Ecological separation among fern species in an old-growth forest

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Abstract

The validity of niche-assembly rules in explaining community structure is revisited by testing for ecological separation among ferns. An intensive, fine-scale survey of fern abundance and environmental variation was done in 1-ha of old-growth forest. Three methods of detecting niche segregation (canonical correspondence analysis, detrended correspondence analysis and GIS mapping) suggested that most fern species at the site are distributed according to distinct environmental preferences. The most important gradients separating fern species are first, the amount of soil moisture and second, soil nitrate concentration. Contrary to other findings, pH had little influence on controlling fern distribution. Spatial autocorrelation, detected by partialled ordinations, obscured the presence of niche partitioning. As well, sampling grain changed the apparent location of some species on environmental gradients and their ecological similarity to other species. Finer-scaled environmental heterogeneity or dispersal-mediated processes may account for the unexplained variation in fern species abundance of this site.

Résumé

La validité des règles d'assemblage de niche dans l'explication de la structure des communautés est ré-etudieé en vérifiant les différences écologiques entre les fougères. Un échantillonnage intensif à grande échelle de l'abondance des fougères et des variations environnementales a été réalisé sur un site d'un hectare dans une vieille forêt. Trois méthodes de détection de la ségrégation des niches (analyse canonique des correspondances, analyse des correspondances redressées et cartographie de système d'informations géospatiales) suggèrent que la plupart des espèces de fougère du site se distribuent selon des préférences environnementales distinctes. Les gradients les plus importants qui séparent les espèces de fougère sont l'humidité du sol et la concentration en nitrate du sol. Contrairement à d'autres résultats, le pH influence peu la distribution des fougères. De l'autocorrélation spatiale, détectée par des ordinations partielles, masque la présence de la sépartion de niche. Également, l'échelle d'échantillonnage change le positionnement apparent de quelques espèces selon les gradients environnementaux et leur similarité écologique aux autres espèces. Une hétérogénéité environnementale plus fine ou les processus de dispersion pourraient représenter la variation inexpliquée de l'abondance des espèces de fougère du site.

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Introduction

The niche and its importance in organizing communities

The niche has been a valuable ecological concept to explain patterns of species distribution and abundance. The concept of a species' "niche" was first used by Grinell in 1917 (Whittaker and Levin, 1975) but has been changed somewhat as we have come to understand more of the forms and functions of species. The niche concept has been reviewed in the past (i.e. Whittaker *et al.*, 1973; Schoener, 1989), including some more recent accounts that stress that the niche of a species is dynamic and occurs as a response to the environment and to its neighbours (Bazazz, 1996). Niche in the context of this thesis will be defined similarly to Hutchinson (1957): the limits to where a species exists in multidimensional environmental space. Resource gradients traditionally are taken as the axes of the environmental space. Integrating resource gradients with the niche concept, offers a way to quantify how species differ ecologically. Tokeshi (1998) recognized that defining a species only by its position on resource gradients is somewhat conceptually restricted, however this approach does make the niche concept more flexible and compatible with experimental methods.

Competition underlies the niche concept; the competitive exclusion principle dictates that only one species can survive on a shared resource. However, for any given habitat there are only a few limiting resources, and how these resources could support so many species has been characterized as a paradox (Hutchinson, 1961). Tilman and Pacala (1993) explored the processes that might allow persistence of numerous species by setting aside each of the assumptions underlying competitive exclusion. These assumptions are: spatial homogeneity, equilibrium conditions, simple trophic structure, simple life histories and absence of limiting physical factors, neighbourhood effects, and habitat patchiness. The presence of trade-offs in the ability to compete under varying conditions and partitioning resources in space and time all enable species to avoid competition and to co-exist.

The niche concept is deeply rooted in ecology and is useful in explaining patterns of occurrence, as attested by a number of recent reviews on the distribution and abundance of a variety of organisms, such as bryophytes (Slack, 1990), peatland plant species (Gignac, 1994), deep-sea macrobenthos (Gage, 1996), soil microorganisms (Giller, 1996) and palms (Svenning, 2001). Each of these community assemblages require that the species differ in their competitive abilities to survive on limiting resources. The species with the most tolerance to the lowest amounts of limiting resources out-competes all other species. When there are two or more limiting resources present, species will have tradeoffs in their competitive abilities at particular ratios of supply rates of the limiting resources (Tilman, 1982). Through competitive interactions species divide resources, so that each species survives on different portions of resource gradients.

