Spatial patterns and habitat characteristics of Atlantic Coastal Plain Flora across lakeshore edges in Nova Scotia

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ABSTRACT

Spatial patterns and habitat characteristics of Atlantic Coastal Plain Flora across lakeshore edges in Nova Scotia

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Lakeshores are hotspots for biodiversity in many temperate regions, including disjunct populations of Atlantic Coastal Plain Flora (ACPF) in Nova Scotia. As ACPF are increasingly endangered, I aimed to provide a framework that can guide decisions regarding the conservation of ACPF habitat by (1) identifying their spatial pattern and relationship with structural diversity along the lakeshore-to-forest gradient and (2) defining their habitat characteristics at landscape and local scales. I characterized common lakeshore ACPF species, vegetation structural elements and abiotic factors on lakes in the Medway watershed. ACPF were positively associated with structural diversity on lakeshores where low levels of structural diversity were found. At a landscape scale, larger watershed area, distance to shrub and gentle slope, with low elevation and shrub cover, presence of sundews, bryophytes and graminoids, and a variety of substrate types, at a local scale, were positively associated with ACPF, which can help to identify ACPF habitat.

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CHAPTER 1 – INTRODUCTION

Riparian zones and more specifically lakeshores are hot spots for biodiversity in many temperate regions (Morris et al. 2002). They provide important habitats for many plant species (Komonen 2009) as flooding displaces competitive terrestrial upland species, creating favored conditions for rare and stress-tolerant species (Rhazi et al. 2006). Woody plant species mortality resulting from hydrological disturbances creates gaps that reduce competitive interactions and allows for the coexistence of a greater number of species (Naiman and Décamps 1997), especially poor competitors (Keddy 1984) and species at risk (Komonen 2009), such as many of the Atlantic Coastal Plain Flora found on lakeshores in southwestern Nova Scotia.

NATURAL HISTORY OF ATLANTIC COASTAL PLAIN FLORA

Atlantic Coastal Plain Flora (ACPF) are a group of taxonomically unrelated herb, grass, sedge and shrub species that share common habitat types, such as freshwater (e.g., lake and river shores, wetlands (fens, bogs)), coastal (e.g., salt marshes, estuaries, rock and sand barrens) and forest habitat (Crowley and Beals 2010). They are mainly restricted to the Atlantic coastal plain physiographic region, representing eight percent of North America (Wisheu and Keddy 1989, 1994; Sweeney and Ogilvie 1993). Considered a major center of endemic biodiversity, this region has a low topographic relief, a temperate climate and a broad range of soil pH and textures, nutrient availability, rainfall patterns and hydrology regimes (Sorrie and Weakley 2006). The range of ACPF extends from Texas to Maine, with important disjunct populations occurring in Nova Scotia and within the Great Lakes region (i.e., Wisconsin, Michigan, Ontario) (Wisheu and Keddy 1989, 1994; Clayden et al. 2010) (Figure 1-1). Some ACPF species can also be found in other Canadian provinces, such as New Brunswick, Quebec, Prince Edward Island, Newfoundland and Labrador and even British Columbia (Crowley and Beals 2010).

Figure 1-1. The distribution of Atlantic Coastal Plain Flora species (modified from Nova Scotia's Atlantic Coastal Plain Recovery and Stewardship 2015).

Many ACPF species are known to have weak competitive abilities for acquiring light and nutrients, but broad stress tolerance (e.g., to floods and soil infertility) (Keddy 1985; Wisheu and Keddy 1989, 1994). Therefore, most of ACPF species are associated with hydrologically disturbed habitats with broad water level fluctuations, ice movements, flooding and wave/wind action, which prevent the establishment of competitive species (Hill and Keddy 1992; Keddy 1985; Wisheu and Keddy 1989, 1994; Clayden et al. 2010).

The majority of ACPF species are found on lakeshores, where they rely on specific habitat characteristics (e.g., water depth, shoreline slope, substrate type and exposure to disturbance), but are abundant within areas that feature those characteristics (Sweeney and Ogilvie 1993). Therefore, most lakeshore ACPF species inhabit gently sloping windward shorelines, with coarse textured (e.g., sand, gravel, cobble) and infertile substrates (e.g., low organic matter, silt and clay contents) and some peaty patches (Wisheu and Keddy 1989; Wisheu et al. 1994; Keddy and Sharp 1994).

ACPF play a fundamental role in maintaining healthy riparian ecosystems and their associated services such as the regulation of flooding, solar energy and stream flow, the stabilization of stream banks and the capture of nutrients and sediments (Naiman et al. 1988; Hedman and van Lear 1995; Hill et al. 1998; Belliveau 2011). Riparian vegetation influences the quantity and quality of resources (e.g., food) for aquatic faunal communities (Hedman and van Lear 1995) and supports other terrestrial plants and animals by offering millions of flowers for pollinators (Belliveau 2011). ACPF also offer important habitat and are geographically associated with migratory birds, fish, wildlife, amphibians, reptiles, plants, lichens, mosses as well as legally listed species, such as Atlantic whitefish (*Coregonus huntsmani*), Blanding's turtle (*Emydoidea blandingii*) and Eastern ribbonsnake (*Thamnophis sauritus*) (Rawinsky and Price 1994; Sorrie 1994; Environment Canada and Parks Canada Agency 2010).

ATLANTIC COASTAL PLAIN FLORA IN NOVA SCOTIA

The occurrence of ACPF in Nova Scotia is an exceptional characteristic of Atlantic Canada's flora and is still not fully understood at this time. It has been widely accepted that the occurrence of ACPF in Nova Scotia resulted from late glacial persistence and early postglacial migration, which created favorable climatic conditions for the migration of ACPF along the continental shelf above sea level from Cape Cod to Nova Scotia (Wisheu and Keddy 1989; Sweeney and Ogilvie 1993; Clayden et al. 2010). However, recent evidence indicates that ice from the late Wisconsin glaciation covered the Atlantic Canadian continental shelf leading to two alternative hypotheses proposed by Clayden et al. (2010). First, ACPF could have migrated through Maine, New Brunswick and Nova Scotia during a warmer period from the early to mid-Holocene, leading to a continuous range of ACPF. Afterwards, an abrupt rise of the Bay of Fundy tidal amplitude in the mid Holocene decreased the summer sea surface temperature and increased coastal precipitation, resulting in a cooling period that led to vegetation change and ACPF range shrinkage between Maine and Nova Scotia. Second, long distance dispersal of USA populations through birds, strong winds and hurricanes/tropical storms could have led to the establishment of ACPF populations in Nova Scotia.

Many ACPF populations show a scattered and sporadic distribution across North America, which might be a result of recent loss of habitat and populations or poor dispersal ability or might simply reflect what remains of their continuous range between Maine and Nova Scotia (Sweeney and Ogilvie 1993; Clayden et al. 2010). Particularly in Atlantic Canada, some plant species seem to incompletely inhabit their potential range in terms of climatic and vegetation conditions. The absence of suitable edaphic conditions in

New Brunswick might act as an obstacle to the migration of plants into Nova Scotia (Clayden et al. 2010). Southern Nova Scotia has regionally unique characteristics, such as the warmest temperatures, the longest frost-free period, the longest growing season and the mildest winters of Atlantic Canada and has an extremely high density of lakes (Wisheu and Keddy 1989; Clayden et al. 2010). ACPF species are sensitive to cold temperatures and consequently are not able to tolerate winter conditions in most adjacent regions, possibly explaining in part their isolated occurrence in southwestern Nova Scotia (Wisheu and Keddy 1989; Clayden et al. 2010). As Nova Scotian populations are at the northern range of the ACPF distribution, colder climatic conditions combined with low fertility of soils might limit sexual reproduction (Wisheu and Keddy 1989; Sweeney and Ogilvie 1993). Consequently, Nova Scotian populations have low seed production and are poorly represented in the seed bank, which, along with their poor dispersal abilities, restricts their distribution (Wisheu and Keddy 1989; Sweeney and Ogilvie 1993; Rawinski and Price 1994).

Nova Scotia supports disjunct populations at the northern edge of the ACPF distribution, which is mainly restricted by continental climate and physiography (Sweeney and Ogilvie 1993, Figure 1-2). Nova Scotia supports 98 ACPF species, one third of which have a high priority for recovery (Environment Canada and Parks Agency Canada 2015), including 13 species protected under the Nova Scotia Endangered Species Act (NSESA) and the Canadian Species at Risk Act (SARA). Nova Scotia has some of the last large, relatively undisturbed populations of ACPF species in the world (Wisheu et al. 1994), as increasing development threatens the remaining populations in the United States (Francis and Munro 1994). This province also contains an important reserve of many nationally rare ACPF species and offers some of the most suitable remaining habitat (Morris et al. 2002).

The conservation of northern edge populations, such as Nova Scotian ACPF (Sweeney and Ogilvie 1993), is important for species survival, especially in the context of climate change (Gibson et al. 2009). Their genotype may be more adapted to external range conditions, their genetic diversity may affect their potential to adapt and their geographic proximity may allow propagules to colonize new habitat (Gibson et al. 2009). Populations at the edge of their distribution can be genetically different and contribute to the species' genetic diversity, as they are often exposed to different environmental conditions, are more isolated and have smaller population sizes (Gibson et al. 2009). Furthermore, individuals from disjunct populations, such as those in Nova Scotia, may be dispersal sources for natural colonization elsewhere (Rawinski and Price 1994). The impact of climate change on ACPF lakeshore species is still uncertain and poorly understood at this time, although increasing storm frequency and severity in Nova Scotia are expected to lead to habitat loss and degradation according to Environment Canada and Parks Agency Canada (2015). It is also important to note that species range expansion due to climate change is limited by a variety of non-climatic factors, such as edaphic properties and biotic interactions; these non-climatic factors could also change under climate change conditions in the longer term (Brown and Vellend 2014).

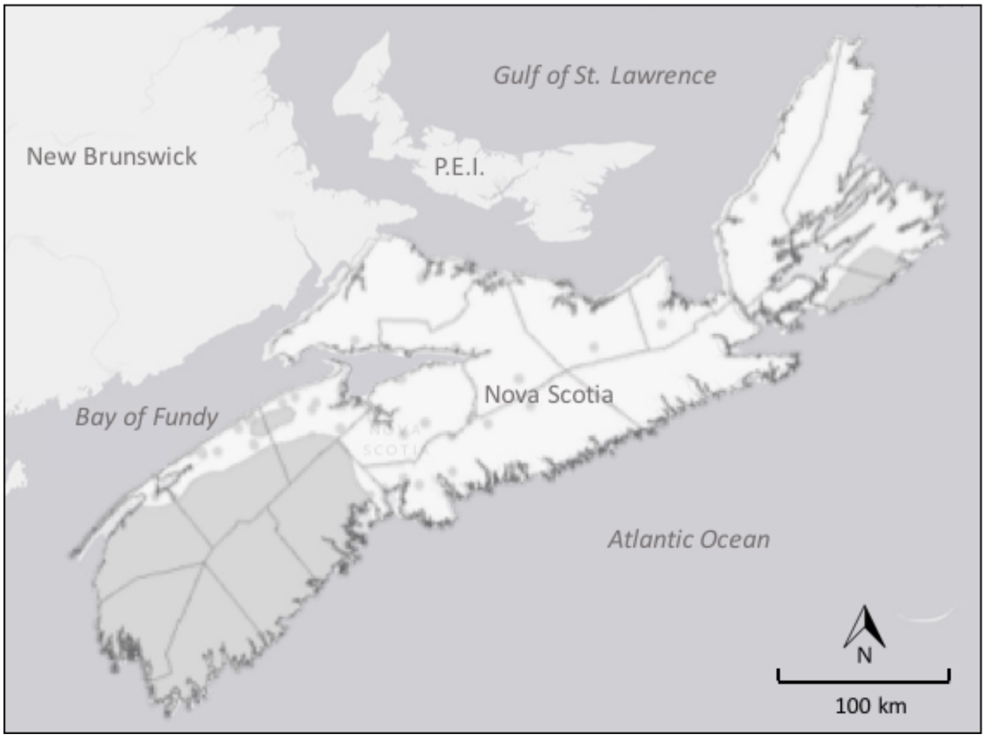


Figure 1-2. Range (in grey shading) for high priority Atlantic Coastal Plain Flora species in Nova Scotia (modified from Environment Canada and Parks Canada Agency 2015).

CONSERVATION OF ATLANTIC COASTAL PLAIN FLORA IN NOVA SCOTIA

ACPF are increasingly endangered as their main range overlaps the industrialized Atlantic seacoast of the United States (Hill and Keddy 1992). Threats mainly arise from urbanization causing habitat loss and changes in ecological processes, which has caused the destruction of approximately fifty percent of all former suitable habitat throughout their range (Wisheu and Keddy 1989, 1994; Sorrie 1994; Keddy and Sharp 1994). High priority threats for lakeshore species in Nova Scotia involve shoreline development and alterations, off-highway vehicle use, infilling, nutrient pollution from animal husbandry and waste water systems (Environment Canada and Parks Canada Agency 2015). In the past, damming has altered approximately half of the former most important lakeshore habitat in Nova Scotia, causing the destruction of nationally rare and imperiled ACPF populations (Hill et al. 1998). Lakeshores support the highest number of high priority species and face the greatest number of threats, as their habitat is more vulnerable to recreational development and supports higher levels of human activity (Wisheu et al. 1994; Environment Canada and Parks Canada Agency 2010). Furthermore, riparian plant communities often show an early response to anthropogenic influences, such as climate change (Naiman et al. 1988). ACPF are found in fifty percent of Nova Scotian watersheds; only eleven watersheds support high priority species, eight of which are located in southwestern Nova Scotia. Only one percent of Nova Scotia's lakes support high priority species; where 36 lakes are defined as high priority lakes (Environment Canada and Parks Canada Agency 2010).

As a result of their similar distribution, habitat and threats, the protection of ACPF habitat would maximize the effectiveness of conservation efforts by benefiting multiple species (Wisheu and Keddy 1989; Environment Canada and Parks Canada Agency 2010) and preserving the ecological functions of riparian communities (Hill et al. 1998). Biodiversity losses in riparian zones can result in a decline in water quality and increased costs from floods (Naiman et al. 1988). Preserving natural levels of flooding and infertility is essential to ACPF survival, as water level stabilization and nutrient enrichment will lead to the establishment of competitive species (Wisheu and Keddy 1989, 1994).

According to the *Recovery Strategy and Management Plan for Multiple Species of Atlantic Coastal Plain Flora in Canada* produced by Environment Canada and Parks Canada Agency (2015), past conservation efforts have not been very strategic. The establishment of appropriate conservation plans is restricted by numerous knowledge gaps, including the identification of potential habitat, population trends, historical distributions and understanding of key habitat characteristics and ecological processes. The Canadian federal government's overall goal is to maintain ACPF populations and habitats in Nova Scotia and Canada, whereas one of their specific objectives is to gain information on the ecological requirements of ACPF for the comprehensive identification of critical habitat (Environment Canada and Parks Canada Agency 2010). Critical habitat is defined as any portion of a lakeshore with the same key ACPF habitat characteristics, regardless of whether the lakeshore is currently occupied or unoccupied by ACPF. Key habitat characteristics are described as habitat features necessary for species survival (Environment Canada and Parks Canada Agency 2015). The protection of these habitats will allow for the maintenance and growth of Nova Scotian ACPF populations by increasing the probability of population persistence and resistance to threats (Wisheu and Keddy 1989; Sweeney and Ogilvie 1993).

RESEARCH OBJECTIVES

The overall goal of my project was to define the habitat requirements, in terms of biotic and biotic factors, of lakeshore ACPF species in southwestern Nova Scotia. I aimed to provide a framework that can guide decision-making regarding the preservation, management, restoration and ecological understanding of ACPF habitat. Offering tools to develop appropriate strategies and management plans will allow managers to better conserve ACPF Nova Scotian populations through the protection of their habitat.

To achieve that goal, I first described some edaphic properties (i.e., pH, organic layer thickness, matrix percentage of sand, matrix chroma) along the lakeshore-to-forest gradient, as they are important drivers of plant communities (Chapter 2). Then, I assessed the spatial distribution of ACPF along the lakeshore-to-forest gradient at the site level (spatial extent of 20 m, spatial grain of 0.2 m, Chapter 3), as spatial patterns can provide essential information on ecological processes, habitat structure and the effect of disturbances (Dale 1999). I also developed structural diversity indices, which reflect habitat complexity and summarize numerous habitat variables that can be linked to important ecological requirements (Noss 1990; Tews et al. 2004; McElhinny et al. 2005). Spatial pattern analysis can relate structural diversity to ACPF richness at different scales and locations along an environmental gradient to determine if structural diversity could be used as an indicator of suitable habitat for ACPF. Scale is defined as the grain (quadrat level) and extent (site level) of the spatial pattern, representing the local and landscape scale, respectively. After looking at the ACPF distribution and using somewhat broad habitat indicators, I defined specific habitat characteristics of lakeshore ACPF (Chapter 4). I assessed the effects and significance of abiotic and biotic habitat variables for ACPF communities at lake, shoreline and individual levels, which could provide essential information for species conservation and management (Brosofske et al. 1999; Williams et al. 2009; Bellamy et al. 2013). A lake is an essential ecological unit where key ecological requirements are found at a shoreline level, but the most fundamental and specific scale of a habitat occurs at the individual level (Environment Canada and Parks Canada Agency 2010). My specific research objectives were:

1. To describe edaphic properties (pH, organic matter thickness, matrix sand content and matrix chroma) along the lakeshore-to-forest gradient, as edaphic properties are closely tied to hydrological disturbances and plant communities; pH influences nutrient availability, the organic matter thickness influences soil fertility and can indicate levels of wave action, and the matrix sand content and the matrix chroma can indicate saturated conditions.
    a. To assess the minimum, maximum and mean of edaphic properties at a site level to report and document the values of pH, organic matter thickness, matrix sand content and matrix chroma found within ACPF hotspots.
    b. To assess general trends in edaphic properties across lakeshores and beyond the forest edge to visually describe how pH, organic matter thickness, matrix sand content and matrix chroma change between the lakeshore and the forest. I would expect that lakeshores have a thinner organic layer and higher sand content due to wave actions that remove fine particles and sediments (e.g., silt and clay) compared to the forest. I would also expect a lower chroma on lakeshores in comparison to the forest, as saturated conditions from flooding lead to an iron depleted matrix with lower chroma.

2. To define spatial patterns of ACPF and their spatial relationships with structural diversity indices in order to determine if structural diversity, which is increasingly

known and used as a surrogate of ecological requirements and processes, could be used as an indicator of habitat suitability for ACPF.

a. To assess spatial transitions of ACPF richness, individual species cover and structural diversity indices along the lakeshore-to-forest gradient. Before looking at spatial relationships, the main objective of this chapter, it is important to first characterize individual spatial patterns of the two variables (i.e., ACPF richness and structural diversity) and collect information on the spatial structure of the system of interest. I would expect that transitions in ACPF richness would be located on lakeshores as ACPF rely on hydrological disturbances, whereas transitions in structural diversity would be at the forest edge due to unique climatic conditions and physical processes that are known to increase the diversity and density of plant communities. I also characterized the spatial patterns of individual ACPF species to see if each species occupied different positions along the lakeshore-to-forest gradient (i.e., zonation).

b. To assess spatial relationships between lakeshore herbaceous ACPF richness and structural diversity indices at different scales and locations. In order to appropriately assess the influence of habitat characteristics or indicators on a species or group of species, it is important to look at the relationships between the two variables at different scales and locations along an environmental gradient, as different types of associations could arise. The concept of scale here is essential as patterns of plant communities (e.g., clumped and dispersed) vary according to scale and the intensity or the effect of different habitat variables changes between scales. Consequently, I would expect a negative relationship between ACPF richness and structural diversity at finer scales as increased structural diversity could directly lead to increased competition and decreased number of ACPF species. I would also expect a positive relationship at coarser scales as a result of increased complexity of the surrounding vegetation and the diversity of niches which could increase the number of ACPF species. I would also expect a positive relationship on lakeshore as ACPF share habitat with a diversity of plants, including graminoids and sundews; however, a negative relationship should occur at the forest edge as increased structural diversity would indicate higher competition due to lower amplitude of hydrological disturbances.

3. To define landscape and local scale habitat characteristics of lakeshore herbaceous ACPF, as plant communities are influenced by numerous abiotic and biotic factors that arise at different scales.

   a. To assess the influence of landscape scale habitat characteristics, such as hydrological processes and topography, on zone width (distance from the waterline to the last ACPF individual), richness and abundance of ACPF at a shoreline (site) level. More specifically, I expected watershed and lake area to influence the amplitude of hydrological disturbances through higher water level fluctuations and wave action, respectively. Wave action would also be reflected by the shoreline type (e.g., mineral or organic), which could indicate soil fertility and the intensity of competition. I would also expect the slope and distance to shrub, through water depth and flooding conditions, to influence the zone width of ACPF on lakeshores.

b. To assess the influence of local scale habitat characteristics, such as elevation, vegetation elements and substrate, on the presence, abundance and richness of ACPF, as well as on the presence of five common ACPF species, at an individual (quadrat) level. I would expect local habitat characteristics to mostly influence the abundance of ACPF due to surrounding resources that can support a certain amount of biomass at a fine scale. More specifically, elevation and shrubs could indicate the relative proximity to hydrological disturbances and the level of competition. Sundews, graminoids and bryophytes would indicate nutrient poor conditions, diverse and moist shorelines, respectively, and consequently disturbed shorelines. Ferns could increase the level of competition. Litter could indicate the limit of wave action and flooding, whereas woody material could result from those disturbances and provide seed establishment sites. Disturbances would also lead to intermediate or coarser size substrate by washing fine soil particles. In order to include all these explanatory variables and have sufficient statistical power, I decided to focus on the five most common species: lance leaved violet, golden pert, redroot, slender fragrant goldenrod and yellow eyed grass. Common species are especially relevant when studying rare or ephemeral plant communities, as they could be used as diagnostics for the whole community by carrying more ecological information.

STUDY AREA

This study was conducted in southwestern Nova Scotia, a region that supports headwaters of several river systems such as the Mersey, Shelburne, Medway and Tusket watersheds where numerous ACPF critical habitats have been identified (Francis and Munro 1994). The Medway watershed is considered a high priority watershed (Environment Canada and Parks Canada Agency 2010) and is the second most important site for ACPF after the Tusket watershed in Nova Scotia (Sweeney and Ogilvie 1993). This region also includes Kejimkujik National Park, an important place to study ACPF as it supports important populations of many species and could offer the organizational measures needed for their conservation (Francis and Munro 1994, Figure 1-3). Southwestern Nova Scotia is generally characterized by sandy acidic soils with mixed drainage and an inland climate with high humidity (Sweeney and Ogilvie 1993). Mean daily annual temperature ranges from -5 °C in January to 19 °C in July and monthly precipitation ranges from 96 to 165 mm at Bridgewater (Climate Canada 2015). The vegetation is dominated by coniferous tree species, although lakeshores support a mixture of coniferous and deciduous tree species including: red maple (*Acer rubrum*), beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), red spruce (*Picea rubens*), white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*). Common woody shrub species include sweet gale (*Myrica gale*), witherod (*Viburnum nudum*), Canada holly (*Ilex verticillata*), royal fern (*Osmunda regalis*) and alder (*Alnus ssp.*) (Sweeney and Ogilvie 1993).

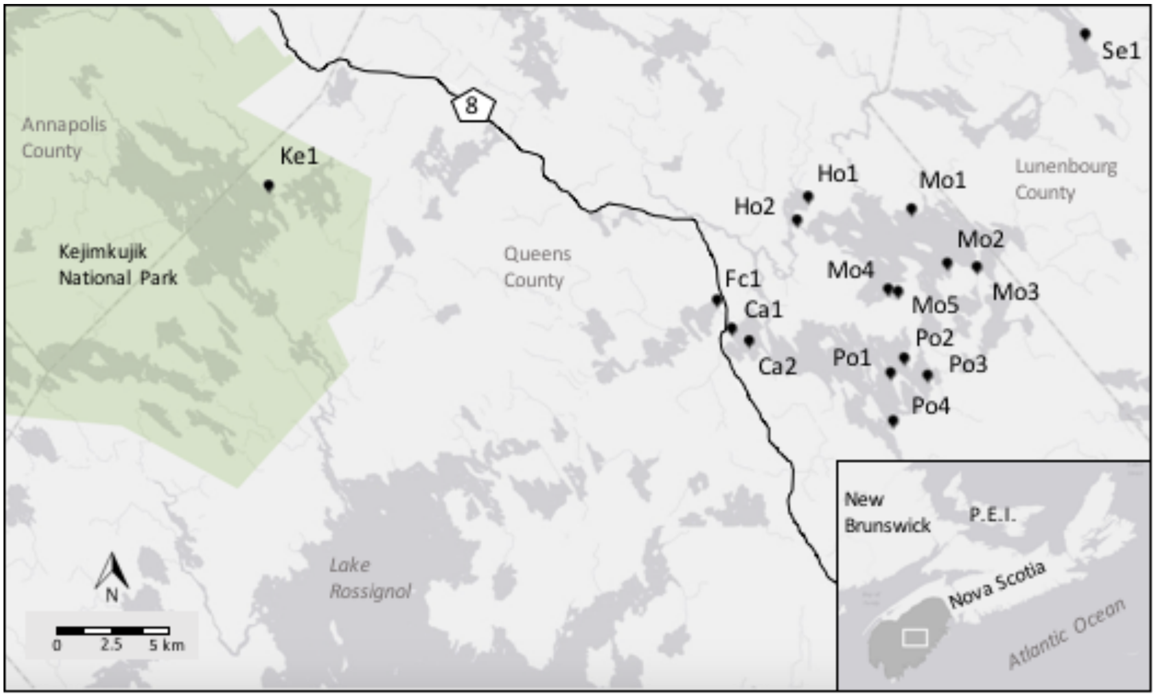


Figure 1-3. Location of sites (n = 16) on seven lakes: Molega (Mo), Kejimkujik (Ke), Ponhook (Po), Seven mile (Se), First Christopher (Fc), Cameron (Ca) and Hog (Ho). Sites for grids are Ca2, Ke1, Se1, Ho2 and Po3. The inset map shows the range of high priority Atlantic Coastal Plain Flora species (darker grey shading) in southwestern Nova Scotia.

SPECIES, LAKE AND SITE SELECTION

I chose lakes located within the Medway and Mersey watersheds and excluded lakes with few ACPF species. I listed species found on each lake using the Mersey Tobeatic Research Institute (2015) ACPF database from 36 high priority lakes. The data were collected as a part of Environment Canada’s Habitat Stewardship Program in partnership with the Atlantic Coastal Plain Flora Recovery Team. I selected a subset of 19 common/abundant ACPF species that mostly co-occur on lakeshores (Table 1-1, Appendix 1). I excluded species that were: relatively uncommon, taxonomically questionable or prone to hybridization, difficult to identify or to find and/or floating and submerged aquatic species. I selected seven lakes that supported the highest number of selected species (Table 1-2).

Table 1-1. Description of the Atlantic Coastal Plain Flora species examined in this study, including the functional group (shrub, herb, graminoids), the scientific and common name, the general habitat of the species and the Nova Scotia general status (and one Species At Risk Act (SARA) status) (Crowley and Beals 2011).

Functional group	Scientific name	Common name	General habitat	NS general status
Shrub	*Cephalanthus occidentalis*	(Common) Buttonbush	Lakeshore, wetlands	Sensitive
	Ilex glabra	Inkberry	Lakeshore, wetlands	Secure
	Morella pensylvanica	Northern bayberry	Lakeshore, wetlands, forest	Secure
	Rosa palustris	Swamp rose	Lakeshore, wetlands	Secure
	Smilax rotundifolia	Round-leaved greenbrier	Lakeshore, waterline	Secure
	Toxicodendron radicans var. radicans	(Eastern) Poison ivy	Forest edge, marshes	Secure
Herb	*Bartonia paniculata var. iodandra*	Branched bartonia (Screwstem)	Peat/cobble lakeshore, bog	Secure
	Euthamia caroliniana	Slender (Carolina) fragrant goldenrod	Sand/gravel lakeshore	Secure
	Gratiola lutea	Golden pert	Waterline of sand/gravel lakeshore	Secure
	Hypericum virginicum	Virginia (Marsh) St. John's-Wort	Lakeshore, wetlands	Secure
	Lachnanthes caroliniana	Redroot	Peat/sand/gravel lakeshore	At risk (SARA: Special concern)
	Lycopodiella appressa	Southern bog clubmoss	Waterline of peat lakeshore	Secure
	Rhexia virginica	Virginia meadow-beauty	Rocky lakeshore	Secure

	Sisyrinchium atlanticum and angustifolium	Eastern and pointed blue-eyed grass	Peat/gravel/sand lakeshore, marshes	Secure
	Viola lanceolata	Lance-leaved violet	Waterline of sand lakeshore	Secure
	Xyris difformis	Lakeshore yellow-eyed grass	Sand/gravel/peat lakeshore, wetlands	Sensitive
Fern	*Woodwardia virginica*	Virginia chain fern	Lakeshore	Secure
Graminoid	*Cyperus dentatus*	Toothed flat-sedge	Sand/gravel lakeshore	Secure
	Panicum virgatum	Old switch panic grass	Sand/gravel lakeshore, bogs	Secure

Table 1-2. Description of selected lakes including the coordinates at the center of the lake, lake area, primary watershed, tertiary watershed area, county and number of sites for each lake.

Lake	Coordinates at lake center	Lake area (ha)	Primary watershed	Tertiary watershed area (ha)	County	Sites (#)
Ponhook	44^{o}31’ N 64^{o}88’ W	1570	Medway	13 900	Queens	4
Cameron	44^{o}32’ N 64^{o}94’ W	230	Medway	13 900	Queens	2
Hog	44^{o}38’ N 64^{o}92’ W	130	Medway	36 400	Queens	2
First Christopher	44^{o}33’ N 64^{o}97’ W	150	Medway	10 200	Queens	1
Molega	44^{o}36’ N 64^{o}85’ W	2150	Medway	36 400	Queens and Lunenburg	5
Seven mile	44^{o}44’ N 64^{o}76’ W	280	Medway	21 000	Lunenburg	1
Kejimkujik	44^{o}38’ N 65^{o}24’ W	2500	Mersey	45 000	Queens and Annapolis	1

I located between one and five sites per lake for a total of 16 sites (Figure 1-3). Criteria for site selection within each lake included: maximizing ACPF species richness, west or southwest facing shorelines to keep environmental factors consistent (e.g., sunlight, wave and wind exposure, Lusk and Reekie 2007) and site accessibility. In order to support a wide riparian zone with the highest ACPF richness and abundance, sites were mostly on intermediate-sized physical substrate (i.e., gravel, cobble) with a gentle slope and western aspect (Table 1-3, Figure 1-4).

