Fig. 2.2). In terms of composition, however, the interaction between disturbance and habitat sensitivity was significant in a few cases. For instance, I found significant interaction effects at the species level for graminoides (Appendix 2.2) and at the functional level for plants with low rooting depth and high drought tolerance (Appendix 2.3).

3.2 Linear and curvilinear relationships between species and functional diversity

I found both linear and curvilinear relationships between species and functional diversity. In fragile habitats I found linear relationships at both extremes of the disturbance gradient (Fig. 2.3A,E), whereas at a moderate intensity of disturbance, the relationship was logarithmic (Fig. 2.3B-D). In stable habitats, this relationship shifted from linear (Fig. 2.3F) to logarithmic (Fig. 2.3G) to quadratic (Fig. 2.3H-J) along a gradient of disturbance intensity. In all cases the best fitting model was either liner or logarithmic as evident from the lowest value of the distance from observed (Table 2.2; Δ_i). The exponential model always deviated significantly from the observed.

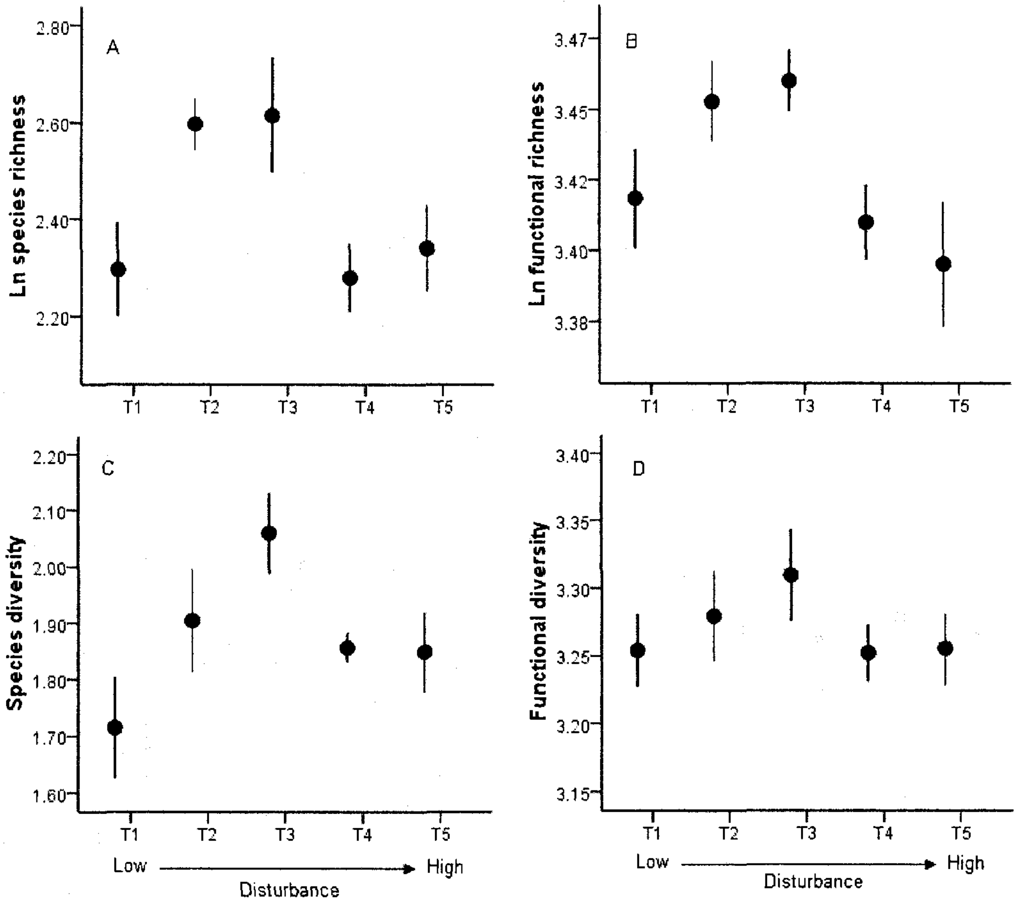

Fig. 2.2 Response of species richness, functional richness, species diversity and functional diversity (±1SE) in a gradient of forest harvesting disturbance. The dark bar represents riparian habitat (fragile) and grey bar represents uplands (stable) habitat. T1, T2, T3, T4 and T5 indicates disturbance treatments: unharvested sites (T1), protected riparian buffer reserves adjacent to the clearcut (T2), protected riparian buffer reserves adjacent to the clearcut plus scarification (T3), clearcut (T4) and clearcut plus scarification (T5). Note that species and functional richness are in $\log_e$ scale. The interval of the abscissas is arbitrarily set equal but do not imply equal scale.

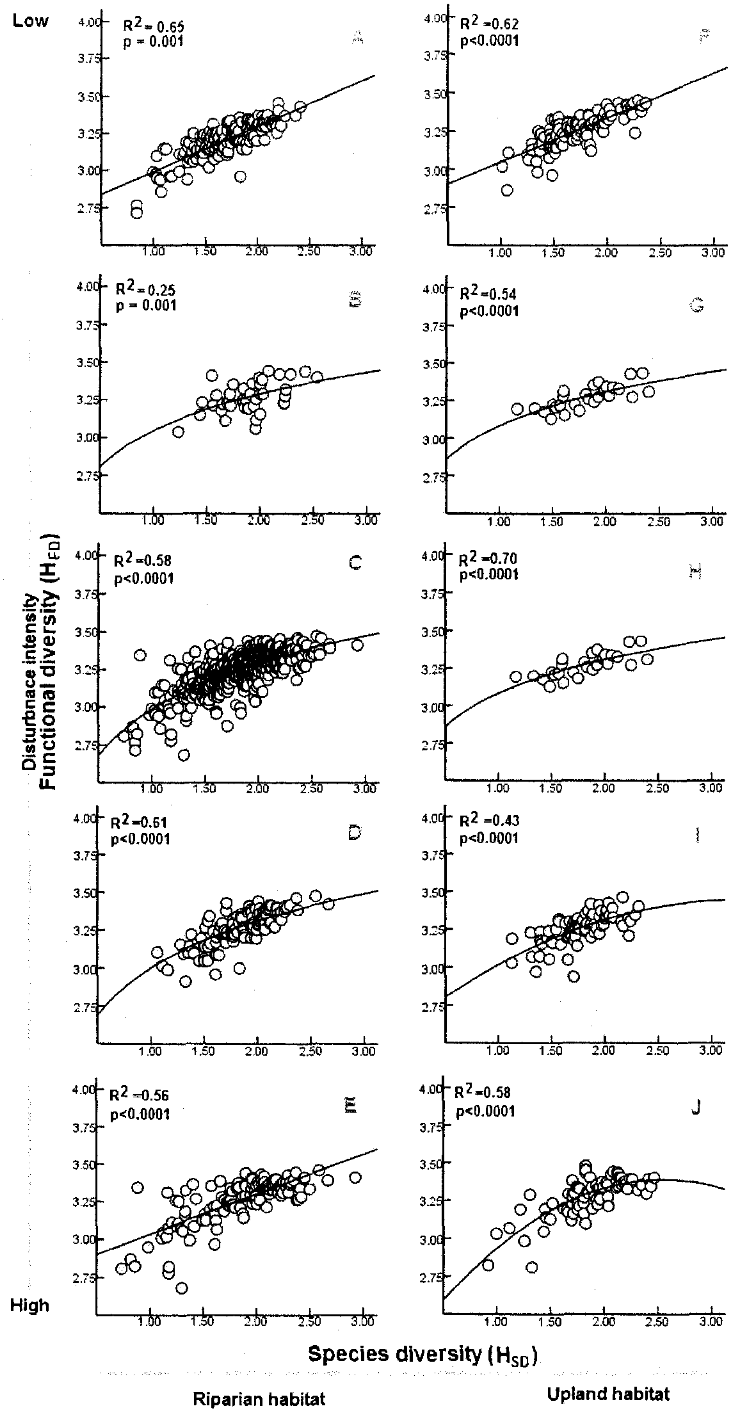

Fig. 2.3 Relationships between species diversity and functional diversity in a gradient of forest harvesting disturbance and habitat sensitivity. The left hand panel is for riparian habitat (fragile) and the right hand panel is for upland habitat (stable). Individual graphs from top to bottom are arranged as unharvested sites, protected riparian buffer reserves adjacent to clearcuts,

protected riparian buffer reserves adjacent to clearcuts plus scarification, clearcut and clearcut plus scarification.

Table 2.2

Values of Akaike's Information Criterion (AIC) used to identify the relationship between species diversity and functional diversity in harvesting treatments and habitat types. Values in the parenthesis indicate distance from the observed (Δ_i).

Disturbance	Habitat sensitivity	Possible models (relationships)				
		Linear	Logarithmic	Quadratic	Cubic	Exponential
T1 Low	Riparian	10.66(AIC_{min})	10.81(0.15)	11.86(1.2)	12.07(1.41)	15.27(4.61)
T2	Riparian	12.98(0.07)	12.91(AIC_{min})	13.84(0.93)	14.73(1.82)	17.99(5.08)
T3	Riparian	12.18(0.04)	12.14(AIC_{min})	12.89(0.75)	13.2(1.06)	16.79(4.65)
T4	Riparian	11.06(0.25)	10.81(AIC_{min})	11.8(0.99)	11.87(1.06)	15.72(4.91)
T5 High	Riparian	9.75(AIC_{min})	10.89(1.14)	10.92(1.17)	10.93(1.18)	14.29(4.54)
T1 Low	Upland	11.68(AIC_{min})	11.76(0.08)	12.69(1.01)	12.75(1.07)	16.29(4.61)
T2	Upland	15.99(0.06)	15.93(AIC_{min})	17.01(1.08)	17.02(1.09)	20.9(4.97)
T3	Upland	14.86(0.89)	14.26(0.49)	13.77(AI_{min})	14.13(0.36)	18.55(4.78)
T4	Upland	12.94(1.04)	12.94(1.04)	11.9(AIC_{min})	12.18(0.28)	16.55(4.65)
T5 High	Upland	12.99(1.37)	12.91(1.29)	11.62(AIC_{min})	12.00(0.38)	16.14(4.52)

4. Discussion

This study presents a comprehensive field test of the response of species diversity and functional diversity to disturbance and the nature of the relationship between species diversity and functional diversity. All of our diversity indices (species richness, functional richness, species diversity, and functional diversity) were significantly higher in the moderately disturbed habitat in comparison to both extremes of disturbance (lowest and highest) resulting in bell shaped curves. Irrespective of habitat sensitivity, species richness and species diversity were significantly lower in high and low disturbance sites in comparison to moderately disturbed habitats. Although at both extremes of disturbance they did not differ, disturbed habitats were characterized by marginally higher species richness and diversity (Fig. 2.2A,B). Seen from a functional perspective, highly disturbed habitats had significantly lower functional richness than low to moderately disturbed habitats (Fig. 2.2C,D). This differential tail was due to a differential rate of trait dispersions (convergence /divergence) (Fig. 2.4) that may lead towards species divergence while traits converge (Fukami et al. 2005). My abundance weighted diversity indices failed to capture these sharp changes because Shannon`s index ($H^{/}$) is more sensitive to higher species abundance. Furthermore, the weighted index was a trade-off for the abrupt changes in species abundance and reflects a gradual and not an immediate change. The idiosyncratic effects of functional diversity with disturbance in the fragile habitat might be due to instability of the riparian habitat. Riparian plant communities are exposed to frequent natural disturbances such as flooding, fire, and beaver activity (Tabacci and Tabacci 2001, Lamb and Mallik 2003). Adaptations of riparian plants to those natural disturbances might equip them in coping with other forms of disturbances such as forest management and scarifications. My result of decreasing functional richness but stable functional diversity in riparian habitat indicates that although the total number of functional groups may not be higher, they are evenly abundant. In a space constrained system like small stream riparian zones, grasses are early colonizing species and they might facilitate other grass species to colonize and maintain higher abundance, hence functional diversity remains unchanged (higher), although species richness and functional richness are decreased. Kimbro and Grosholz (2006) observed similar facilitation by early colonizing species in a space-constrained benthic oyster community on the Californian coasts. My results support the growing consensus of using species richness as a better predictor to capture disturbance response than species diversity (O'Connor and Crowe 2005).

My data did not support my hypothesis of different shapes of disturbance - diversity curves as a product of disturbance - habitat sensitivity coupling. I found non-significant disturbance – habitat sensitivity interaction, with very low effect size (see Table 2.1). Although the traits are related to disturbance, in natural communities environmental heterogeneities often are a trade-off for the treatment responses that may mask a significant relationship (Wright et al. 2006). Although I am rejecting the effect of disturbance habitat sensitivity interactions on diversity, my present study provides some clues for future thought, especially at species compositional levels. For instance, I found an exponential increase of graminoides and a decrease of lichens as a result of disturbance (Appendix 2.2). At a functional level, productivity

(C: N ratio, growth rate), potential to support other species (flower colour), site stability (rooting depth) and adaptability to drought and fire tolerance functions showed a gradual decline (Fig 2.5 and Appendix 2.3).