The niche, or the consequent ecological separation among species in a community (demonstrated by environmental preferences), should be most apparent where there is a high number of species over a small spatial scale. Niche apportionment models show that with the incorporation of new species, existing species in the community must decrease their relative resource use, though not necessarily in equivalence. As Rosenzweig (1995) explained with regard to habitat diversity among birds, "the more species, the more narrowly they specialize". Competitive interactions will be strong amongst a group of functionally similar species. For a guild of species to co-exist in a community, each species will have to subdivide resources to avoid competition. A study on wetland plants found that species that were more similar with respect to ecological traits, experienced increased intensity of competition (Johansson and Keddy, 1991). Within a community, this translates into fine-scale environmental differentiation. Forest herbs have been found to be distributed according to numerous sources of fine scale heterogeneity: distance to trees, logs and rocks (Bratton, 1976), soil moisture, depth, and microtopography (Hicks, 1980), litter type, canopy density, and canopy composition (Mann and Shugart, 1983), decaying tree falls (Christy and Mack, 1984), pits and mounds

(Beatty, 1984), soil moisture and nutrient properties (Velland *et al.*, 2000), and logs, stumps and root throws (Lee and Sturgess, 2001).

The presence of niche partitioning will vary with scale. Variations in the environment will be viewed differently depending on the species. Bacteria in the soil will be dependent on small pockets (at the mm scale) of water, air and nutrients. Trees growing in the same soil will not perceive these small differences and will respond to larger scale variations, like soil type (at the scale of decimetres to ten's of metres). The grain chosen to detect niche partitioning should therefore reflect the scale of heterogeneity that is perceived by the species. The spatial extent will also be influential in what role the niche plays in community assemblages. By increasing extent, i.e. the distance over which observations are made, the cause of species' differences in distribution changes (Nekola and White, 1999). Over increasing distance, the environment can become less similar and species turnover will be due to competitive sorting of broadly different environmental tolerances. On the other hand, with increasing extent, the landscape will have different resistances to the movement of organisms. To ensure that species are being sorted based on environmental preferences, an extent should be chosen that does not pose any dispersal restrictions to the species.

If we assume that the propagules of an organism can potentially arrive to all sites within an area, the distribution and abundance of a species should reflect its ecological niche. Communities of species formed by species occurring at sites where they have evolved to be the best competitor, are said to be niche-assembled. There will be as many species present as there are available niches. When species occurrence is largely due to chance, historical factors or random dispersal, the community is said to be dispersal-assembled. There is no systematic differentiation among species; their occurrence is only a matter of what gets there first. Dispersal-assembled communities are said to be open, the number of species only restricted by the regional pool of species available to colonize a site (Hubbell, 2001).

Niche separation among ferns

We can expect that fern distribution will be explained more by niche-assembly than dispersal-assembly rules, which assert there are no ecological differences among species and that stochasticity plays a major role in determining species distribution and abundance (Hubbell, 2001). Environmental preferences of ferns have been well documented in floristic guides and also in the scientific literature. Temperature, soil moisture and pH have been cited as the dominant factors influencing fern distribution (Lellinger, 1985). Climatic differences are prominent at regional scales (Marqez *et al.*, 1997; Dzwonko and Kornas, 1994) and soil conditions are more influential at local scales ranging from a square metre to one hectare (Richard *et al.*, 1999; Tuomisto and Poulsen, 1996 and 2000; Odland *et al.*, 1990; Greer *et al.*, 1997; Ruokolainen *et al.*, 1997; Petersen, 1985 and citations therein; Wherry, 1920).

The influence of the abiotic environment on fern distribution patterns is seen at all life stages. The majority of studies on fern ecology (including the aforementioned) examine the sporophytic phase of the fern. However, the gametophyte is also sensitive to its environment, most notably of moisture conditions. Successful fertilization requires moisture for the flagellated sperm to swim to the egg contained in the archegonium. In addition to the biologically based high moisture requirements among all ferns, Hill (1971) showed that gametophytes have interspecific differences to light intensity, temperature and substrate pH, all representative of sporophytic habitat preferences. Despite their lengthy and successful existence in the earth's flora in evolutionary terms (510-440 mya; Rothwell, 1996), ferns have not evolved to have many biotic interactions throughout their life cycle (e.g. spore dispersers and herbivores). Consequently, their distribution and abundance is more linked to the abiotic environment (Barrington, 1993). However, there is a lack of quantitative studies in which rigorous techniques unambiguously attest to the ecological differences among fern species and the degree to which they differ.