Table 1-3. Description of selected sites including geographical coordinates of the transect, slope along the transect (average difference in height in cm over a distance of one meter), shoreline type (mineral or organic), distance to shrub (distance from the waterline to the occurrence of continuous shrub), distance from the waterline to the last ACPF herb individual, ACPF herb richness, ACPF herb abundance (sum of ACPF herb cover per transect) and the presence/absence of grid sampling at that site.

Site	Coordinates	Average slope (cm/m)	Shoreline type	Distance to shrub (m)	Distance to last ACPF herb (m)	ACPF herb richness (# per transect)	ACPF herb abundance (% cover)	Grid sampling (Y/N)
Po1	44°309’ N 64°862’ W	17.8	Mineral	3.8	2.6	6	436	N
Po2	44°315’ N 64°854’ W	26.4	Mineral	0.8	0.8	3	22	N
Po3	44°309’ N 64°841’ W	20.3	Mineral	5.6	5.4	6	296	Y
Po4	44°291’ N 64°860’ W	7.1	Mineral	3.4	6.2	7	199	N
Ca1	44°327’ N 64°950’ W	10.1	Organic	0.2	2.0	2	12	N
Ca2	44°322’ N 64°940’ W	21.2	Mineral	3.6	3.0	6	51	Y
Ho1	44°380’ N 64°907’ W	11.4	Organic	1.4	4.8	6	361	N
Ho2	44°371’ N 64°913’ W	10.8	Mineral	2.6	6.0	9	359	Y
Fc1	44°339’ N 64°958’ W	10.6	Organic	4.6	3.8	5	184	N
Mo1	44°375’ N 64°850’ W	10.3	Organic	4.2	6.2	5	310	N
Mo2	44°354’ N 64°830’ W	5.5	Mineral	3.2	4.2	4	273	N
Mo3	44°352’ N 64°813’ W	10.3	Organic	0.8	4.8	4	226	N
Mo4	44°343’ N 64°863’ W	5.5	Organic	3.6	4.6	3	40	N
Mo5	44°342’ N 64°857’ W	14.4	Organic	6.6	6.0	1	6	N
Se1	44°445’ N 64°753’ W	8.9	Mineral	7.2	7.6	7	1709	Y
Ke1	44°384’ N 65°208’ W	6.35	Mineral	8.2	7.2	6	81	Y

Figure 1-4. Picture showing a typical shoreline for ACPF sampling at Seven Mile Lake (Se1): gravel and cobble shoreline with a gentle slope.

THE CHALLENGE OF SAMPLING RARE SPECIES

Some species are rare in time and/or space, which can result from their association with microsites that are ephemeral or distributed as patches (Edwards et al. 2005). Many ACPF species have a natural rarity that arises from their biological limitations such as low seed production, low dispersion abilities, typically small population sizes, slow growth and small plant size, specific climatic requirements (i.e., minimum/average winter temperature, amount of insolation, average summer temperature (Sorrie 1994)) and physiological tolerances, along with the scarcity of suitable habitat (Keddy 1985; Wisheu and Keddy 1989, 1994; Environment Canada and Parks Canada Agency 2010). ACPF are consequently restricted to specific habitat types within a limited geographical region (Wisheu and Keddy 1989); only five percent of Nova Scotian lakes have a watershed area that is large enough to support rare ACPF communities in the long term (Morris et al. 2002). The detection of many rare plants demands sufficient sampling effort, especially for herbs as they can re-sprout the following year, live only underground and present different levels of detectability (e.g., seedlings vs flowering) (Philippi 2005). Small changes in water level influence the germination of many ACPF species (Moore and Keddy 1988; Keddy and Sharp 1994), which explains in part why species composition varies greatly between growing seasons (Sorrie 1994; Hill et al. 1998). Some ACPF species are only present during specific periods of the hydrologic cycle (Rawinski and Price 1994) and will survive in the seed bank to escape high water periods (Keddy 1984). For example, golden pert (*Gratiola lutea*) will produce flowers and seeds only during low water levels, such as in shallow water or when completely outside the water (Keddy and Reznicek 1982).

Predicting the distribution of suitable habitat for rare species is a challenge as a small number of locations are often found within relatively large areas (Franklin et al. 2009). Standard sampling methods undoubtedly provide the least biased estimates; however, they are often not appropriate for low abundance or rare species, as an insufficient number of individuals are encountered (Edwards et al. 2005), resulting in sparse and difficult to obtain data (Parviainen et al. 2008). Random sampling of rare plants leads to the absence of individuals in the majority of quadrats (Philippi 2005). Consequently, habitat explanatory models for rare species often include a high number of explanatory variables, but with few species occurrences (Breiner et al. 2015), leading to difficulties in distinguishing important explanatory variables (Williams et al. 2009). Therefore, sampling designs of rare species require an adequate level of detection (Edwards et al. 2005).

As understanding species' distributions and associated environmental factors is essential to protect rare species (Parviainen et al. 2008), alternative sampling designs that include a larger proportion of individuals are used (Philippi 2005). Examples of alternative methods are adaptive cluster sampling (Philippi 2005) and model-based stratifications by using abundant species related to the targeted rare species or focusing on species' habitat requirements to generate sampling strata (Edwards et al. 2005). Sampling other species from the communities is very relevant for rare species by carrying additional information to modelled relationships with environmental factors (Elith et al. 2006).

Presence/absence models (sampling both presence and absence sites) perform best for characterizing habitat (Williams et al. 2009). However, absence data can be difficult to collect for rare species as intensive population surveys are difficult to achieve (Pearce and Boyce 2006; Rebelo and Jones 2010) and could include false absences in the case of imperfect detection, which biases model predictions (Rebelo and Jones 2010). Alternatively, sampling from presence sites or presence only data consist of observations with no reliable data on where the species is not found (Pearce and Boyce 2006); these are increasingly available from museums and herbarium records and used to predict new occurrences of rare species (Williams et al. 2009; Rebelo and Jones 2010). However, sampling designs to collect presence data are often biased towards collection efforts

(Elith et al. 2006; Rebelo and Jones 2010; Stolar and Nielsen 2015). Presence-only models usually provide broad predictions characterized by environmental conditions only associated with species presence, but are still valuable, especially for rare species that are poorly understood (Pearce and Boyle 2006). These models cannot provide reliable information on species frequency or predict the probability of species presence with accuracy, but can provide relative indices of habitat suitability (Elith et al. 2006).

PROTECTION OF HABITAT

Conservation plans using the 'habitat method' consist of the protection of whole habitat units instead of individual species (Sweeney and Ogilvie 1993). By conserving habitat, the probability of self-maintenance and resistance to future disturbances of ACPF populations will increase (Wisheu and Keddy 1989; Sweeney and Ogilvie 1993; Wisheu et al. 1994). Furthermore, the habitat method contributes to the protection of many species (Sweeney and Ogilvie 1993; Wisheu et al. 1994) and the services/benefits from ecological processes such as the provision of migratory corridors, the reduction of erosion and the maintenance of water quality (Naiman et al. 1993). The similarities in habitat of many ACPF species suggest that the habitat method should be a priority for the conservation of ACPF populations in Nova Scotia (Wisheu et al. 1994). A conservation plan that integrates habitat requirements of ACPF communities is therefore needed (Rawinsky and Price 1994). The identification of potential habitat for conservation purposes needs to be assessed at different spatial scales in order to maintain essential habitat features, including critical structures (Franklin 1993). Using habitat indicators, such as structural diversity indices, along with specific habitat characteristics associated with ACPF communities at landscape and local scales, will direct conservation efforts towards potential watersheds, lakes and shorelines (Hill et al. 1998). Furthermore, a community level approach allows the protection of cryptic, ephemeral or poorly understood species that are associated with these communities (Rawinski and Price 1994). Some ACPF species may not be present every year or only present during favorable times of the hydrological cycle (Rawinsky and Price 1994). Therefore, a habitat and community level approach are the most efficient ways to conserve ACPF.

CHAPTER 2

Edaphic properties along the lakeshore-to-forest gradient

INTRODUCTION

Many organisms are influenced by abiotic factors as much as vegetation structure; the presence of some species is determined by specific abiotic factors even in suitable habitat in terms of vegetation structure (Chen et al. 1996). The gradient of abiotic factors at forest edges usually affects vegetation structure and other biotic factors (Marchand and Houle 2006). Consequently, it is important to include abiotic along with biotic factors to appropriately define habitat requirements for conservation purposes (Chen et al. 1996). Niches of plants are mainly defined by light quantity and quality, as well as plant litter, soil nutrients and soil moisture (Lundholm 2009). In addition, other abiotic factors influence species composition, such as elevation, organic matter (which affects soil fertility), soil texture and pH (which affects nutrient availability) and litter depth (Marchand and Houle 2006; Laughlin and Abella 2007). The amount of organic matter can be quantified using the thickness of the organic layer which consists of dead and decomposing plant material found beneath live plants, mosses and lichens (U.S. Army Corps of Engineers 2011). Soil texture refers to the percentage by weight of sand (0.05 – 2.0 mm), silt (0.002 – 0.05 mm) and clay (< 0.002 mm) particles in the fine earth fraction (< 2 mm) of the mineral soil, defined as the matrix (Keys et al. 2010; Schoeneberger et al. 2012).

Riparian zones, defined as areas at the interface of terrestrial and aquatic ecosystems, are essential components of lake ecosystems where hydrology, soil and vegetation are interconnected (Lu et al. 2007). Wetlands are mostly delimited by the occurrence of vegetation adapted to saturated soil and anaerobic conditions, such as along the shores of many lakes and ponds (U.S. Army Corps of Engineers 2011). Wetland plant communities rely on these edaphic conditions, where herbaceous plant composition can show drastic turnover between drought and pluvial years (U.S. Army Corps of Engineers 2011). Some edaphic characteristics, such as the texture and moisture of soils, usually fluctuate along the elevation gradient on lakeshores (Keddy and Reznieck 1982).

Indicators of hydric soils (i.e., wetlands) consist mostly of the accumulation or loss of iron, but also manganese, sulfur or carbon compounds in the soil. In a saturated and anaerobic environment, soil organisms reduce these elements; the reduced form of iron, now soluble, enters the soil solution where it can move and translocate. Some areas of the soil will consequently lose iron in a process called redox depletion, creating a depleted matrix with a low chroma (< 2) and a grayer color. The chroma is an index of relative purity or strength of the matrix color, which has a range from 0 to 8 indicating neutral to the most intense colors, respectively. When aerobic conditions are reached, the soluble iron will rapidly oxidize and concentrate as masses, named redox concentrations, now having their own color with a higher chroma (U.S. Department of Agriculture 2010; U.S. Army Corps of Engineers 2011). Consequently, the chroma is especially useful in riparian zones as it can help to determine if the soil is usually under saturated conditions.

In order to characterize soil properties on lakeshores where ACPF were present, I sampled different edaphic properties at each site. My specific objectives were:

1. To define the minimum, maximum and mean condition of the pH, organic matter thickness, matrix sand content and matrix chroma from the lakeshore to the forest of each selected site.
2. To characterize general trends (non-statistical) of pH, organic matter thickness, matrix sand content and matrix chroma along the lakeshore-to-forest gradient.

METHODS

At each site (except in Kejimkujik National Park (Ke1) where soil digging was not allowed), I located two approximately 22 m (18-26 m) transects perpendicular to the waterline. Transects were separated by 20-50 m along the shoreline, depending on the suitable locations. I chose transect positions to avoid rocky areas (to facilitate use of the soil auger) and to include ACPF shrub species or possible ACPF habitat, as selected herbaceous ACPF species had not emerged at that time. I only established one transect at Ca1, as it was too narrow for two transects. From mid-June to mid-July 2015, I sampled 16 m of the transect from the waterline to at least 5 m into the forest. During the next sampling period (vegetation transects from mid-July to mid-August 2015), the water levels had dropped and I extended the transects at least 4 m towards the lake until they reached the beginning of vegetation in the water. Consequently, the transect length mainly depended on the width of the riparian vegetation zone.

Sampling points were positioned every two meters along the transect. At each point, I used a clinometer (Laser Technology Inc) to measure the slope to the next point and a soil tester (Kel Way) to measure pH. I used a soil auger to measure the organic layer thickness and assess the dominant von Post class (e.g., degree of peat humification) (Keys et al. 2010, Appendix 2A). For each mineral layer, I measured the thickness, determined the matrix color with a Munsell color chart (Soil survey staff 1993) and assessed the soil matrix texture (Keys et al. 2010, Appendix 2B). I did not auger deeper than 40 cm of organic soil and 30 cm of mineral soil. I also noted the depth to water (i.e., water table or ground water) and depth to soil saturation (e.g., glistening). As the collected data depended mostly on long term processes or disturbances (e.g., seasonal water level fluctuations), only extreme rainfall events (e.g., hurricanes, tropical storms) could have slightly impacted the results in the following days. I only noted one heavy rainfall event during the soil sampling period.

For each site, I calculated the minimum, maximum and mean of the pH, organic thickness, matrix sand content and matrix chroma. Afterwards, I plotted each soil property along the transects (lakeshore-to-forest gradient).

RESULTS

In general, the pH of the soil was acidic (i.e., < 7.0) and had a range of 3.7 (extremely acid) to 6.9 (neutral) across all sites, with a mean per site between 5.2 (strongly acid) and 6.3 (slightly acid) (Table 2-1). However, pH was not recorded in moist or rocky areas, consequently excluding areas in water, lakeshores with coarser substrates (e.g., cobble) and other sampling points along the transect. The range of the thickness of the organic layer was 0.0 to 40.0 cm (i.e., the maximum depth), with a mean of 4.0 to 22.3 cm per site. It is important to mention that the organic layer thickness depended, in some cases, on the depth I was able to reach with the auger without hitting a rock. The matrix sand content range from 5 to 95%, with a mean per site of 15 to 79%. The range of matrix chroma was from 1.0 to 6.0 and a mean between 1.4 and 3.5 per site.

Table 2-1. The minimum, maximum and mean (± standard deviation) of the pH, the organic layer thickness, the matrix sand content and the matrix chroma (0 indicating neutral color and 8 representing the most intense colors) for each site (n indicated for each site).

Site	n	pH	Organic thickness (cm)	Matrix sand content (%)	Matrix chroma
Fc1	20	4.0 – 6.8 (6.0 ± 0.6)	0.0 – 23.7 (9.4 ± 6.3)	0.13 – 0.63 (0.49 ± 0.16)	1.0 – 4.0 (2.4 ± 1.3)
Ca1	10	5.8 – 6.6 (6.2 ± 0.2)	0.0 – 34.0 (15.3 ± 12.0)	0.13 – 0.22 (0.15 ± 0.04)	1.0 – 2.0 (1.4 ± 0.5)
Ca2	20	5.0 - 6.8 (6.0 ± 0.6)	0.0 – 19.0 (9.6 ± 6.3)	0.42 – 0.95 (0.72 ± 0.20)	1.0 – 4.0 (2.7 ± 1.0)
Mo5	20	5.3 – 6.8 (6.0 ± 0.4)	0.0 – 40.0 (14.7 ± 11.2)	0.22 – 0.83 (0.64 ± 0.19)	1.0 – 4.0 (2.6 ± 1.1)
Po3	21	4.6 – 6.8 (5.8 ± 0.7)	0.0 – 18.0 (7.0 ± 5.2)	0.22 – 0.95 (0.46 ± 0.25)	1.0 – 6.0 (2.4 ± 1.6)
Po2	20	3.7 – 6.6 (5.2 ± 0.9)	0.0 – 40.0 (13.4 ± 10.0)	0.22 – 0.95 (0.47 ± 0.19)	1.0 – 4.0 (2.7 ± 0.9)
Mo4	20	4.2 – 6.1 (5.2 ± 0.8)	4.5 – 27.0 (14.9 ± 7.5)	0.22 – 0.83 (0.39 ± 0.20)	1.0 – 6.0 (2.7 ± 1.4)
Mo2	23	3.7 – 6.7 (5.5 ± 0.7)	0.0 – 40.0 (11.8 ± 10.4)	0.22 – 0.95 (0.62 ± 0.23)	2.0 – 4.0 (2.9 ± 0.8)
Ho1	21	5.0 – 6.9 (6.3 ± 0.5)	0.0 – 40.0 (11.4 ± 11.0)	0.22 – 0.95 (0.69 ± 0.26)	1.0 – 4.0 (2.7 ± 1.1)
Mo1	25	4.5 – 6.8 (5.9 ± 0.6)	4.0 – 40.0 (14.8 ± 8.7)	0.13 – 0.63 (0.31 ± 0.18)	1.0 – 6.0 (2.9 ± 1.3)
Po4	23	4.2 – 6.8 (5.7 ± 0.8)	0.0 – 40.0 (22.3 ± 15.3)	0.22 – 0.95 (0.63 ± 0.21)	1.0 – 4.0 (2.5 ± 1.2)
Se1	21	3.9 – 6.8 (5.3 ± 0.9)	0.0 – 20.0 (7.9 ± 6.6)	0.22 – 0.95 (0.46 ± 0.26)	1.0 – 6.0 (3.5 ± 2.1)
Ho2	22	5.2 – 6.9 (6.0 ± 0.5)	0.0 – 25.0 (4.0 ± 6.9)	0.05 – 0.95 (0.48 ± 0.39)	1.0 – 3.0 (2.1 ± 0.6)
Po1	20	4.6 – 6.9 (5.8 ± 0.7)	0.0 – 32.0 (16.4 ± 10.2)	0.13 – 0.95 (0.79 ± 0.21)	1.0 – 4.0 (2.4 ± 1.2)
Mo3	21	4.9 – 6.7 (6.0 ± 0.5)	4.0 – 26.0 (12.9 ± 6.0)	0.05 – 0.95 (0.66 ± 0.30)	1.0 – 4.0 (1.8 ± 1.0)

Rather than use statistical analysis for this chapter, I visually described the distribution of each edaphic characteristic along the lakeshore-to-forest gradient. The objective was to determine if there was a general or potential trend by looking at the location of concentrations of lower and higher values, indicated by the darker points on the graphs. Lower and higher pH did not seem to exhibit any general trend in pH along the lakeshore-to-forest gradient (Figure 2-1a). Lower organic matter thickness looked more concentrated at the beginning of the transect (i.e., in the water), whereas higher organic matter thickness appeared to be located along the middle to the end of transect in the forest (Figure 2-1b). Lower matrix percentages of sand seemed to be more concentrated near the waterline (e.g., smaller distance from the waterline) whereas higher values appeared to be located farther from the waterline (Figure 2-1c). In contrast, lower matrix chroma looked more concentrated at the beginning of the transect, whereas higher matrix chroma seemed to be located at the end of the transect (Figure 2-1d).

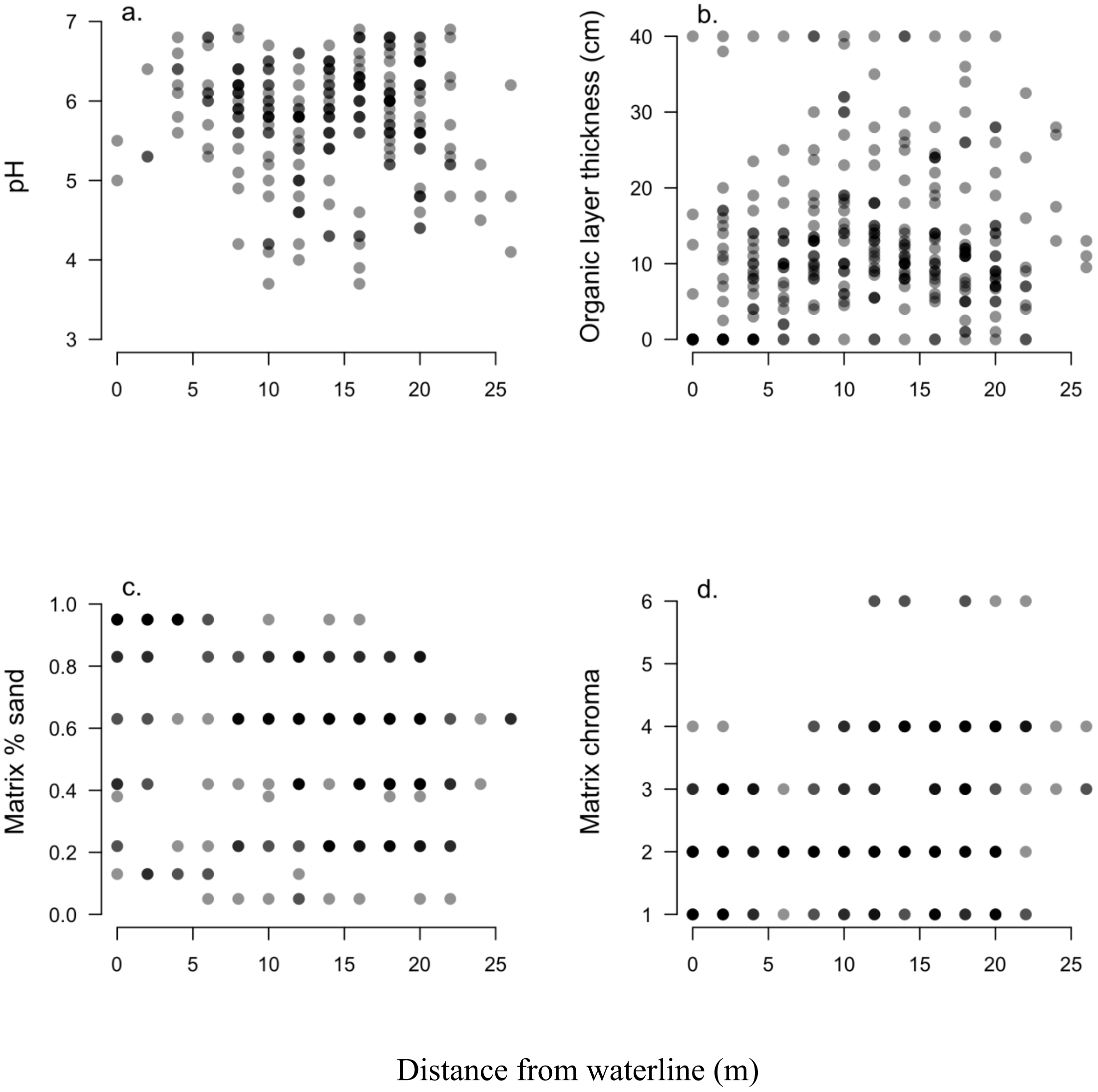


Figure 2-1. The distribution of pH, organic layer thickness, mineral sand content and mineral chroma (0 indicating neutral color and 8 representing the most intense colors) along the lakeshore-to-forest gradient. Grey shading represents the intensity of superimposed data points.

DISCUSSION

At the time of the sampling, water levels were high and the majority of ACPF herb species had not yet emerged. As I was not able to position the soil transect right beside the vegetation transect, it would not have been appropriate to directly relate the edaphic factors to ACPF communities. Furthermore, as I was often hitting rocks and was consequently not able to characterize the soil for numerous sampling points, a lot of data were missing. Because edaphic factors are often qualitative (e.g., color, texture, decomposing state), the database could not be quantitatively analyzed for all variables. Therefore, I only reported the values and general trends along the lakeshore-to-forest gradient of four edaphic characteristics: pH, organic layer thickness, matrix sand content and the matrix chroma of the dominant mineral layer (i.e., the thickest layer) without any statistical analysis.

Soil organisms mostly use carbon compounds from organic matter as an energy source. In saturated and anaerobic conditions, the rate of carbon utilization is reduced from decreased respiration rates. Wetlands can consequently accumulate a thick layer of partially decomposed organic matter, often as a form of peat or muck (U.S. Department of Agriculture 2010; U.S. Army Corps of Engineers 2011). However, ACPF are found on lakeshores that are exposed to high levels of wave action, which remove organic matter and other fine particles in the soil (Keddy 1982; Holt et al. 1995). My results could only suggest a visual positive trend in the organic layer thickness with distance from water within ACPF hotspot zones.

Many ACPF species are known to inhabit shorelines with low silt and clay content (Wisheu et and Keddy 1989) and are strongly correlated with the percentage of sand (Hill and Keddy 1992). A visual description of the matrix percentage of sand along the lakeshore-to-forest gradient suggests a negative trend in the matrix percentage of sand with distance from water within ACPF hot spot zones.

Saturated conditions in wetlands cause the translocation of different soil elements, from reduction by soil organisms, creating depleted matrices with lower chroma. As flooding and saturated conditions decrease with increasing distance from the waterline, aerobic conditions become dominant, which prevents the loss of elements and the matrices will consequently display a higher chroma (U.S. Department of Agriculture 2010; U.S. Army Corps of Engineers 2011). My results suggest an increase in the matrix chroma with distance from water within ACPF hotspot zones.

In summary, at the beginning of the transect, in the water, I found most of the lowest values of organic layer thickness and most of the highest values of matrix percentage of sand. This could indicate disturbed shorelines through higher levels of wave action, which restrict the accumulation of organic matter on shorelines and remove fine particles such as silt and clay in the mineral matrix. I also found that soils in the water displayed most of the lowest values of the matrix chroma, whereas matrices with lower chroma usually indicate saturated conditions from iron loss. These three characteristics would suggest disturbed and saturated shorelines, which could indicate possible suitable habitat for many herbaceous ACPF species.

CHAPTER 3

Spatial pattern and relationship of Atlantic Coastal Plain Flora and structural diversity along the lakeshore-to-forest gradient

** Based on the submitted manuscript: Daze Querry N, Harper KA. Spatial pattern of Atlantic Coastal Plain Flora and structural diversity across Nova Scotian lakeshore edges. Plant Ecology.*

ABSTRACT

Riparian zones often provide favored habitats for rare stress tolerant species where hydrological disturbances displace competitive species. Atlantic Coastal Plain Flora (ACPF) are a group of taxonomically unrelated plants mostly found along lakeshores in the Atlantic coastal region of North America. Vegetation structure, defined by the height, cover and types of plants, can be used to characterize their habitat requirements. The objectives of this study were to assess spatial patterns and relationships of ACPF richness and structural diversity indices at different scales and positions along the lakeshore-to-forest gradient. I selected 7 lakes, 19 ACPF species and 16 sites in southwestern Nova Scotia. For each site, I used 20 m transects, perpendicular to the waterline, and 5 x 5 m grids located between the lake and the forest edge with contiguous 20 x 20 cm quadrats to measure the cover of ACPF species and structural elements at different heights. I calculated structural diversity indices using the Shannon index and analyzed the data with wavelet position variance and wavelet covariance with randomization tests. Along the lakeshore-to-forest gradient, the average distance of the last transition for ACPF richness (the edge of their distribution) coincided with the average first transition in structural diversity, indicating higher levels of structural diversity. ACPF richness was positively

associated with structural diversity at finer scales and on lakeshores, whereas a negative association was detected at coarser scales and closer to the forest edge. Structural diversity had the strongest association with ACPF richness within the lakeshore, suggesting that it could be used as an indicator of suitable ACPF habitat at a fine scale. This could help to identify and protect potential habitat for ACPF, allowing the maintenance and growth of ACPF populations in Nova Scotia.

INTRODUCTION

Edges, defined as zones of transition between plant communities, are important parts of landscapes as they control the flow of energy and materials across ecosystems and are characterized by unique abiotic and biotic gradients (Harper et al. 2005). Edges usually support a higher level of structural diversity because of interactions occurring between physical processes and unique microclimatic patterns (e.g., increased solar radiation and exposure to wind; Fraver 1994; Ploff et al. 1997). Vegetation structure is defined by the height, coverage and types of vegetation (Tews et al. 2004) and represents the physical organization of plants (Noss 1990). Vegetation structure is considered one of the most important components of ecosystems because it provides resources and shelter for many species (Tews et al. 2004; McElhinny et al. 2005; Ozdemir and Donoghue 2013). As high levels of structural diversity offer a variety of habitat niches (Tews et al. 2004), vegetation structure is usually positively correlated with increased biodiversity (Neumann and Starlinger 2001; McElhinny et al. 2005).

Riparian zones are expected to support increased structural diversity because they are shaped by moderate levels of disturbances, contain vegetation elements from both lakeshore and forest communities, and experience tree mortality from flooding (Komonen 2009). Vegetation at edges between terrestrial and aquatic ecosystems (e.g., riparian zones) is influenced by hydrological disturbances resulting from lacustrine/fluvial processes (e.g., soil saturation, erosion, periodic flooding, ice damage) and hill slopes (Fetherston et al. 1995; Pabst and Spies 1998). Two main hydrological gradients, wave exposure and elevation, influence riparian plant communities and affect soil properties (e.g., fertility and particle size) by washing out nutrients/fine sediments and determining water depth, respectively (Keddy 1983; Weiher and Keddy 1999). Other edaphic characteristics, such as soil texture and moisture, will also vary along a gradient of relative elevation (Keddy and Reznieck 1982).

Riparian zones support complex habitat patches that are created and destroyed at different spatial and temporal scales by hydrological disturbances, resulting in an annual redistribution of species (Naiman et al. 1993; Naiman and Decamps 1997). As habitat patches are mostly delimited by vegetation structure (Chen et al. 1996), characterizing vegetation structure can assist in the identification of potential habitat and associated biotic habitat characteristics (Pabst and Spies 1998; Ibanez et al. 2014). Vegetation structure can also be integrated into different indices of structural diversity, such as the diversity or richness of structural elements (Dodonov 2015). By synthesizing the spatial distribution, functional diversity and composition of vegetation, structural diversity could be used as a summary variable to characterize the diversity of microhabitat types and ecological processes (McElhinny et al. 2005).