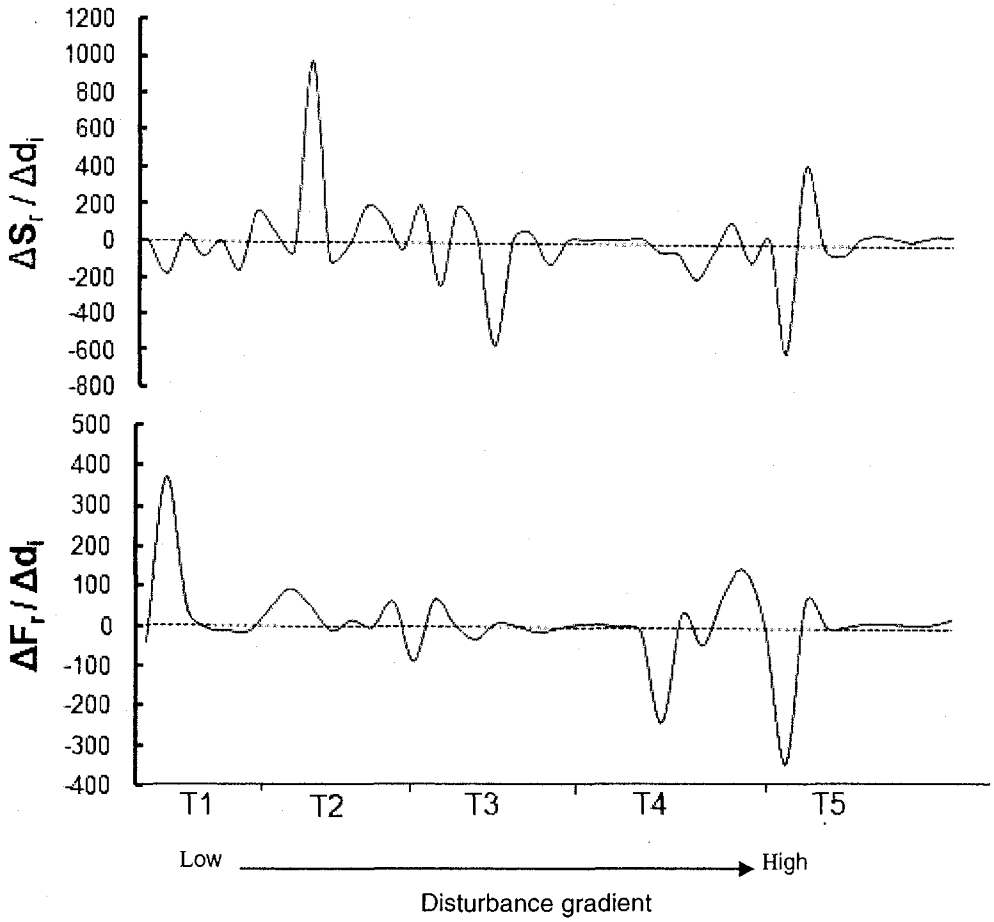

Fig. 2.4 Species and trait dispersions in response to disturbance. Increasing species richness also increases functional richness but at a decreasing rate. After ascending the composite disturbance index and corresponding species and functional richness, I calculated the marginal increase in species richness ($\Delta S_r/\Delta d_i$) and functional richness ($\Delta F_r/\Delta d_i$) per unit of disturbance when IDS was used as a measure of disturbance (Δd_i). Fluctuation above 0 means divergence while negative values correspond to convergence. See Box1.for the quantification of trait dispersions. T1, T2, T3, T4 and T5 represent corresponding disturbance treatments as mentioned in Fig. 2.2. The interval of the abscissa in Fig. 2.4 and 2.5 are arbitrarily set equal but do not imply equal scale.

Box 1

Quantification of trait dispersions

I measured the mean and rate of trait dispersions (convergence/divergence) in a disturbance gradient. I defined the rate of trait dispersion as the marginal change in the trait richness per unit of disturbance increment.

Let t_1 be the trait richness at a disturbance level d_1. If the level of disturbance increase to $d_2, d_3, d_4 \ldots d_n$ and $t_2, t_3, t_4 \ldots t_n$ are the trait abundance for the corresponding levels of disturbances; then the marginal change in the trait richness Δt's are $(t_2 - t_1)$, $(t_3 - t_2)$, $(t_4 - t_3)$, $\ldots(t_n - t_{n-1})$. Therefore, mean trait convergence/divergence (t_c) can be expressed as:

$$\textit{Mean trait dispersion } \boldsymbol{t_c} = \overline{(\Delta t_1 + \Delta t_2 + \Delta t_3 + \Delta t_4 + \ldots\ldots\ldots + \Delta t_n)}$$

$$\boldsymbol{t_c} = \overline{\{(t_2 - t_1) + (t_3 - t_2) + (t_4 - t_3) + \ldots + (t_n - t_{n-1})\}}$$

Consider that the marginal increase of disturbance (I used IDS as a measure of disturbance) is Δd_1, and then it can be quantified as,

$$\boldsymbol{d_c} = \overline{(\Delta d_1 + \Delta d_2 + \Delta d_3 + \Delta d_4 + \ldots + \Delta d_n)}$$

$$\boldsymbol{d_c} = \overline{\{(d_2 - d_1) + (d_3 - d_2) + (d_4 - d_3) + \ldots + (d_n - d_{n-1})\}}$$

The rate of trait convergence /divergence (rt_c) can be expressed as

$$\textit{Rate of trait convergence /divergence } \boldsymbol{rt_c} = \overline{(\Delta t_1 / \Delta d_{1\,+,}\, \Delta t_2 / \Delta d_{2\,+}\, \Delta t_3 / \Delta d_{3\,+}}$$

$$\overline{\Delta t_4 / \Delta d4_{+} \ldots\ldots\ldots + \Delta t_n / \Delta d_{n)}}$$

In this exercise I considered number and abundance of traits; therefore, if t_c is negative ($t_c < 0$) then it is said to be convergence whereas for the positive value ($t_c > 0$) it will be divergent (if anyone considers abundance of a particular trait state, then positive values will indicate convergence).

If it is assumed that a system with low species diversity is dominated by disturbance-sensitive species, then it will not be surprising to see the disturbance diversity curve to be idiosyncratic (Schlapfer and Schmid 1999). It also confirms the fact that choice and number of functional traits is an important factor in determining disturbance response to functional diversity (see review of Lavorel et al. 2008).

The level of functional redundancy can explain the overall shape of the species diversity – functional diversity relation (Walker 1992, Lawton and Brown 1993, Naeem 1998). My result of a curvilinear (quadratic) species-functional diversity relationship was at the cost of uneven and low functional redundancy. In a disturbed habitat, where plants with disturbance-related traits dominate, many generalists can also survive for quite a long period (Grime 1973). This creates a pulse in functional redundancy which ultimately leads to deviation from a straight-line relationship. The uneven functional redundancy can be explained as follows: with natural disturbance (of low to intermediate intensity), three groups of plants can co-occur – generalist, disturbance specialist and some disturbance-sensitive species, which can provide diversity of ecological functions. Therefore, an increase in the number of species also means increasing number of life forms and functional groups, i.e., low functional redundancy. With increasing disturbance such as clearcutting in my case, habitat becomes less suitable for generalist and disturbance sensitive species, whereas the habitat favours the disturbance specialists with disturbance-related functional traits. This creates high functional redundancy for few functions (disturbance responsive functions), while a very low redundancy for many other functions (Fig. 2.5) causes very uneven functional redundancies. With uneven functional redundancy, the species diversity – functional diversity curve can move into two possible directions, either closer to a parabolic or an exponential relation (Fig. 2.1). My data showed that a second degree polynomial fit in a disturbed stable habitat. Linear and logarithmic relationships in the fragile habitat exist because of habitat instability and are less predictable. Secondly, floristic recovery might be more rapid in a riparian zone than in an adjacent upland because of flow facilitated propagule arrival. My results are consistent with those of Mayfield et al. (2005) who found differential responses in species and trait-state relationships between forested and deforested tropical habitats. There remains a paucity of studies exploring the effects of habitat sensitivity on the species diversity – functional diversity relationship, highlighting the need for future attention to this topic.

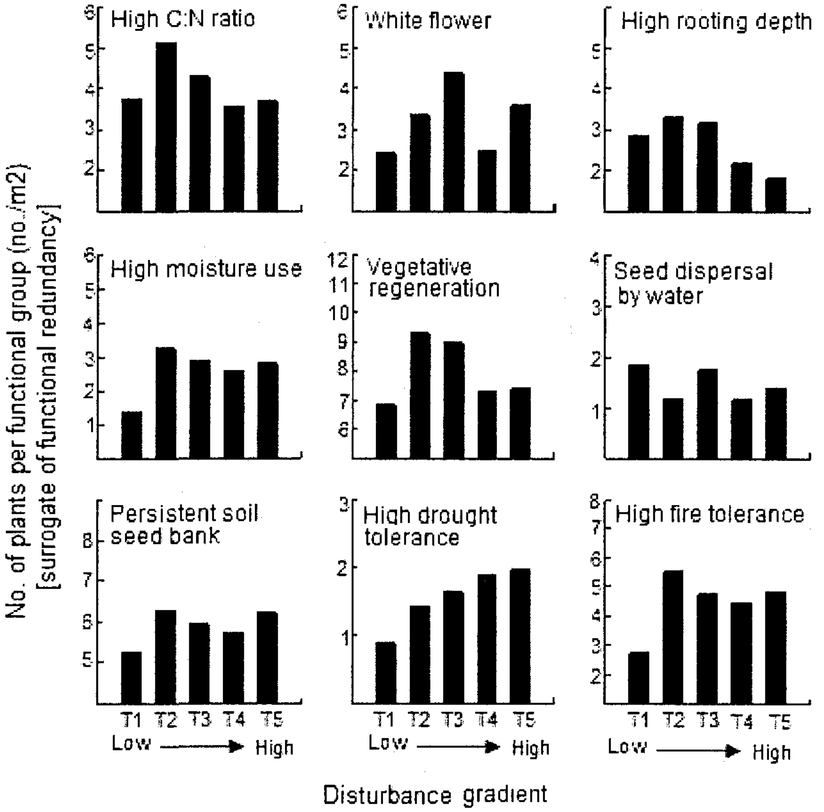

Fig. 2.5 Number of plants per functional group (surrogate of functional redundancy) of selected traits in a gradient of forest harvesting disturbance and habitat sensitivity. Note that we present traits which show significant differences between disturbed and undisturbed habitat. T1, T2, T3, T4, and T5 represent corresponding disturbance treatments as mentioned in Fig. 2.2

Several assumptions are associated with my findings and must be considered in data interpretations. I conducted this study in habitats where plant colonization occurred naturally under field conditions. Although I selected my sites very carefully with similar terrain, pre-disturbance vegetation and in the same watershed and bioclimatic region, I cannot completely reject the possibility of habitat heterogeneity. I was aware of this at the beginning and tried to overcome the challenge by increasing my sample size. I sampled over large riparian areas along the 30 small streams (1 m^2 quadrats, n = 1044) and considered diverse life forms, including trees, shrubs, herbs, ferns, grasses, lichens, mosses and liverworts.

5. Conclusions

I can draw three main conclusions from this study. First, both species diversity and functional diversity reached its peak in moderate intensity of disturbance, producing a bell shaped disturbance-diversity curve. Second, disturbance-habitat sensitivity coupling has very little effect on overall diversity although the effect on particular life forms and functions may be significant. Third, in natural communities, species-functional diversity relationships are linear at low disturbances but this relationship shifts to curvilinear (quadratic) with moderate to high intensities of disturbance. My result signifies that in disturbed habitats, functional redundancy becomes low implying that failure to implement careful conservation measures may result in functional collapse. To overcome these risks I suggest that both number of species (richness) and functional groups be considered in determining disturbance impact on biodiversity in order to safeguard the natural ecosystem functions.

Chapter 3

The refuge concept extends to plants as well: riparian buffer reserve as a biodiversity refuge in the cut-over North American boreal forest*

Abstract

Understanding the role of remnant habitats in human dominated forests is important for effective conservation planning. The riparian buffer reserve is a thin, remnant habitat in the cut-over North American boreal forest. Here I tested if a riparian buffer reserve can act as refuge for forest plants after clearcutting. I sampled naturally colonized plants along small streams (n = 10) within the clearcut forest, adjoining riparian buffer reserves and the uncut reference forest. I predicted the potential plant colonization from their regeneration and dispersal traits. I quantified buffer affinity of the sampled species using Ivlev (1961) electivity coefficient. I found that both species richness (p = <0.0001) and colonization traits were higher in riparian buffers than adjacent clearcuts (p<0.0001) and uncut (p = <0.0002) forests. Multiple response permutation procedure (MRPP) showed significant differences in the composition of colonization traits between habitats (p = <0.0001). Using non-metric multidimensional scaling (NMDS), I explain that additional species in riparian buffers were seed regenerating plants, mostly dispersed by wind, water and vertebrates suggesting that these plants might have arrived from the adjacent clearcuts. My findings add a novel conservation value to the riparian buffers as they act as refuges for disturbance sensitive plants from the clearcut boreal forest. This signifies that careful management of riparian buffers may help in reducing the risk of local extinction of many disturbance sensitive plant species from the boreal forest.

Key words: Buffer affinity, clear-cutting, dispersal traits, plants migration, Ivlevs electivity coefficient, small stream riparian plants

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1. Introduction

Given the increasing human disturbance in the boreal forest, conservation ecologists are curious to know if remnant forest patches contiguous to disturbed habitats provide shelter for plants displaced from the disturbed habitats (Fahrig 2003, Owen-Smith 2008). This concept of biodiversity maintenance by the remnant habitat is known as refuge (Berryman and Hawkins 2006, Owen-Smith 2008). The concept and mechanisms of refuge are well developed for animal ecology (Berryman and Hawkins 2006, Bihn et al. 2008); however, the approach remains to be widely adopted for plants (Haddad et al. 2003, Owen-Smith 2008). Using riparian buffer reserves as representative patches of remnant forest after clearcutting, I evaluate if the refuge concept extends to plants as well.