In addition to their relative absence of biotic interactions, ferns are widely dispersed, thus, discounting dispersal limitation as an explanation to patterns of fern species occurrence. Despite leptokurtic spore dispersal patterns (Conant, 1978), regular long distance spore dispersal and a viable soil spore bank makes fern spores an almost ubiquitous part of the environment (Dyer and Lindsay, 1992). Viable spore banks were found 50 m from the nearest fertile fern in an old deciduous woodland, suggesting that short distance travel is common (Dyer and Lindsay, 1992). Historic accounts of spores travelling up to 3200 kilometres (Tryon, 1970) and more recent accounts of spore transport from New Zealand and Australia to Antarctica (Paganelli, 1997) provide evidence that fern spores are not dispersal limited. However, Peck *et al.* (1990) in a study that outlined the limiting factors in fern establishment, found that only 8% of trapped spores were found more than 5 m from source plants. Nonetheless, Clark (1998) accounted for the rapid spread (100-1000m$\cdot$ yr^{-1}) of trees at the end of the Pleistocene by modeling dispersal distributions that allowed for rare, long-distance dispersal. Given that it is not unreasonable for tree seeds to travel 100 m$\cdot$ yr^{-1}, it is likely that fern spores, which are more plentiful and lighter than tree seeds, are widespread over an area of approximately one hectare. The ubiquitous nature of fern spores within a community diminishes the role of neutral processes, which assert that stochastic effects dominate over adaptation.

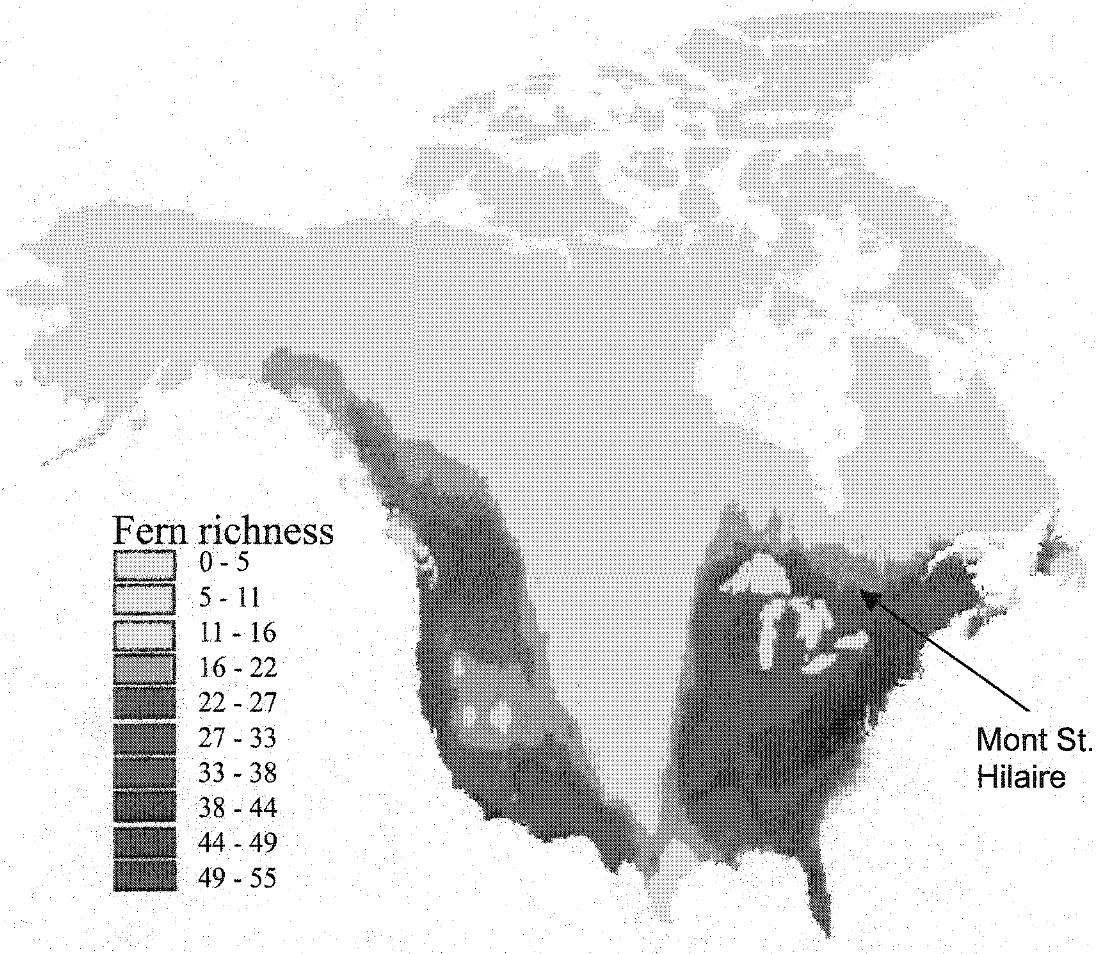
Recently, the concept of neutrality has challenged the role of the niche in community assemblages. Niche partitioning contributed less than chance events in maintaining tropical tree species diversity and neutral theories that recognized species as ecologically equivalent have explained patterns like relative species abundance (Bell, 2000), community dynamics and speciation (Hubbell, 2001). However, the evidence for niche versus neutral factors in explaining community diversity remains equivocal (Brokaw and Busing, 2000). In light of this debate, my objective in this thesis is to test for niche separation of ferns at the fine-scale. There is little doubt that species do ecologically differ across large scales, i.e. "coconuts cannot be successfully established in boreal peat bogs" (Bell, 2001), but there is ambiguity at finer scales. Specifically, the questions I am addressing are: 1. Is there evidence that ferns in general, show environmental preferences from locality to locality across a region? 2. Do ferns show environmental preferences at the fine-scale? 3. What are the main gradients that control fern distributions and how does spatial structure alter the importance of these gradients? 4. How do the demonstrated environmental affinities expressed locally for the ferns compare with previous results from observations at larger scales?