Spatial pattern is defined by the spatial arrangement (e.g., clumped vs dispersed) and size (i.e., scale) of areas with high and low levels of certain vegetation attributes (e.g., density, coverage) (Dale 1999). Using spatial pattern analysis with structural diversity indices can consequently provide important information on the structure of habitat, as it would allow for the assessment of the size and physical organization of patches (Dale 1999; Lindenmayer et al. 2000) of structural diversity, which can indicate habitat suitability in terms of vegetation structure. Spatial patterns of vegetation mainly depend on competition and edaphic factors (Dodonov 2015) and could provide information on plant populations and the role of disturbance (Chen et al. 1996). In riparian zones, spatial patterns are influenced by physical and disturbance features: propagule dispersal, seed germination, seedling survival, power and frequency of floods and site specific erosion (Naiman and Decamps 1997).

Scale is a key component of spatial patterns and relationships, such as between structural diversity and biodiversity (Noss 1990; Spellerberg and Fredor 2003; McElhinny et al. 2005). The structure of communities and the distribution of plant patches vary with the scale of observation (Dale 1999; Kembel and Dale 2006). Riparian communities offer insight into the variation of species richness at different scales, as disturbances act as a direct source of vegetation spatial heterogeneity, creating a variety of niches (Naiman et al. 1988; Naiman and Decamps 1997). Fine scale heterogeneity is an important determinant of general pattern in plant communities (Lundholm 2009), as local resources mainly determine biodiversity (Marchand and Houle 2006; Rooney and Bayley 2011).

Two major external factors are known to limit plant biomass: disturbance, which partly or completely destroys biomass, and stress, which restricts the production of biomass due to deficiencies or excesses of abiotic factors such as light, water and mineral nutrients (Grime 1977). Disturbance and stress are considered to be the precursors of three different plant evolutionary strategies: competitive (low stress, low disturbance habitat), stress-tolerant (high stress, low disturbance habitat) and ruderal (low stress, high disturbance habitat) (Grime 1977). Different types of stress, like nutrient deficient habitat, displace competitive species with stress-tolerant species (Grime 1977). Therefore, flooding and low fertility soils in riparian zones provide favored habitat for some rare species (Rhazi et al. 2006; Komonen 2009), particularly species that have weak competitive abilities for acquiring light/nutrients and broad tolerances to stress (e.g., soil infertility, floods) and disturbance (e.g., ice scouring, wave action) (Keddy 1985; Wisheu and Keddy 1989, 1994), such as many Atlantic Coastal Plain Flora (ACPF).

ACPF are a group of taxonomically unrelated plant species, including herbs, graminoids and shrubs, that mainly inhabit lakeshores and wetlands in the Atlantic coastal plain physiographic region of North America (Wisheu and Keddy 1989, 1994; Sweeney and Ogilvie 1993). ACPF have numerous biological limitations that mostly arise from their stress-tolerant evolutionary strategy, such as small plant size, slow growing rate, small population size and low seed production, resulting in weak abilities to compete for resources (e.g., light and nutrients) (Keddy 1985; Wisheu and Keddy 1989, 1994). Disjunct from their main range in eastern United States (Wisheu and Keddy 1989, 1994), southwestern Nova Scotia has some of the most suitable remaining habitats for ACPF (Environment Canada and Parks Canada Agency 2010). Nova Scotian populations are some of the last large undisturbed ACPF populations in the world and contain many rare ACPF species (Wisheu et al. 1994; Morris et al. 2002). However, knowledge gaps, such as the identification of key habitat characteristics and potential habitats, restrict the establishment of strategic conservation plans (Environment Canada and Parks Canada Agency 2010). The objectives of this study were (1) to assess spatial patterns of ACPF richness, individual ACPF species cover and different structural diversity indices along the lakeshore-to-forest gradient; and (2) to assess spatial relationships of ACPF richness with structural diversity indices at different scales and positions along the lakeshore-to-forest gradient.

METHODS

Sampling design and data collection

At each site, I located one 20 m transect (i.e., spatial extent) perpendicular to the waterline with 0.2 x 0.2 m contiguous quadrats (i.e., spatial grain) (16 sites x 100 quadrats = 1600 quadrats) (Figure 3-1a, Appendix 3). Contiguous small-scale quadrats were chosen as this sampling design to minimize the probability of missing small-scale spatial patterns while allowing for small and large-scale pattern assessment (Dale 1999). Between mid-June and mid-July 2015, I established the start of transects where vegetation emerged (approximately 1-2 m in the water at that time of the year) to at least 5 m beyond the forest edge. I subjectively located transects in areas with wider shorelines and the highest abundance/richness of ACPF species along the lakeshore-to-forest gradient.

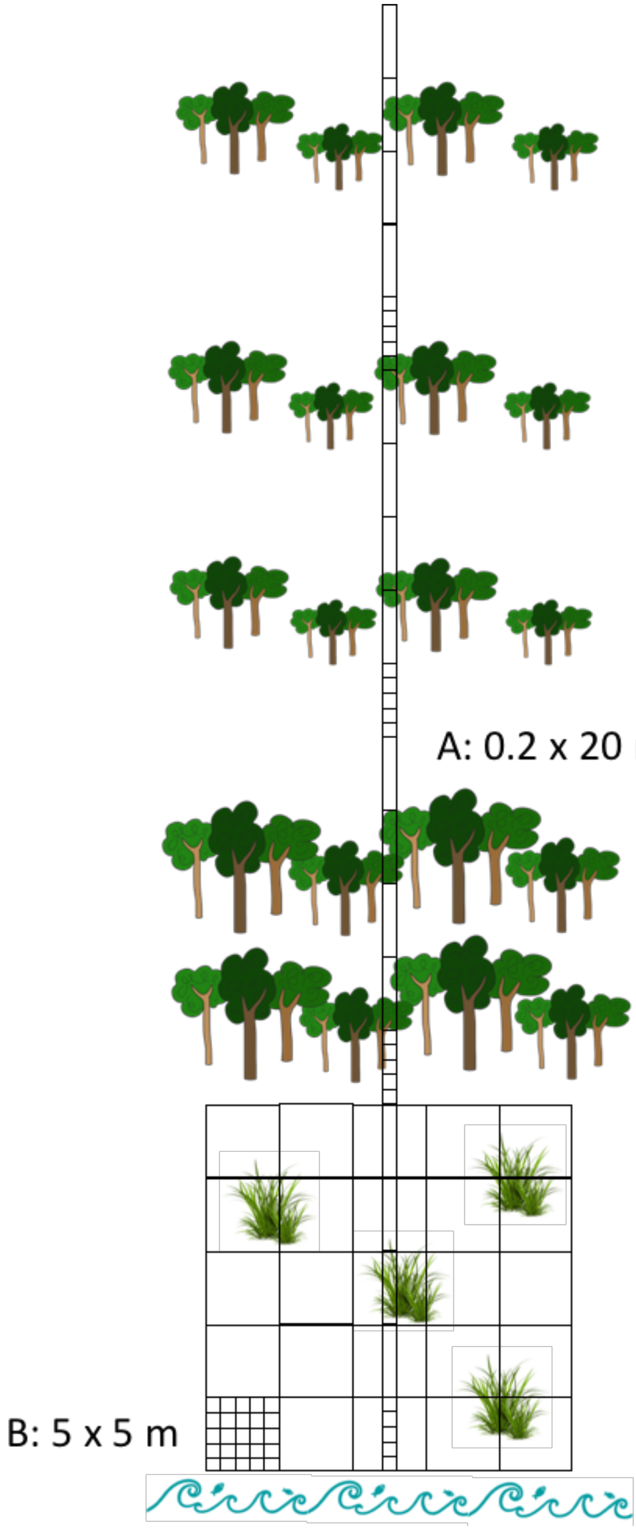


Figure 3-1. Diagram showing the locations of a transect (a) and a grid (b) with respect to the waterline and the forest edge (e.g., first trees). Contiguous quadrats were 0.2 x 0.2 m (only some shown due to clarity).

I also used a two-dimensional sampling approach for exploring the spatial relationship of ACPF with structural diversity, my second objective. Hufkens et al. (2009) advocate two dimensional analysis over one dimensional analysis, as it offers more appropriate and representative insights into ecosystems processes and structures. This different sampling method also captures the second dimension of spatial patterns (Camarero et al. 2006) while collecting more data on ACPF habitat. From mid-August to the beginning of September 2015, I established five 5 x 5 m grids (i.e., spatial extent), divided into 0.2 x 0.2 m contiguous quadrats (i.e., spatial grain) (5 grids x 625 quadrats = 3125 quadrats) (Figure 3-1b). Grids started where vegetation emerged (near the waterline at that time of the year) and extended approximately to the forest edge. I centred the grids on the transects, except at the Se1 site where the shoreline was not straight enough at that location for a sufficient distance to accommodate the grid. Five sites on different lakes were chosen to conduct grid sampling (Figure 1-3), based on the transects with the highest ACPF richness and widest shorelines to maximize the number of quadrats with ACPF.

Within each quadrat along transects and in grids, I visually estimated the cover of 19 ACPF species and different structural elements within different height/diameter categories using cover classes of < 5%, 6-25%, 26-50%, 51-75% and > 76%. Structural elements included ground elements such as leaf and needle litter, twigs of different diameters and other woody material, bryophytes and lichens, as well as above-ground functional groups of plants such as herbs, graminoids, ferns, evergreen species and woody species (Table 3-1).

Table 3-1. Description of structural elements with associated measurement categories.

Structural group	Structural element	Measurement categories
Litter	Needle litter	
	Leaf litter	
Woody material	Twigs	Diameter: < 1 cm, 1-5 cm
	Log	
	Snag	
	Other (debris)	
Other living plant material	Roots	
	Seeds	
	Trunk	
Plants	Bryophytes	
	Lichens	
	Sundews	
	Horsetails	
	Graminoids	
	Ferns	Height: 0.2, 0.4, 0.6, 0.8, > 0.8 m
	Evergreen herbs	Height: 0.2, 0.4, > 0.4 m
	Deciduous herbs	Height: 0.2, 0.4, 0.6, > 0.6 m
	Vines	
	Deciduous woody plants	Height: 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.8, 2.0, 2-3, 3-5, > 5 m
	Coniferous woody plants	Height: 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.4, 1.8, 2.0, 2-3, 3-5, > 5 m
Other	Algae	
	Rock	
	Fungus	

Spatial pattern analysis

Spatial pattern describes the arrangement of plants in space by assessing patch size (e.g., average width of clumps) and scale (e.g., distance between patches) (Dale 1999). Wavelet analysis quantifies spatial patterns at different scales and positions in one (e.g., transect) or two dimensions (e.g., grid). This spatial analysis has the advantage of not requiring stationarity of the data, meaning that the characteristics (e.g., mean and variance, Brosofske et al. 1999) of the spatial pattern don’t have to be constant across positions (Bradshaw and Spies 1992; Dale and Mah 1998; Rosenberg and Anderson 2011). Wavelet analysis consists of a moving template that assesses the similarity between the template and the data at each position along the transect or grid, and at several scales by increasing the size of the template (see Figure 3-2 for example in one dimension).

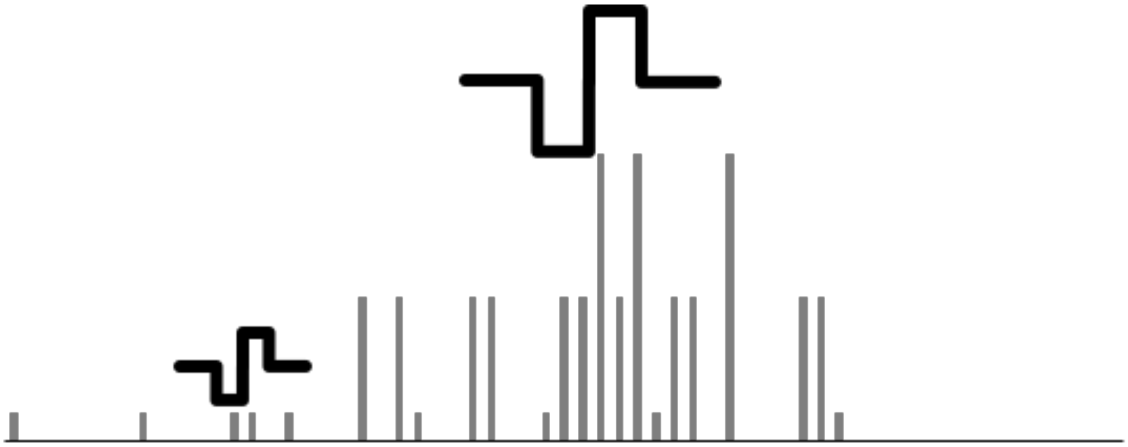


Figure 3-2. Wavelet continuous transforms evaluate the similarity between the template (black) and the data (gray) at each position and at several scales by increasing the size of the template.

The template represents the shape of a spatial structure, such as transitions (Haar template) or patches (Mexican hat template) (Figure 3-3a). High wavelet transform indicates a match between the template and the data, and consequently a non-random spatial association, revealing the presence of the spatial structure defined by the template (Dale and Mah 1998; Kembel and Dale 2006; James and Fleming 2010; James et al. 2011). For two dimensional analysis, three different templates based on the Haar and French Top Hat templates are available (Rosenberg and Anderson 2011) (Figure 3-3b).

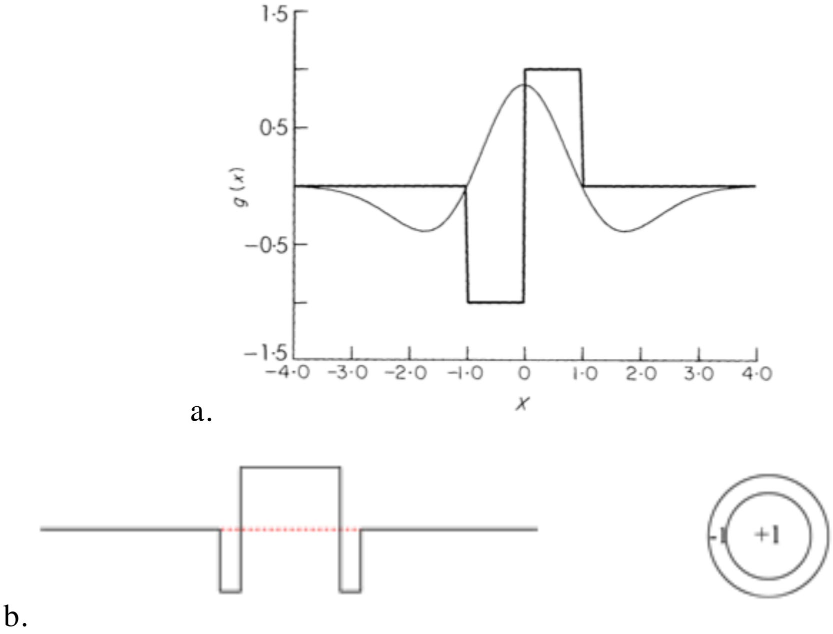


Figure 3-3. (a) Haar (bold line) and Mexican hat template for one dimensional analyses (Bradshaw and Spies 1992), and (b) Boater template for two dimensional analyses (Rosenberg and Anderson 2011).

Wavelet variance is used to assess spatial patterns across scales by calculating the average square of the wavelet transform (i.e., similarity between the template and data) at every position for a given scale (Bradshaw and Spies 1992). Wavelet position variance assesses spatial patterns across positions and is mostly used to identify patches or transitions in species composition along transects (Dale and Mah 1998). Wavelet position variance sums wavelet variance across all scales for each position. Peaks/shoulders of the wavelet variance indicate the scales or locations of the spatial patterns (Kembel and Dale 2006). Wavelet covariance multiplies the wavelet transforms of two variables to assesses spatial relationships between two variables at different scales and positions (Kembel and Dale 2006). A positive wavelet covariance implies that the two variables vary in the same direction, whereas a negative value indicates that the variables vary in opposite directions.

Before performing the analysis, a maximum scale needs to be set. The scale is defined as the percentage of quadrats to group together, up to the selected maximum scale. For example, one hundred contiguous 0.2 m long quadrats are distributed along the 20 m transect (one dimensional analysis); a maximum scale of 30% means that quadrats would be grouped together up to 30 quadrats for a maximum scale of 6 m. The maximum scale that can be used is often restricted by the template chosen. For example, the maximum scale for two dimensional analyses with the Boater template cannot be greater than 25%. However, a scale of 30% is commonly used for one dimensional analyses.

Using wavelet analysis with null models (e.g., randomization tests) permits the identification of significant scales and locations of spatial patterns and relationships. Null models represent spatial processes deprived of pattern (e.g., under stochasticity processes) and involve the same analysis but with a random resampling of the data along transects (James and Fleming 2010).

After the analysis, a wavelet variance or covariance value, along with the value from the null models (95% confidence intervals), is given for each scale up to the maximum scale or for each position (see example in Table 3-2). There is also a graphical output available (Figure 3-4). Scales and positions for which the wavelet variance or covariance value is higher than the value provided by null models (i.e., above the 95% confidence interval) are considered significant (James and Fleming 2010; James et al. 2011). Afterwards, I calculated the mean of significant wavelet variance or covariance value per site for each scale or position (see example in Table 3-3).

Table 3-2. Example of wavelet position variance for the first five positions along a transect, where a wavelet position variance value, along with the value from null models, is given for each position. The significant values (higher value than null model) were kept, whereas the non significant values were changed to zeros.

Position	Wavelet position variance	Null model (95%)	Significant wavelet value
1	0.00	4.00	0
2	1.63	3.13	0
3	1.68	1.42	1.68
4	0.25	1.44	0
5	0.64	0.96	0

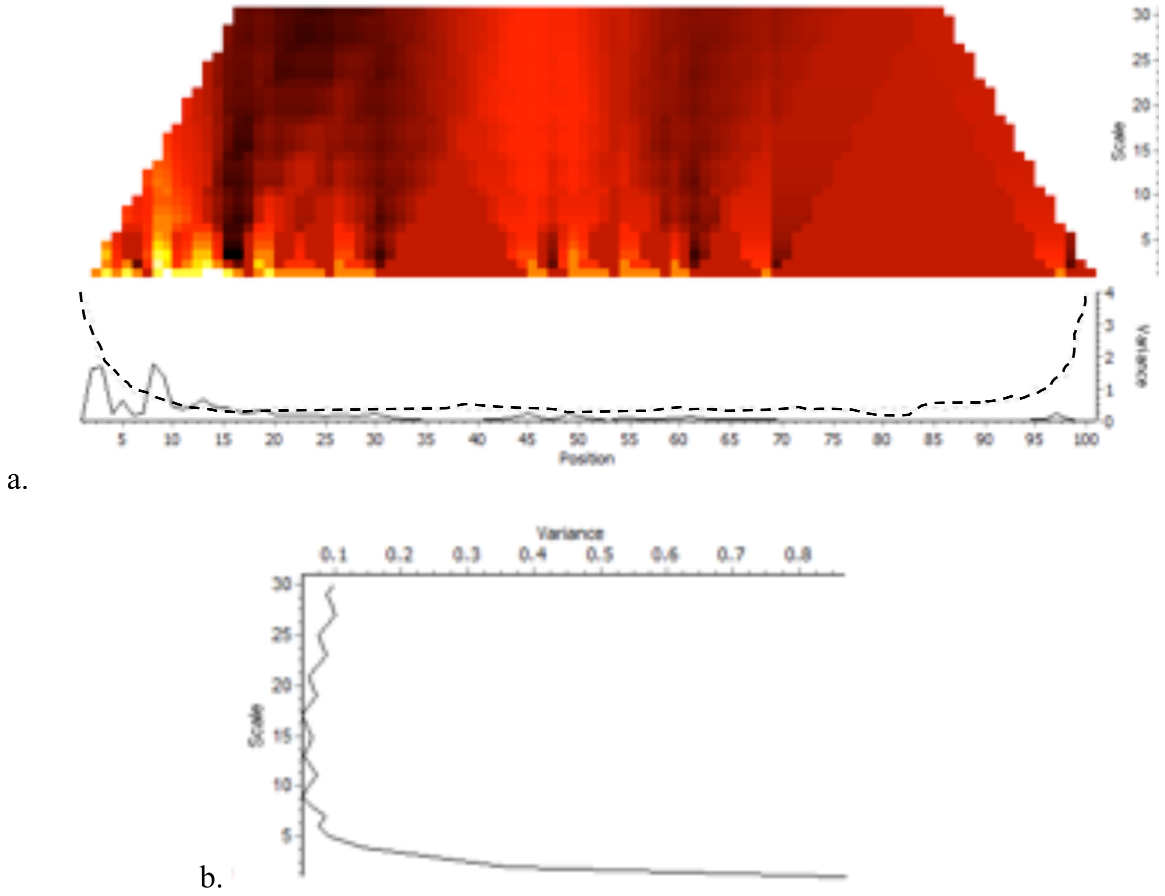


Figure 3-4. Example of graphical output after wavelet analysis (not related to the example in Table 3-2). (a) the top graph is a heatmap (sometimes grayscale), which represents wavelet transform values across positions for given scales. The bottom graph shows the wavelet position variance; which is the sum of wavelet variance across all scales for each position, with the dashed line representing values from the null model. (b) the graph is called scalogram, which is the wavelet variance (average square of the wavelet transform across positions) for each scale.

Table 3-3. Significant wavelet position variance for the first five positions for ten sites and the mean of significant wavelet position variance value per site for each position.

Position	Fc1	Ca2	Ca1	Ho1	Ho2	Ke1	Mo1	Mo2	Mo3	Po1	Mean
1	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	30.5	0	0	0	0	7.63	0	3.16
3	16.27	1.68	0	12.46	0	2.67	7.18	7.73	1.68	0	3.32
4	5.35	0	0	7.69	0	0	0	6.45	2.09	0	1.68
5	3.08	0	0	0	0	0	2.27	5.68	0	3.34	0.96

Data analysis

I calculated different indices of structural diversity for each quadrat by calculating the Shannon index using structural elements as pseudo-species (McElhinny et al. 2005). In ecology, the Shannon index is described as $H = -\sum p_i \ln(p_i)$ where p_i represents the proportion (e.g., number, coverage) of individuals belonging to a certain species. All cover classes were first converted to their midpoint value of 3%, 16%, 38%, 63% and 88%. I calculated an overall structural diversity index using the cover of each structural element (described in Table 3-1). I also divided structural elements into two main categories (e.g., ground layer or above ground) and calculated their Shannon index, defined as substrate diversity (e.g., litter, twigs, log, bryophytes, algae, lichen) and plant diversity (e.g., graminoids, shrubs, ferns, evergreen, trees at different heights). I calculated a shrub diversity index with the cover of coniferous and deciduous woody species at every 0.2 m height up to 2 m. It is important to note that ACPF species were not included in the structural diversity indices. All Shannon diversity indices were calculated using the Vegan package (Oksanen et al. 2015) in R 3.2.2. (R Core Team 2015). ACPF richness was defined as the number of ACPF species in each quadrat.

To assess spatial patterns of ACPF richness and different structural diversity indices (structural, substrate, plant, shrub) along the lakeshore-to-forest transects, I used wavelet position variance with the Haar template to allow for the detection of transitions, edges and gradients (Bradshaw and Spies 1992). As ACPF richness included numerous individual species, I expected a non-random spatial distribution of ACPF richness in the form of transitions in the number of species instead of patches of similar number of ACPF species. Similarly, I expected gradients and changes in structural diversity and not distinct patches of similar levels of structural diversity through the lakeshore-to-forest gradient. The Haar template is also known as the simplest wavelet function and is the most used (Rosenberg and Anderson 2011). I assessed patches of individual ACPF herb and shrub species that were present in at least 30 quadrats overall with the Mexican hat wavelet (Dale and Mah 1998). I only included sites where the species was present in a minimum of 5% of the quadrats to ensure a certain amount of data to be detected by wavelet analysis. As opposed to ACPF richness and structural diversity, I expected a non-random spatial distribution of individual ACPF species in the form of patches along the lakeshore-to-forest gradient with respect to their specific range of positions due to zonation processes, which is why I used the Mexican hat wavelet.

To assess spatial relationships between ACPF herb richness and different structural diversity indices at different scales and positions along the transects, I performed wavelet covariance analysis (Kembel and Dale 2006). I used ACPF herb richness as different functional groups of plants may not be influenced by structural diversity in the same way. Most ACPF selected species were herbs and they were more abundant and diverse along the lakeshore-to-forest gradient compared to shrubs and graminoids. I used structural diversity indices that excluded herb cover to eliminate any possible autocorrelation.

I also used wavelet covariance analysis in two dimensions to assess spatial relationships between ACPF herb richness and structural diversity indices (structural, substrate, plant) at different scales in the grids. I did not use shrub diversity as shrubs were only present in low abundance in only two grids. For each grid, I selected herb species that were in a minimum 10% of the quadrats, and I also performed wavelet covariance between individual species and the structural diversity indices. For these two dimensional analyses I used the Boater template, which is based on the Haar template and has equal magnitudes of outer and inner data (Rosenberg and Anderson 2011). Not enough studies have been done to distinguish among these three templates; however, they are expected to give similar results because of their similar shapes (Rosenberg and Anderson 2011).

I used a maximum scale of 30% and 25% for the one and two dimensional analyses, respectively (scales of 6 m and 1.2 x 1.2 m = 1.44 m^2). For every analysis, I conducted randomization tests using 999 iterations with a 95% confidence interval. Wavelet variance/covariance was considered significant when it was above the confidence interval (James and Fleming 2010; James et al. 2011). I calculated the mean of wavelet variance/covariance for significant values only across sites for each scale or position in order to summarize the results for all transects. All wavelet analyses were performed with PaSSAGE 2.0 (Rosenberg and Anderson 2011).

RESULTS

Before going into wavelet analysis results, I visually inspected the distribution of ACPF richness and structural diversity indices along the lakeshore-to-forest gradient. The objective was to visualize the data and to determine if there was a general trend (non statistically significant), by looking at the location of lower and/or higher values concentrations, indicated by the darker points on the graphs. Along the lakeshore-to-forest gradient, higher values of ACPF richness appeared to be found within the first half of the transect (i.e., between 0 and 10 m) (Figure 3-5a). In contrast, lower values of structural diversity seemed to be more concentrated at the beginning of the transect compared to most of the values found within the second half of the transect (i.e., between 10 and 20 m) (Figure 3-5b). However, there was more variation in structural diversity closer to the waterline compared to the second half of the transect. Lower values of shrub diversity appeared to be mostly located at the beginning (i.e., waterline) and end (i.e., forest interior) of the transect (Figure 3-5c). Lower and higher values of plant and substrate diversity did not seem to be visually concentrated at any location along the transect and showed more variation in the data (Figure 3-5d and e).

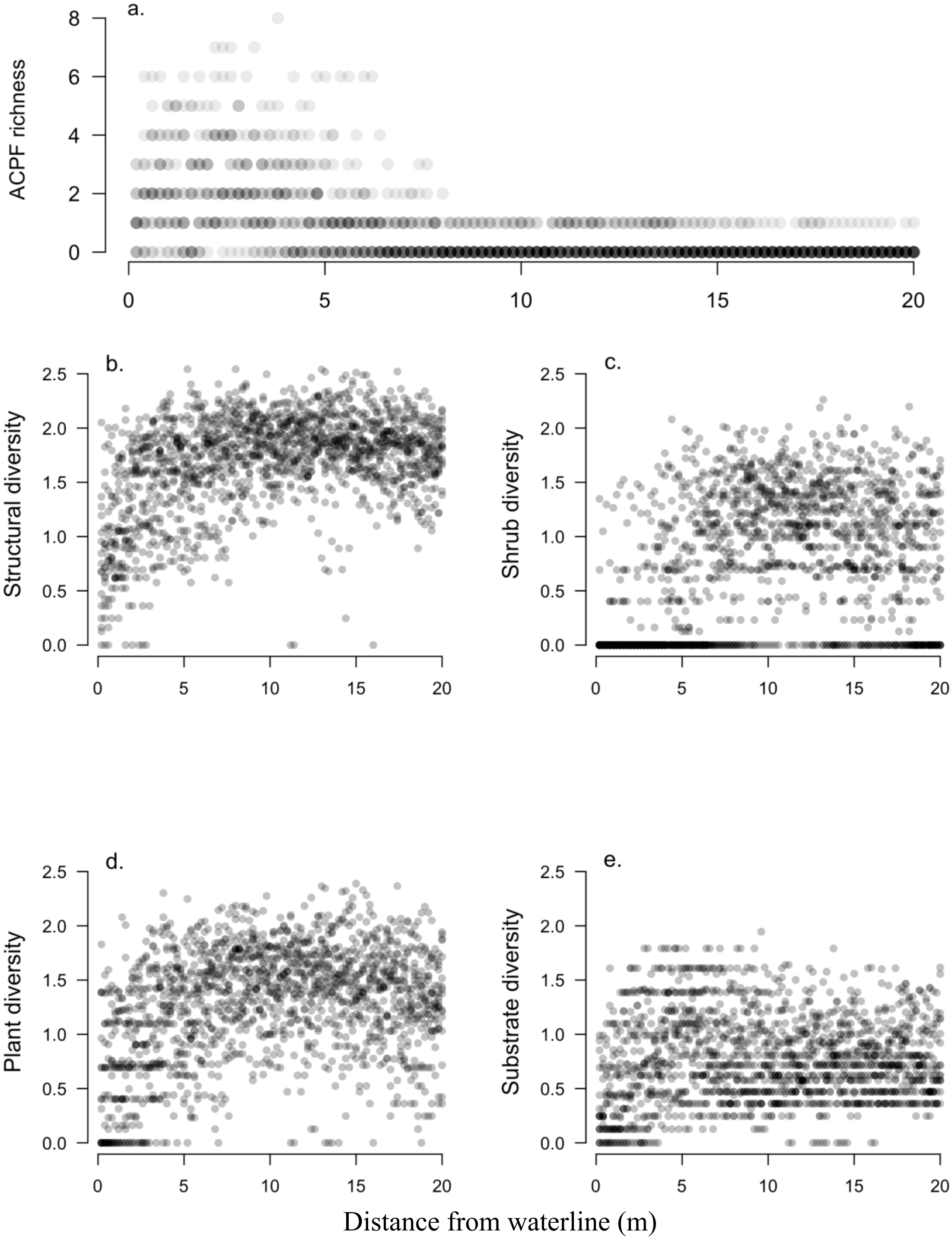


Figure 3-5. ACPF richness (number of ACPF species, a) and structural diversity indices (using the Shannon index of different structural elements cover, b to e) along the lakeshore-to-forest gradient (n = 16 for each 0.2 m distance). Grey shading represents the intensity of superimposed data points.