Borrowing the idea from social science, I define a refuge for plants as a habitat that can be used by plants as a shelter in the event of disturbance. These disturbances may be caused by anthropogenic activities such as forest harvesting as well as natural occurrences such as forest fire, flooding, insect infestation etc. Clearcutting of the forest is one form of human induced disturbance (Keenah and Kimmins 1993, Lamb et al. 2003) that opens the canopy and alters the micro-environment (e.g. light, moisture etc) and that may affect plants (Hamilton and Yearsley 1988, Naiman et al. 2005). In order to minimize these disturbances, the concept of riparian buffer reserve management was introduced (O'Laughlin and Belt 1995) and now riparian buffer reserve management is an integral component in management of the North American boreal forest (Lee et al. 2004, Naiman et al. 2005). A typical riparian buffer reserve consists of a ~30 m wide unharvested forest along both sides of a stream. Retention of the riparian buffer reserve sustains key ecosystem functions (Malanson 1993, O'Laughlin and Belt 1995) including water quality, wildlife habitat, stream temperature and stream bank stability (Naiman et al. 2005, Lamb et al. 2003). However, the role of a riparian buffer reserve to the plant community, especially to the ground vegetation remains unexplored.

Ecological theory predicts that a protected habitat adjacent to a disturbed habitat helps in maintaining species diversity (Fahrig 2003). In this theoretical context, riparian buffer reserves may represent the protected habitats adjacent to clearcut forests (disturbed habitat) and likely play an important role in maintaining plant diversity. There are two ways riparian buffer reserves may help in maintaining plant diversity. First, because of the interconnectedness of forest streams, riparian buffer reserves are interconnected (Gomi et al. 2002). Therefore, in the clearcut forest landscape, riparian buffer reserves provide habitat connectivity that may facilitate plant propagule dispersal. Second, riparian buffer reserves could also support migratory plants (hereafter referred as colonized plants and relevant traits as colonization traits) from the clearcut forest. I define plant migration as a combined phenomenon of dispersal of propagules and establishment of progeny rather than movement of the same individual. After forest harvesting, the altered habitat conditions (e.g. light) creates stress for the understory plant community (Fredricksen et al. 1999, Hart and Chen 2008). Many plant species may persist by adopting colonization strategies that allow them to colonize a nearby protected habitat (Gibbs 2000), and riparian buffer reserves represent the remnant protected habitats adjacent to the clearcuts. Addition of these newly colonized species would enrich the species pool in the riparian buffer reserve. I speculate that overall species richness and cover of colonized species would be higher along small streams in a riparian buffer reserve than along small streams in the clearcut or the uncut reference forest where there are no adjacent habitat disturbances and no colonization events occurring.

Fig. 3.1 Panoramic view of a typical boreal forest landscape showing the riparian buffers and its adjacent clearcut areas.

Which plants will colonize from a stressed habitat to a protected habitat? The answer depends on the possession of certain traits (i.e. colonization traits) that determines plants ability to survive the disturbance and colonize a new habitat (Brunet and Oheimb 1998, Graae and Sunde 2000). The mode of regeneration (Bond and Midgley 2001) and the mode of seed dispersal (Grashof-Bokdam 1997, Takahashi and Kamaitani 2004) are two important traits that influence plants dispersal and colonization (Matlack 1994). Typically, a stress sensitive plant with a set of dispersal traits can colonize a protected forest patch (Matlack 1994, Graae and Sunde 2000), and may persist in response to land use changes (McIntyre et al. 1999). I predict that any addition of colonized species in a riparian buffer reserve would be reflected in the trait display. In other words the prevalence of colonization traits will be diverse and abundant in the riparian buffer reserve.

In this study, in keeping with the overall goal of testing the potential of riparian buffers as a plant refuge, I evaluate two hypotheses: i) riparian buffer reserves support more plant species than a clearcut and an uncut reference forest and ii) the prevalence of colonization traits is higher in a riparian buffer reserve than a nearby clearcut and an uncut reference forest. To test these hypotheses, I studied naturally established plants around small streams within the clearcut, the uncut reference forest and the riparian buffer reserves adjacent to the clearcuts.

2. Methods

2.1 Study sites

My study sites were located in the Mckenzie River and Current River watersheds, on the north shore of the Lake Superior, about 30 km northwest of Thunder Bay, Canada ($48^0 22'$ N, $89^0 19'$ W; 199 m above sea level). Ground slope of the study sites ranged from 5 - 15^0. This area has low rolling relief with underlying bedrock composed of primarily Precambrian granite and gneiss. Climate is boreal temperate, with minimum and maximum temperature ranging from -50^0C to $+40^0$C. Total annual precipitation varies from 700 to 850 mm (Baldwin et al. 2000). Vegetation is predominantly coniferous such as *Picea mariana, Picea glauca,* and *Pinus banksiana*. Dominant understory and ground layer plants include *Aster* spp*, Clintonia borealis, Cornus canadensis, Viola* spp., *Lycopodium* spp. and others. Ages of the reference sites and the riparian buffers were 80 - 100 years old whereas the clearcut sites were 3-5 years old.

2.2 Sampling design

I selected 10 small streams in the clearcut forest and riparian buffers adjacent to that clearcut forest. Small streams that flow from the clearcut forest through a riparian buffer reserve and into larger streams were selected. I also selected an equal number (n = 10) of small streams from the nearby uncut reference forest. Study sites were selected with similar vegetation, ground slope and soil characteristics. On each stream, I laid my sampling transects in two different locations: two transects within the clearcut area and one transect within the riparian buffer reserves. This sampling choice allowed me to compare the ground vegetation within a clearcut forest (stressed; A in Fig. 3.2) and a riparian buffer reserve (protected patch $A^{/}$ in Fig.3.2). On each transect, I placed 1 m^2 consecutive quadrats in the riparian zones. I recorded presence of vascular and non vascular plant species and visually estimated their percent cover in the quadrats.

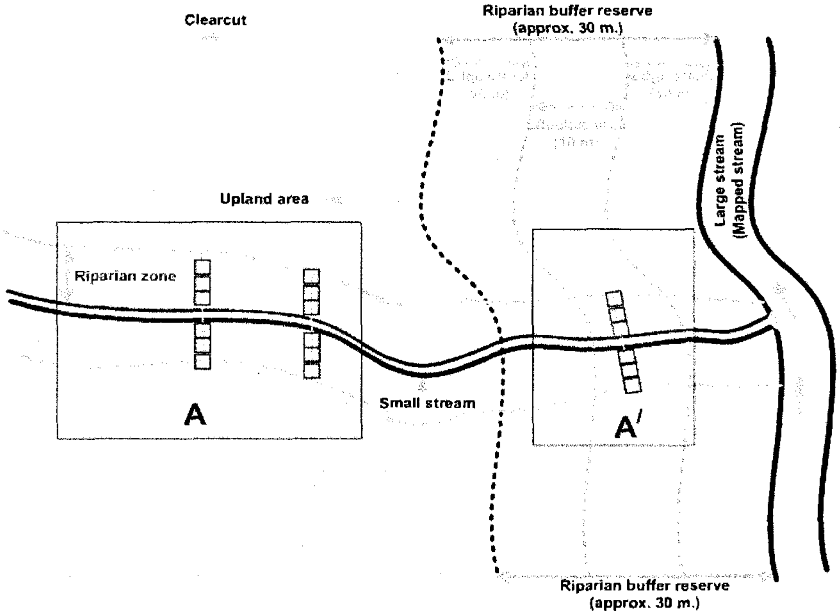

Fig. 3.2 Schematic of sampling layout showing transects and quadrat positions along a small stream in two locations: clearcut (A. stressed habitat) and riparian buffer reserves of a large stream ($A^{/}$. protected habitat).

2.3 Quantification of buffer affinity

I considered a species to be a colonized (immigrant) if it had higher mean abundance in a riparian buffer reserve than in an uncut reference forest and in a clearcut forest. Secondly, I identified the species that were absent in the uncut reference forest but present both in a riparian buffer reserve and an adjacent clearcut forest. I described the buffer affinity of a species using a coefficient (C_{BA}) derived from Ivlev's (1961) electivity coefficient. Shitzer et al. (2008) found this coefficient useful while quantifying affinity of the grazing sensitive plant species to small rock refuge. I calculated the coefficient of buffer affinity (C_{BA}) as:

$$C_{BAi} = \frac{C_{rb} - C_{cf}}{C_{rb} + C_{cf}},$$

Where, C_{rb} and C_{cf} are the mean cover of species *i* in a riparian buffer reserve and a clearcut forest, respectively. Values of C_{BA} were set between -1 to +1. Following the protocol of Shitzer et al. (2008), I set a cut off value of +0.50 to +1 for a colonized species (i.e. positive buffer affinity) and - 0.50 to -1 for a disturbance specialist species (negative buffer affinity). Species that showed a C_{BA} value between - 0.50 to +0.50 were categorized as generalist species. I limited the quantifications of buffer affinity to vascular plants only, due to limited information on nonvascular dispersal traits.

2.4 Colonization traits

I considered three major sets of plant functional traits that influence a plant's colonization and/or migration (e.g. Matlack 1994, Grashof-Bokdam 1997, Brunet and Oheimb 1998, Graae and Sunde 2000, Takahashi and Kamaitani 2004). The selected traits were: i) mode of seed dispersal (wind, water and vertebrate), ii) presence of soil seed bank (persistent, transient) and iii) mode of regeneration (seed, vegetative). In conjunction with buffer affinity, I used a trait based dichotomous key (Fig. 3.3) to qualitatively verify the colonized species in case of any dispute between colonization and habitat mediated flourishing (high abundance). I compiled my trait data base from published literature and the USDA plant data base (www.usda.org).

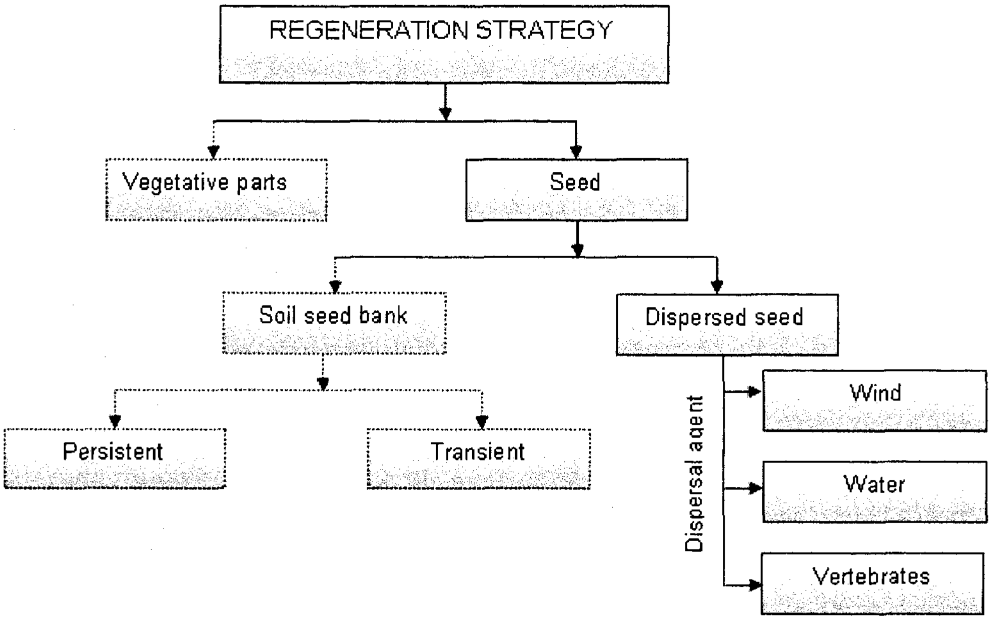

Fig. 3.3 Plant's trait contributing to their colonization. Colonization traits are indicated by solid line whereas non-colonization traits are indicated by dotted lines. I used this trait based dichotomy in conjunction with cover based buffer affinity to identify the colonized plants in a riparian buffer by rejecting the potential dispute of habitat mediated higher abundance.

2.5 Statistical analyses

To test if species richness differed significantly between habitats, I ran one way analysis of variance (ANOVA) using type III sum of squares followed by Tukeys Honest Significant Difference *post-hoc* test with species richness as the dependent variable. To meet the assumptions of ANOVA I checked the residuals for normality (Kolmogorov-Smirnov test; p=0.05) and homogeneity of the variance (Levene test; p=0.05). I transformed species richness to $\log_e$ for the analysis.

To identify potential colonized species in riparian buffer reserves, I first compared the mean percent cover of a species in a riparian buffer reserve and in a reference site by using one way ANOVA. To test if the composition of colonization traits differs between habitats, I ran a multiple response permutation procedure (MRPP) test with Sorensen distance measure. MRPP is a nonparametric technique for detecting the difference between *a priori* classified groups. Although MRPP is analogous to parametric tests it is more attractive than its parametric counterparts because of its robustness under violations of parametric assumptions (Mielke and Berry 1994). Also, MRPP derives the exact probabilities associated with a test statistic, rather than approximate values obtained from common probability distributions (Mielke and Berry 2001).

To test the display of colonization traits, I ran a non-metric multidimensional scaling (NMDS) ordination using the slow and thorough analysis option and the default settings (Sorensen distance measure) in the PC-Ord version 5.11 (McCune and Mefford 1999). NMDS is a non parametric ordination method well suited to community data that avoids many assumptions about the underlying structure of the data made by traditional ordination methods (Clarke 1993).

3. Results

I found a significantly higher number of species along small streams in the riparian buffer than along small streams in the clearcut and in the uncut reference forest ($F_{2,29} = 21.08$, $p = <0.0001$, Fig. 3.4). Richness of shrubs, herbs and lichens was significantly higher in the riparian buffer than each of the other two habitats (Fig. 3.5). Based on the buffer affinity coefficient, 17 species were colonizing species (i.e. showed strong affinity toward the riparian buffer), 35 species were disturbance specialists and the remaining were generalists (Appendix 3.1). The composition of plant colonization traits was significantly different in the riparian buffer reserve than in the clearcut and in the uncut reference forest ($p= 0.000017$, Table 3.1). NMDS ordination gave a three dimensional optimal solution for predicting trends in the abundance weighted functional traits. The solution accounted for 97% of the cumulative variance of the data sets. First, second and third NMDS axes explained 15, 31 and 51% variance of the data sets. The dominant axis three represents a gradient of very few to a high number of colonization traits. The buffer reserve sites are clearly separated from the clearcut and uncut sites and are distributed at the top of the ordination space (Fig. 3.6A,B). Axes one and two, on the other hand, are not as clear as axis three, but represent a weak gradient of water (axis 1) and wind dispersed plants (axis 2) in a gradient of low to high species richness.