I address these questions by examining a community of ferns located on Mont Saint-Hilaire (MSH), which is within a relatively fern-rich area of the continent (Figure x-1). There are 60 fern species present in the province of Quebec, Canada (excluding varieties and hybrids) (Fleurbec, 1993), of which 36 species are found on MSH (Bell, Lechowicz and Waterway, unpublished data) (Figure x-2) (species nomenclature used herein is from Flora of North America Editorial Committee, 1993). Compared to the number of fern species on the continent, the number of ferns at MSH, represents only 8% of the North American fern species but greater than 50% of the fern species present in Quebec (Table x-1). Based on a comprehensive survey in 1996, *Dryopteris intermedia* is the most abundant fern species on the mountain followed by *Dryopteris marginalis*, *Polystichum acrostichoides*, *Athyrium filix-femina*, *Adiantum pedatum* and *Dryopteris carthusiana* (Figure x-2). The least abundant fern species are *Dryopteris cristata*, *D. clintoniana*, and *Botrychium lanceolatum* (*Botrychium* species are ephemeral and not well censused in the survey, although the species always occurs in low numbers). Of the eight families present on the mountain, many of the genera are represented by a single species, but others such as *Dryopteris*, *Polystichum* and *Botrychium* have as many as eight species representing the genus (Table x-1).

The studied fern community is found in a heterogeneous setting. The Gault Nature Reserve (1200 hectares) situated on Mont Saint-Hilaire, is the largest tract of old-growth forest in the St. Lawrence River valley. The reserve is geologically complex, as it was formed by a series of magmatic intrusions, and is one of the few isolated mountains that remain in the region (Currie *et al.*, 1989). The geology, microclimate, hydrology, vegetation and natural history of the mountain have been described elsewhere (Maycock, 1961; Rouse and Wilson, 1969; Feininger and Goodacre, 1995).