Significant peaks in wavelet position variance for any variable using the Haar template indicate a transition, gradient or boundary of that variable, which can be either a positive (increase) or negative (decrease) change (see data analysis for more details). For ACPF richness, almost all transitions were located between 0.2 and 7.6 m from the waterline (Figure 3-6a). First transitions (closest to the waterline) in ACPF richness were more abrupt compared to last transitions, indicated by higher wavelet position variance values. Two peaks often represent the first and last transitions of a variable, indicating the presence of one patch. ACPF richness showed more than two transitions per transect (average number of peaks, Table 3-4); which indicates that there could be one patch of different levels of ACPF richness (e.g., skewed distribution) or multiple patches of ACPF along the lakeshore-to-forest gradient. The average last significant transition in ACPF richness (5.5 m) was located before the average first significant transition in structural diversity (6.8 m, Table 3-4).

Table 3-4. Average distance and standard deviation of first and last significant peaks and number of significant peaks of ACPF richness and structural diversity indices along the lakeshore-to-forest gradient (n = 16). Structural diversity indices were calculated using the Shannon index. Significant peaks in wavelet position variance using the Haar template represent transitions.

Indices	Average distance of first peak (m)	Average distance of last peak (m)	Average number of peaks
ACPF richness	1.0 ± 0.6	5.5 ± 4.3	3.3 ± 1.2
Structural diversity	6.8 ± 3.5	13.2 ± 4.3	2.5 ± 1.2
Shrub diversity	6.2 ± 2.9	12.6 ± 5.8	3.0 ± 1.6
Substrate diversity	3.6 ± 2.3	14.1 ± 5.1	3.8 ± 1.1
Plant diversity	5.7 ± 2.6	14.3 ± 4.7	3.1 ± 1.2

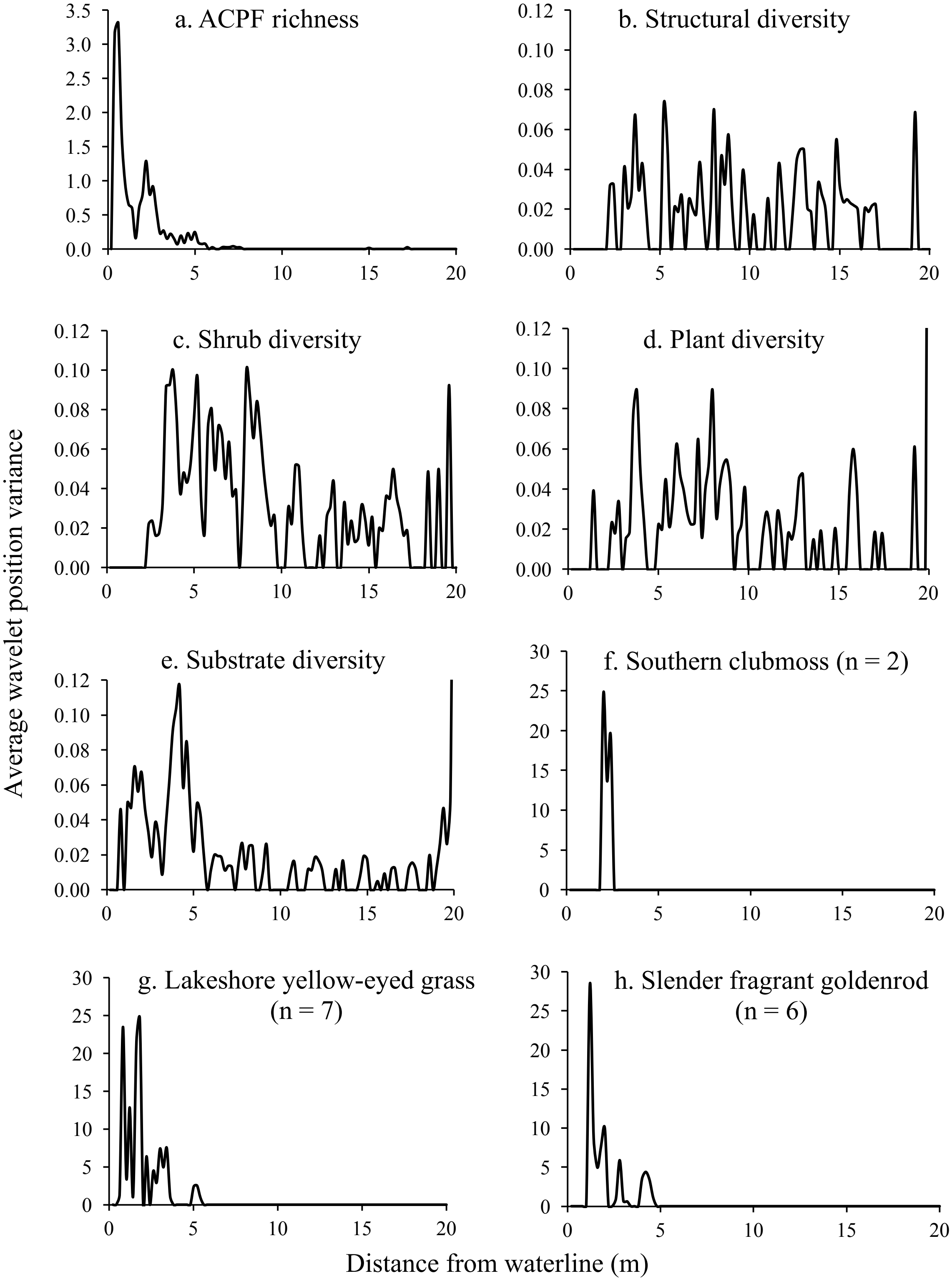
Most transitions in structural diversity had similar intensities (i.e., similar wavelet position variance values); all transitions were located between 2.4 and 19.2 m from the waterline (Figure 3-6b). All transitions in shrub diversity were located between 2.4 and 19.8 m, whereas all transitions in plant diversity were situated between 1.4 and 20.0 m from the waterline (Figure 3-6c and d). All transitions in substrate diversity occurred between 0.8 and 20.0 m from the waterline; abrupt transitions were located between approximately 1 and 5 m, as indicated by higher peaks in wavelet position variance (Figure 3-6e). Numerous transitions in vegetation structure appeared along the lakeshore-to-forest gradient, indicated by many peaks per transect for each structural diversity index (Table 3-4). Transitions in ACPF richness were more abrupt than transitions in structural diversity indices, shown by higher wavelet position variance values.

Patches of individual herb ACPF species, indicated by significant peaks in wavelet position variance with the Mexican hat template, were mainly found at closer distances to the waterline (< 5 m), with a total of 1-2 closed patches per transect (Figure 3-6f – l, Table 3-5). Patches of shrub species were located at farther distances from the waterline compared to herb species (> 5 m) and were distributed with 1-2 patches along the transect (Figure 3-6m and n, Table 3-5). Here, it is important to note that some species have small sample sizes (n < 3), which highly limits the ability to make broad predictions regarding the position occupied by the species.

Table 3-5. Average distance and standard deviation of the start and end of significant peaks and average number of significant peaks along the transects for individual species (with a frequency of > 5% quadrats (n = # transects)). Significant peaks in wavelet position variance using the Mexican hat template represent patches.

Functional group	Species	Average distance of peak start	Average distance of peak end	Average number of peaks
Herb	Virginia meadow-beauty (n = 3*)	0.6	0.8	1.0
	Golden pert (n = 7)	1.1 ± 0.8	1.2 ± 0.7	1.3 ± 0.5
	Lakeshore yellow-eyed grass (n = 7)	1.8 ± 0.9	2.9 ± 1.4	1.7 ± 0.8
	Redroot (n = 5)	1.4 ± 0.9	1.9 ± 0.8	1.3 ± 0.6
	Lance-leaved violet (n = 10)	2.9 ± 1.4	4.0 ± 1.2	1.7 ± 0.8
	Slender fragrant goldenrod (n = 6)	1.9 ± 0.9	3.0 ± 1.1	1.4 ± 0.6
	Southern clubmoss (n = 2*)	2.0	2.4	1.0
Shrub	Northern bayberry (n = 5)	8.4 ± 5.9	13.1 ± 4.7	1.8 ± 0.8
	Inkberry (n = 2)	6.2 ± 2.8	9.3 ± 5.5	2.0 ± 0

* Only one site had significant wavelet variance values (i.e., above the confidence interval determined by randomization tests).


a. ACPF richness
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
b. Structural diversity
0.12
0.10
0.08
0.06
0.04
0.02
0.00
c. Shrub diversity
d. Plant diversity
e. Substrate diversity
f. Southern clubmoss (n = 2)
g. Lakeshore yellow-eyed grass (n = 7)
h. Slender fragrant goldenrod (n = 6)
30
25
20
15
10
5
0
0
5
10
15
20
Average wavelet position variance
Distance from waterline (m)

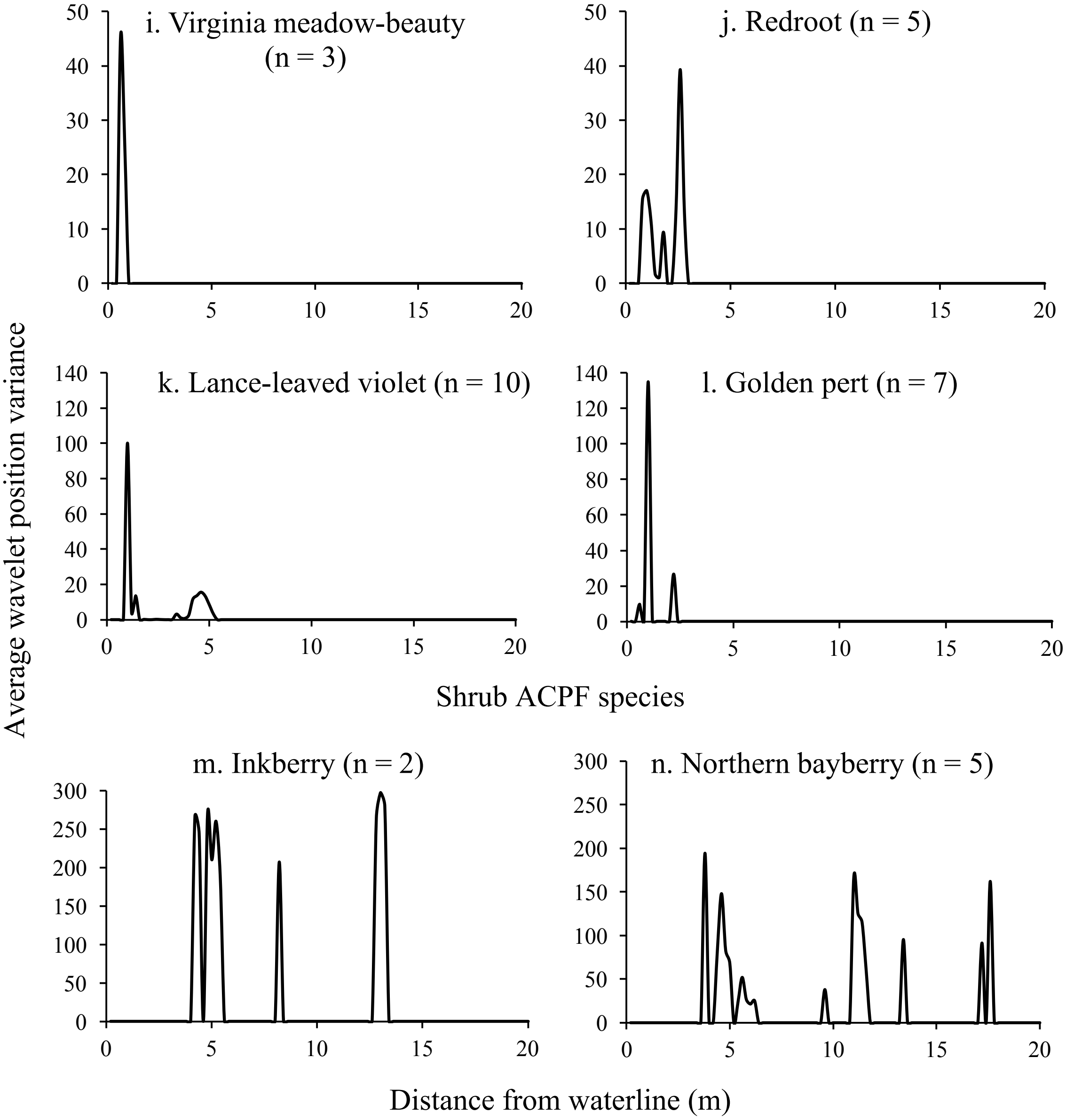


Figure 3-6. Average of significant wavelet position variance of ACPF richness, different structural diversity indices and individual species across sites for each position along the transects (n = 16 unless otherwise indicated). Data were analyzed with wavelet analysis using the Haar template for richness and structural diversity indices, and the Mexican hat template for individual species, which were analyzed only for transects with a frequency of > 5% quadrats. The maximum scale was 30%. See Appendix 4 for results for standard deviation.

Spatial relationships at different scales and positions

Along the lakeshore-to-forest gradient, ACPF herb richness was positively associated with structural diversity at finer scales (< 2.8 m) and became negatively associated at coarser scales (> 2.8 m up to 6.0 m). Here, wavelet analysis defines scale as the template size and consequently the size of grouped quadrats at which the analysis was performed. This scale could be defined as the spatial grain, which is the minimal unit size of a measure (Rosenberg and Anderson 2011). Similarly, positive associations with ACPF herb richness became negative at a scale of 1.6 m for plant diversity and 1.2 m for substrate and shrub diversity, respectively (Figure 3-7a). Positive associations with shrub diversity were very low compared to the other structural diversity indices. The highest positive associations occurred with structural diversity, then plant, substrate and finally shrub diversity, at a dominant scale of 0.4 m. There was no common scale for negative associations.

In the grids, the association between ACPF herb richness and structural diversity, as well as substrate diversity, was positive at each scale up to the maximum scale of 1.44 m^2 (Figure 3-7b). However, some species showed a negative association at coarser scales (> 0.64 m^2 = 0.8 x 0.8 m). A positive association with plant diversity became negative at a scale of 1.44 m^2, but was very low and at one site only. The highest positive associations occurred with structural diversity, then substrate and finally plant diversity at a dominant scale of 0.36 m^2.

Along the lakeshore-to-forest gradient, a positive association between ACPF herb richness and structural diversity became negative mostly after 3.2 m (Figure 3-8a). A negative association with substrate and plant diversity mainly arose after 4.0 m and 2.8

m, respectively, along the transect (Figure 3-8b and c). The association of ACPF herb richness with shrub diversity was almost always negative, except between 1.6 and 2.4 m, with a low positive association compared to the other structural diversity indices (Figure 3-8d).

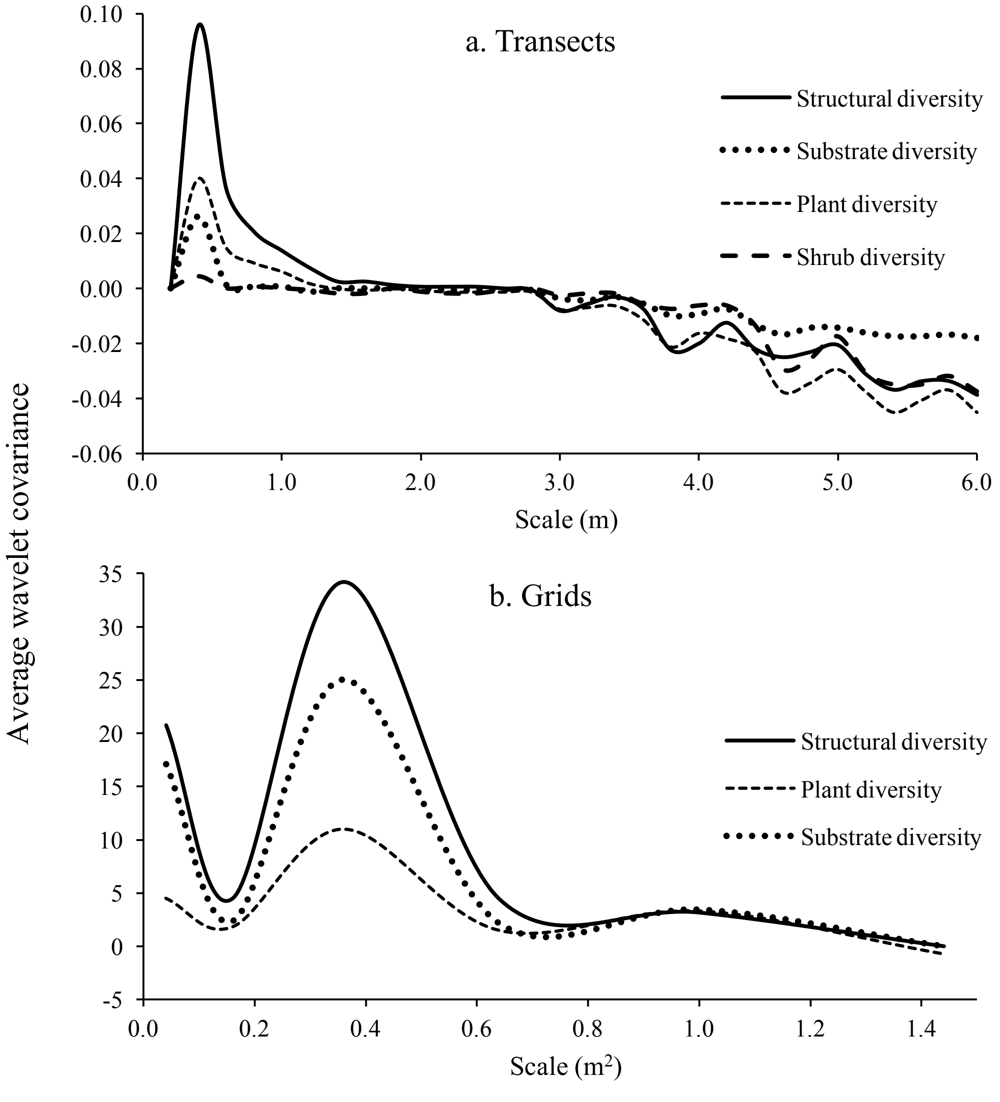


Figure 3-7. Average of significant wavelet covariance between ACPF herb richness and structural diversity indices across sites for each scale along the transects (n = 16) and within the grids (n = 5). Data for transects were analyzed with wavelet analysis in one dimension with the Haar template and a maximum scale of 30% (6 m). Data for grids were analyzed in two dimensions with the Boater template and a maximum scale of 25% (1.2 x 1.2 m = 1.44 m^2). See Appendix 4 for results for standard deviation.

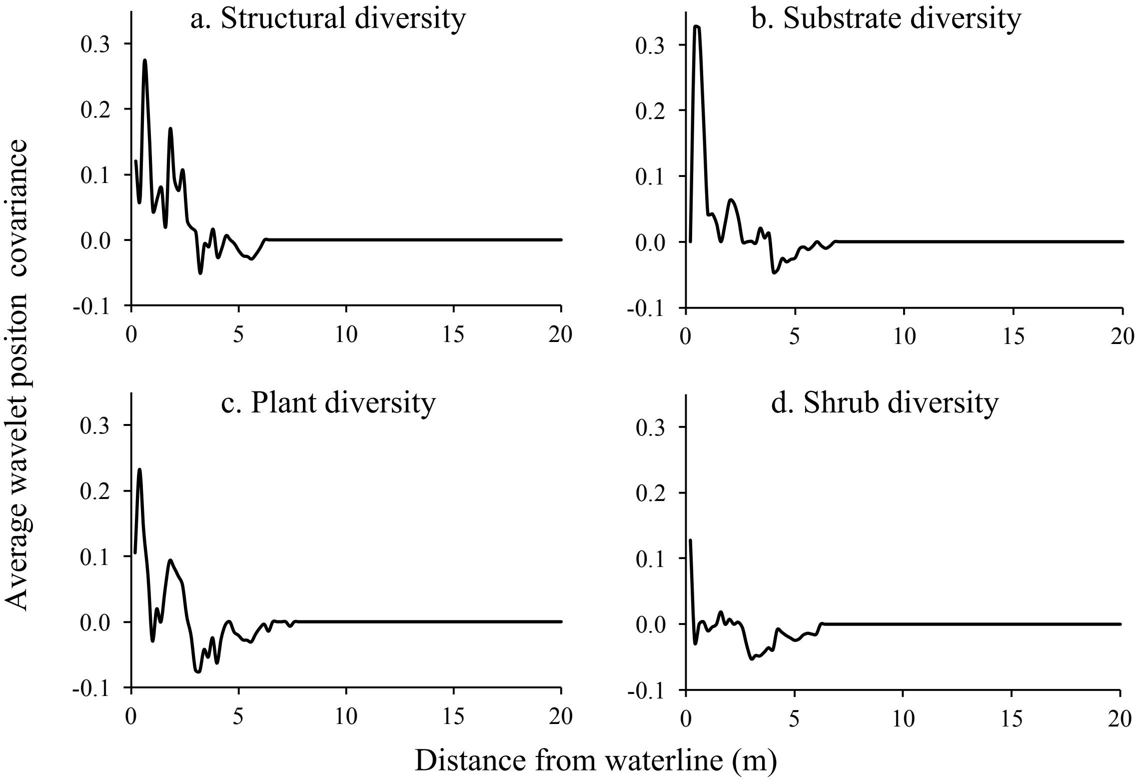


Figure 3-8. Average of significant wavelet position covariance between ACPF herb richness and different diversity indices across sites for each position along the transects (n = 16). Data were analyzed with wavelet analysis in one dimension using Haar template and a maximum scale of 30%. See Appendix 4 for results for standard deviation.

DISCUSSION

Spatial patterns along the lakeshore-to-forest gradient

Transitions in ACPF richness appeared closer to the waterline (i.e., beginning of the transect) compared to the forest interior (i.e., end of the transect) (Figure 3-6a). ACPF are closely associated with hydrological disturbances (e.g., water level fluctuations, flooding, ice scouring, wave action) that reduce competition on lakeshores (Keddy 1985; Wilson and Keddy 1986; Wisheu and Keddy 1989, 1994; Hill and Keddy 1992). The highest ACPF richness (e.g., seven ACPF herbaceous species in one quadrat) was found at approximately the middle positions on the lakeshore (i.e., first half of the transect) (Figure 3-5a). Species richness has been shown to be highest at a moderate level of disturbance (Wilson and Keddy 1986; Nilsson et al. 1989; Schneider 1994; Hill et al. 1998). Higher water levels and wave exposure may exceed the hydrological tolerance of some species and lead to insufficient accumulation of organic matter (Sorrie 1994; Hill et al. 1998). Furthermore, plant diversity and seed density has been shown to decline at low elevation due to flooded conditions (Schneider 1994), possibly explaining why the highest number of ACPF species was not found at the waterline.

Selected herb species of ACPF are all generally defined as lakeshore species (Table 1-1; Crowley and Beals 2011) and showed different ranges of positions mostly within the first 5 m of the transect (Figure 3-6 f - l). In contrast, the occurrence of ACPF shrub species started at a farther distance from the waterline (Figure 3-6 m and n), compared to ACPF herb species, and were distributed up to the forest interior (i.e., end of the transect, 20 m). The occurrence of woody species usually delimits the upper boundary of lakeshore plant communities (Schneider 1994), as the majority of shrubs are sensitive to flooding (Keddy and Reznieck 1982; Keddy 1985; Wisheu and Keddy 1989, 1994; Hill and Keddy 1992). Similar to what Schneider (1994) found with rare lakeshore plant communities, the edge of the distribution of ACPF richness coincides with increased shrub diversity, as well as structural and plant diversity (Table 3-4), indicating the boundary between lakeshore and forest plant communities.

The first and last transitions on a transect often represent the beginning and end of the response variable (e.g., species cover) and consequently the zone of its occurrence (e.g., one patch). Individual transects showed an average of 2.5 significant transitions in structural diversity along the lakeshore-to-forest gradient (Table 3-4). The first and last transitions for each transect could represent an increase in structural diversity followed by a decrease in structural diversity, respectively (average distance of first and last transitions in Table 3-4). Consequently, the zone between these two transitions could suggest the presence of the forest edge with a higher level of structural diversity (e.g., one patch of higher structural diversity). Alternatively, these transitions could simply indicate different levels of structural diversity along the lakeshore-to-forest gradient. Plant communities at natural edges tend to be more diverse and dense, as edges are characterized by different microclimatic conditions, such as increased solar radiation, resulting in higher air and soil temperature and lower humidity (Naiman et al. 1988; Fraver 1994; Ploff et al. 1997; Marchand & Houle 2006). Lakeshore edges are no exception and are expected to harbor high levels of structural diversity as wave and wind action causes seedling uproot, stem and root breakage, along with woody species mortality (Keddy 1982, 1985; Komonen 2009). Canopy gaps enhance regeneration and allow a greater number of species to coexist from reduced competition, whereas woody debris resulting from these shrub mortalities provide microsites (e.g., light, nutrient) for seed establishment and germination (Keddy 1984; Fetherston et al. 1995; Naiman and Decamps 1997; Pabst and Spies 1998; Komonen 2009). Intermediate levels of hydrological disturbances combined with increased exposure to wind and solar radiation, create canopy gaps and woody debris which increase the density and diversity of plant communities at lakeshore edges and consequently the level of structural diversity.

Some substrate elements, such as leaf litter, seeds and twigs, could indicate the limit of flooding, as wave action removes large amounts of plant materials (Keddy 1982, 1985). For example, Day et al. (1988) used litter removal on lakeshores to quantify the level of disturbance mostly from winter and spring erosion. Therefore, substrate elements would be more influenced by current hydrological disturbances by being physically carried away, whereas increased levels of structural diversity from woody species occurrence would be mainly determined by long-term water level fluctuations (e.g., high waterline) and flooding conditions (Schneider 1994). This could explain why changes in substrate diversity appeared at closer distance from the waterline compared to the other structural diversity indices.

Spatial relationships at different scales and positions

In theory, two plants or structural elements have a negative spatial relationship at very fine scales, as they cannot share the same space (Figure 3-9). In this study, I found a positive association between ACPF herb richness and structural diversity indices at finer scales, indicating that 0.04 m^2 (e.g., one quadrat) is large enough to accommodate both ACPF plants and structural elements. This positive covariance suggests that high level of ACPF richness is associated with high levels of structural diversity. However, this positive covariance only occurred within a zone of low structural diversity, indicated by the gap between the edge of ACPF richness (i.e., average last transition) and the beginning of higher structural diversity levels (i.e., average first transition) (Table 3-4). Furthermore, a positive covariance between ACPF herb richness and structural diversity indices was only located at closer distances to the waterline compared to farther distances where a negative covariance was found between the two variables (Figure 3-8).

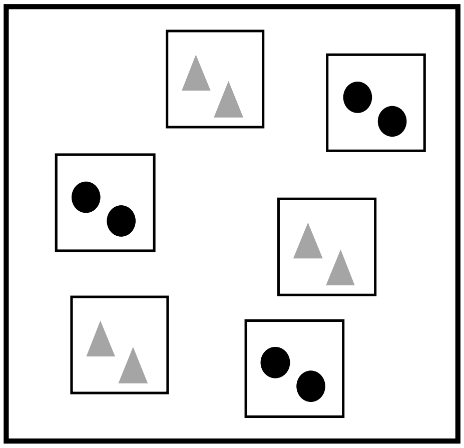


Figure 3-9. Diagram showing negative covariance at finer scales (e.g., small squares) and positive covariance at larger scales (e.g., bold large square) between two elements (e.g., black circles and grey triangles) in two dimensional sampling.

As wave action washes seeds, seedlings, plant parts, fine sediments, nutrients and organic matter (Keddy 1982; Day et al. 1988), lakeshores support relatively low levels of structural diversity (e.g., sundews, graminoids) compared to the forest edge (e.g., deciduous and coniferous shrubs and trees, evergreen herbs, leaf litter). This leads to a negative association between ACPF herb richness and structural diversity indices at coarser scales, at which ACPF richness decreases from the lakeshore to the forest interior. The hydrological gradient on lakeshores is a complex combination of stress and disturbance created by the removal of nutrients/organic matter (restricting growth) and biomass, respectively (Wilson and Keddy 1986). Therefore, suitable habitat would be provided for species that tolerate those conditions, such as many lakeshore ACPF species (Shipley et al. 1991). With decreasing flooding and nutrient poor conditions (Pabst and Spies 1998), ACPF and other lakeshore species are replaced by more dominant competitors like shrubs (Shipley et al. 1991). Woody species are highly competitive species and easily outcompete ACPF (Hill and Keddy 1992), which explains why shrub diversity had a negative association with ACPF herb richness across almost all scales and positions or a relatively low positive association compared to other structural diversity indices (Figure 3-7a and 3-8d). In contrast to ACPF richness, structural diversity increased along the lakeshore-to-forest gradient, as interfaces between plant communities are characterized by abiotic and biotic gradients that impact the structure of plant communities, a phenomenon called edge influence (Harper et al. 2005). Consequently, at coarser scales, ACPF herb richness (decrease) and structural diversity (increase) vary in opposite directions, resulting in a negative covariance (Dodonov 2015); high ACPF herb richness is consequently associated with low levels of structural diversity. The location of this negative association also appeared at a further distance from the waterline (i.e., closer to the forest edge than the waterline) (Figure 3-8).

As grids were approximately located between the lake and the forest edge and reached only five meters from the waterline, the majority of quadrats were on lakeshores and supported ACPF species along with similar structural elements (e.g., sundews, graminoids, bryophytes). In comparison, the transect sampling design included the forest edge and consequently higher levels of structural diversity, shown by the average distance to the first significant transition in structural diversity (i.e., 6.8 m in Table 3-4). Including the forest edge led to a negative association between ACPF herb richness and structural diversity at coarser scales along the lakeshore-to-forest gradient, whereas ACPF herb richness showed a strong relationship with structural diversity across all scales in the grids, supported by the highest positive association (Figure 3-7). Structural diversity indices shared a similar spatial relationship with ACPF herb richness (e.g., strongest spatial association at 0.44 m^2 scale, Figure 3-7b), although different levels of association occurred at the dominant scale. ACPF herb richness was more related to structural diversity and showed a higher relationship with substrate diversity than plant diversity. Hydrological disturbances on lakeshores lead to erosion and deposition of litter and silt (Naiman and Decamp 1997), creating microsites with heterogeneous substrate and moisture conditions (Pabst and Spies 1998). Furthermore, woody debris produced from hydrological disturbances (Komonen 2009), influence seedling germination and survival by holding plant propagules and providing protection from abrasion, drought and herbivory (Naiman and Decamp 1997). By retaining sediment, organic matter and nutrients, woody debris also offer favorable conditions for plant colonization (Fetherston et al. 1995). Organic content can directly influence seed bank germination, a critical process in lakeshore plant communities (Moore and Keddy 1988).