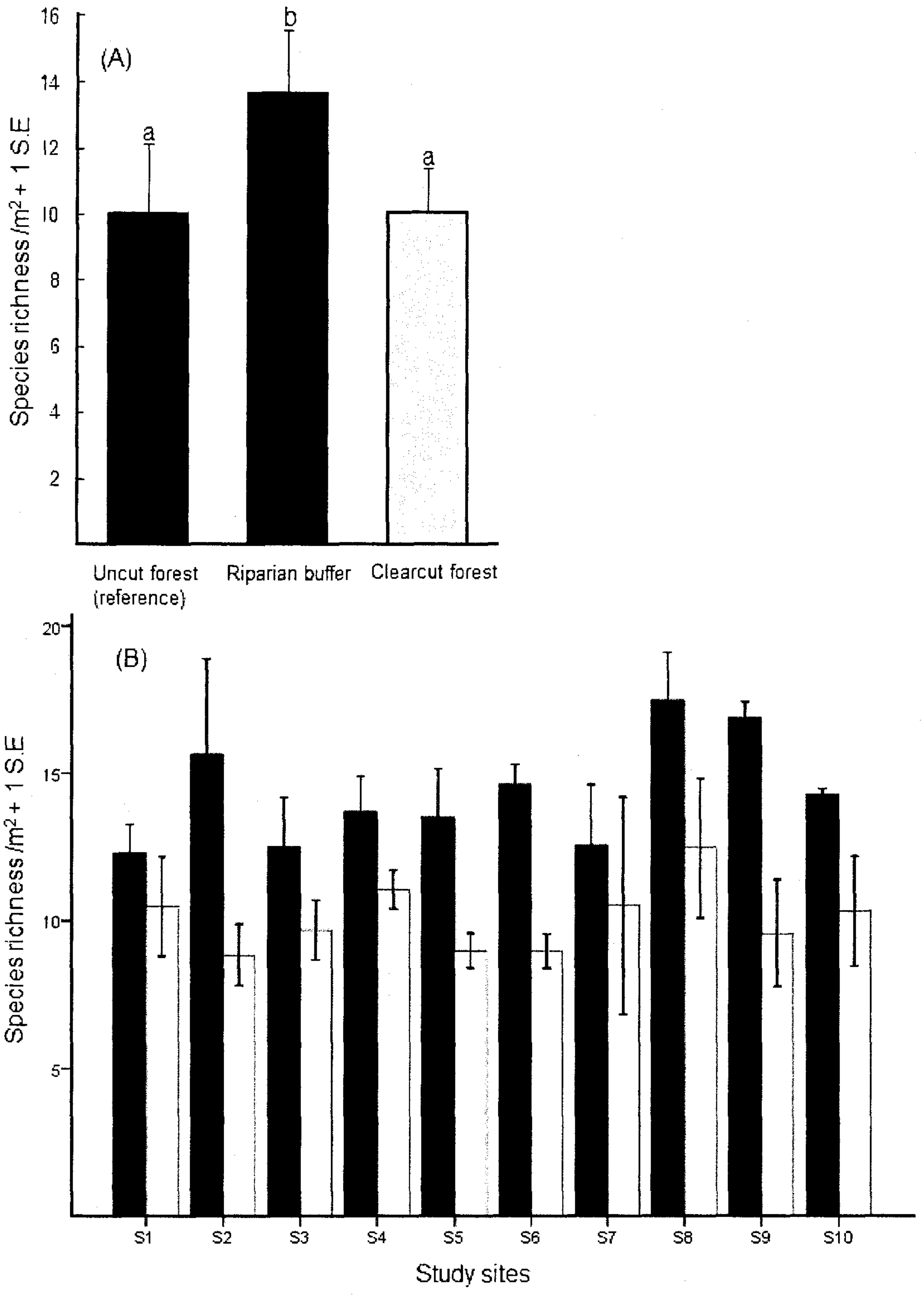

Fig. 3.4 (A) Species richness (Mean +1S.E.) in the riparian buffer compared to the clearcut and the uncut reference forest. Bars with same letter do not differ significantly at $p = 0.05$. (B) Pair wise comparison of the riparian buffer (dark bar) and nearby clearcut sites.

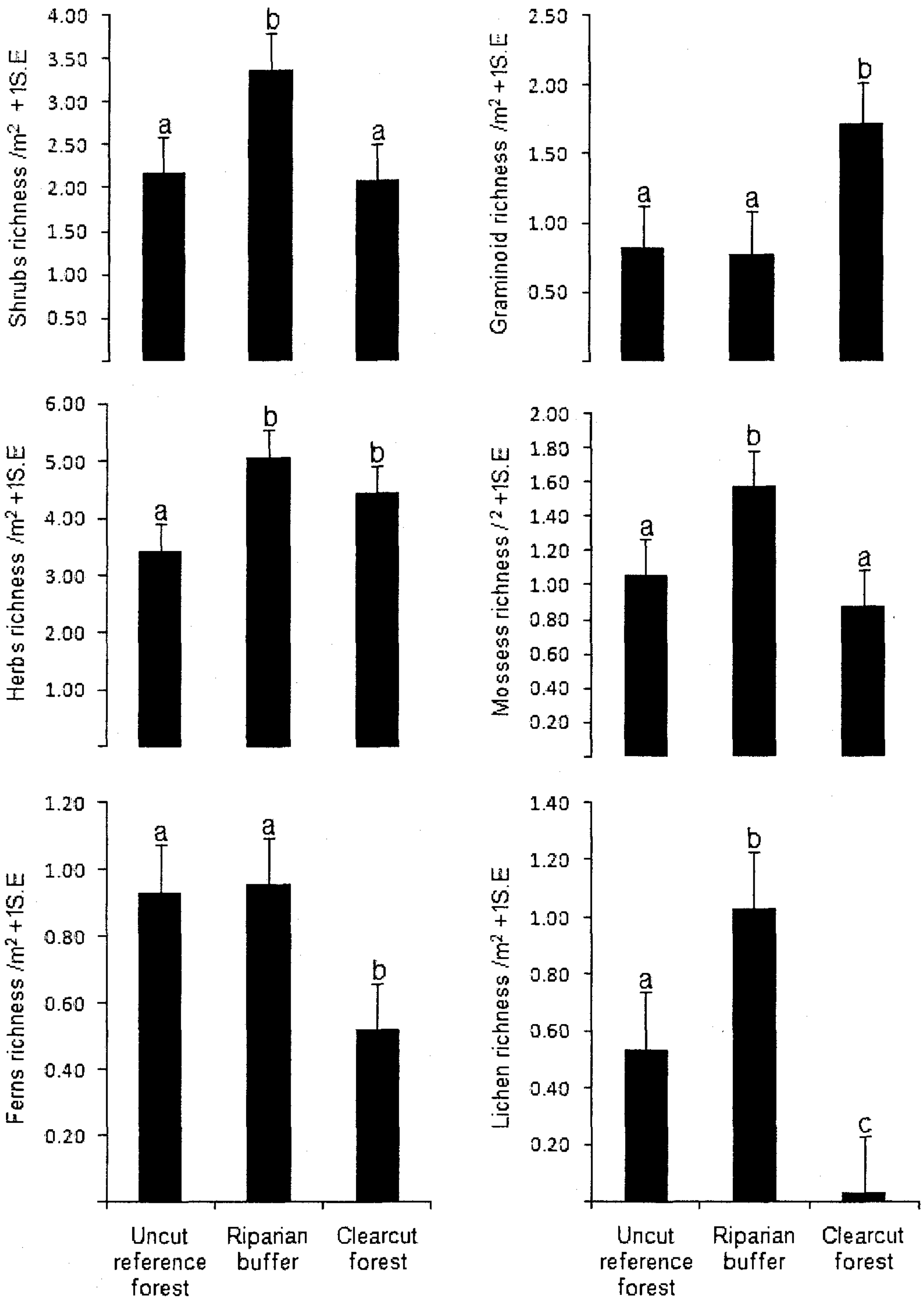

Fig. 3.5 Mean species richness (+1S.E.) based on the life forms of vascular and nonvascular plants in the riparian buffer compared to the clearcut and uncut reference forest. Bars with same letter do not differ significantly at $p = 0.05$.

Table 3.1

Results of the Multiple Response Permutation Procedure (MRPP) testing the null hypothesis of no significant difference in the composition of colonization traits between uncut reference forest, clearcut forest and riparian buffers. The observed delta is calculated from the data while the expected delta is derived from a null distribution. T is the MRPP statistics. A is the chance corrected within group agreement.

Multiple comparisons	T	A	*P*	MRPP statistics
Uncut reference vs Riparian buffer	-7.255	0.257	**<0.0001**	T = -7.5124053
Uncut reference vs clearcut	-0.091	0.003	0.38251127	Observed delta = 0.37567
Riparian buffer vs clearcut	-8.053	0.299	**<0.0001**	Expected delta = 0.50000
				Variance of delta = 0.000274
				Skewness of delta = -1.1646
				A = 0.24866587
				p = **0.00001689**

In the ordination space (Fig. 3.6A) clearcut sites are distributed on the top left hand side (support disturbance specialist species) and uncut sites on the top right hand side (support disturbance tolerant species) while riparian buffer reserves are spread all over, but more concentrated in the middle indicating that they support both groups of species. In Fig. 3.6B clearcut, uncut and riparian buffer reserve sites are sorted in left, middle and right hand sides that run a gradient of abundance of lower to higher water and wind dispersed plants.

4. Discussion

I found that both species richness and associated colonization traits were higher in a riparian buffer reserve than the adjacent clearcut and the uncut reference forest. My findings of higher species richness in a riparian buffer reserve are in accordance with the current understanding of the secondary edge processes of species addition (*sensu* Harper et al. 2005). The possible source of the additional species in the riparian buffer reserve might be the adjacent clearcut forest. Harper et al. (2005) predicted similar patterns of species invasion along clearcut forest edges. This raises the question as to how these additional species arrive in a riparian buffer reserve.

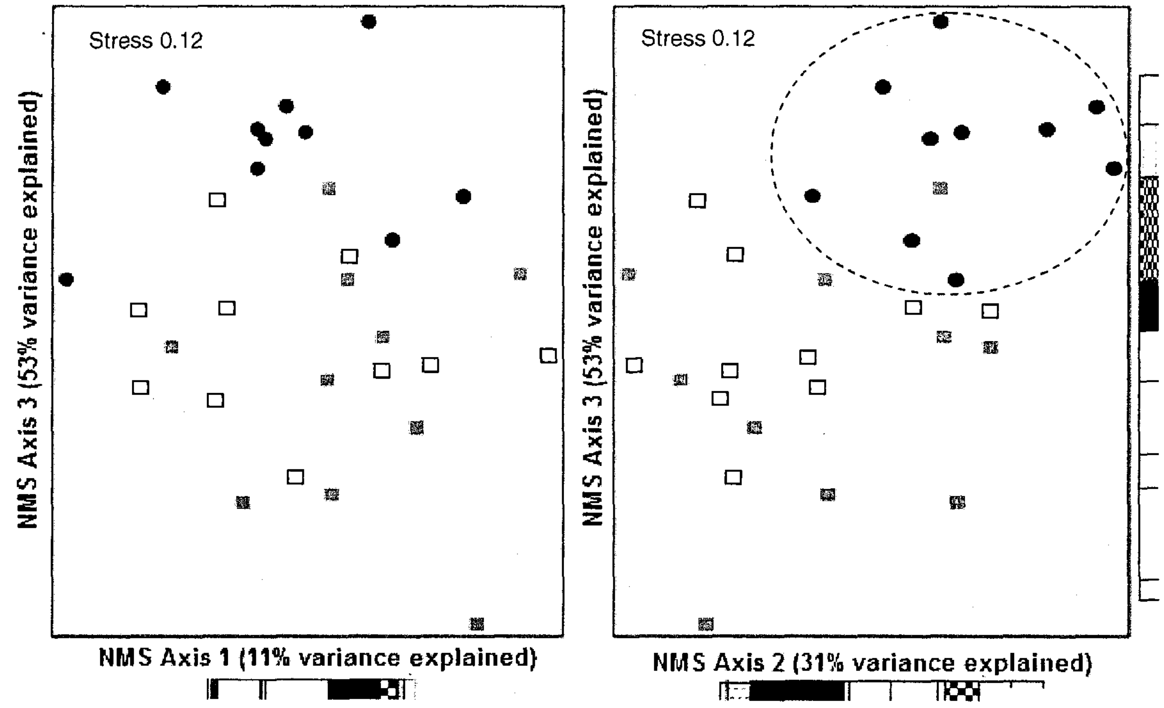

Fig. 3.6 Non-metric multidimensional scaling ordination (NMDS) diagram of the abundance weighted functional traits in three habitats: riparian buffer reserve (●, clearcut forest (☐) and uncut reference forest (▨). The ordination gives a three dimensional solution. (a) Axis 1 vs axis 3 (b) axis 2 vs axis 3. Scale along the ordination axis depicts the estimated effects of colonization traits on the explained variances highlighting the contribution of vertebrate (▩) wind (■) and water (⬚) dispersal traits. I calculated the effects size as the ratio of the variance of the factor to the total explained variance by an axis.