The presence of other functional groups of plants, such as ferns, graminoids, sundews and shrubs, could indicate suitable habitat for plants on lakeshores (i.e., not too moist, some organic matter present). Water level fluctuations bring diverse plant communities, from submerged and emerged aquatic plants to sedges (Naiman et al. 1988). Therefore, it is not surprising that ACPF species could occur in the same quadrats as other functional groups of plants, shown by a positive association between ACPF herb richness and plant diversity index. Carnivorous species, such as sundews, are associated with ACPF as they also inhabit low fertility habitat by exploiting a different nutrient source (Wilson and Keddy 1986; Wisheu and Keddy 1989, 1994; Wisheu et al. 1994). However, a high diversity of plants could also lead to competition for light and nutrients, resulting in a lower positive association with ACPF herb richness and even a negative association at coarser scales or with some ACPF species, compared to structural and substrate diversity.

CONCLUSION

Atlantic Coastal Plain Flora (ACPF) herb richness was associated with structural diversity. Different relationships (e.g., positive and negative) between ACPF herb richness and structural diversity indices arose at different scales and locations along the lakeshore-to-forest gradient. Structural diversity showed positive covariance with ACPF herb richness at finer scales and at close distances from the waterline, whereas negative covariance occurred at coarser scales and at farther distances from the waterline. These results highlight the importance of measuring and defining habitat characteristics for species conservation at numerous scales and positions along the entire environmental gradient, for example by including the forest edge (Gaudet and Keddy 1995; Tews et al. 2004; Estes et al. 2010).

I conclude that ACPF herb richness was associated with overall low levels of structural diversity along the whole lakeshore-to-forest gradient (i.e., coarser scales). The distribution of ACPF on lakeshores also seemed to be restricted by higher levels of structural diversity, as the edge of structural diversity coincided with the edge of ACPF distribution on lakeshore. Higher levels of structural diversity could consequently be used as a tool to manage riparian zones and control the quantity of suitable habitat for ACPF. For example, increasing the distance on lakeshores to higher levels of structural diversity would provide larger areas for the establishment and growth of ACPF populations. However, ACPF were positively associated with structural diversity on lakeshores where relatively low levels of structural diversity were found. Overall structural diversity had the strongest positive association with ACPF herb richness within riparian zones, suggesting that it would be the best indicator of suitable habitat for ACPF, compared to the other structural diversity indices that I have developed.

Consequently, structural diversity could assist the development of more appropriate conservation measures through the identification of potential suitable habitat in terms of structural diversity. Quantitative indicators are increasingly known and should be used for conservation purposes (Pabst and Spies 1998; Ibanez et al. 2014); structure-based indicators are especially appropriate for the assessment of biodiversity and habitat sustainability (Lindenmayer et al. 2000; Ozdemir and Donoghue 2013). Using low structural diversity along the lakeshore-to-forest gradient but high levels of structural diversity on lakeshore as indicators of suitable habitat for ACPF would allow private owners and managers to quickly and easily assess favorable sites for future protection. For example, by prioritizing the protection of shorelines that support various structural elements, such as graminoids, ferns, sundews, bryophytes, litter and woody material, but avoiding bare shorelines (low structural diversity) or shorelines with levels of structural diversity similar to the forest edge. The presence of extremely dense plant communities and increased woody species cover and height would lead to too high structural diversity shorelines and increased competition that many ACPF lakeshore herbs are not able to tolerate. The level of structural diversity could also be potentially used as an index for the intensity of hydrological disturbances and soil fertility, as disturbed shorelines with poor nutrient content would support low biomass (e.g., low structural diversity) compared to undisturbed nutrient rich shorelines that would be densely vegetated (e.g., high structural diversity). Furthermore, for the restoration as well as the maintenance of known ACPF habitats, simply increasing the level of structural diversity by establishing structural elements (e.g., bryophytes, woody material, graminoids) on bare shorelines or reducing the level of structure by trimming tall plants and woody species on densely vegetated shorelines could help ACPF populations colonize new shorelines and persist in Nova Scotia.

CHAPTER 4

Habitat characteristics of Atlantic Coastal Plain Flora lakeshore herbs at landscape and local scales

ABSTRACT

Atlantic Coastal Plain Flora (ACPF) are a group of taxonomically unrelated plants mostly found on lakeshores and in wetlands along the Atlantic coastal region of the United States with Canadian disjunct populations in Nova Scotia and Ontario. Lakeshore plant communities are driven by habitat processes at larger scales (e.g., hydrological disturbances), which influence habitat characteristics at smaller scales (e.g., soil fertility). In order to appropriately define ecological requirements of ACPF, the objective of this study was to determine their habitat characteristics at both landscape and local scales. I selected 16 sites on seven lakes in southwestern Nova Scotia where I sampled 20 m transects perpendicular to the waterline and 5 m x 5 m grids located between the lake and forest edge. I estimated the cover of ten common ACPF herb species and vegetation elements, and measured elevation and substrate in 20 cm square contiguous quadrats. I analysed the data using t-tests, simple linear regressions and spatial generalized linear mixed models. Larger watershed areas, gentle slopes, and greater distance from the waterline to shrub occurrence were significantly correlated with increased width of ACPF distribution along lakeshores. ACPF richness was significantly higher on mineral shorelines compared to organic shorelines. Lower elevation and shrub cover, intermediate-sized physical substrate and greater cover of sundews, graminoids and bryophytes were significantly correlated with increased ACPF presence, abundance and

richness at a local scale. Individual species occupied specific zones across lakeshores and consequently were influenced by different habitat characteristics. Defining landscape and local scale ecological requirements will improve the identification, conservation and management of ACPF habitat for the growth and maintenance of their populations in Nova Scotia.

INTRODUCTION

The distribution of species is determined by the presence of suitable habitat, dispersion barriers and/or stochastic factors (Williams et al. 2009). Although the range of a species can be defined at the landscape scale, understanding habitat occupancy at the local scale is essential for the proper identification of species habitat requirements for conservation purposes (Williams et al. 2009). At a landscape scale, indirect effects (e.g., transport of materials) and the general climate govern species composition, whereas at local scales, direct effects (e.g., light, temperature, soil nutrients, water, dispersal, competition, herbivory) and stochasticity (e.g., mortality, predation, interactions) determine plant distributions (Marchand and Houle 2006; Kembel and Dale 2006; Lundholm 2009; Rooney and Bayley 2011). Moreover, the distributions of many species are affected by interactions between landscape and local scale environmental factors (Parviainen et al. 2008).

For lakeshore plant communities, watershed area (defined as a terrestrial area where running water will converge into a water body, Hill and Keddy 1992), is related to the amplitude of hydrological disturbances (e.g., water level fluctuations, flooding, ice scouring and wave action), which are important drivers of species composition among lakes at a landscape scale (Hill and Keddy 1992; Morris et al. 2002). Water level fluctuates annually due to variable rainfall and evaporation patterns, which affect the timing, duration and number of floods (Nilsson and Wilson 1991). Low water levels provide an exposed shore for colonization (Sorrie 1994) and allow recruitment from the seed bank, whereas high water levels prevent the establishment of woody plants at low elevation positions on shorelines (Hill et al. 1998). Therefore, small changes in water level affect the germination of many lakeshore herbaceous plants (Moore and Keddy 1988; Keddy and Sharp 1994), which often explains the variability in species composition between growing seasons (Sorrie 1994; Hill et al. 1998). Ice scouring is an important disturbance on lakeshores that creates gaps in vegetation (Holt et al. 1995); gap dynamics is a critical process for recruitment, competition and mortality within plant communities (McElhinny et al. 2005). Ice scouring is also important in creating substrate heterogeneity by transporting pieces of soil (e.g., litter, organic matter) and plants (Figure 4-1), which improves colonization of nearby shorelines and creates new populations or occurrences of lakeshore plants (Sweeney and Ogilvie 1993; Holt et al. 1995; Day et al. 1988; Hill et al. 1998). Wave action further influences lakeshore communities by physically removing plant biomass, as well as washing nutrients and fine sediments from the soil, consequently reducing soil fertility and competitive interactions (Keddy 1985; Wilson and Keddy 1986).

Figure 4-1. Picture showing a potential impact of ice scouring at Hog Lake, Site 2 (Ho2). Ice scouring dislodges and transports mats of soils and plants, creating patches of peat, shown by the white circles.

At local scales, lakeshore vegetation varies along two major gradients of water depth and soil fertility, resulting from shoreline topography (i.e., relative elevation) and exposure to wave action, respectively (Keddy 1983; Weiher and Keddy 1999). These two gradients also influence edaphic characteristics on lakeshores by determining the moisture, nutrient content and particle size composition of soil (Keddy and Reznieck 1982; Keddy 1983). A variety of niches will consequently be created across the riparian zone, where each species occupies a certain position, a phenomenon called zonation (Keddy 1984; Pabst and Spies 1998). Species' positions on lakeshores mainly depend on their competitive abilities and organic matter content, mostly determined by the exposure to wave action (Wilson and Keddy 1986), along with winter inundation (i.e., high waterline) and summer drawdown (i.e., low waterline), which determines flooding and saturated conditions (Sorrie 1994). The main factors influencing the competitive abilities of lakeshore plant species are first determined by their capacity to colonize after disturbance and subsequently by shade tolerance (Pabst and Spies 1998). Consequently, poor competitor (e.g., stress tolerant) species are mostly found on disturbed infertile mineral shorelines/areas, whereas competitive species (e.g., stress intolerant) mainly inhabit undisturbed nutrient-rich organic shorelines/areas (Wilson and Keddy 1986; Gaudet and Keddy 1995). Alternatively, poor competitors would be found at low elevation positions in contrast to high elevation positions inhabited by good competitors.

As lakeshores are exposed to stress (e.g., soil infertility, floods) and disturbances (e.g., ice scouring, wave action), they provide habitat for plants that have broad tolerance but poor competitive abilities (i.e., stress tolerant or ruderal species according to Grime (1977)), such as many herbaceous Atlantic Coastal Plain Flora (ACPF) species found on lakeshores (Wisheu and Keddy 1989). ACPF are a group of taxonomically unrelated plants species that share common habitat types (e.g., lakeshores, wetlands) along the Atlantic coastal plain physiographic region of United States (Wisheu and Keddy 1989, 1994; Sweeney and Ogilvie 1993). Disjunct from that range (Wisheu and Keddy 1989, 1994), southwestern Nova Scotia supports some of the last large ACPF populations in the world, many provincially, and in some cases nationally, rare ACPF species, and some of the most suitable remaining habitat for ACPF species (Wisheu et al. 1994; Morris et al. 2002). With increased industrial development along the east coast of the United States

(Francis and Munro 1994) and climate change, environmental conditions are becoming less suitable (e.g., increased temperature, lower humidity) for ACPF through their main range, highlighting the importance of disjunct populations in the northern part of their distribution.

As ACPF have poor physiological tolerances and are sensitive to numerous climatic factors, such as minimum/average winter temperature, amount of insolation and average summer temperature (Sorrie 1994), winter climatic conditions temperatures in most regions adjacent to southwestern Nova Scotia restrict their distribution (Wisheu and Keddy 1989; Clayden et al. 2010). There are also physiography restrictions, such as the low topographic relief characteristic to the coastal plain physiographic region (Sweeney and Ogilvie 1993, Sorrie and Weakley 2006). At the landscape level, watershed area, which affects the amplitude of hydrological disturbances such as water level fluctuations that determine flooding conditions, as well as anthropogenic pressures (e.g., land use), determine if a lake can support ACPF communities (Keddy 1985; Morris et al. 2002). Both an excess of nutrients from agriculture and housing and the stabilization of water levels from hydrological damming promote the establishment of shrubs and competitive species and eliminate ACPF on lakeshores (Naiman and Décamps 1997; Hill et al. 1998). At the lake level, the amplitude of wave action (related to lake area) and the level of exposure (depending on the shoreline aspect) influence soil fertility and consequently competition intensity on shorelines (Keddy 1984, 1985; Wilson and Keddy 1986; Holt et al. 1995). Higher levels of wave action wash nutrients and fine sediments (e.g., silt, clay), creating an infertile substrate with coarser particle sizes (e.g., mineral shoreline), whereas lower levels of wave action would lead to an accumulation of organic material (e.g., organic shorelines). At a shoreline level, the lakeshore slope influences water depth and the width of the riparian zone, which defines flooding conditions and suitable habitat for lakeshore plant communities (Morris et al. 2002).

Knowledge gaps, such as the identification and ecological understanding of key habitat characteristics, restrict the establishment of strategic conservation plans for the preservation of ACPF populations in Nova Scotia (Environment Canada and Parks Canada Agency 2010). As riparian communities are thought to be driven by landscape and local factors (Behren et al. 2013), a multi-scale approach is essential to identify critical habitat characteristics and ecological requirements for ACPF (Environment Canada and Parks Canada Agency 2015). Some characteristics of ACPF communities have already been related to landscape scale habitat variables, whereas relationships with numerous local scale habitat variables have not commonly been studied. Consequently, the objectives of this study were: (1) to determine what influences ACPF zone width, ACPF species richness and ACPF species abundance at a landscape scale (i.e., watershed, lake and shoreline levels) in terms of hydrological disturbances and topography, and (2) to determine what influences ACPF presence (total and for five individual species), ACPF species richness and ACPF species abundance at a local scale (i.e., quadrat level) in terms of substrate, elevation and vegetation structural elements.

METHODS

Sampling design and data collection

To characterize lakeshore ACPF communities, I selected the ten provincially common and/or abundant ACPF herbaceous species from the 19 ACPF species previously selected (Introduction – Species, lake and site selection). Herbs characterize the majority of ACPF lakeshore communities and have similar habitat characteristics that might differ from other functional group of plants, such as woody ACPF species that also occur beyond the forest edge. Selected ACPF herb species were also more abundant and diverse along shorelines compared to shrub and graminoid species.

At each site, I located one 20 m transect perpendicular to the waterline with 0.2 m x 0.2 m contiguous quadrats. Between mid-June and mid-July 2015, I established the start of transects where vegetation emerged (approximately 1-2 m into the water at that time of the year) and extended them to at least 5 m beyond the forest edge. I subjectively located transects in areas with wider shorelines and the highest abundance/richness of ACPF species along the lakeshore-to-forest gradient.

I also used a two-dimensional sampling approach to capture the within-shoreline gradient and to obtain more data on ACPF habitat. From mid-August to the beginning of September 2015, I established 5 m x 5 m grids, divided into 0.2 m x 0.2 m contiguous quadrats. The lakeside edge of each grid was placed on the boundary of emergent vegetation (near the waterline at that time of the year), with the landward edge extending towards the forest edge. I centred the grids on the transect positions, except at the Se1 site where the shoreline was not straight enough to accommodate the grid. Five sites on different lakes were chosen to conduct the grid sampling (Figure 1-3). These sites were selected based on the transects with the highest ACPF richness and widest shorelines in order to maximize the number of quadrats with ACPF.

Within each quadrat, I visually estimated the cover of the ten selected lakeshore herb ACPF species and different vegetation elements (e.g., leaf and needle litter, bryophytes, sundews, twigs (diameter < 5 cm) and other woody material (debris), graminoids, ferns and deciduous/coniferous woody species at every 0.2 m height up to 2 m) using cover classes of < 5%, 6-25%, 26-50%, 51-75% and > 76%. I also assessed the main substrate using particle size classes for mineral soil: sand (0.005-0.2 cm), gravel (0.2-7.5 cm), cobble (7.6-25 cm), stone (26-60 cm) or boulders (> 60 cm) (Keys et al. 2010) (Figure 4-2a). When algae, leaf litter, organic soil or peat material covered the majority of the quadrat, the main substrate was characterized as organic (Figure 4-2b). I measured the difference in elevation (in cm) from the previous quadrat using a level and a ruler for each quadrat along the transects and at the middle line of the grid that was not at the same position as the transect (Se1) (Figure 4-3).

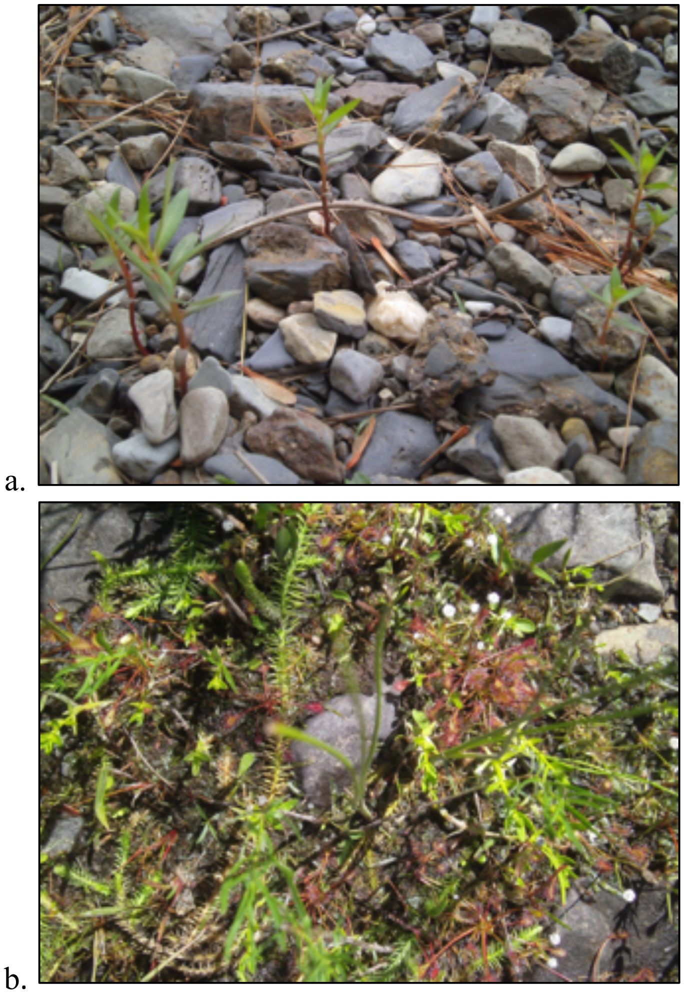


Figure 4-2. Pictures showing different substrates: (a) gravel/cobble and (b) organic (e.g., mostly algae, peat) substrate.

Figure 4-3. Picture showing fine scale elevation measurement with a level and a ruler along the lakeshore-to-forest gradient.

Data analysis

Landscape scale habitat characteristics

To address my first objective, which was to determine landscape scale habitat characteristics of lakeshore herbaceous ACPF species, I used the data from the transects. For each of the seven selected lakes, I calculated lake and tertiary watershed area using the Forest Inventory – Geographic Information Systems data (Nova Scotia Department of Natural Resources 2013). Some lakes were in the same watershed due to their physical proximity, such as Cameron and Ponhook Lake, as well as Hog and Molega Lake.

All ACPF/vegetation cover classes were first converted to their midpoint values of 3%, 16%, 38%, 63% and 88%. For each transect, I calculated the total number of selected ACPF species and the total cover of all selected ACPF species in all quadrats, respectively defined as ACPF richness and ACPF abundance. I calculated the distance from the beginning of the transect (from the waterline) to the last selected ACPF species individual, as well as the distance to the beginning of continuous woody species occurrence (i.e., first quadrat with > 3% cover of shrubs) for each transect, defined as ACPF zone width and distance to shrub, respectively. I also calculated the slope of the entire transect by dividing the difference in elevation between the first and last quadrat of the transect by the transect total length (i.e., 20 m). To determine if the shoreline was either mineral or organic (shoreline type), transects were considered mineral when > 50% of the quadrats on lakeshores were either sand, gravel or cobble, or organic when > 50% of the quadrats were dominated by organic matter (i.e., organic substrate).

As sample size (here n = 16) should be 10 times larger than the number of explanatory variables (Breiner et al. 2015), I performed 12 simple linear regressions (3 response variables x 4 explanatory variables) in R 3.2.2. (R Core Team 2015). Response variables were ACPF zone width (Gaussian distribution), ACPF richness (Gaussian distribution) and ACPF abundance (exponential distribution). I did a log transformation of ACPF abundance and used the Shapiro-Wilk test of normality to confirm the normality of the response variables. Gaussian distribution of errors is a critical assumption when performing linear regressions. Explanatory variables were watershed area, lake area, slope and distance to shrub. For all significant linear regressions, post hoc analysis using the Shapiro-Wilk test of normality indicated that residuals were normally distributed (p-value > 0.28). I also performed three t-tests to determine whether ACPF zone width, richness and abundance were significantly different between mineral and organic shorelines.

Local scale habitat characteristics

To address my second objective (to determine local scale habitat characteristics of lakeshore herbaceous ACPF species), I used the data from the grids with 2469 quadrats that supported ACPF (compared to 283 quadrats for the transect data). For each quadrat, I assigned the value of 1 to indicate ACPF presence and 0 for absence of ACPF. I calculated the total number of selected ACPF species and the total cover of all selected ACPF species for each quadrat, defined as ACPF richness and ACPF abundance respectively. I selected the five most common selected ACPF species (presence in > 500 quadrats) and assigned the value of 1 to indicate their presence and 0 for their absence in each quadrat. Along the middle line of each grid, I calculated the difference in elevation of each quadrat relative to the first quadrat (near the waterline). I calculated the sum of fern and deciduous/coniferous woody species cover at every 0.2 m height up to 2.0 m, defined as fern and shrub, respectively. I calculated the sum of twigs and other woody debris cover, defined as woody material, as well as the sum of needle and leaf litter cover, defined as litter.

In order to assess the effect and significance of each local habitat characteristic on lakeshore herbaceous ACPF, I performed spatial Generalized Linear Mixed Models (GLMMs) for eight response variables. I used the glmmPQL function from the package MASS (Venables and Ripley 2002) and nlme (Pinheiro et al. 2015) in R 3.2.2. (R Core Team 2015), as suggested by Dormann et al. (2007). Spatial GLMMs are based on penalized quasi-likelihood (PQL) and fit overall fixed (non-random) effects with linear predictors containing random effects (group errors) and spatially autocorrelated within-group errors (i.e., nested structure) (Dormann et al. 2007). This type of model accounts for site differences while assuming autocorrelation between observations from the same site. Spatial GLMMs are known as the most flexible method to address spatial autocorrelation for non-Gaussian error distributions (Dormann et al. 2007).

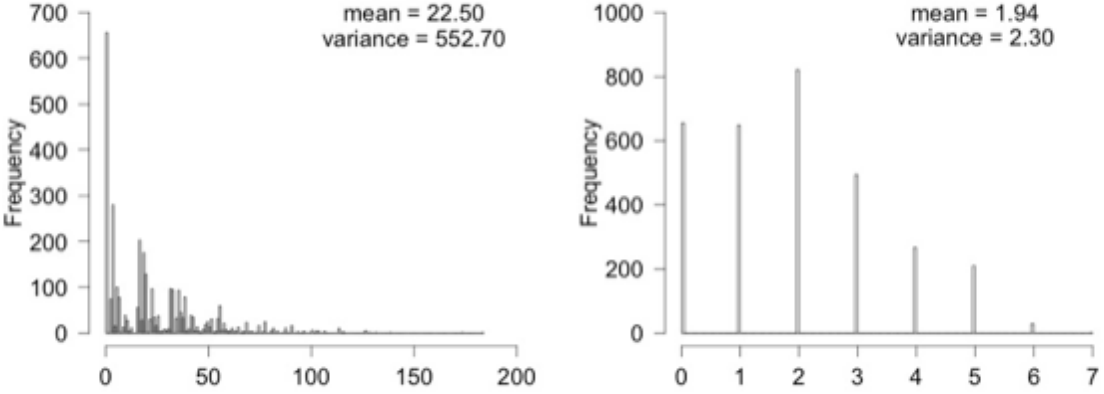
Because a nested structure resulted from the numerous quadrats included in one individual grid, the letter of the grid (a, b, c, d, e) was used as a random effect in the model to capture the correlation between quadrats from the same grid (Kassahun et al. 2014). Statistical analyses of data with nested structures, which are not considered, make biased predictions (Dormann et al. 2007). It is also probable that quadrats that are close together share similar attributes compared to ones farther apart, violating the assumption of error independence (Stephenson et al. 2006). Therefore, spatial dependence also needed to be incorporated in the model by indicating a spatial structure and including plot coordinates; otherwise unrealistically small standard errors and p-values could have been given (Stephenson et al. 2006). Similar to Stephenson et al. (2006), an exponential spatial correlation argument containing the quadrat x and y position within each grid was included in the model.

One important characteristic of rare species data is the excess proportion of zero values (i.e., zero inflated data), which often leads to over-dispersed data (i.e., variance > mean) and causes biased parameter estimates (Cunningham and Lindenmayer 2005; Potts and Elith 2006; Yesilova et al. 2010). The Poisson distribution is commonly used for species count data; however, it should only be used when the mean and variance are almost equal (Yesilova et al. 2010) or it will result in excessively optimistic conclusions about the significance of explanatory variables (Potts and Elith 2006). A negative binomial distribution could therefore be used to account for over-dispersion (Yesilova et al. 2010), as the variance is a multiple of the mean (Potts and Elith 2006). However, this distribution does not control for zero inflated data (Cunningham and Lindenmayer 2005) because the number of zero values is often exceeded under that distribution (Martin et al. 2005). This problem led to two-part modelling, such as the Hurdle model, where the first part consists of a binary model indicating presence (positive counts) and absence (zero counts), which controls for the zero inflation effect. The second part includes only positive counts (truncated at zero counts) under a Poisson or negative binomial distribution, accounting for the over-dispersion effect (Potts and Elith 2006). Therefore, the Hurdle model distinguishes the processes/mechanisms that determine the presence of a species from the ones that determine the abundance (e.g., number of individuals) once the species is present (Cunningham and Lindenmayer 2005; Potts and Elith 2006). According to Martin et al. (2005). Using methods that directly model the sources of zero observations such as the Hurdle model will increase the robustness of statistical analyses and improve ecological understanding.

Following the Hurdle model, I first performed the model with ACPF presence as the response variable (binomial distribution). Then I performed the model only for the presence of ACPF with ACPF abundance (negative binomial distribution, variance > mean, Figure 3-4) and afterwards with ACPF richness (Poisson distribution, variance ~ mean, Figure 3-4) as response variables. Histograms are shown in Figure 4-4 to visualize the proportion of zeroes and the over dispersion effect. I also executed the model with the presence of the five individual species (binomial distributions) as response variables for lakes where the species were present; the majority of studies on individual species distributions are only based on presence and absence data (Dormann et al. 2007). I used the following explanatory variables for all eight spatial GLMMs: substrate (categorical: sand, gravel, cobble, stone, boulder, organic), elevation and the cover of litter, woody material, shrubs, ferns, sundews, graminoids and bryophytes. Explanatory variables were checked for collinearity ($r < 0.6$) using the pair function. I also used grayscale diagrams to represent ACPF herb richness and the cover of the individual five species in each quadrat of each grid.

Positive and zero counts

a. b.



Positive counts

c. d.

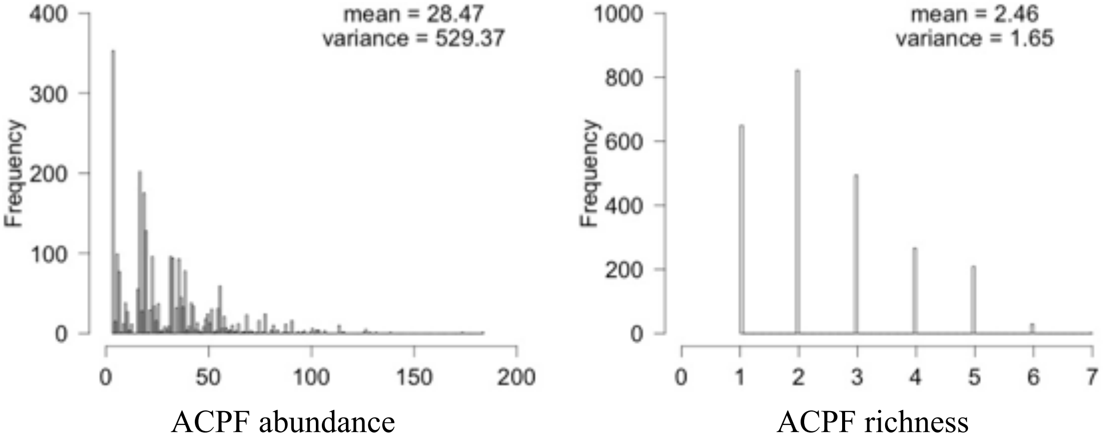


Figure 4-4. Histograms of ACPF abundance and richness according to positive and zero counts (n = 3125, a and b) and positive counts only (n = 2469, c and d), with the mean and variance for each.

RESULTS

I visually inspected the distribution of ACPF richness, ACPF abundance and shrub cover along the lakeshore-to-forest gradient. The objective was to visualize the data and to determine if there was a general trend (non statistically significant) by looking at the location of lower and/or higher values concentrations, indicated by the darker points on the graphs. Along the lakeshore-to-forest gradient, higher values of ACPF richness and abundance appeared to be found within the first half of the transect (i.e., between 0 and 10 m) (Figure 4-5a and b). Lower values of shrub cover seemed to be more concentrated at the beginning (i.e., waterline) and end (i.e., forest interior) of the transect (Figure 4-5c).

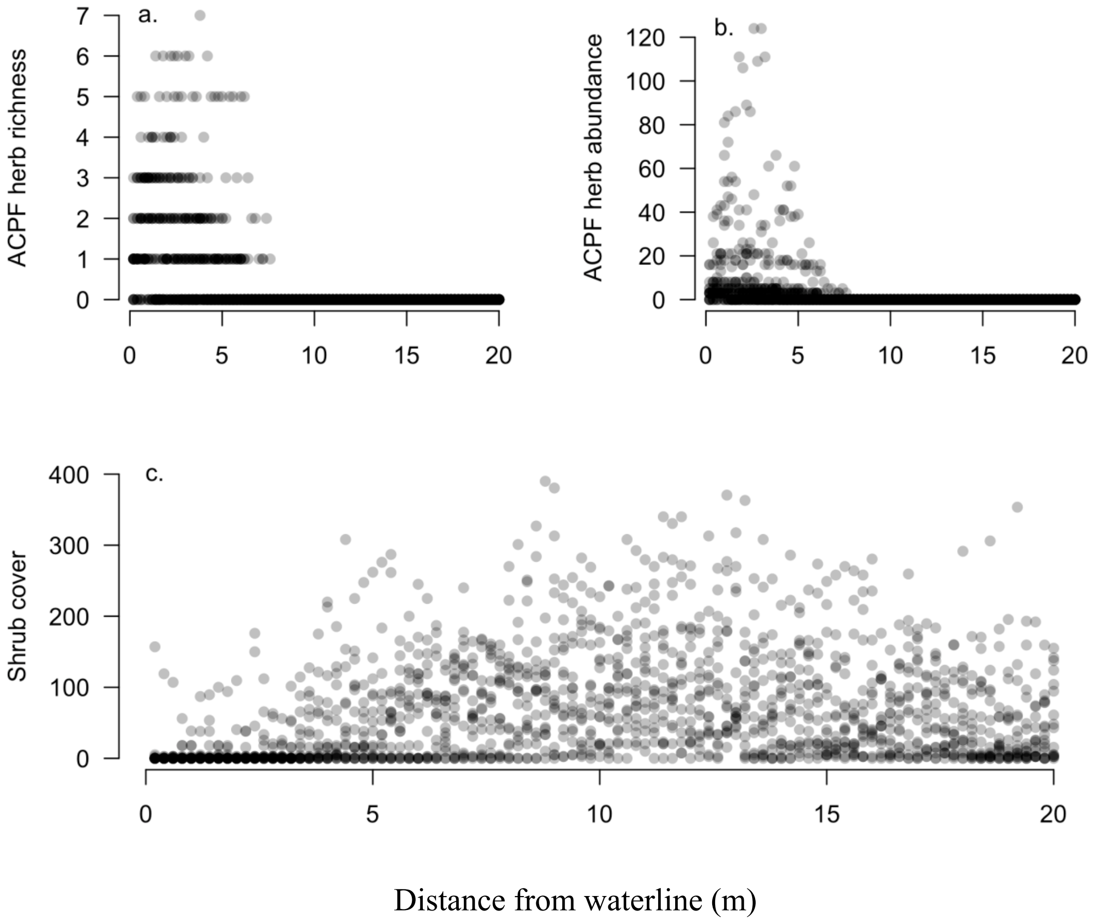


Figure 4-5. ACPF richness (# ACPF herb species per quadrat, a), ACPF abundance (sum of all ACPF herb species cover per quadrat, b) and shrub cover (sum of coniferous and deciduous woody species cover at each 0.2 m height up to 2 m per quadrat, c) along the lakeshore-to-forest gradient (n = 16 for each 0.2 m distance). Grey shading represents the intensity of superimposed data points.

Landscape scale habitat characteristics

Distance to shrub (from the waterline to the beginning of continuous woody species occurrence) explained the highest proportion of the variation in ACPF zone width; greater distance to shrub was significantly correlated with increased zone width of selected ACPF species (Table 4-1, Figure 4-6). Steeper slopes were significantly correlated with decreased ACPF zone width and explained the second highest proportion of ACPF zone width variation. Increased ACPF zone width was also significantly correlated with greater watershed area, explaining the smallest proportion of the variation in ACPF zone width of the significant explanatory variables. It is also important to mention that distance to shrub was not significantly correlated with watershed area (regression coefficient = 3.33×10^{-9}, p-value = 0.51, $R^2 = 0.031$) or transect slope (regression coefficient = -0.070, p-value = 0.50, $R^2 = 0.033$). No significant correlation was found between lake area and ACPF zone width and ACPF zone width did not differ between mineral and organic shorelines.

ACPF richness was significantly higher on mineral compared to organic shorelines (Table 4-1, Figure 4-6 j). No significant correlation was found between ACPF richness and watershed area, lake area, slope and distance to shrub. ACPF abundance was not significantly correlated with any explanatory variables (watershed area, lake area, slope, distance to shrub) and did not differ between shoreline types (mineral and organic).

Table 4-1. Regression coefficient, R^2, and *p-value (*bold if significant*)* for the 12 simple regression analysis between ACPF zone width, ACPF richness and log ACPF abundance, and four landscape scale habitat variables (watershed area, lake area, slope and distance to shrubs); and significance (with *p-values*) of the difference between mean values of ACPF zone width, ACPF richness and log ACPF abundance between mineral (M) and organic (O) shorelines from t-tests.

ACPF shoreline characteristics	Watershed area (ha)	Lake area (ha)	Slope (cm/m)	Distance to shrubs (m)	Shoreline type (M/O)
ACPF zone width	0.055 R^2 = 0.28 ***0.035***	0.00040 R^2 = 0.038 *0.47*	-0.18 R^2 = 0.33 ***0.020***	0.55 R^2 = 0.46 ***0.0038***	M = 4.8 O = 4.6 *0.85*
ACPF richness	-0.024 R^2 = 0.0034 *0.83*	-0.00085 R^2 = 0.14 *0.15*	-0.028 R^2 = 0.0066 *0.76*	0.18 R^2 = 0.040 *0.46*	M = 6.0 O = 3.7 ***0.024***
log ACPF abundance	0.0069 R^2 = 0.0021 *0.96*	-0.00014 R^2 = 0.038 *0.47*	-0.025 R^2 = 0.057 *0.37*	0.046 R^2 = 0.027 *0.55*	M = 2.3 O = 1.9 *0.24*

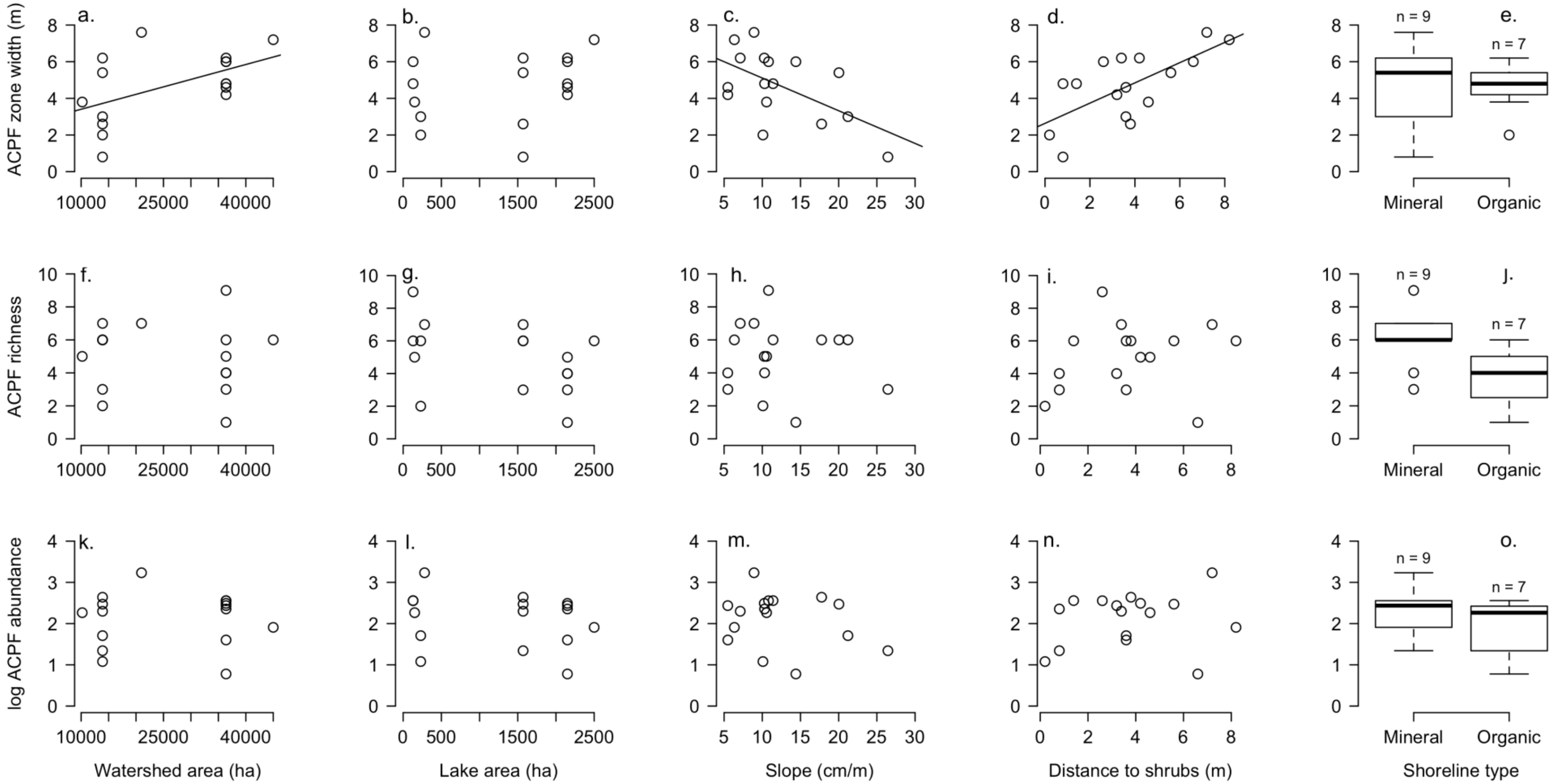


Figure 4-6. ACPF zone width (distance from the waterline to the last individual, a to e), richness (number of ACPF species, f to j), and abundance (log of total ACPF cover, k to o) in relation with five landscape scale habitat variables (watershed area, lake area, slope, distance to shrub and shoreline type) (n = 16). Regression lines are only shown if they were significant. Bold line of boxplots show mean values of ACPF zone width, richness and abundance according to shoreline type: mineral (n = 9) and organic (n = 7).

Local scale habitat characteristics

Lower elevation and shrub cover, as well as greater cover of sundew were significantly correlated with increased presence, abundance and richness of ACPF at the quadrat level (Table 4-2). Greater cover of graminoids was significantly correlated with increased ACPF presence as well as abundance, but had no significant correlation with ACPF richness. Quadrats with greater bryophyte cover were significantly correlated with increased ACPF abundance but were not significantly correlated with either the presence or the richness of ACPF. As substrate is a categorical variable, the model used the first category (in alphabetical order, here boulders) as a baseline to compare the effect of the other categories. Consequently, cobble, gravel and organic substrate were significantly correlated with increased presence and abundance of ACPF. Sand substrate was significantly correlated with increased ACPF abundance only, whereas stone substrate had no significant correlation with any response variables. No substrate was significantly correlated with ACPF richness. The cover of litter, woody material and fern did not have a significant correlation with the presence, abundance or richness of ACPF.

Table 4-2. Results from spatial Generalized Linear Mixed Models for ACPF presence, and ACPF abundance and richness only when ACPF were present. Estimates of regression coefficient ± standard error with *p-value* of each explanatory variable used in the model (n = 3125 for ACPF presence, n = 2469 for ACPF richness and abundance).

Variables	ACPF presence	ACPF abundance	ACPF richness
Elevation	-0.019 ± 0.004 ***< 0.0001***	-0.0084 ± 0.0023 ***0.00020***	-0.0094 ± 0.0014 ***< 0.0001***
Shrub	-0.0097 ± 0.0017 ***< 0.0001***	-0.0019 ± 0.0009 ***0.032***	-0.0011 ± 0.0005 ***0.039***
Sundew	0.10 ± 0.03 ***0.00010***	0.011 ± 0.003 ***0.0011***	0.0048 ± 0.0015 ***0.0016***
Graminoids	0.010 ± 0.000 ***0.0042***	0.0036 ± 0.0010 ***0.00030***	0.0010 ± 0.0006 *0.065*
Bryophytes	0.0084 ± 0.0057 *0.14*	0.0031 ± 0.0012 ***0.0090***	0.00099 ± 0.00061 *0.10*
Cobble	1.6 ± 0.4 ***0.00010***	0.44 ± 0.22 ***0.046***	0.19 ± 0.12 *0.13*
Gravel	1.7 ± 0.4 ***0.00010***	0.45 ± 0.22 ***0.041***	0.21 ± 0.12 *0.086*
Sand	0.69 ± 0.68 *0.31*	0.67 ± 0.29 ***0.023***	0.091 ± 0.152 *0.55*
Organic	1.8 ± 0.4 ***0.00010***	0.56 ± 0.22 ***0.012***	0.20 ± 0.12 *0.11*
Stone	0.62 ± 0.42 *0.15*	0.061 ± 0.231 *0.79*	0.059 ± 0.129 *0.65*
Litter	-0.0036 ± 0.0047 *0.45*	0.0024 ± 0.0016 *0.14*	0.0010 ± 0.0009 *0.25*
Woody material	-0.0011 ± 0.0064 *0.86*	-0.0023 ± 0.0021 *0.27*	0.00046 ± 0.00112 *0.68*
Fern	-0.011 ± 0.001 *0.26*	-0.00059 ± 0.00484 *0.90*	0.0015 ± 0.0024 *0.52*

Lower elevation was significantly correlated with increased presence of golden pert (*Gratiola lutea*), yellow-eyed grass (*Xyris difformis*) and redroot (*Lachnanthes caroliniana*), whereas lower shrub cover was significantly correlated with increased redroot, lance-leaved violet (*Viola lanceolata*) and slender fragrant goldenrod (*Euthamia caroliniana*) presence (Table 4-3). Quadrats with greater sundew cover were significantly correlated with increased presence of all species except redroot. Greater cover of graminoids and bryophytes were significantly correlated with increased lance-leaved violet and slender fragrant goldenrod presence, respectively. Cobble and gravel substrate were significantly correlated with increased presence of lance-leaved violet, yellow-eyed grass and redroot, whereas quadrats with organic substrate were significantly correlated with increased presence of lance-leaved violet and redroot. Sand and stone substrate were not significantly correlated with any species. The presence of golden pert and slender fragrant goldenrod was not significantly correlated with any substrate. The cover of litter, woody material and ferns did not have a significant correlation with any species.

Although only five sites were sampled, patterns of ACPF herb richness seemed to differ among sites; the highest richness zone appeared closer to the waterline compared to the forest edge. Regarding individual species, lance-leaved violet was very abundant and distributed along the upper part of the lakeshore gradient (Ponhook, Kejimkujik), or the lower part (Hog, Seven Mile, Cameron). The vegetation zone inhabited by lance-leaved violet was clearly delimited at the Cameron and Ponhook sites, compared to the Kejimkujik and Seven Mile sites where this inhabited zone was less clearly demarcated (Figure 4-7). Golden pert inhabited a conspicuous and well defined vegetation zone closer to the waterline, but showed a more dispersed distribution at the Kejimkujik site. Golden pert was also very abundant at some sites (Ponhook, Seven Mile), but less abundant at others (Cameron, Hog, Kejimkujik). Yellow-eyed grass was distributed along the lower boundary of the grid, and was either abundant (Kejimkujik, Seven Mile) or more dispersed (Cameron, Hog, Ponhook) within that zone. Slender fragrant goldenrod was present at four sites, with a high abundance and no particular zone (Hog, Seven Mile) or a low abundance with a localized zone (Kejimkujik, Cameron). Redroot was present at three sites, with three different patterns: very abundant covering almost the entire grid, very abundant within a clear zone at the lower boundary or very localized with a low abundance. Some species, such as slender fragrant goldenrod and redroot, had an uneven distribution along the lakeshore gradient (i.e., from the left to the right side of the grid).

Table 4-3. Results from spatial GLMMs for the presence of common ACPF species in grids where the species was present. Estimates of regression coefficient ± standard error with *p-values* are given for each explanatory variable used in the model (n = 3125 for lance-leaved violet, golden pert, and lakeshore yellow-eyed grass, n = 2500 for slender fragrant goldenrod, n = 1875 for redroot).

Variables	Lance-leaved violet	Golden pert	Yellow eyed grass	Slender fragrant goldenrod	Redroot
Elevation	0.00047 ± 0.0038 *0.90*	-0.11 ± 0.01 ***< 0.0001***	-0.068 ± 0.007 ***< 0.0001***	-0.0096 ± 0.0069 *0.17*	-0.043 ± 0.009 ***< 0.0001***
Shrub	-0.0048 ± 0.0016 ***0.0025***	-0.017 ± 0.013 *0.18*	-0.011 ± 0.006 *0.10*	-0.0048 ± 0.0021 ***0.024***	-0.0060 ± 0.0020 ***0.0029***
Sundew	0.038 ± 0.010 ***0.00010***	0.038 ± 0.020 ***0.051***	0.086 ± 0.014 ***< 0.0001***	0.033 ± 0.013 ***0.0096***	0.0098 ± 0.0122 *0.42*
Graminoids	0.0078 ± 0.0022 ***0.00050***	-0.00017 ± 0.00550 *0.98*	-0.0012 ± 0.0038 *0.74*	0.0042 ± 0.0035 *0.22*	0.0035 ± 0.0035 *0.32*
Bryophytes	-0.00068 ± 0.00278 *0.81*	0.0028 ± 0.0072 *0.70*	0.0052 ± 0.0052 *0.32*	0.0060 ± 0.0032 ***0.057***	0.0071 ± 0.0040 *0.080*
Cobble	1.1 ± 0.4 ***0.012***	1.4 ± 1.2 *0.23*	1.8 ± 0.9 ***0.041***	0.089 ± 0.532 *0.87*	1.2 ± 0.6 ***0.030***
Gravel	1.1 ± 0.4 ***0.0091***	1.6 ± 1.2 *0.17*	1.9 ± 0.9 ***0.032***	0.21 ± 0.54 *0.70*	1.1 ± 0.6 ***0.052***
Sand	0.66 ± 0.61 *0.28*	1.5 ± 1.4 *0.29*	0.85 ± 1.01 *0.40*	0.010 ± 0.720 *0.99*	-
Organic	0.98 ± 0.43 ***0.023***	1.7 ± 1.2 *0.15*	1.6 ± 0.9 *0.064*	0.36 ± 0.54 *0.50*	1.4 ± 0.6 ***0.0094***
Stone	0.54 ± 0.43 *0.22*	0.39 ± 1.20 *0.74*	1.4 ± 0.9 *0.13*	-0.27 ± 0.55 *0.62*	1.1 ± 0.6 *0.0621*
Litter	-0.0045 ± 0.0034 *0.19*	0.014 ± 0.011 *0.19*	-0.0031 ± 0.0074 *0.68*	0.0051 ± 0.0047 *0.28*	-0.0023 ± 0.0049 *0.64*
Woody material	0.0023 ± 0.0042 *0.59*	-0.027 ± 0.016 *0.11*	0.0073 ± 0.0092 *0.42*	-0.0079 ± 0.0058 *0.18*	0.0095 ± 0.0061 *0.12*
Fern	-0.0043 ± 0.0070 *0.54*	0.0028 ± 0.0299 *0.93*	0.023 ± 0.018 *0.20*	0.0041 ± 0.0117 *0.73*	0.0000087 ± 0.0105000 *1.0*

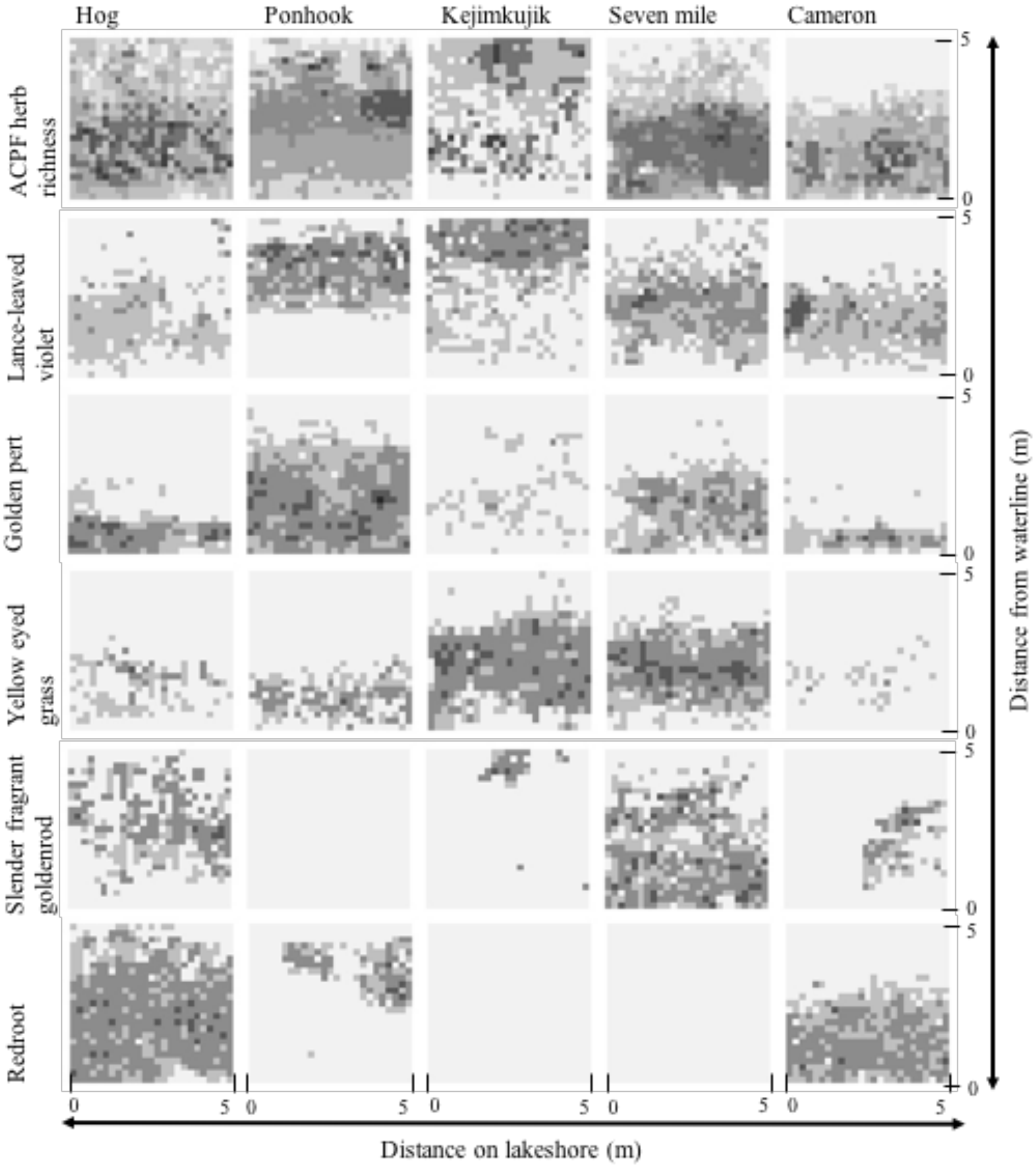


Figure 4-7. Gray scale diagrams showing the richness of ACP herbs and the cover of five common ACPF species within quadrats in the five grids. Darker quadrats represent higher richness or cover.

DISCUSSION

Landscape scale habitat characteristics

Although the effect of each landscape habitat variable might be interrelated, each significant linear regression will be discussed individually, as they were analyzed individually as a result of low sample size (n = 16). For example, watershed area and topography are known to influence water level fluctuations and the high waterline, which usually defines the distance to shrub. Furthermore, some landscape scale habitat characteristics might have shown a non-significant linear relationship as a result of interactions between different explanatory variables that were not included in the simple linear regression.

The width of the inhabited zone by ACPF on lakeshores was explained in part by watershed area. By controlling the amount of water that a lake will receive, watershed area influences water level fluctuations (Hill and Keddy 1992), which control the width of the riparian zone by defining the low waterline from decreased rainfall and increased evaporation during summer/fall, and the high waterline from winter/spring flood (Sorrie 1994; Morris et al. 2002). Consequently, these factors determine flooding conditions and suitable habitat for many ACPF herbs and other lakeshore plants among lakes. According to Hill and Keddy (1992), because watershed area is a constant variable influencing hydrological disturbances, it may be a better way to characterize these disturbances instead of the actual events that are more variable from year to year.

The amplitude of water level fluctuations and flooding conditions depends on watershed area (Holt et al. 1995), but also on shoreline slope (Morris et al. 2002). Steeper slopes result in a smaller area affected by hydrological disturbances (e.g., smaller riparian zone width), whereas a gentle slope would offer a larger area (e.g., larger riparian zone width) (Figure 4-8). Lakeshore slope also influences, in part, within-lake variation of ACPF by determining the zone of flooding conditions and the first occurrence of shrubs, consequently defining suitable habitat for many herbaceous ACPF species. This explains why transect slope was an important variable in explaining the variation in ACPF zone width. Therefore, lakes with greater watershed area experience higher water level fluctuations, along with gentle slopes that increase the area affected by those disturbances, would result in a larger width of riparian zone and habitat for herbaceous lakeshore ACPF species.

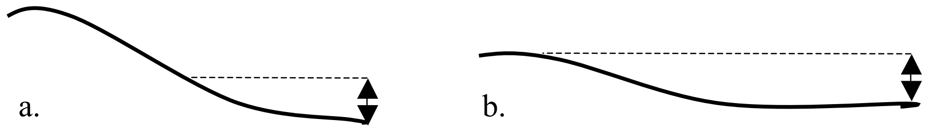


Figure 4-8. Diagram showing the amplitude (e.g., area affected) of water level fluctuations and flooding conditions according to (a) steeper and (b) gentle slope.

Distance to shrubs appears to be the most important factor explaining the distance that ACPF individuals will reach along the lakeshore-to-forest gradient (ACPF zone width). High waterline usually coincides with the first occurrence of shrubs and the limit of flooding conditions (Hill and Keddy 1992). As the amplitude of hydrological disturbances, including the degree of soil saturation and infertility, decreases along the lakeshore-to-forest gradient (Keddy 1984), suitable habitat is provided for competitive and stress-intolerant species such as shrubs and other woody species. ACPF are mostly found below that shrub zone (Wisheu et al. 1994), as woody species are highly competitive and are able to replace ACPF species on lakeshores (Wisheu and Keddy 1989).

ACPF richness was explained in part by the shoreline type, either mineral or organic. Organic shorelines have a higher organic matter content, indicated by the presence of litter, peat and a soil organic layer, compared to coarser substrates, such as cobble and gravel, on mineral shorelines. Because hydrological disturbances, and more specifically wave action, remove organic matter by washing out fine sediments and nutrients, shorelines with a higher organic matter content shows that the intensity of hydrological disturbance is relatively low (Wilson and Keddy 1986; Sorrie 1994; Holt et al. 1995). Higher soil fertility, resulting from lower levels of wave action, provides more nutrients to sustain competitive species and consequently creates suitable shorelines for woody species that have the ability to outcompete ACPF (Wisheu and Keddy 1989, 1994; Wilson and Keddy 1986). Organic shorelines can provide suitable habitat for some ACPF shrub species, such as swamp rose (*Rosa palustris*) and common buttonbush (*Cephalanthus occidentalis*), but are less suitable for most herbaceous lakeshore ACPF species, consequently reducing the richness (i.e., number) of ACPF species found on those shorelines. Although watershed area did not have a significant effect on ACPF richness in this study, it was previously related to ACPF richness (Hill and Keddy 1992), as well as to the presence of rare species in eastern Canada (Holt et al. 1995). Rare plant richness has been shown to have a strong relationship with the amplitude of water level fluctuations (Keddy 1985; Wisheu and Keddy 1994; Hill et al. 1998). Lakes with greater watershed areas experienced more hydrological disturbances reducing soil fertility, shrub establishment and competitive interactions, consequently promoting biodiversity and richness of lakeshore plant communities (Holt et al. 1995).

Within-lake variation of ACPF communities is mostly due to the level of exposure to wave action on shorelines (Keddy 1984), creating infertile soils and removing biomass, which are important habitat characteristics for the maintenance of many ACPF and other lakeshore plant communities that have poor competitive abilities. Morris et al. (2002) have stated that lake surface area influences wave action and Hill and Keddy (1992) also found that ACPF herb richness was positively correlated with lake area. Contrary to this, I found that lake area did not influence either the zone width and richness of ACPF. However, lake area alone might not carry sufficient information to quantify the wave action regime on shorelines. The perimeter:surface area ratio of the lake would indicate the level of sheltered bays and consequently the strength of possible wave action on shorelines (Wilson and Keddy 1986). The aspect of the shoreline could further indicate the level of exposure to dominant wind (Komonen 2009); ACPF have been found to be more abundant on windward shorelines (Wisheu et al. 1994; Morris et al. 2002). The level of exposure to wave and wind action on shorelines could also be influenced by the distance of open water to nearby land.

In my study, none of the landscape scale habitat characteristics was correlated with ACPF abundance at a shoreline level, suggesting that ACPF abundance might be more influenced by local scale habitat characteristics. This further highlights the importance of combining both landscape and local scale habitat characteristics to define ecological requirements of ACPF.

Local scale habitat characteristics

Low elevation had a strong correlation with the presence, richness and abundance of ACPF. As many ACPF species rely on hydrological disturbances, distance to water seems to be consequently an important factor to characterize the habitat of ACPF. However, as mentioned earlier, the amplitude of hydrological disturbances and the degree of flooding conditions also depends on the elevation, as shorelines with a gentle slope would offer a larger area influenced by disturbances, compared to steeper slope shorelines (Morris et al. 2002). Elevation influences numerous hydrological processes, such as the duration of flooding, the intensity and area affected by wave action and ice scouring, water depth, litter deposition and organic matter content (Day et al. 1988). Therefore, the proximity to hydrological disturbances depends more on the difference in height above the water, compared to the distance to water. In other words, for a given distance to water position, it is the elevation of that position that will determine if it is suitable or not for ACPF, making relative elevation an important habitat characteristic for ACPF.