It is likely that one dominant dispersal vector or a combination of several dispersal vectors including wind, water, and vertebrates may facilitate this dispersal and colonization. In the NMDS ordination space (Fig. 3.6A,B), riparian buffer reserves are grouped at the top of axis 3 (a gradient of the diversity of colonization traits) indicating higher diversity of plant colonization traits.

These results are predictable as small windblown seeds can easily be deposited in a riparian buffer reserve which acts as a wind barrier. Secondly, harvesting and site preparation leads to channel bed deformation and interrupted water flow in small streams, therefore, it is likely that seeds can be dispersed only a short distance. The riparian buffer reserve is the closest protected habitat; hence, higher colonization potential for wind and water dispersed plants. Thirdly, if I consider herbivores, after grazing they prefer to take shelter in a shaded place. It is likely that increased frequency of vertebrate movement between the clearcut and uncut riparian buffer reserve facilitate plants dispersal in the riparian buffer reserves. My current study did not allow me to provide direct evidence that additional species in the riparian buffer reserve are coming from a clearcut forest. However, the prevalence of the higher number and abundance of functional traits that determines the colonization potential of plants is in agreement with my arguments.

Stress created by forest harvesting may affect plant species differently depending on their autecological attributes (Haila 1999, Dupre and Ehrlen 2002). Species cover value may be a good predictor to capture this response. For the encountered species, my pair-wise comparison of the cover in the uncut reference forest with the clearcut forest and the riparian buffer reserves made it clear that apart from the addition of new species in the riparian buffer reserve, as indicated by their higher cover some species were showing strong affinity towards the riparian buffer reserve (Appendix 3.1). Although it can be argued that after forest harvesting and edge creation, the altered and improved habitat conditions in the riparian buffer reserve (Murcia 1995, Stewart and Mallik 2006) may increase abundance of some species, however, my careful qualitative evaluation of the dispersal traits following the trait based dichotomous key (see Fig. 3.3 for screening methods) should account for that possibility (Graae and Sunde 2000). Roy and Blois (2006) used a similar trait based analysis while evaluating hedgerow corridors as an environmental filter for forest herbs.

My results showed that plants from all life forms have the colonization potential (Table 3.2). For instance, *Diervilla lonicera, Thalictrum dasycarpum, Matteuccia struthiopteris* and *Carex intumescens* represents colonization and refuge use potential from shrubs, herbs, ferns and graminoides life forms, respectively. However, among the vascular plants, shrubs have more affinity toward riparian buffer reserves than other plants. Dispersal of shrubs into the riparian buffer reserves can be enhanced by their height, growth forms and fleshy fruits that facilitate their dispersal by wind, water and vertebrates (Shitzer et al. 2008).

Table 3.2

Buffer affinity and colonization traits of the selected plant species that are confirmed or speculated to be colonizers in a riparian buffer reserve from an adjacent clearcut. The complete set of colonization traits for the encountered species is available upon request. For a complete list of buffer affinity see Appendix 3.1.

Life form	*Species*	*Buffer affinity*	*Colonization traits*				
			Mode of regeneration		*Mode of seed dispersal*		
			Seed	*Vegetative*	*Wind*	*Water*	*Vertebrates*
Shrub	*Diervilla lonicera*	*0.543*	+++[1]	+++[2]	+[1]	+[1]	+++[3]
Herbs	*Thalictrum dasycarpum*	*0.589*	+++[1]		+++[4]	+[1]	
Ferns	*Matteuccia struthiopteris*	*0.559*	+++[1]	+[5]	+++[5]	++[5]	
Grass	*Carex intumescens*	*0.595*	+++[1]	++[1]	+++[6]	++[1]	

[1]USDA plant data base, [2]Leck et al. 1989, [3]Arnup et al. 1995, [4]Lamb 2002, [5]Prange and Vonaderkas 1985, [6]Byers and Meagher 1997. +++, ++ and + stands for primary, secondary, occasional process.

Several assumptions are associated with my conclusions and they should be interpreted with caution. My findings regarding this vegetation response were obtained shortly after clearcutting (3-5 yrs). Given the fact that most of the common open habitat species arrive at a site soon after disturbance (Connell and Slayter 1977) this study should be considered in the context of a disturbance-colonization scenario. Secondly, I predicted the immigrant species in a riparian buffer reserve based on their functional traits instead of direct tracking. Thirdly, I limited the quantifications of the buffer affinity to vascular plants, due to limited information on the nonvascular dispersal traits. From this study, I am also unable to infer how long an incoming species persists in a riparian buffer reserve. It would be worthwhile to study whether these colonized (immigrant) species in the riparian buffer reserves contribute to recovery of the adjacent clearcut forest. A chronsequence study covering wide range of post-harvest times of clearcuts may answer these questions.

In conclusion, this study provides evidence that, in the boreal forest, riparian buffer reserves could act as a refuge for plants, especially at an early stage after clearcutting. These findings have several implications for riparian management and conservation. For instance, in riparian management, two issues are emerging in importance: i) protection of water quality and aquatic environment and ii) reducing the risk of local extinction of boreal plants. Ecologists and managers are trying to address these concerns separately with more focus on water quality and aquatic environment. My findings imply that a careful management and conservation of riparian buffers may reduce the risk of local extinction of many disturbance sensitive plant species from the boreal forest. If these two issues are integrated then both of the problems can be solved with a minimal conservation effort. However, there remains a paucity of studies on this topic highlighting the need for future research attention in this topic.

Chapter Four

General discussion

I studied plant communities along small streams in northwestern Ontario by focusing on three aspects: i) current state of knowledge on small stream riparian plant communities, ii) disturbance effects on the relationship between species diversity and functional diversity and iii) if riparian buffer reserves act as refuges for plants in the cut-over boreal forests.

I found that riparian plant communities of small forest streams are very poorly studied (chapter 1). Studies of small stream riparian plant communities occupy only five percentages of the total riparian studies (see Fig. 1.2). Several studies (e.g. Gomi et al. 2002, Richardson and Danehy 2007) have shown the structural and functional connectivity between small headwater streams and larger streams. Because of the connectivity between small and large streams in a watershed, it is logical that adversely affected small streams may affect the larger streams. Secondly, riparian habitats are considered to be biodiversity hotspots in the North American boreal forest (Sabo et al. 2005). Plants provide habitat templates for fauna and adversely affected plant community might affect the faunal community. In the synthesis I found that forest management disturbances along unprotected small streams may affect the riparian plant community in terms of reducing plant species richness, and more importantly, shifts the herbaceous dominance to shrubs. It can be predicted that if the plant composition changes, the associated fauna will also be changed leading to a possible danger of functional anomalies. In the recent years, wetland ecologists have become interested in small streams as evident from the increasing number of publications on small stream riparian systems (see section 3.1 in chapter 1 for details). However, one inadequacy is the study on plant communities and future study needs more focus on this topic.

Conservation ecology traditionally relies on the number of species to evaluate if ecosystem functions are maintained, with an understanding that with higher numbers of species a higher the diversity of functions will be achieved. I found that the relationship between species diversity and functional diversity remains linear in lightly disturbed habitat but that relationship shifts to curvilinear with increasing disturbance intensity (see section 3.2 in chapter 2). Danovaro et al. (2008) found an exponential relationship between species diversity and functional diversity in a deep sea benthic community; their findings are opposite of my findings in terms of the curvature of this relationship. The nature of disturbance and resiliency of the investigated community may have contributed to the differing results. However, a common but key message is that the relationship between species diversity and functional diversity is not consistently linear and in fact, this relationship is very much dynamic, like a dynamic natural system.

I suggested that uneven functional redundancy was one of the underlying mechanisms causing the differential relationships. From the perspectives of community assembly, in low disturbed sites competition is the dominant filter structuring plant communities resulting in more or less even redundancy (Grime 1973, Grime 1979, Tilman 1999). In the disturbed habitat, however, abiotic filters become dominant allowing only disturbance tolerant and disturbance specialist species to colonize, followed by competitive filtering that structures the final community of disturbance specialists (Diamond 1975, Weiher and Keddy 1995). Therefore, the final communities in disturbed habitats are inclined towards a limited number of functional groups that can provide only a limited number of functions, resulting in high redundancy for some functions while no or low redundancy for other functions. In my study I found evidence of this type of uneven functional redundancy with increasing disturbance (see section 3, Fig. 2.5; in chapter 2). This finding might add to the growing interest to explain the assembly of natural communities from a functional basis. However, this may be a concern for conservation biologists because in conservation it is common to use species richness (number of species) as a surrogate of ecosystem functions. From the above explanations of functional redundancy, my findings and Danovaro's (2008) findings, it is clear that in disturbed habitats a high number of species does not always correspond to a high number of functions. Conservation activities concentrate more on disturbed habitats where the relationship between species diversity and functional diversity does not follow a straight line. It is the right time to evaluate whether conservation is meeting its goal of functional sustenance. Detailed studies using functional traits may be an avenue for this sort of understanding.

Another emerging concept in contemporary conservation biology is the refuge concept where ecologists are arguing that remnant/protected habitats adjacent to a disturbed habitat could act as a refuge for biota from the disturbed landscape (Fahrig 2003). Animal ecologists have found evidences in support of this concept (e.g. Berryman and Hawkins 2006, Bihn et al. 2008). However, in plant ecology it is still discussed at a theoretical level (Owen-Smith 2008) with little empirical evidence. Using riparian buffer reserves as protected habitats and adjacent clearcuts as disturbed habitats, I empirically evaluated this concept and found some 'preliminary evidence' that the refuge concept is applicable to plants. I use the term preliminary evidence because I did not directly track the plant's movement. That is a long term and difficult task in the field as opposed to radio telemetry to track animals. I used two surrogates: i) a functional dichotomy that may identify possible migratory plants and ii) changes in plant cover due to addition of migratory plants using Ivlev's coefficient (Ivlev 1961). In addition to theoretical unification of the refuge concept, this finding also added a new conservation value to the riparian buffer reserves in clearcut landscape. I should caution however, that these findings are from a small scale study covering only the early phase (3-5 years) after clearcutting. Research covering all ages would be helpful to develop a clear understanding of refuge concept as well as the role of riparian buffer reserves to adjacent disturbed plant communities.

One interesting aspect throughout the thesis is the use of functional trait in conjunction with species level analysis. Using this simultaneous measure I showed possible risks involved, if reliance is placed only on species level analysis. My use of functional traits for qualitative evaluation of plant colonization showed the power and wide applicability of functional traits in understanding the natural systems (Ackerly and Cornwell 2007). One shortcoming in the trait based analysis is the availability of trait data. Europe is far advanced in developing and using the exhaustive trait data bank, in North America, however, efforts continue to develop a trait data bank. Once detailed trait information is available it can be used as a powerful tool for ecological inference.

Future research directions

More research is needed in the following ecological aspects of riparian vegetation of small streams:

1. Is there any functional difference between riparian plant communities of small and large streams?
2. Do small stream riparian plant communities interact differently in presence and absence of habitat disturbances? What is the threshold of disturbance that shifts competitive filtering to abiotic filtering in natural communities?
3. Do small streams in the forest act as a seed dispersal corridor for plants in the boreal watersheds?
4. Do the riparian buffer reserves facilitate recovery of clearcut forests? If so, how?
5. Which faunal groups use riparian buffer reserve as a refuge? After clearcutting does the movement of herbivores increase in the riparian buffer reserves?
6. Does disturbance around small streams facilitate spread of invasive species in the down streams and the protected riparian buffer reserves?

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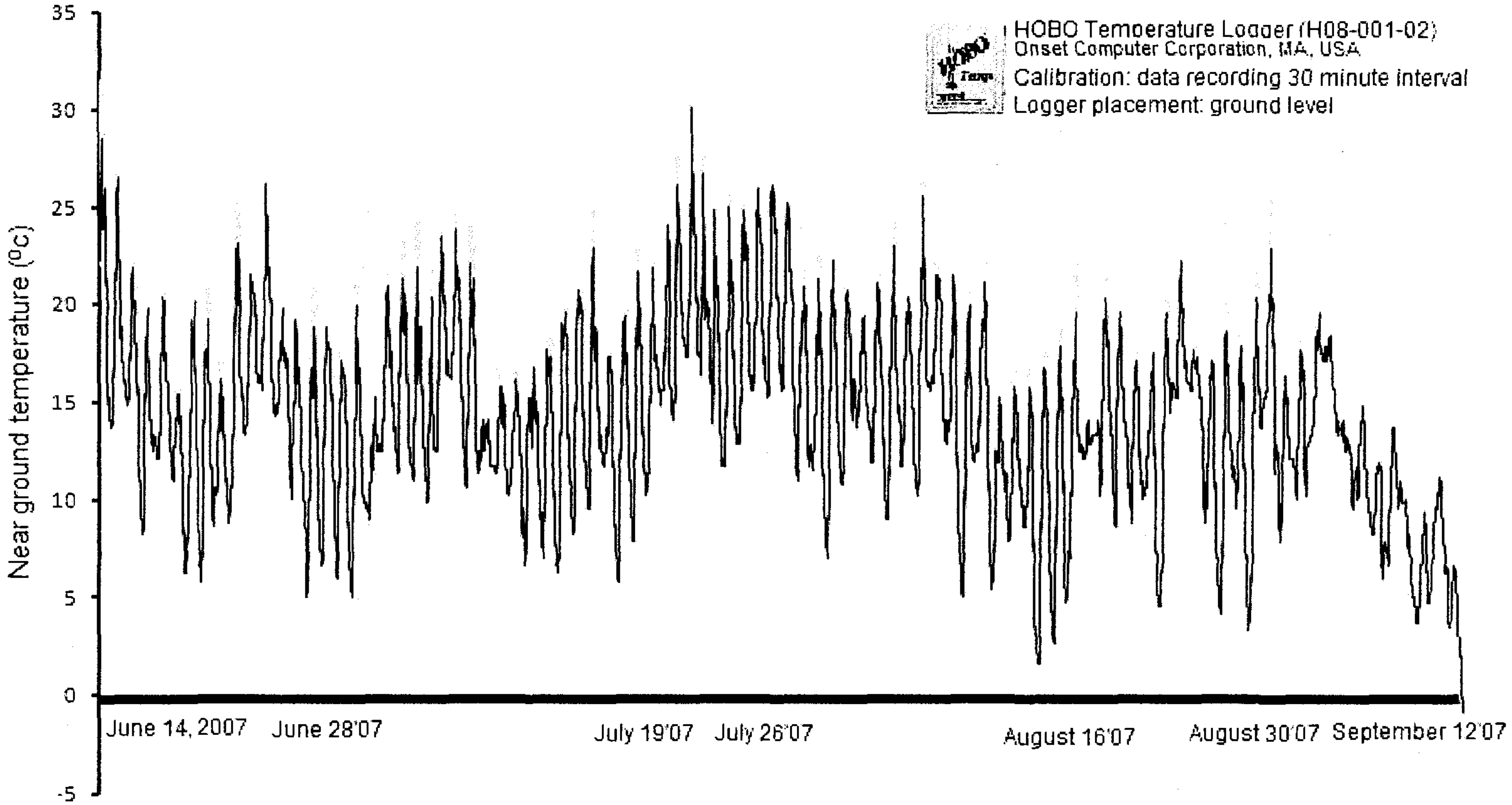
Appendices

Appendix.1

Near-ground air temperature of the study area during the study period



Appendix 2.1A

List of plant functional traits considered in this study with their surrogate functions

Trait category	*Trait states*	*Surrogate functions*	*Explanations /references*
C/N Ratio	• Plants with high C/N ratio • Plants with moderate C/N ratio • Plants with low C/N ratio	Productivity	C: N ratio indicates Carbon output per unit of atmospheric Nitrogen intake. Hence, C: N ratio is reflective of above ground productivity.
Flower colour	• Plants with white flower • Plants with colourful flower	Supporting other biodiversity	Plants with coloured flowers attract more insects than white flowers
Rooting depth	• Plants with high rooting depth • Plants with moderate rooting depth • Plants with low rooting depth	Structural stability, effective functional areas	Plants with a deeper and dense root system reinforce mechanical strength and hold soil more tightly than shallow rooting plants.
Moisture use	• Plants with high moisture use • Plants with moderate moisture use • Plants with low moisture use	Competition ability	Competitive
Growth rate	• Plants with fast growth rate • Plants with moderate growth rate • Plants with low growth rate	Competition ability	Competitive
Life span	• Annual plants • Perennial plants	Productivity	Annual plant spends more energy on reproduction than growth and they also produce more seed for their sustenance. Therefore, presence of annual or perennial plants depicts where the lion share of the resource is utilized.

Trait category	*Trait states*	*Surrogate functions*	*Explanations /references*
Stem tissue	• Plants with woody stem tissue • Plants with herbaceous stem tissue	Structural stability	Structural stability
Leaf longevity	• Evergreen leaves • Deciduous leaves	Productivity	
Regeneration	• Seed regeneration • Vegetative regeneration	Plants migration and recovery	Matlack et al. 1994
Seed dispersal	• Plants with vertebrate seed dispersal • Plants with wind seed dispersal • Plants with water seed dispersal	Plants migration and recovery	Matlack et al. 1994
Resprouting ability	• High resprouting ability • Low or no resprouting ability	Plants migration and recovery	Matlack et al. 1994
Seed bank	• Persistent seed bank • Transient seed bank	Plants migration and recovery	Diversity in the soil seed bank is an important predictor of community recovery after disturbance (Lavorel et al. 1994, Matlack et al. 1994)
Drought tolerance	• Plants with high drought tolerance • Plants with moderate drought tolerance • Plants with low or no drought tolerance	Adaptation	Ability of plants to adjust to environmental stress
Fire tolerance	• Plants with high fire tolerance • Plants with moderate fire tolerance • Plants with low or no fire tolerance	Adaptation	Ability of plants to adjust to environmental stress

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Appendix 2.1B

Example of a partial trait matrix used in this study

Species	Life –form	Life span	Stem tissue	Competition ability	Leaf type	Regeneration method	Seed dispersal vector	Resprouting ability	Colonial growth	Seed bank	Drought tolerance	Flood tolerance	Fire tolerance
Abies balsamea	T^1	P^6	W^1	F^{42}	E^1	S^4	Wi^{42}, V^1		L^1	T^1			
Acer spicatum	S^1	P^6	W^1		D^1	S^6	Wi^1, Wa^6		L, R, S^1	P^1			L^6
Achillea millefolium	H^2	P^2	H^2	M^7	E^2	S, V^2	Wi, V^2	$none^7$	R^2	T^2	H^2	L^2	H^7
Actaea rubra	H^7	P^7											
Agrostis scabra	G^7	P^7		M^7		S^7, V^{48}	Wi^{66}	$none^7$	$none^7$		L^7		L^7
Alnus incana	S^1, $T^{5,31}$	P^3	W^1	F^{31}	D^1	S^6, V^{31}	Wi^1, Wa^6	H^{32}	L, R, S^1	P^1		L^{31}	H^6
Alnus viridis	S^5	P^6				S^6	Wi^6		R^6	T^6			H^6
Amelanchier stolonifera	$S^{1,5}$	P^6	W^1		D^1	S^6, V^8	V^1		R, S^1	T^1			
Anaphalis margaritacea	H^7	P^7	H^{30}	F^7		S, V^4	Wi^{30}	$none^7$	R^7	P^{26}	M^7	L^{30}	L^7
Anemone quinquefolia	H^1	P^7	H^1		D^1	S^4			R^1	T^1			
Aquilegia canadensis	H^7	P^7				S, V^7				P^{26}			H^7
Aralia nudicaulis	H^1	P^7	W^1		D^1	S, V^4	$V^{1,66}$	H^4	R^1	P^1			H^4
Aster ciliolatus	H^7	P^7				S, V^4	Wi^{66}						
Aster lateriflorus	H^7	P^7		M^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7			L^7	H^7
Aster macrophyllus	H^1	P^6	H^1		D^1	S, V^4	Wi, V^1		R^1	P^1			L^6
Aster modestus	H^7	P^7		M^7		S^7	Wi^{66}	$none^7$	R^7		M^7		L^7
Aster puniceus	H^1	P^7	H^1	S^7	D^1	S, V^7	Wi^1	$none^7$	R^1, S^7	T^1	L^7		M^7
Aster umbellatus	H^1	P^7	H^1		D^1		Wi^1		R^1	T^1			
Athyrium filix-femina	P^1	P^2	H^1	M^7	D^1	S^2, V^7	Wi^1	$none^7$	$R^{1,2}$	$P^{1,46}$	L^7		L^7
Betula papyrifera	T^1	P^6	W^1	F^7	D^1	S, V^4	Wi^1	H^7	L, R^1, S^6	$P^{1,28;}$ T^6	L^7	L^{29}	L^6
Brachyelytrum erectum	G^7	P^7		M^7		S^7	Wi^{66}	$none^7$			L^7		L^7
Bromus ciliatus	G^7	P^7					Wi^{66}			P^{37}		L^{58}	
Calamagrostis canadensis	G^1	P^6	H^1	F^4	D^1	S, V^4	$Wi^{1,66}$	$none^7$	R^1	P^1	L^7/H^{45}		H^6/L^{45}
Caltha palustris	H^2	P^2	H^2		D^2	S, V^2	Wa^2	L^2	R, S^2	$unknown^2$	$none^7$	L^2	
Campanula aparinoides	H^1	P^7	H^1		D^1	S, V^7	Wi^1	$none^7$	R^1	T^1	L^7		H^7
Cardamine pensylvanica	H^7	A, P^7			D^7	S^7		$none^7$			$none^7$		$none^7$
Carex adusta	G^7	P^7					Wi^{66}						
Carex aenea	G^7	P^7					Wi^{66}						
Carex aquatilis	G^1	P^7	H^1	M^7	D^1	S^7	Wa^1, Wi^{66}	$none^7$	R^1	T^1	L^7		L^7
Carex arctata	G^7	P^7	H^{26}				Wi^{66}			P^{26}			
Carex canescens	G^7	P^7		S^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		$none^7$		H^7
Carex crawfordii	G^7	P^7					Wi^{66}						
Carex crinita	G^7	P^7		M^7	D^7	S^7	Wi^{66}	$none^7$			L^7		L^7
Carex deflexa	G^1	P^7	H^1		D^1		Wa^1, Wi^{66}		R^1	P^1			
Carex disperma	G^7	P^7		M^7	D^7	S, V^4	Wi^{66}		R^7		L^7		H^7
Carex flava	G^7	P^7					Wi^{66}						
Carex gracillima	G^7	P^7		S^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		L^7		H^7
Carex houghtoniana	G^7	P^7					Wi^{66}						
Carex interior	G^7	P^7		S^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		L^7		H^7
Carex intumescens	G^7	P^7		M^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		$none^7$		H^7
Carex laxiflora	G^7	P^7					Wi^{66}						
Carex leptalea	G^7	P^7		M^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		$none^7$		H^7
Carex rostrata	G^7	P^7		M^7	D^7	S, V^7	Wi^{66}	$none^7$	$R^{7,59}$	P^{16}	H^{59}	$H^{27,59}$	H^7
Carex stipata	G^7	P^7		S^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		H^{59}	H^{59}	H^7
Carex trisperma	G^7	P^7		M^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		$none^7$		H^7
Carex vulpinoidea	G^7	P^7		M^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		L^7		L^7
Chamaedaphne calyculata	S^1	P^6	W^1	M^7	E^1	S^6	Wi^1	H^7	R, S^1	T^1	L^7		H^6
Cinna latifolia	G^7	P^7		M^7	D^7	S, V^7	Wi^{66}	$none^7$	R^7		L^7		H^7
Circaea alpina	H^7	P^7		M^7	D^7	S^4, V^7		L^4	R^7	P^{39}	L^7		L^7
Circium arvense	H^2	P^2				S, $V^{2,60}$	Wi^{51}, Wa^{60}	H^{50}	$R^{2,60}$	$P^{2,60}$	H^{45}	L^{60}	H^{45}
Cirsium muticum	H^1	P^7	H^1		E^1		Wi^1			P^1			
Clintonia borealis	H^1	P^7	H^1	M^7	D^1	rarely S^{44}, $V^{4,44}$	$V^{1,66}$	$none^7$	R^1	T^1	L^7		M^7
Coptis trifolia	H^1	P^7	H^1		E^1	V^{28}			R^1	T^1			
Cornus canadensis	H^1	P^6	H^1	S^7	D^1	S, V^4	V^1	H^4	R, S^1	P^1	L^7		H^6
Cornus stolonifera	S^1	P^6	W^1	M^7	D^1	S^6, V^7	V^1	H^7	L, R, S^1	P^1	L^7	M^{47}	L^6