The presence of shrubs is commonly known as a major biotic control on understory plant and herbaceous communities (Pabst and Spies 1998; Dale 1999). More specifically, shrub height and cover can explain herb diversity within plant communities (McElhinny et al. 2005); lakeshore plant diversity is higher in the absence of shrubs (Holt et al. 1995). Long submersion periods prevent the establishment of woody species (Rhazi et al. 2006), where the high waterline indicates less saturated conditions and marks the presence of shrubs (Hill and Keddy 1992). Shrubs have been previously shown to outcompete and exclude ACPF on shorelines (Wisheu and Keddy 1989). The absence of shrubs is consequently an important habitat characteristic of many herbaceous ACPF species, shown by an increased presence, abundance and richness of ACPF correlated with low cover of shrubs at different heights.

Greater cover of sundews is an important habitat characteristic for many ACPF species at a local scale, as it was correlated with increased presence, abundance and richness of herbaceous lakeshore ACPF. Sundews are known to share habitat types with ACPF, as they exhibit the same evolutionary strategy as stress-tolerant species (Wilson and Keddy 1986). They have adapted to these low fertility ecosystems by obtaining their nutrients from an external source such as insects and are known as indicator of infertile soil (Wilson and Keddy 1986; Wisheu and Keddy 1989, 1994; Wisheu et al. 1994).

Greater cover of graminoids is another important factor for ACPF habitat suitability, shown by increased presence and abundance of ACPF. Hydrological disturbances on lakeshores create areas free of competitive species that are suitable for numerous stress tolerant species outside of ACPF. Ice scouring and wave action are also known to carry seeds and seedlings which contribute to high plant diversity on lakeshores, including sedges and other graminoids (Naiman et al. 1988). In Nova Scotia, numerous graminoids species, such as panic grasses, sedges, rushes and bulrushes, are found on sandy lakeshores, and consequently share habitat with many herbaceous ACPF species (Sweeney and Ogilvie 1993).

Bryophytes, such as mosses and liverworts, are usually found in moist environments as they don’t have vascular tissue to ensure the transport of water through the plant. Several species of mosses are associated with ACPF communities (Environment Canada and Park Canada 2010). Greater cover of bryophytes is an important habitat characteristic of ACPF, as it was correlated with increased abundance of ACPF at a local scale. Sundews, graminoids and bryophytes could potentially be used as indicators of disturbed shorelines with infertile, diverse plant communities and flooded conditions, which consequently indicate suitable habitat for many herbaceous ACPF species.

Substrate is a critical determinant of plant communities (Ibanez et al. 2014) and is also known as a common predictor of vegetation diversity by characterizing plant niches (Lundholm 2009). By having a strong influence on germination, substrate governs species composition (Moore and Keddy 1988). Many herbaceous ACPF species inhabit hydrologically disturbed areas, which reflect the particle size composition of the substrate (Holt et al. 1995). A finer substrate indicates low wave action and results in a greater accumulation of organic matter that can support the high nutrient demand of competitive species, which outcompete ACPF (Wisheu and Keddy 1994). Therefore, lakeshores with higher levels of wave action, such as most shorelines that support herbaceous ACPF species, are usually shaped by coarser substrates as a result of wave action that removes fine particles of sediments and nutrients (e.g., silt, clay) from the soil (Keddy 1985; Wisheu et al. 1994). Many ACPF communities have been shown to mostly occur on sand or gravel shorelines with some peat patches, mostly from ice scouring (Keddy and Sharp 1994). Similarly, I found that substrates such as cobble, gravel, sand and organic (e.g., peat) are important habitat characteristics of ACPF habitat suitability as they enhance the presence and abundance of ACPF. In general, intermediate-sized substrates such as cobble and gravel were preferred compared to large-sized substrates, like stone and boulder. ACPF inhabit areas with diverse substrates, such as boulder, gravel, sand and peat, where preferred substrate type greatly varies depending on the species (Sweeney and Ogilvie 1993).

Substrate was not an important factor in explaining the total number of ACPF species (i.e., richness) at a local scale, although it might influence ACPF species composition. As the richness of ACPF at a local scale was only correlated with low elevation position, low shrub cover and greater cover of sundews, ACPF richness seemed to be mostly influenced by the overall shoreline type at the landscape scale (i.e., mineral or organic shorelines), with less importance accorded to local scale habitat characteristics compared to ACPF presence and abundance. Alternatively, landscape scale habitat characteristics did not seem to influence ACPF abundance on shorelines, but ACPF abundance at a local scale had the highest number of significant local scale habitat characteristics compared to ACPF presence and richness.

The cover of litter and woody material were not important factors for explaining the presence, abundance and richness of ACPF. Hydrological disturbances are known to remove plant material, litter and organic matter from lakeshores (Holt et al. 1995). Litter removal has been previously used to quantify hydrological disturbances on shorelines (Day et al. 1988). However, flooding and ice scouring generates physical heterogeneity from the erosion and deposition of litter and organic matter in riparian zones, creating patches of various substrate (Naiman and Décamps 1997). Also, storm and other meteorological events can depose large amounts of litter and plant material on lakeshores in a very short time period. Therefore, the cover of litter and woody material on lakeshores might be too variable to have a significant effect on ACPF communities, and consequently could not be considered as important habitat characteristics for herbaceous

ACPF species. Ferns were not commonly found on lakeshores, which explains why fern cover did not have a significant correlation with the presence, abundance and richness of ACPF.

Elevation was not an important habitat characteristic for lance-leaved violet as this species appeared to be distributed either near the waterline or the forest edge. Its presence was associated with both graminoids and sundews, and was displaced by shrubs. Cobble, gravel and organic substrates were preferred for lance-leaved violet. Because golden pert and yellow eyed grass were commonly found in the water or near the waterline, low elevation was an important habitat characteristic for these species. Sundew was the only vegetation element associated with their presence, suggesting that elevation has a critical role in their distribution compared to vegetation elements. Even shrubs were not correlated with the presence of those species, probably because shrubs were very rarely found in the water. Substrate was not important for golden pert; however, cobble and gravel were preferred substrates for yellow eyed grass. Slender fragrant goldenrod had an apparent random distribution on lakeshores, resulting in the lack of importance of elevation as a habitat characteristic for this species. Habitat characteristics of this species only included vegetation elements; its presence was associated with a greater cover of bryophytes and sundews, but avoided shrubs. Low elevation and shrub cover were important habitat characteristics of redroot, as this species was mostly found closer to the water. Different substrates were also correlated with redroot; cobble, gravel and organic substrate were preferred habitat characteristics.

By studying those five individual species, four different patterns of habitat requirements emerged. All patterns included surrounding vegetation elements, indicating their importance in characterizing species habitat. The presence of some species (yellow eyed grass and redroot) depended on elevation, vegetation, as well as substrate. The presence of other species, such as lance-leaved violet, was correlated with substrate and vegetation; however, golden pert presence depended on elevation and vegetation. Finally, the presence of some species (slender fragrant goldenrod) only depended on vegetation elements. These patterns suggest differences in preferred habitat for individual species and that some species were related to more habitat characteristics compared to others, highlighting the importance of studying individual species as well as communities as a whole.

CONCLUSION

In my study, landscape scale habitat characteristics appeared to be very important in determining the width of riparian zone and consequently the quantity of suitable habitat for lakeshore herbaceous ACPF species, but also the overall shoreline ACPF species richness. Local scale habitat characteristics seemed to be more important in determining the abundance of ACPF in comparison to landscape scale habitat characteristics. Landscape scale habitat requirements can be related to the richness and in some case the abundance of ACPF communities. First, the watershed area has to be large enough to create hydrological disturbances on lakes, mostly through higher water level fluctuations. Second, the shoreline slope needs to be gentle enough to support a wider flooded area influenced by those disturbances, which also leads to greater distance to shrubs. Third, shorelines also need to be exposed to a sufficient level of wave activity, leading to a mineral, infertile and coarser substrate, to sustain richer ACPF communities.

None of the landscape scale habitat requirements influenced the abundance of ACPF at a shoreline level, suggesting the importance of local scale habitat requirements in characterizing the abundance of ACPF, but also the presence and richness of ACPF at a local scale, along with landscape scale habitat requirements.

The importance and influence of local scale habitat characteristics have not been extensively quantified and related to ACPF communities. In my study, a variety of local scale habitat requirements were correlated with the presence, abundance and richness of ACPF in different ways. In general, low elevation positions and shrub cover, as well as intermediate substrate particle sizes (cobble, gravel, sand) with some peat material were important habitat characteristics for ACPF. Other groups of plants also shared lakeshores with ACPF, such as sundews, graminoids and bryophytes. Greater cover of these plants were associated with increased occurrence of ACPF, suggesting that they could be used as indicators of suitable habitat for many herbaceous ACPF species. Only sundews have been previously mentioned as an indicator of suitable habitat for ACPF.

It is important to determine habitat requirements of ACPF as a group, but also to characterize the habitat of individual species as difference in habitat requirements should occur. Habitat characteristics of individual ACPF species have been previously defined, however the focus was mostly on species at risk and not on common ACPF species. Common ACPF species should not be disregarded as they could be used as diagnostics of ACPF communities and habitat that might also support endangered or rare ACPF species. Individual ACPF species were correlated with different habitat characteristics, which might be due to the specific positions that they inhabit on lakeshores. The distributions of certain species varied along the lakeshores, confirming the presence of a within-lakeshore gradient in addition to the lakeshore-to-forest gradient. Some species also seemed to strongly depend on elevation, whereas other species were correlated with vegetation elements and/or substrate regardless of elevation.

Within their range and habitat, species are related to different abiotic and biotic environmental factors occurring at many scales (Bellamy et al. 2013). Therefore, it is essential to define ecological requirements at both landscape and local scales in order to appropriately preserve ACPF habitat. This will benefit not only individual species but also plant communities and ecosystems, as well as associated ecological processes (Franklin 1993; Tews et al. 2004).

CHAPTER 5 – CONCLUSION

STRUCTURAL DIVERSITY AS A HABITAT INDICATOR

Vegetation structure is an important component of habitat variability (Chen et al. 1996) underscoring the importance of improved knowledge on structural diversity and its role in the development of more appropriate conservation measures for plant species, such as Atlantic Coastal Plain Flora (ACPF) (Pabst and Spies 1998; Ibanez et al. 2014). Structural diversity, defined as the number and types of structural elements, can be used as an index of vegetation complexity and provide essential information on plant communities and associated ecological processes (Dodonov 2015). Species' relationships with structural diversity and other habitat characteristics should be defined at relevant scales, where keystone structures reflect habitat requirements of the species of interest (Noss 1990; Tews et al. 2004; Estes et al. 2010).

Major findings from Chapter 3 indicated that the width of the zone inhabited by ACPF communities on lakeshores was restricted by higher levels of structural diversity. ACPF richness was positively associated with structural diversity on lakeshores where low levels of structural diversity were found, and became negatively associated near the forest edge (Table 5-1). The level of structural diversity could potentially serve as an indicator for the intensity of hydrological disturbances and soil infertility, and consequently the intensity of competition, which determines the suitability of lakeshore habitat for many herbaceous ACPF species. Disturbed lakeshores usually have nutrient poor substrates and consequently support low plant biomass leading to low levels of structural diversity, which promotes the establishment of many ACPF species that are known to have weak competitive abilities and can be excluded by competitors on lakeshores.

For the identification of shorelines with potential ACPF habitat, overall low levels of structural diversity along the lakeshore-to-forest gradient (e.g., low woody species cover, smaller sized shrubs), but high structural diversity on lakeshores (e.g., a variety of substrate materials and life forms including graminoids, litter, algae, bryophytes, sundews, woody material), could be used as an indicator of suitability. For example, structural diversity would be a tangible criterion for land owners and managers to quickly identify suitable ACPF habitat. The majority of ACPF habitat is on privately owned land because of the popularity of cottage development around ACPF lakes in southwestern Nova Scotia. I also found that different functional groups of plants were positively associated with ACPF, such as sundews, graminoids and bryophytes, or negatively associated, such as woody species. However, land owners might not be able to recognize these different groups of plant, whereas low and high levels of structural diversity (e.g., bare vs dense vegetation) could be easier to assess for the majority of the public.

For the management and restoration of ACPF habitat, simply reducing higher levels of structural diversity (e.g., by removing woody species and cutting taller plants) would allow patches of ACPF to expand or spread to new shorelines. The amount of ACPF habitat (e.g., lakeshore width) could also be manipulated by increasing the distance from the waterline to higher levels of structural diversity (usually found at the forest edge) creating larger areas with low structural diversity that are suitable for ACPF. Using structural diversity as a tool to identify, manage and restore ACPF habitat will improve the conservation and maintenance of their populations in Nova Scotia.

Table 5-1. Positive (+) or negative (-) relationships between ACPF and structural diversity indices at lakeshore and forest (including the forest edge) positions along study transects.

Indices	Lakeshore	Forest
Structural diversity	+	-
Substrate diversity	+	-
Plant diversity	+	-
Shrub diversity	-	-

Layers of foliage, canopy gaps, variation in diameter at breast height (DBH), dead wood, tree height and density have been previously used to characterize microhabitat diversity and ecosystem services (McElhinny et al. 2005). Structural diversity has typically been measured as the diversity, variance or standard deviation of tree size classes (Staudhammer and LeMay 2001; McElhinny et al. 2005; McRoberts et al. 2008; Valbuena et al. 2012), but has not normally included other structural components (e.g., vegetation other than trees). In this study, I included a variety of structural elements and functional groups of plants at ground and above ground level to better represent the entire complexity of the vegetation. Structural diversity has also already been related to species diversity (Tilman 1982; McIntire and Fajardo 2013), but has never been related to ACPF communities. According to Hill et al. (1998) and Morris et al. (2002), understanding the relationship between disturbance regimes and diversity or structural patterns will help to protect ACPF communities.

My study provides insights on how to characterize structural diversity and assess its influence at different scales and locations along an environmental gradient, with the main goal of using structural diversity as an indicator of habitat suitability for conservation purposes. A review of the scientific literature indicates that structural diversity has not been applied to characterize and identify potential ACPF habitat in conservation or species at risk recovery plans. The method that I have developed for ACPF could be used for other species at risk and be expanded to measure the success or relevance of biodiversity management practices (Lindenmayer et al. 2000).

IMPLICATIONS OF HABITAT CHARACTERISTICS FOR THE CONSERVATION OF ATLANTIC COASTAL PLAIN FLORA

Habitat management is an essential component for the long term protection and conservation of ACPF populations (Wisheu and Keddy 1989). The amplitude of hydrological disturbances, such as ice scouring and wave action, are essential for transporting soil, seeds and plants, which improve colonization of nearby shorelines and create new ACPF occurrences/populations (Day et al. 1988; Sweeney and Ogilvie 1993; Hill et al. 1998). Furthermore, as ACPF individuals move frequently due to among-year and within-year variability in hydrological disturbances, potential habitats are essential for the persistence of ACPF communities in Nova Scotia.

Identifying habitat where ACPF are not currently present, is an existing knowledge gap that, if filled, will improve conservation efforts on several fronts (Alain Belliveau, personal communication). It will help create specific maps of critical (occupied and unoccupied) habitat, which could be shared with municipal planners and private landowners (Megan Crowley, personal communication). Habitat characteristics of many ACPF species overlap with high-use recreational areas; lakeshore development is a common and increasing occurrence on ACPF lakes (i.e., 353% increase in 55 years, Environment Canada and Parks Canada Agency 2010), and may be the biggest threat to ACPF in Nova Scotia (Alain Belliveau, personal communication). Many suitable shorelines for ACPF are on small private landholdings making land tenure the greatest barrier to the protection of ACPF habitat, where the participation of landowners is the key to overcome that barrier in the longer term (Sweeney and Ogilvie 1993; Wisheu et al. 1994). Defining the specific habitat characteristics where ACPF are actually found and determining the significance of their impact on ACPF (either positive or negative) allows concerned members of the public, government and conservation groups to better understand and identify potential ACPF habitat in order to protect, manage and restore it.

Although I did not directly link edaphic characteristics to ACPF in Chapter 2, I quantified these characteristics along the lakeshore and beyond the forest edge. As many ACPF species inhabit lakeshores, predictions could be made regarding the edaphic properties of ACPF habitat. Compared to the forest, main edaphic properties of lakeshores included a thinner organic layer and a higher relative content of sand, which indicate disturbed (e.g., higher levels of wave action) shorelines and a lower chroma of the mineral matrix, which indicates saturated conditions (Table 5-2). These three characteristics suggest the presence of wetland soil on lakeshores and upland soil beyond the forest edge, which could therefore be used as indicators of possible suitable habitat for many herbaceous ACPF species. The pH did not differ between the lakeshore and the forest, suggesting that it would not be a good criterion of lakeshore habitat.

Table 5-2. Highest (+) or lowest (-) values of edaphic characteristics according to lakeshore and forest (including the forest edge) position along the transect. Blank spaces indicate that there was no apparent change in pH between the lakeshore and forest.

Edaphic characteristics	Lakeshore	Forest
pH		
Organic layer thickness (cm)	-	+
Matrix % sand	+	-
Matrix chroma	-	+

In Chapter 4, I assessed the association of specific habitat characteristics with ACPF at landscape and local scales within sites that are known to support abundant ACPF. These characteristics can be used to identify suitable shorelines that are either occupied or not occupied by ACPF. In order to protect potential habitat for the maintenance of ACPF populations, the first step would be to determine which lakes have a watershed area that is large enough to support hydrological disturbances that are sufficient to create wider shorelines and restrict the establishment of competitive and woody species; this mainly occurs through flooding and changes to soil fertility (Table 5-3). Some lakes, such as Kejimkujik and Ponhook in Nova Scotia, have already been highlighted by Wisheu and Keddy (1989), and 34 other lakes were defined as high priority lakes by Environment Canada and Parks Canada Agency (2015).

An additional measure would be to identify windward shorelines, which are more exposed to wave and wind action, both of which remove organic matter and restrict the establishment of competitive species, creating mineral shorelines that will support a higher number of ACPF species (Table 5-3). Finally, selecting gentle slopes and prioritizing the conservation of shorelines where the continuous occurrence of shrubs is far from the waterline, indicating the zone affected by hydrological disturbances such as flooding conditions, will provide a larger area of suitable habitat for ACPF.

In my study, none of the landscape scale habitat characteristics influenced the abundance of ACPF at a shoreline level, highlighting the importance of combining both landscape and local scale habitat characteristics to appropriately define ecological requirements of ACPF. Landscape scale habitat characteristics seemed to be more important in determining the quantity of ACPF habitat along with the overall shoreline species richness (and probably species composition), whereas local scale habitat characteristics were mostly linked to ACPF abundance.

Table 5-3. Positive (+) or negative (-) significant correlation between landscape scale habitat characteristics and ACPF zone width, richness and abundance. Blank spaces indicate that there was no significant correlation between the two variables.

Landscape scale habitat characteristics	ACPF zone width	ACPF richness	ACPF abundance
Watershed area	+		
Lake area			
Slope	-		
Distance to shrubs	+		
Mineral shoreline		+	

Local scale habitat characteristics can be used to further refine the selection of potential shorelines for the protection, maintenance and growth of ACPF populations. Following the landscape scale selection of shorelines, the protection of gravel and cobble shorelines should be prioritized. Shorelines with organic material patches (e.g., litter, peat, organic matter) on the soil surface and sand substrate could also be selected;

however, coarser substrates such as stone and boulders should be disregarded (Table 5-4). The presence of graminoids, bryophytes and sundews can be used as indicators of suitable habitat for many lakeshore herbaceous ACPF species, with a preference for shorelines with the lowest abundance of shrubs. Finally, the protection of low elevation slope positions should be a conservation priority.

Table 5-4. Positive (+) or negative (-) significant correlation between local scale habitat characteristics and the presence, richness and abundance of ACPF, as well as the presence of five common species. Blank spaces indicate that there was no significant correlation between the two variables.

Local scale habitat characteristics	ACPF presence	ACPF abundance	ACPF richness	Violet	Golden pert	Yellow eyed	Goldenrod	Redroot
Elevation	-	-	-		-	-		-
Shrub	-	-	-	-			-	-
Sundew	+	+	+	+	+	+	+	
Graminoids	+	+		+				
Bryophytes		+					+	
Cobble	+	+		+		+		+
Gravel	+	+		+		+		+
Sand		+						
Organic	+	+		+				+
Stone								
Litter								
Woody material								
Fern								

To restore or maintain habitat for ACPF, local scale habitat characteristics could specifically be used by conservation organizations and private land owners. Landscape scale habitat characteristics are more difficult to control or to act on as they mostly rely on climatic events (e.g., rain fall, drought, wind intensity) and land use patterns (e.g., housing, agriculture, damming). Creating the specific conditions which develop from natural hydrological disturbance regimes, such as the restriction of shrub growth and low soil fertility, will allow ACPF to colonize new shorelines previously defined as unsuitable. Removing/reducing organic material at a shoreline level will reduce soil fertility and consequently provide an insufficient level of nutrients for the establishment and survival of competitive species, although leaving patches of peat and organic material will create substrate heterogeneity and provide diverse niches for ACPF. Afterwards, the original substrate could be kept, as ACPF are found on a variety of substrates from organic to cobble. However, coarser substrates such as boulders or stones should be removed to facilitate germination from the seedbank. Sundews, graminoids and bryophytes are common groups of plant found on lakeshores and will eventually colonize the restored shorelines along with ACPF. ACPF were positively associated with structural diversity, but only within a zone of low structural diversity; consequently, promoting heavily vegetated shorelines will restrict the establishment of ACPF communities. As woody species are the biggest obstacles to ACPF colonization, trimming shrubs and young trees is the key for shoreline restoration. Removing and uprooting shrubs could leave shorelines more prone to erosion with a reduction in nutrient uptake, both of which could have a negative impact on the eutrophication of lakes and ACPF populations. As the shoreline topography should not be manipulated, prioritizing habitat restoration at low elevation positions would provide a larger area for the establishment of ACPF.

STUDY LIMITATIONS

The majority of herbaceous ACPF species had not yet emerged at the time of the soil sampling, resulting in the survey of soil and ACPF transects that were not at the same position along the shoreline (see Chapter 2 for more information). Consequently, measured edaphic properties could not be directly related to ACPF communities along the lakeshore-to-forest gradient. Thus I was only able to characterize soil properties at a broad site level and define their variation along the lakeshore-to-forest gradient. Ideally, I would also have assessed the effect and significance of these soil properties on ACPF communities by including them as explanatory variables in the spatial GLMMs developed for the study.

For my study, I selected a limited number of ACPF species; ideally, I would have included and recorded the cover of every ACPF species encountered during the sampling of the quadrats. As I had never been in contact with those species before fieldwork and as they were only present from mid-July as seedlings to mid-September as flowering individuals, recognizing and identifying more than 90 species was unrealistic. Consequently, I selected a subset of abundant or common species that were found together to gain enough information to characterize habitat requirements of ACPF lakeshore communities as a whole. It is important to note that selecting only common species might limit the application of my results to rare or uncommon species; however, ACPF species share similar habitats and ecological requirements, forming assemblages of numerous ACPF species.

I defined the habitat characteristics of ACPF lakeshore communities on shorelines where they were present during the growing season in 2015, which coincides with my period of survey – June 18 to September 4, 2015. Many ACPF plants and patches are known to change location frequently and are somewhat ephemeral (i.e., not consistently present in previously occupied habitat locations), mostly as a result of hydrological disturbances that vary greatly among and within-years. For example, the intensity of ice scouring allows the transportation of mats of plants and soil to nearby shorelines, whereas water level fluctuations promote or discourage the germination of different species in the seed bank (Sorrie 1994). Therefore, ecological studies on ACPF communities should ideally be conducted over numerous growing seasons to appropriately define their habitat requirements (Rawinski and Price 1994).

Numerous limitations arose from my study sampling design that was somewhat subjective. First, sites were selected with one major criterion, which was to be located within an ACPF hot spot. The main reason for that is that ACPF are associated with specific habitats, leading to relatively rare occurrence (e.g., only fifty watersheds support ACPF in Nova Scotia). To evaluate the spatial pattern of ACPF and their spatial relationships with structural diversity, ACPF presence within sites was crucial, especially within a limited sampling period and ACPF growing season (e.g., only low water levels). Furthermore, in order to performed models with numerous explanatory variables, having enough data on ACPF but also for individual species was needed. This also means that I selected sites that had similar characteristics, such as similar aspect and richness of

ACPF, although I sampled sites with different slopes as well as mineral and organic shorelines, which could limit the inferences of my results to specific habitat types. The disadvantage of that sampling design is that I could not define the characteristics that makes a habitat unsuitable and consequently could not define the absolute habitat requirements of ACPF. Sampling a variety of habitats as well as shorelines with the presence (i.e., occupied) and absence (i.e., unoccupied) of ACPF could have provided broader inferences and results applications. However, it is important to note that ACPF have an irregular occurrence due to the variability in hydrological disturbances that are highly linked with ACPF, making it hard to distinguish suitable occupied habitat from suitable but unoccupied habitat. Such false absences could bias model predictions. Consequently, this sampling design was still relevant, especially for rare or poorly understood species such as many ACPF species, as it helped to define what was and was not associated with ACPF within ACPF hot spots and characterize habitat with higher levels of suitability.

As a result of this sampling design, the number of sites for each lake consequently depended on the number of ACPF hot spot zones. For example, if Seven Mile lake supported one ACPF hot spot (according to Alain Belliveau from Atlantic Canada Conservation Data Center), I only selected this site, regardless of the size of the lake size. Larger lakes generally had more sites with the exception of Kejimkujik lake that only had one site as soil sampling was not allowed. This led to different number of transects per lake and consequently an uneven sampling of lakes, which could limit the application of my results to specific lakes only by shifting the results towards the most sampled lakes. Sampling a higher number of lakes in a more even way would have provided broader inferences, although ACPF are known to inhabit specific habitats within and between lakes.

SIGNIFICANCE AND NOVELTY OF THE STUDY

The use of spatial pattern analysis, and more specifically wavelet analysis, has never been documented in the scientific literature to characterize ACPF richness, including the range of individual ACPF species (i.e., zonation). By conducting spatial pattern analysis, I was able to locate important breaks in patterns of herbaceous ACPF richness, and patches of individual species along the lakeshore-to-forest gradient. This type of information will help to define the specific distribution of ACPF on lakeshores and consequently the location of suitable habitat. Spatial pattern can also be related to underlying ecological processes and requirements (McIntire and Fajardo 2009). Furthermore, other studies on ACPF have only focused on the within lakeshore gradient and not normally included the lakeshore-to-forest gradient (i.e., they disregarded the forest edge). However, forest edges could have a direct effect on ACPF communities; decreased pollination activities on lakeshores might result from the degradation of the shrub zone, affecting pollinators' overwintering and nesting behavior (Environment Canada and Parks Canada Agency 2010).

From the scientific literature, habitat indicators including numerous variables (only sundew is known as an ACPF habitat indicator) such as structural diversity indices, have never been related to ACPF communities. Indicators are increasingly recognized as surrogates for habitat suitability, where they can be used to help in the identification of potential ACPF habitat. I showed that the association of habitat suitability indices varies according to the scale and the position along an environmental gradient. The relationship between ACPF richness and structural diversity was positive at finer scales and on lakeshores, but negative at coarser scales and beyond the forest edge. Therefore, it is essential to assess habitat requirements at different scales and positions in order to first define the range of habitat characteristics, and then to assess the occurrence of different relationships with those characteristics. This is especially relevant when studying species, such as ACPF, that are found in dynamic ecosystems and along a complex gradient of stress and disturbances.

It is increasingly known that ecological understanding must address multiple scales (Bellamy et al. 2013). Landscape scale habitat characteristics have been commonly related to ACPF; however, local scale habitat characteristics have rarely been studied. In previous studies (e.g., Hill et al. 1998; Morris et al. 2002), ACPF richness and abundance at the shoreline level have been related to landscape scale habitat characteristics such as watershed area, lake area and shoreline width/slope, but the width of the zone that ACPF inhabit along the lakeshore-to-forest gradient has not been commonly related to those characteristics. I concluded that none of the landscape scale characteristics had a significant correlation with the abundance of ACPF at a shoreline level. This highlighted the importance of combining both landscape and local scale characteristics in order to appropriately define habitat requirements for ACPF.

In the documented scientific literature, local scale habitat characteristics defined at a scale as small as 0.44 m^2 have rarely been related to ACPF communities. In my study, I specifically quantified the influence of numerous local scale habitat characteristics, such as the cover of different plant functional groups, different types of substrate, as well as a very minute (centimeter scale) changes in elevation. I distinguished characteristics that are important in determining the presence of ACPF from those influencing ACPF abundance and richness. I also defined habitat characteristics of common ACPF herb species, which has not been commonly done in the past; previous studies and recovery plans mainly focused on ACPF species at risk (e.g., *Coreopsis rosea*, *Hydrocotyle umbellata*, *Lophiola aurea*, *Sabatia kennedyana*). Common species that are part of the same plant community and/or habitat are highly relevant when studying rare species as they allow us to better understand the whole plant community, including rare species, and the broader ecosystems within which they are embedded.

FUTURE DIRECTIONS

Some further steps could be achieved in order to better define the habitat requirements of ACPF in southwestern Nova Scotia. First, soil transects should be established at the same locations as the ACPF plant transects to statistically assess the influence and significance of specific soil properties on ACPF communities. It is also important that data for both transects are measured at the same scale (e.g., one sampling point at 1 m intervals along the transect).

Establishing permanent transects and resampling the same quadrats every year (at approximately the same time of year) would allow for the quantification of the variability between growing seasons and provide more information on ACPF habitat and population persistence. Analyses similar to the ones applied in this study could be utilized to compare results among years (e.g., significance and effect size of explanatory variables). Other statistical analyses (e.g., t-test, ANOVA) could also be done to assess the significance of differences in the characteristics of ACPF communities (zone width, presence, abundance, richness) and in the influence of individual habitat characteristics on ACPF between growing seasons.

Sampling sites with and without ACPF might be a more appropriate means to characterize the habitat requirements of ACPF. Defining the habitat characteristics of sites where ACPF cannot grow could help to distinguish shorelines that are unsuitable for ACPF from suitable but unoccupied shorelines. Using a random sampling design would be the least biased approach to data collection, but it would limit the potential for using study data to model rare species habitat. Consequently, a partially random sampling within a suitable area for ACPF or known locations of ACPF populations, by using the ACPF database from Mersey Tobeatic Research Institute (2015) or other database, could be a better alternative. For example, windward shorelines of larger lakes with larger watershed areas could be randomly selected.