Species	Life –form	Life span	Stem tissue	Competition ability	Leaf type	Regeneration method	Seed dispersal vector	Resprouting ability	Colonial growth	Seed bank	Drought tolerance	Flood tolerance	Fire tolerance
Corydalis sempervirens	H^{7}	A, B, P^{7}											
Corylus cornuta	S^{1}	P^{6}	W^{1}	M^{7}	D^{1}	S, V^{4}	V^{1}	H^{7}	R, S^{1}	T^{1}	M^{7}		L^{6}/H^{7}
Cypripedium acaule	H^{7}	P^{7}											M^{43}
Diervilla lonicera	S^{1}	P^{6}	W^{1}	S^{7}	$D^{1,5}$	S, V^{4}	V^{6}	H^{7}	R, S^{1}	P^{1}	H^{7}		H^{6}
Drosera rotundifolia	H^{7}	P^{7}											
Dryopteris carthusiana	P^{7}	P^{7}											
Dryopteris expansa	P^{1}	P^{7}	H^{1}		E^{1}		Wi^{1}		R^{1}	$P^{1, 46}$			
Elymus trachycaulus	G^{7}	P^{7}		F^{7}	D^{7}	S^{7}	Wi^{66}	$none^{7}$			H^{7}	L7	H^{7}
Epilobium angustifolium	H^{6}	P^{6}	H^{25}	F^{4}	D^{7}	S^{4}, V^{25}	Wi^{25}, V^{6}	L^{4}	R^{6}	T^{4}/P^{35}	L^{7}	M^{25}, L^{30}	H^{4}
Epilobium ciliatum	H^{2}	P, can function as A^{2}	H^{2}	F^{2}		S,V^{2}	Wi^{2}	L^{2}	R^{2}	P^{2}			H^{45}
Epilobium palustre	H^{2}	P^{2}			D^{2}	S, V^{2}	Wi^{2}	H^{2}	R^{2}				
Equisetum arvense	H^{7}	P^{2}		F^{7}	D^{2}	S,V^{2}		$none^{7}$	R, S^{2}		$none^{7}$		$none^{7}$
Equisetum sylvaticum	H^{7}	P^{7}		F^{7}	D^{7}	V^{4}		H^{4}	$R^{7, 49}$		$H^{7, 49}$		$H^{4, 49}$
Erigeron strigosus	H^{7}	A, P^{7}		M^{7}	D^{7}	S^{7}	Wi^{66}	$none^{7}$			M^{7}		L^{7}
Erysimum cheiranthoides	H^{7}	A, P^{7}								P^{57}			
Eupatorium maculatum	H^{1}	P^{7}	H^{1}	F^{7}	D^{1}	V^{7}	Wi^{1}	$none^{7}$	R^{1}	P^{1}	L^{7}		H^{7}
Eupatorium perfoliatum	H7	P^{7}				S, V^{63}	Wi^{63}						
Euthamia graminifolia	H^{7}	P^{7}				S, V^{7}			R^{7}		L^{24}	L^{24}	
Fragaria virginiana	H^{7}	P^{7}											
Fraxinus nigra	T^{7}	P^{7}		M^{7}	D^{7}	S, V^{7}		H^{7}	R^{7}, S^{23}		L^{7}	H^{23}	M^{7}
Galium asprellum	H^{7}	P^{7}		F^{2}		S^{7}		$none^{7}$			M^{7}		
Galium boreale	H^{7}	P^{7}		M^{7}		$S^{7, 52}$, V^{52}	V^{52}	$none^{7}$	R^{52}		M^{7}		L^{7}
Galium trifidum	H^{7}	P^{7}		M^{7}	D^{7}	S^{7}		$none^{7}$	$none^{7}$		$none^{7}$		$none^{7}/H^{45}$
Galium triflorum	H^{1}	P^{6}	H^{1}		D^{1}	S^{6}	Wi^{6}, V^{1}		R^{1}	P^{1}			L^{6}
Gaultheria hispidula	S^{7}	P^{7}		S^{7}	E^{1}	S, V^{4}		H^{7}	R, S^{7}		M^{7}		H^{7}
Gentiana rubricaulis	H^{7}	P^{7}											
Geocaulon lividum	H^{7}	P^{7}											
Geum rivale	H^{7}	P^{7}		M^{7}	D^{7}	$S^{7, 22}$, V^{22}	V^{35}	$none^{7}$	R^{22}	P^{15}	L^{7}	H^{22}	M^{7}
Geum triflorum	H^{7}	P^{7}		M^{7}	D^{7}	S, V^{7}	Wi, V^{53}	$none^{7}$	R^{7}		H^{7}		M^{7}
Glyceria borealis	G^{7}	P^{7}		M^{7}	D^{7}	V^{7}	Wi^{66}	$none^{7}$			L^{7}		L^{7}
Glyceria canadensis	G^{7}	P^{7}		M^{7}	D^{7}	V^{7}	Wi^{66}	$none^{7}$			L^{7}		L7
Goodyera repens	H^{7}	P^{7}		S^{4}	E^{21}	S^{4}		L^{4}	R^{21}	T^{45}			
Gymnocarpium dryopteris	P^{7}	P^{7}				V^{36}		$none^{7}$		P^{46}			
Heracleum lanatum	H^{7}	P^{7}		M^{7}	D^{7}	S^{7}					L7		H^{7}
Hieracium aurantiacum	H^{7}	P^{7}				S^{54}							
Hieracium caespitosum	H^{7}	P^{7}											
Hieracium scabriusculum	H^{7}	P^{7}											
Hypericum ellipticum	H^{7}	P^{7}											
Iris versicolor	H^{7}	P^{7}										H^{7}	
Juncus brevicaudatus	G^{7}	P^{7}											
Juncus effusus	G^{7}	P^{2}		F^{2}	E^{2}/D^{7}	S,V^{2}	Wi, V^{2}	$none^{7}$	R^{2}	P^{2}	H^{2}		H^{7}
Juncus filiformis	G^{7}	P^{2}			D^{7}								
Juncus nodosus	G^{7}	P^{3}		M^{7}	D^{7}	S^{3}, V^{7}		$none^{3}$	R^{3} (?)		M^{7}		M^{7}
Lactuca biennis	H^{7}	A, P^{7}											
Larix laricina	T^{4}	P^{7}		F^{7}	D^{5}	S^{5}, V^{7}		$none^{7}$	R^{7}		L^{7}	L^{7}	$none^{7}$
Ledum groenlandicum	$S^{1,5}$	P^{6}	W^{1}	S^{7}	$E^{1,5}$	S^{6}	Wi^{1}	none7	L^{1}	P^{1}	M^{7}		H^{6}
Linnaea borealis	S^{1}	P^{7}	W^{1}		E^{1}	V^{4}	V^{1}		L^{1}	$P^{1, 46}$			$none^{8}$
Listera cordata	H^{7}	P^{7}											
Lonicera canadensis	S^{7}	P^{7}				S, V^{4}							
Lonicera hirsuta	H^{7}	P^{7}											
Lonicera involucrata	S^{5}	P^{7}		M^{7}	D^{5}	S, V^{7}		H^{7}	R^{7}		L^{7}		M^{7}
Lonicera oblongifolia	S^{7}	P^{7}											
Lonicera villosa	S^{6}	P^{6}				S^{6}	V^{6}		R, S^{6}				H^{6}
Luzula acuminata	G^{7}	P^{7}											
Lycopodium annotinum	P^{1}	P^{7}	H^{1}	M^{7}	E^{1}	V^{7}	Wi^{1}	$none^{7}$	L, R^{1}	T^{1}	L^{7}		H^{7}
Lycopodium clavatum	P^{7}	P^{7}											
Lycopodium complanatum	P^{7}	P^{7}											
Lycopodium dendroideum	P^{1}	P^{7}	H^{1}		E^{1}		Wi^{1}		R^{1}	T^{1}			
Lycopodium lucidulum	P^{7}	P^{7}											
Lycopodium selago	P^{7}	P^{7}											
Lycopus uniflorus	H^{1}	P^{7}	H^{1}		D^{1}		Wa, V^{1}		R^{1}	P^{1}			
Lysimachia thyrsiflora	H^{7}	P^{7}		M^{7}	D^{7}	S, V^{7}		$none^{7}$			$none^{7}$		H^{7}
Maianthemum canadense	H^{1}	P^{7}	H^{1}		D^{1}	S, V^{4}	V^{1}	H^{4}	R^{1}	T^{1}			H^{4}

Species	Life –form	Life span	Stem tissue	Competition ability	Leaf type	Regeneration method	Seed dispersal vector	Resprouting ability	Colonial growth	Seed bank	Drought tolerance	Flood tolerance	Fire tolerance
Matteuccia struthiopteris	P^7	P^7				S, V^{20}	Wi^{20} (stolons by $Wa)^{20}$		R^{20}		L^{20}	L^{20}	
Mentha arvensis	H^1	P^7	H^1 or G^{38}	M^7	D^1	V^7	$Wa^{1, 34}$	$none^7$	R^1	P^1	L^7		$none^7$
Menyanthes trifoliata	H^7	P^7		M^7	D^7	S, V^7		$none^7$			$none^7$		H^7
Mertensia paniculata	H^1	P^7	H^1		D^1				R^1	T^1			
Mitella nuda	H^1	P^7	H^1		E^1	S^4			R^1	P^1			
Moneses uniflora	H^7	P^7											
Monotropa uniflora	H^7	P^7											
Myrica gale	S^1	P^7	$W^{1,5}$	M^7	D^1	S, V^7	Wa, Wi^1	H^7	R, S^1	T^1	M^7	H^{17}	H^7
Oenothera biennis	H^7	$B^{7, 55}$		F^7		$S^{7,55}$, V^{55}	Wi, Wa, V^{62}	H^{55}	$none^7$/R, S^{55}	$P^{55, 57}$	M^7		L^7
Onoclea sensibilis	P^7	P^7											
Orthilia secunda	S^7	P^7											
Oryzopsis asperifolia	G^1	P^7	H^1		E^1	S, V^4			R^1	P^1			
Osmunda claytoniana	P^7	P^7		M^7	D^7	S, V^7			S^7		L^7		L^7
Osmunda regalis	P^7	P^7		M^7	D^7	S, V^7			S^7		L^7		L^7
Petasites frigidus	H^7	P^7											
Petasites sagittatus	H^7	P^7		M^7	D^7	S, V^7					L^7		H^7
Phalaris arundinacea	G^7	P^2		F^2	D^2	S,V^2	Wa ^{2}	H^2	R, S^2	$P^{2, 57}$	H^7	H^2	H^7
Phegopteris connectilis	P^1	P^7	H^1		D^1		Wi^1		R^1	$P^{1, 46}$			
Physocarpus opulifolius	S^5	P^7		S^7	D^5	S, V^7		H^7	R, S^7		H^7		M^7
Picea glauca	T^4	P^6		S^7	E^5	S^4, V^7	Wi, V^6	$none^7$		T^6	L^5/H^7		L^7
Picea mariana	T^1	P^6	W^1	S^7	E^1	S^4, V^7	Wi, V^6	$none^7$	L^1	P^1; T^6	L^5		H^4/$none^7$
Pinus banksiana	T^4	P^5		F^7	E^5	S^4, V^7	Wi, V^6	L^4		P^6	L^7		H^4
Platanthera hyperborea	H^7	P^7											
Polygala paucifolia	H^7	P^7											
Polygonum cilinode	H^7	P^7				S^4				P^{26}			
Polypodium virginianum	P^7	P^7				S, V^7		$none^7$	R^7		M^7		H^7
Populus balsamifera	T^5	P^6		F^7	D^5	S^6, V^7	Wi, Wa^6	H^7	S^6	T^6	L^7		H^6
Populus tremuloides	T^4	P^6		F^7	D^5	S, V^4	Wi^6	H^4	S^4	T^6	L^7		H^4
Potentilla fruticosa	S^5	P^7		S^7	D^5	S, V^7		H^7	R^7		L^7		L^7
Potentilla norvegica	H^7	A, B, $P^{7, 61}$				S^{61}	$undetermined^{61}$			P^{57}			
Potentilla palustris	H^7	P^7								P^{16}			
Prenanthes alba	H^7	P^7											
Prunus pensylvanica	S^6	P^6		F^7	D^7	S^4, V^7	V^6	H^7	S^6	P^4	L^7		H^7
Prunus virginiana	$S^{1,5}$ T^5	P^6	W^1	F^7	D^1	S^6, V^7	V^1	H^7	R, S^1	P^1	M^7		H^7
Pteridium aquilinum	P^7	P^7			D^{64}	V^{64}	Wi, Wa^{64}		R^{64}	T^{64}	L when young, H when $older^7$	L^{64}	
Pyrola elliptica	S^7	P^7											
Rhamnus alnifolia	S^7	P^7		M^7	D^7	S, V^7		H^7	R^7		L^7		L^7
Ribes glandulosum	S^7	P^7				S^4							
Ribes hirtellum/R. oxycanthoides	S^7	P^7											
Ribes hudsonianum	S^7	P^7		M^7	D^7	S, V^7			R, S^7		M^7		H^7
Ribes lacustre	S^7	P^7											
Ribes triste	S^1	P^7	W^1		D^1		V^1		L, S^1	P^1			
Rosa acicularis	S^1	P^6	W^1	F^7	D^1	S, V^4	V^1	H^7	R, S^1	P^1	L^7		H^6
Rubus acaulis	H^7	P^7											
Rubus chamaemorus	H^7	P^7		F^7	D^7	S, $V^{7, 65}$	V^{67}	$none^7$	R^{65}		L^7		H^7
Rubus idaeus	S^1	P^6	W^1		D^1	S, V^4	V^1		R, S^1	$P^{1, 15}$			H^6
Rubus parviflorus	S^7	P^7				S, V^7		H^7	R^7		M^7		H^7
Rubus pubescens	S^1	P^7	W^1		D^1	S, V^4	V^1		R^1	T^1			
Sagittaria latifolia	H^7	P^3		M^7	D^7	S^3		none ^{3}	R^3 (?)		$none^7$		$none^7$
Salix spp.	S, T^2	P^2	W^2	F^2	D^2	S,V^2	Wi^2, Wa^6	H^2	S^2	T^2			H^6
Sanicula marilandica	H^7	P^7											
Schizachne purpurascens	G^7	P^7				S^{28}	Wi^{66}			P^{28}			
Scirpus cyperinus	G^1	P^7	H^1	M^7	D^1	S, V^7	Wi^{66}	$none^7$	R^1	P^1	L^7		M^7
Scirpus hudsonianus	G^7	P^7					Wi^{66}						
Scutellaria galericulata	H^7	P^7											
Sium suave	H^7	P^3											
Smilacina trifolia	H^7	P^3											
Solidago canadensis	H^7	P^3		F^7	D^7	S, V^7		L^7	R, S^7		M^7		H^7

Species	Life –form	Life span	Stem tissue	Competition ability	Leaf type	Regeneration method	Seed dispersal vector	Resprouting ability	Colonial growth	Seed bank	Drought tolerance	Flood tolerance	Fire tolerance
Solidago uliginosa	H^7	P^7											
Sonchus asper	H^7	$A^{2,7}$			D^2	S^2	Wi^2	L^2	none^2	$P^{2, 46}$			
Sorbus americana	T^5	P^7		M^7	D^5	S, V^7		H^7	R, S^7		L^7		L^7
Sparganium emersum	H^7	P^7		H^{11}	D^{10}	S, V^9	Wa, V^9	H^{11}	R^9			H^{11}	
Spiraea alba	S^7	P^7		M^7	D^7	S, V^7		H^7	R^7		L^7		H^7
Streptopus roseus	H^1	P^7	H^1		D^1	V^{28}	$V^{1, 66}$		R^1	T^1			
Taraxacum officinale	H^2	P^2	H^{56}	F^7	E^{56}	S, V^2	$Wi^{2, 56}$, Wa, V^{56}	H^{56}	R, S^{56}	$T^{2, 56}$ $P^{56, 57}$	H^{56}		
Taxus canadensis	S^7	P^7		M^7	E^7	S, V^7		H^7	R^7		M^7		
Thalictrum dasycarpum	H^1	P^7	H^1		D^1		Wi^1		S^1	T^1			
Thuja occidentalis	T^5	P^7		S^7	E^5	S, V^7		none^7	R^7		L^7		L^7
Triadenum fraseri	H^7	P^7											
Trientalis borealis	H^1	P^3	H^1		D^1	S, V^4			$R^{1, 3}$	P^1			
Trillium cernuum	H^7	P^7											
Typha latifolia	H^7/G^{58}	P^2		F^7		$S, V^{2, 58}$	Wi, Wa^2		$R, S^{7,2}$	P^2	L^7	$H^{7, 58}$	H^7
Vaccinium angustifolium	S^1	P^6	W^1	M^7	D^1	S, V^4	V^1	H^7	R, S^1	$P^{1,4}$	M^7		H^6
Vaccinium myrtilloides	S^1	P^6	W^1		D^1	S^6, V^6	V^1		R^1	T^1			H^6
Viburnum edule	S^7	P^7							R^1	P^1			
Viola adunca	H^7	P^7								P^8			
Viola cucullata	H^7	P^7											
Viola nephrophylla	H^7	A, P^7											
Viola pubescens	H^7	P^7		M^7	D^7	S, V^7	ballistic and ants^{13}	H^7	R, S^7/none^{13}	P^{13}	M^7		L^7
Viola renifolia	H^7	P^7				S, V^{28}				P^{28}			

Life Form: T = tree, S = Shrub, H = herb, G = graminoid, P = pteridophyte; **Life Span**: A = annual, P = perennial; **Stem Tissue**: W = woody, H = herbaceous; **Competition Ability** – F = fast growth, M = moderate growth, S = slow growth; **Leaf type**: D = deciduous, E = evergreen; **Regeneration method:** S = seed, V = vegetative; **Seed dispersal vector**: V = vertebrate, Wi = wind, Wa = water; **Resprouting ability**: H = high, L = low; **Clonal growth** Rh = rhizome (extends from parent ramet to where daughter ramet is produced), Sp = resprout (new ramet from existing collar), L = layer (adventitious from stem or branch); **Seed bank**: P = persistent (at least more than 1 year), T = transient (only from one growing season to next); **Drought tolerance; Flood tolerance, Fire tolerance**

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Appendix 2.2

Compositional difference in plants life forms due to disturbance

Results from Tukeys *post-hoc* test after two way ANOVAs, each with the number of species of a certain life form as response variable and disturbance intensity and habitat sensitivity as fixed factors with factorial interactions. Values with same superscript do not differ significantly at $\alpha=0.05$. Symbol ↑ indicates increasing dominance whereas ↓ means decreasing and ♣ indicates where habitat sensitivity (disturbance x habitat interaction) is significant.

Life form	Disturbance F-ratio (p - value)	Control	Buffer adjacent to clearcut	Buffer adjacent to clearcut plus scarification	Clearcut	Clearcut plus scarification
Tree	6.51 (0.000)	2.27^{a}	2.51^{a}	2.56^{ab}	2.22^{c}	2.31^{bc}
Herbs	4.18 (0.059)	3.56^{a}	4.12^{ab}	4.81^{b}	4.13^{ab}	4.40^{ab}
Shrubs	6.97 (0.000)	2.23^{a}	3.48^{a}	3.20^{a}	2.20^{b}	2.24^{b}
Ferns	5.58 (0.000)	0.75^{abc}	0.90^{bc}	0.99^{c}	0.41^{a}	0.54^{ab}
↑Graminoids♣	16.95 (0.000)	0.59^{a}	0.81^{a}	0.62^{a}	1.39^{b}	1.23^{b}
Mosses and liverworts	5.45 (0.001)	0.98^{ab}	1.29^{b}	1.43^{b}	0.63^{a}	0.95^{ab}
↓Lichens	11.10 (0.000)	0.57^{ab}	0.84^{bc}	1.18^{c}	0.17^{a}	0.07^{a}

Appendix 2.3

Compositional difference in plant functional traits in a gradient of habitat disturbance

Results from Tukeys *post-hoc* test after nested ANOVAs, each with the number of plant species with a specific functional trait as response variable and disturbance and habitat type as fixed factors and site as random factor. Values with same superscript do not differ significantly at $\alpha = 0.05$. Symbol ↑ indicates increasing dominance whereas ↓ means decreasing and ♣ indicates where habitat sensitivity (disturbance x habitat interaction) is significant.

Plants functional traits	Response direction	Disturbance F-ratio (p - value)	Control	Buffer adjacent to clearcut	Buffer adjacent to clearcut plus scarification	Clearcut	Clearcut plus scarification
High C/N ratio	↓	27.910 (0.000)	5.00^{a}	5.14^{a}	4.89^{a}	2.97^{b}	3.50^{b}
Medium C/N ratio		4.172(0.004)	2.65^{a}	2.13^{b}	2.18^{b}	3.70^{ab}	3.60^{ab}
Low C/N ratio		2.621 (0.040)	0.34^{a}	0.56^{ab}	0.84^{b}	0.93^{ab}	0.85^{ab}
Colourful flower	↓	22.527(0.000)	3.63^{a}	3.90^{a}	3.68^{a}	3.16^{b}	3.09^{b}
White flower	↑	1.726 (0.005)	1.74^{a}	1.57^{a}	1.55^{a}	2.75^{b}	2.89^{b}
High rooting depth	↓	15.734(0.000)	5.64^{a}	5.72^{a}	5.73^{a}	3.63^{b}	4.32^{b}
Medium rooting depth		1.162 (0.333)	2.25	2.64	2.38	3.11	2.97
Low rooting depth	♣	1.080 (0.371)	1.12	1.49	1.36	2.35	1.88
High moisture use		9.564(0.000)	3.33^{a}	3.43^{ab}	3.67^{a}	3.05^{bc}	2.87^{c}
Moderate moisture use		4.171 (0.004)	3.12^{a}	3.28^{ab}	2.91^{a}	3.45^{b}	3.67^{b}
Low moisture use		0.953 (0.438)	0.61	0.73	1.15	1.07	0.83
Fast growth rate	↓	11.975(0.000)	4.41^{a}	5.39^{a}	4.98^{a}	2.74^{b}	3.03^{b}
Moderate growth rate		7.886(0.000)	2.31^{a}	1.70^{b}	1.93^{b}	2.46^{b}	2.41^{b}
Slow growth rate		1.689(0.159)	1.71	2.50	2.37	3.40	2.05
Annual		2.958 (0.024)	0.02^{a}	0.09^{ab}	0.03^{ab}	0.34^{b}	0.25^{ab}
Perennial	↑	18.487(0.000)	2.97^{a}	2.85^{bc}	2.81^{b}	3.14^{cd}	3.17^{d}
Woody stem tissue		15.275(0.000)	4.95^{a}	4.60^{bc}	4.50^{b}	4.32^{cd}	4.65^{d}
Herbacious stem tissue		6.878(0.000)	1.63^{a}	1.40^{b}	1.70^{ab}	1.92^{b}	1.95^{b}
Evergreen		3.559(0.010)	1.66^{ab}	1.99^{ab}	2.51^{b}	1.14^{a}	1.64^{ab}
Deciduous		11.517(0.000)	3.00^{a}	2.92^{b}	2.70^{b}	3.12^{b}	3.25^{b}
Vegetative regeneration		8.658(0.000)	2.60^{a}	2.93^{ab}	2.80^{ab}	3.21^{bc}	3.21^{c}
Seed regeneration	↑	18.586(0.000)	3.15^{a}	3.13^{bc}	3.05^{b}	3.30^{cd}	3.29^{d}
Vertebrate dispersal		1.466(0.2190	2.46	2.68	2.60	3.54	3.56
Wind dispersal	↓	20.611(0.000)	4.24^{a}	4.09^{b}	4.19^{ab}	3.49^{c}	3.67^{c}
Water dispersal	↓	16.222(0.000)	5.15^{a}	4.09^{b}	4.68^{ab}	1.88^{c}	2.51^{c}
High resprouting ability	↓	12.248(0.000)	4.71^{a}	4.36^{b}	4.23^{ab}	3.20^{c}	3.59^{c}
Low resprouting ability	↑	0.401(0.0087)	2.00^{a}	2.50^{a}	2.42^{a}	3.77^{b}	3.83^{b}
Persistent seed bank		12.220 (0.000)	3.32^{a}	3.13^{bc}	3.02^{b}	3.46^{bc}	3.40^{c}
Transient seed bank		10.672(0.000)	3.06^{a}	2.60^{b}	2.74^{b}	2.66^{b}	2.96^{b}
High drought tolerance	↑ ♣	6.365(0.000)	1.22^{a}	1.29^{a}	1.80^{a}	4.21^{b}	3.52^{ab}
Moderate drought tolerance	♣	0.715 (0.584)	1.60	2.11	1.76	3.19	3.10
Low or no drought tolerance	↓	19.278(0.000)	3.91^{a}	4.03^{b}	4.12^{ab}	3.43^{c}	3.59^{c}
High fire tolerance*		1.1008(0.408)	2.54	3.31	3.06	3.95	3.98

Plants functional traits	Response direction	Disturbance F-ratio (p - value)	Control	Buffer adjacent to clearcut	Buffer adjacent to clearcut plus scarification	Clearcut	Clearcut plus scarification
Moderate fire tolerance		12.752 (0.000)	3.37^a	1.92^b	1.98^b	1.54^b	1.56^b
Low or no fire tolerance	↓	13.345(0.000)	4.55^a	3.74^b	3.60^b	2.16^c	1.81^c

Appendix 3.1

Buffer affinity of the encountered vascular plants

Species	Buffer affinity (C_{IA})	Species cluster
Acer spicatum	0.48	G
Alnus incana	0.479	G
Alnus viridis	0.129	G
Amelanchier stolonifera	0.31	G
Cornus stolonifera	-0.125	G
Corylus cornuta	1.000	Bs
Diervilla lonicera	0.543	Bs
Gaultheria hispidula	-0.502	Ds
Ledum groenlandicum	0.186	G
Linnaea borealis	-0.322	G
Lonicera hirsute	-0.143	G
Lonicera villosa	-0.600	Ds
Prunus pensylvanica	0.50	Bs
Prunus virginiana	1.000	Bs
Ribes glandulosum	-0.098	G
Ribes hudsonianum	0.111	G
Ribes oxycanthoides	0.208	G
Rosa acicularis	-0.116	G
Rubus acaulis	-0.267	G
Rubus idaeus	-0.255	G
Rubus pubescens	-0.208	G
Salix spp.	0.184	G
Vaccinium angustifolium	-0.227	G
Vaccinium myrtilloides	-0.169	G
Viburnum edule	0.199	G
Anaphalis margaritacea	-1	Ds
Anemone quinquefolia	1	Bs
Aralia nudicaulis	0.429	G
Aster ciliolatus	0.263	G
Aster conspicuous	-0.351	G
Aster macrophyllus	0.318	G
Aster umbellatus	0.25	G
Caltha palustris	0.538	Bs
Circaea alpine	-0.053	G
Cirsium muticum	-1	Ds
Clintonia borealis	0.131	G
Coptis trifolia	-0.147	G
Cornus Canadensis	-0.177	G
Drosera rotundifolia	0.633	Bs
Epilobium angustifolium	-0.346	G
Epilobium ciliatum	-1	Ds
Epilobium palustre	0.061	G
Equisetum arvense	0.180	G
Equisetum sylvaticum	0.196	G
Fragaria virginiana	-0.040	G
Galium asprellum	-0.347	G
Galium boreale	0.325	G
Galium triflorum	-0.062	G
Geocaulon lividum	1	Bs
Hieracium aurantiacum	-1	Ds
Hieracium caespitosum	-1	Ds
Iris versicolor	1	Bs
Lactuca spp.	-0.123	G
Lycopus uniflorus	-1	Ds
Maianthemum canadense	-0.095	G
Mentha arvensis	-1	Ds

Species	Buffer affinity (C_{IA})	Species cluster
Mertensia paniculata	0.049	G
Mitella nuda	0.083	G
Oenothera biennis	-1	Ds
Petasites frigidus	0.060	G
Petasites sagittatus	-1	Ds
Polygonum cilinode	-1	Ds
Potentilla norvegica	-1	Ds
Potentilla palustris	-1	Ds
Pyrola elliptica	1	Bs
Sanicula marilandica	-1	Ds
Scutellaria galericulata	1	Bs
Smilacina trifolia	1	Bs
Solidago canadensis	0.047	G
Sonchus asper	-1	Ds
Streptopus roseus	0.257	G
Taraxacum officianale	-1	Ds
Thalictrum dasycarpum	0.589	Bs
Trientalis borealis	0.099	G
Trillium cernuum	0	G
Typha latifolia	-1	Ds
Viola adunca	-1	Ds
Viola nephrophylla	-0.003	G
Viola pubescens	-1	Ds
Viola renifolia	0.039	G
Athyrium filix-femina	0.314	G
Dryopteris expansa	0.321	G
Gymnocarpium dryopteris	0.263	G
Lycopodium annotinum	0.530	Bs
Lycopodium clavatum	1	Bs
Lycopodium dendroideum	0.046	G
Matteuccia struthiopteris	0.559	Bs
Osmunda claytoniana	-1	Ds
Osmunda regalis	-1	Ds
Phegopteris connectilis	-1	Ds
Woodsia	0.132	G
Agrostis scabra	-1	Ds
Calamagrostis Canadensis	-0.472	G
Carex bebbii	-1	Ds
Carex brunnescens	-1	Ds
Carex deweyana	-1	Ds
Carex diandra	-1	Ds
Carex interior	0.132	G
Carex intumescens	0.595	Bs
Carex lasiocarpa	-1	Ds
Cinna latifolia	-1	Ds
Elymus canadensis	-1	Ds
Glyceria grandis	-1	Ds
Poa pratensis	-1	Ds
Schizachne purpurascens	-0.450	G
Scirpus cyperinus	-1	Ds
Scirpus hudsonianus	-1	Ds

Where, Bs = buffer specialist, Ds =disturbance specialist and G = generalist; N.B. Here, we listed species with minimum 2% mean cover in any of the three habitat types.