Another relevant and well known statistical analysis that could be done is path analysis, which assesses the magnitude and significance of causal connections between the different explanatory variables (Shipley 1997). For example, it would allow us to distinguish among possible combination of factors that affect ACPF communities, such as hydrological disturbances, edaphic properties and vegetation structure individually; hydrological disturbances that influence vegetation structure that affects ACPF; or hydrological disturbances that influence edaphic properties that affect vegetation structure and then ACPF (Figure 5-1). Understanding these causation links between different habitat characteristics of ACPF will help to better understand their ecological requirements and the complexity of their dynamic habitat.

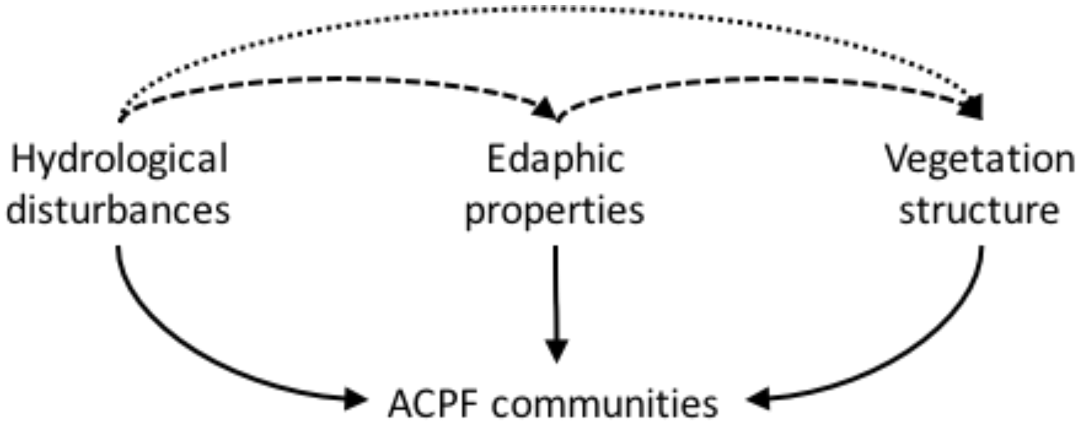


Figure 5-1. Diagram showing possible causation links (solid lines) between hydrological disturbances, edaphic properties, vegetation structure and ACPF communities. The dotted line shows hydrological disturbances that influence vegetation structure, which then affects ACPF. The dashed line shows hydrological disturbances that influence edaphic properties, which then affect vegetation structure and then ACPF.

In order to effectively protect ACPF communities, habitat protection needs to be combined with watershed management (Francis and Munro 1994), where the natural level of fertility and hydrological disturbances, such as water level fluctuations, must be maintained (Wisheu and Keddy 1989, 1994). Numerous threats to ACPF arise at a watershed scale, such as nutrient run-off from agriculture and housing as well as stabilization of water levels from damming, which respectively promote the establishment of competitive species and shrubs on lakeshores (Naiman and Décamps 1997; Hill et al. 1998). Including lake chemistry properties (e.g., pH, turbidity, chlorophyll, nitrate/nitrite and phosphorous) and developing water eutrophication indices would allow for the assessment of the amplitude as well as the influence of some anthropogenic pressures on ACPF communities and to improve our understanding of their habitat at a watershed scale.

Novel and creative approaches are needed to develop conservation plans for ACPF (Sweeney and Ogilvie 1993). Habitat management is an essential part of their conservation (Wisheu and Keddy 1989); the protection of remaining habitat in the shorter term, as well as the maintenance and restoration of habitat in the longer term will allow their persistence and growth in Nova Scotia (Rawinsky and Price 1994). Preserving habitat is an essential way to conserve the existing biodiversity that provides numerous ecological services (Franklin 1993; Tews et al. 2004).

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APPENDIX 1 – SELECTED ACPF SPECIES

A. Shrub ACPF species

Northern bayberry (*Morella pensylvanica*)	Poison ivy (*Toxicodendron radicans var. radicans*)
	
Round-leaved greenbrier (*Smilax rotundifolia*)	Inkberry (*Ilex glabra*)
	

Common buttonbush (*Cephalanthus occidentalis*)	Swamp rose (*Rosa palustris*)
	

B. Herbaceous ACPF species

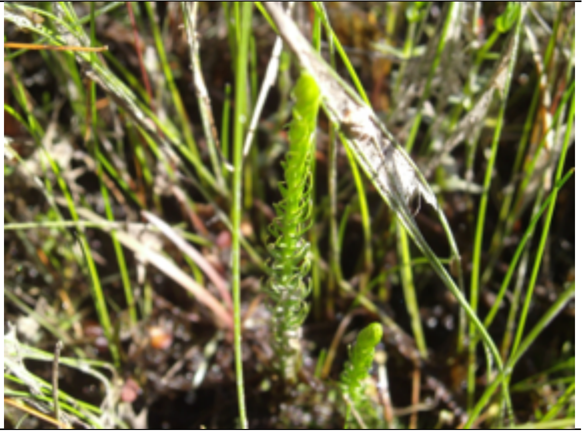
Redroot (*Lachnanthes caroliniana*)	Slender fragrant goldenrod (*Euthamia caroliniana*)
	

Lance-leaved violet (*Viola lanceolata*)

Virginia St-John’s-wort (*Hypericum virginicum*)

Golden pert (*Gratiola lutea*)

Branched bartonia (*Bartonia paniculata var. iodandra*)

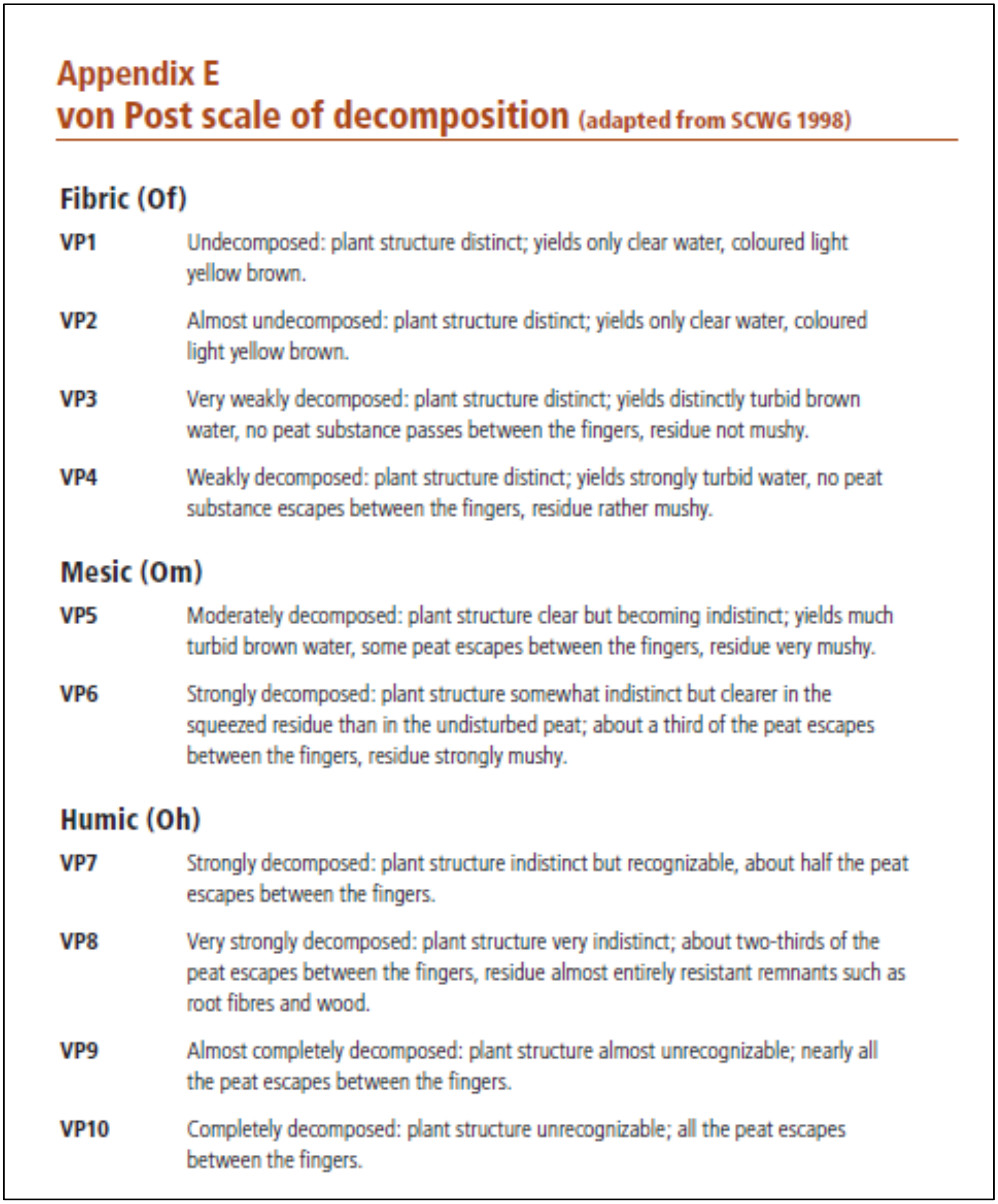
Blue-eyed grass (*Sisyrinchium* sp.)	Virginia meadow-beauty (*Rhexia virginica*)
	
Lakeshore yellow-eyed grass (*Xyris difformis*)	Southern bog clubmoss (*Lycopodiella appressa*)
	

C. Graminoid ACPF species

Toothed flat-sedge (*Cyperus dentatus*)	Old switch panic grass (*Panicum virgatum*)
	

APPENDIX 2 – EDAPHIC KEYS

A. von Post scale of decomposition from Keys et al. (2010).



Appendix E
von Post scale of decomposition (adapted from SCWG 1998)

Fibric (Of)

VP1	Undecomposed: plant structure distinct; yields only clear water, coloured light yellow brown.
VP2	Almost undecomposed: plant structure distinct; yields only clear water, coloured light yellow brown.
VP3	Very weakly decomposed: plant structure distinct; yields distinctly turbid brown water, no peat substance passes between the fingers, residue not mushy.
VP4	Weakly decomposed: plant structure distinct; yields strongly turbid water, no peat substance escapes between the fingers, residue rather mushy.

Mesic (Om)

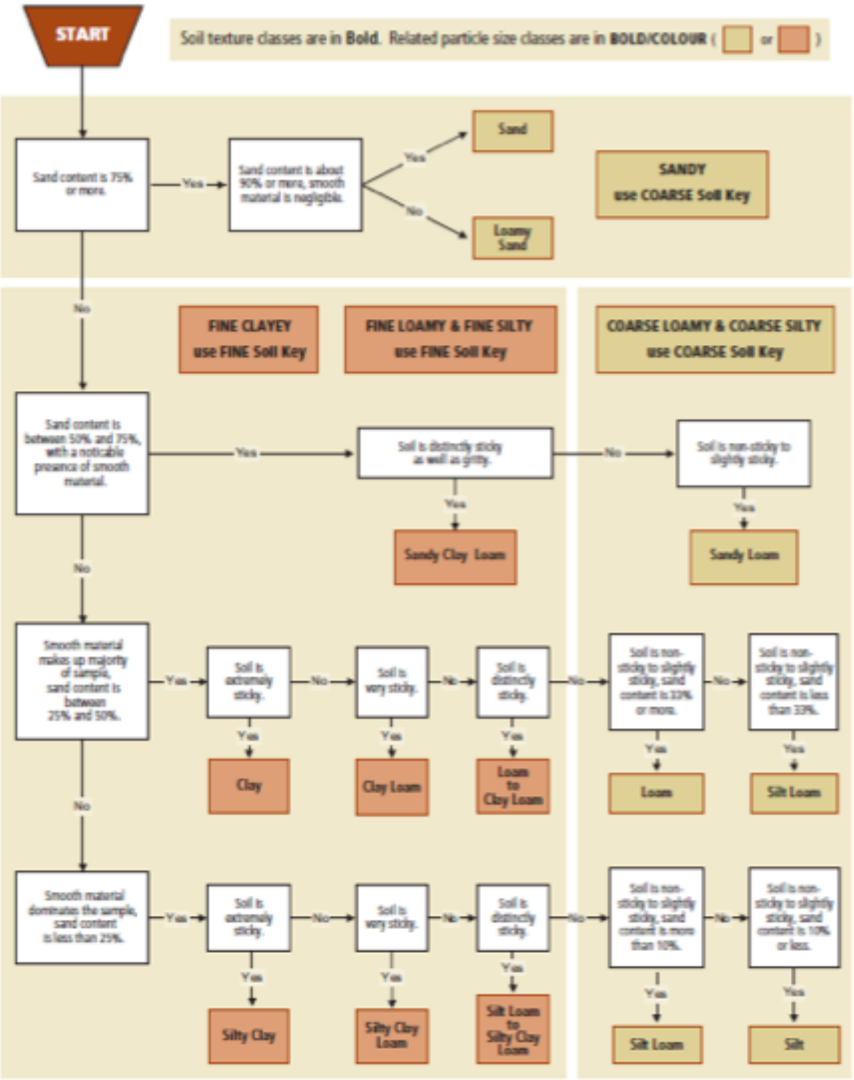
VP5	Moderately decomposed: plant structure clear but becoming indistinct; yields much turbid brown water, some peat escapes between the fingers, residue very mushy.
VP6	Strongly decomposed: plant structure somewhat indistinct but clearer in the squeezed residue than in the undisturbed peat; about a third of the peat escapes between the fingers, residue strongly mushy.

Humic (Oh)

VP7	Strongly decomposed: plant structure indistinct but recognizable, about half the peat escapes between the fingers.
VP8	Very strongly decomposed: plant structure very indistinct; about two-thirds of the peat escapes between the fingers, residue almost entirely resistant remnants such as root fibres and wood.
VP9	Almost completely decomposed: plant structure almost unrecognizable; nearly all the peat escapes between the fingers.
VP10	Completely decomposed: plant structure unrecognizable; all the peat escapes between the fingers.

B. Soil texture class and particle size class key from Keys et al. (2010).

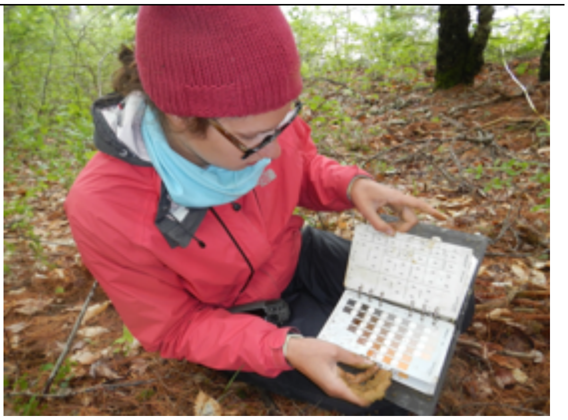
Figure 3. Soil texture class and particle size class key



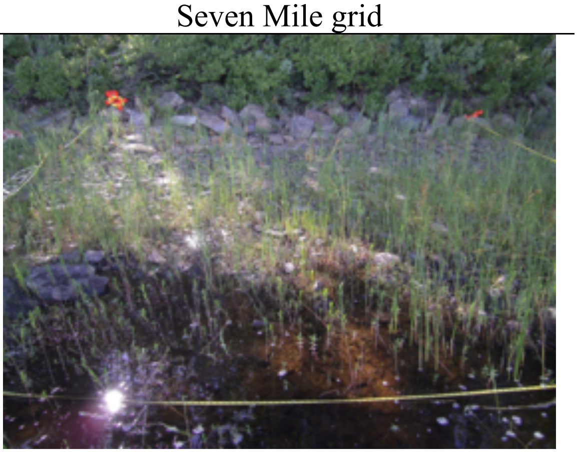
APPENDIX 3 – FIELDWORK PICTURES

A. Data collection

Soil auger	Soil pH
	
Inclination	Canopy cover
	

Mineral matrix texture	Mineral matrix Munsell color
	

B. Sites for the grid sampling design

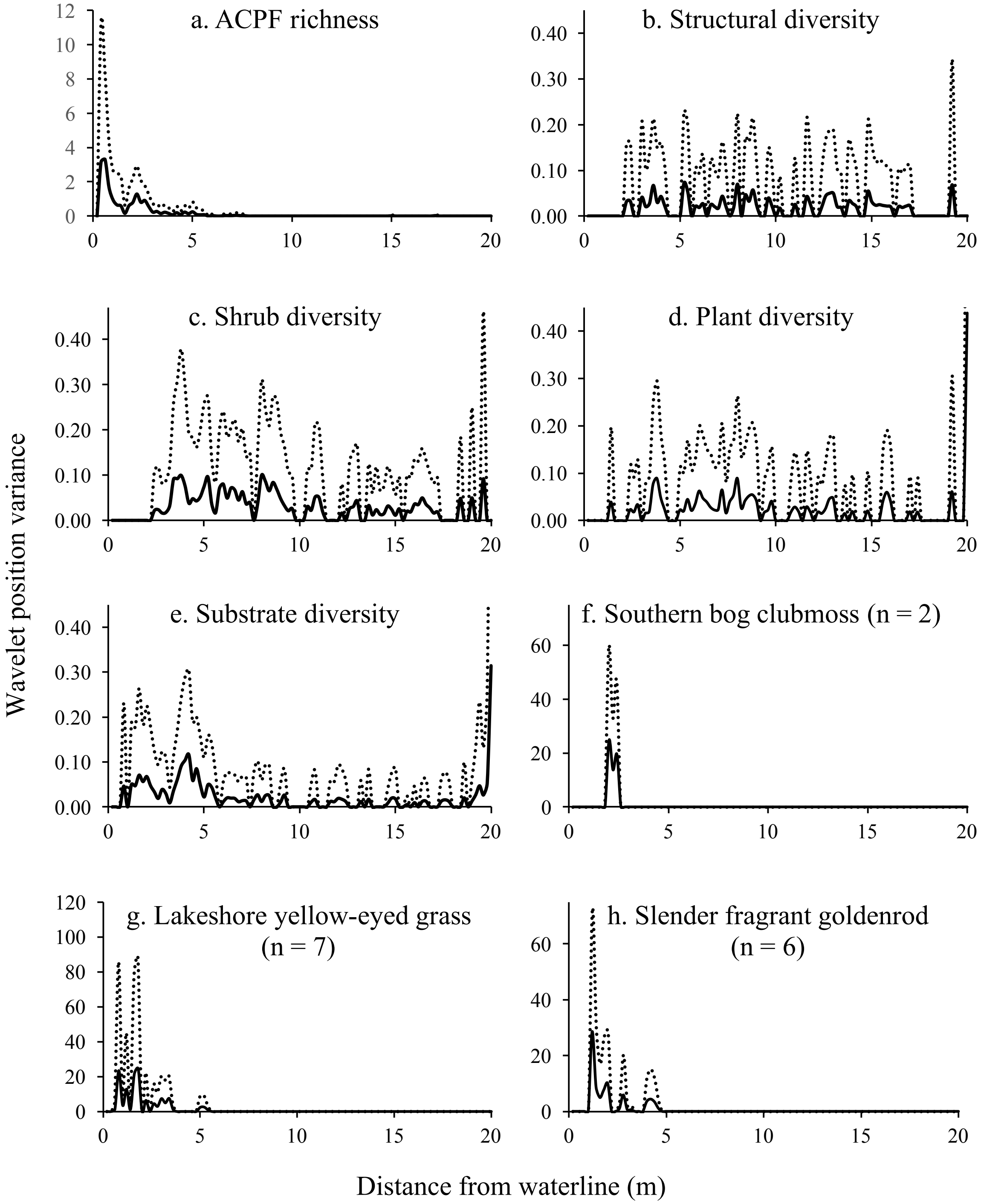
Cameron grid	Kejimkujik grid
	
Ponhook grid	**Seven Mile grid**
	

Hog grid	20 cm x 20 cm quadrat
	

C. Common species found with ACPF

Shrub: huckleberry and cranberry	Herb : spoon-leaved sundew
	

APPENDIX 4 – CHAPTER 3 FIGURES WITH AVERAGE (SOLID LINE) AND POSITIVE STANDARD DEVIATION (DOTTED LINE)



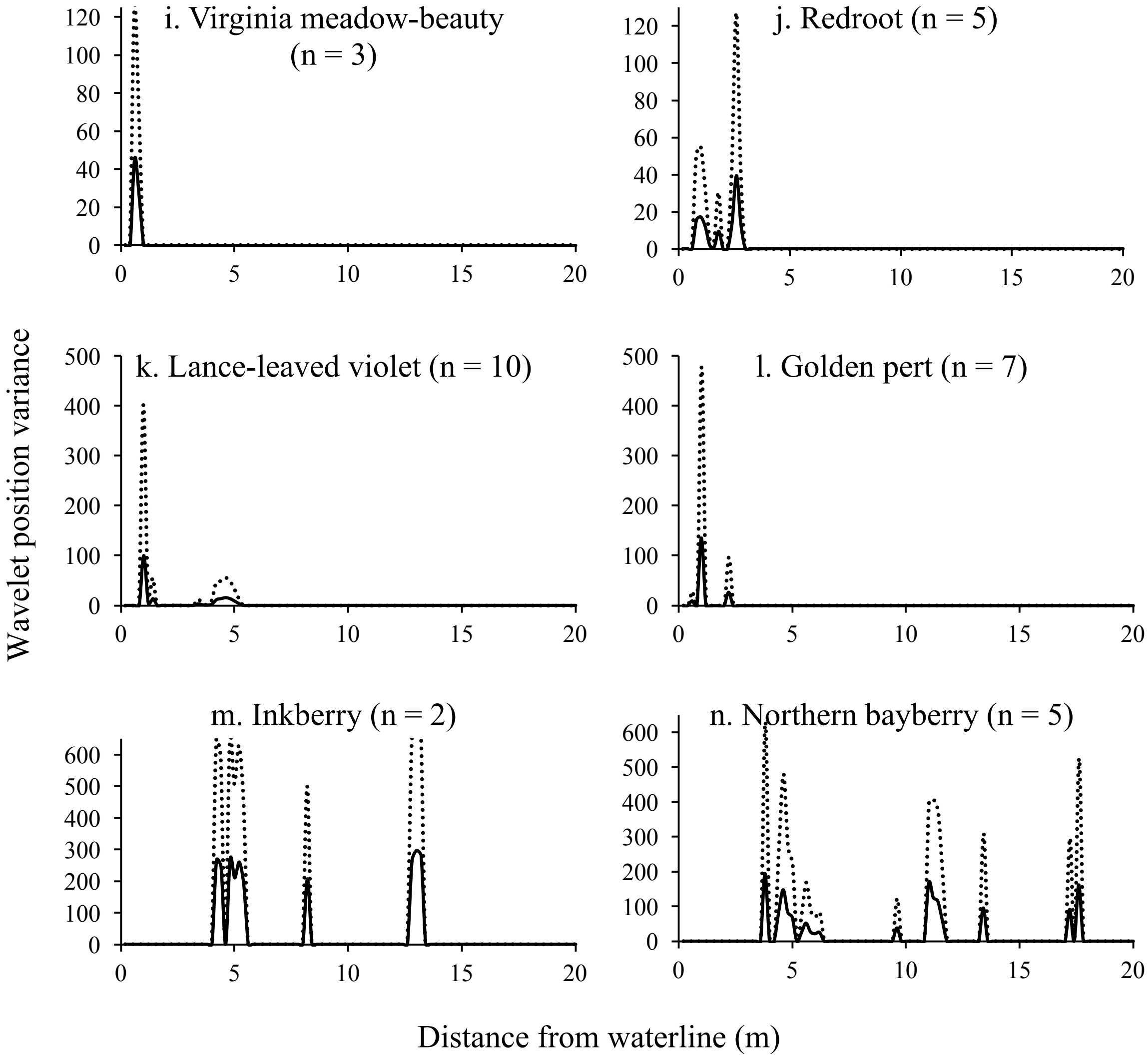


Figure 3-6 with positive standard deviation lines.

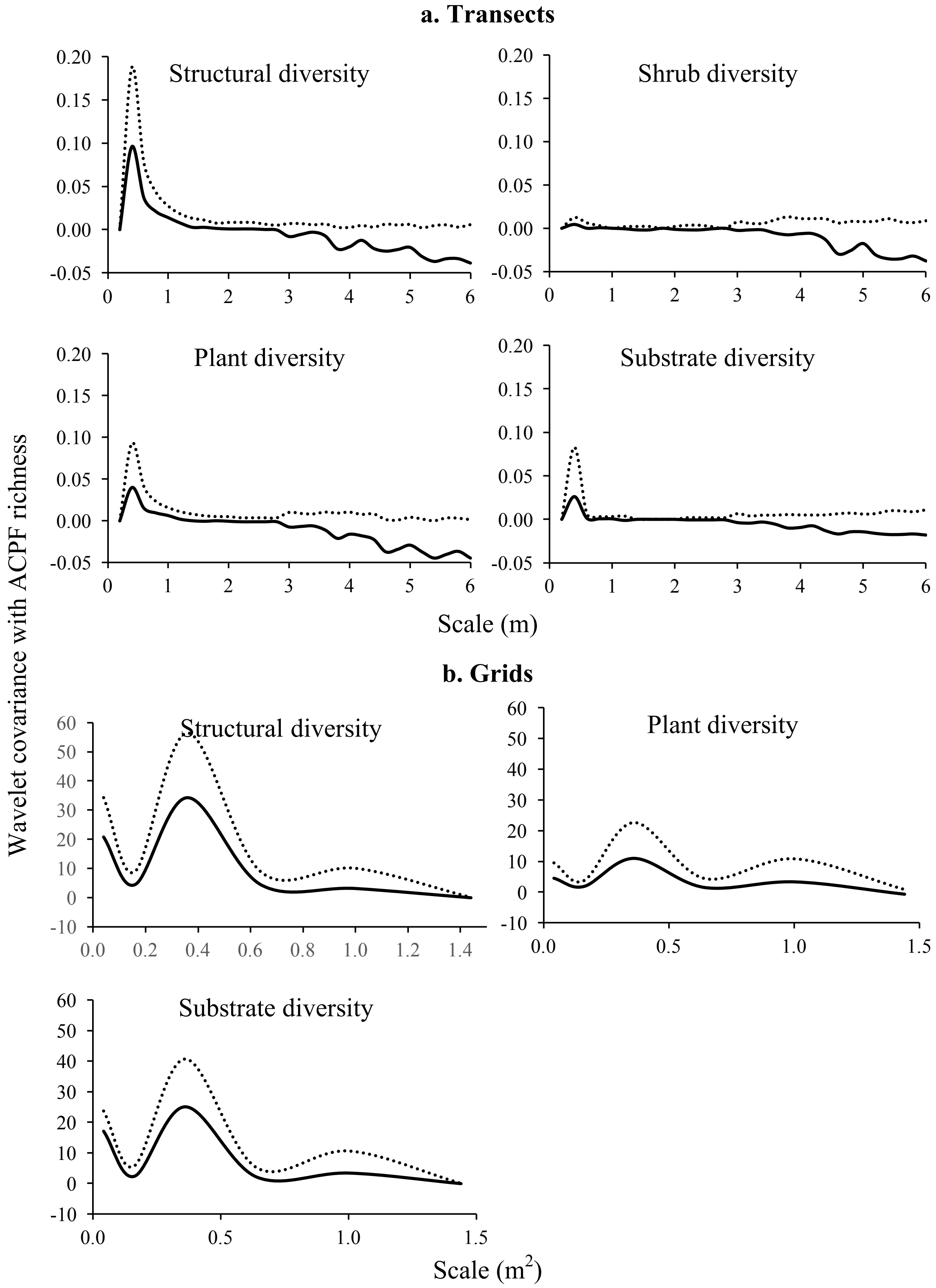


Figure 3-7 with positive standard deviation lines.

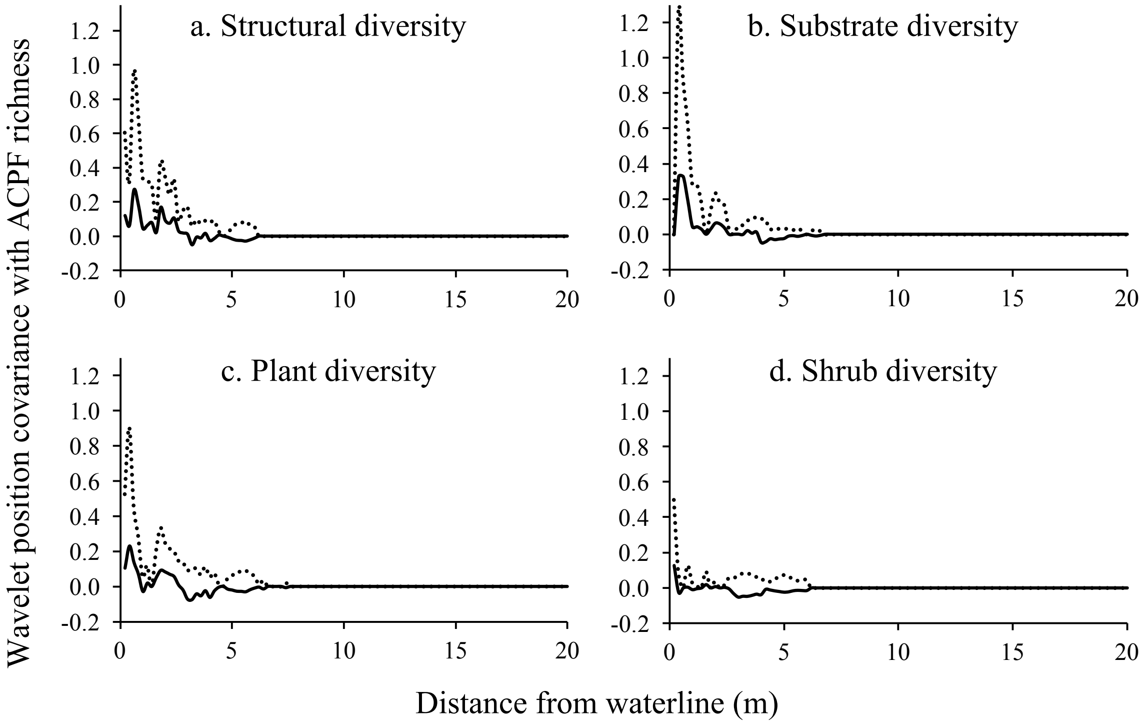


Figure 3-8 with positive standard deviation lines.