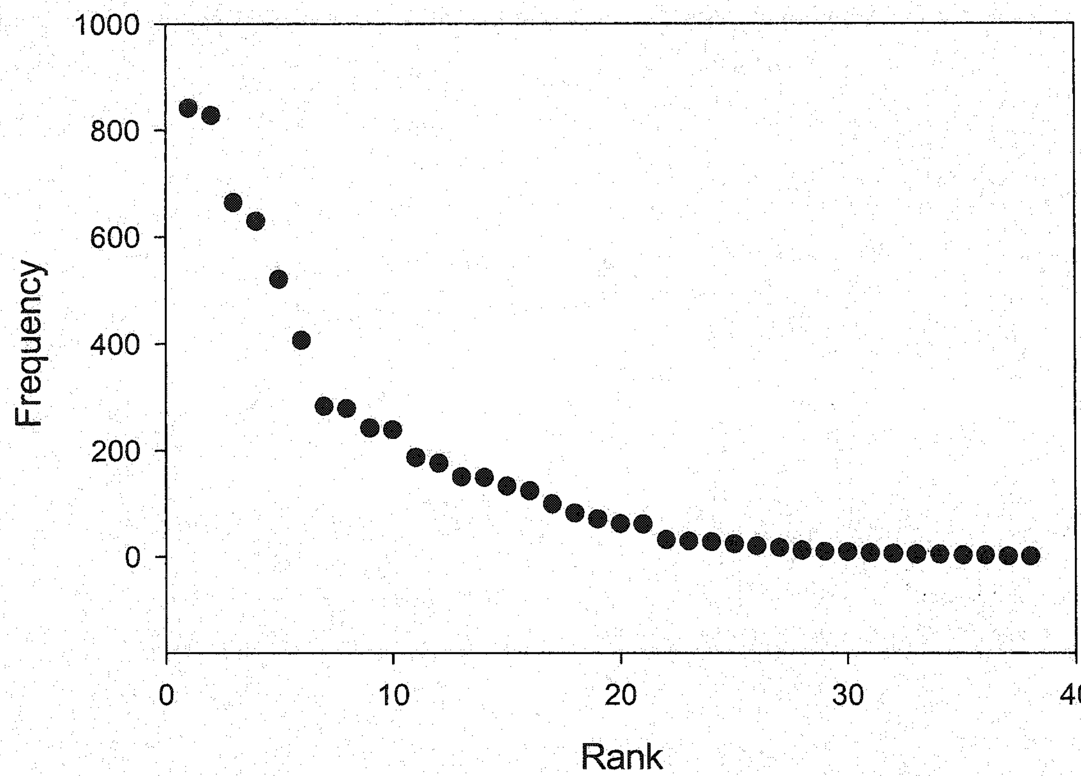
Figure x-1: Fern species richness of North America[1].

[1]Species richness data are from Kemi Fakambi (unpublished report) who downloaded species range maps from the online version of Flora of North America, Volume 2 (http://hua.huh.harvard.edu/FNA/). The printed range maps were digitized in Arcedit and converted into shape files for Arcview 3.2. Species richness was obtained for each pixel (0.5^0 x 0.5^0 or approximately 3600 km^2) of North America by first importing the shape files into Idrisi 32, overlaying the maps using this software and counting the number of species falling in each pixel.



Fern richness
0 - 5
5 - 11
11 - 16
16 - 22
22 - 27
27 - 33
33 - 38
38 - 44
44 - 49
49 - 55
Mont St.
Hilaire

Figure x-2: Dominance-diversity curve for fern species of Mont Saint-Hilaire, Quebec based on 1996 survey of presence of each fern species within each hectare of mountain (1015 hectares in total) (source: Bell, Lechowicz and Waterway, unpublished data).



Rank position (decreasing in frequency): *Dryopteris intermedia*, *D. marginalis*, *Polystichum acrostichoides*, *Athyrium filix-femina*, *Adiantum pedatum*, *D. carthusiana*, *Botrychium virginianum*, *Polypodium virginianum*, *Onoclea sensibilis*, *Deparia acrostichoides*, *Cystopteris fragilis*, *Pteridium aquilinum*, *Dennstaedtia punctilobula*, *Gymnocarpium dryopteris*, *Matteuccia struthiopteris*, *Phegopteris connectilis*, *Thelypteris noveboracensis*, *Cystopteris bulbifera*, *Osmunda cinnamomea*, *Woodsia ilvenis*, *Osmunda claytoniana*, *Osmunda regalis*, *Thelypteris palustris*, *D. goldiana*, *Asplenium trichomanes*, *Botrychium dissectum*, *Diplazium pycnocarpon*, *Polystichum braunii*, *Phegopteris hexagonoptera*, *Botrychium matricariifolium*, *D. campyloptera*, *Botrychium mutifidum*, *Botrychium lanceolatum*, *D. clintoniana*, *Asplenium rhizophyllum* and *D. cristata* (see Appendix A for full species names).

Table x-1: Representative fern families and genera of Mont Saint-Hilaire, Quebec and their counts at continental, regional and local scale compiled from Flora of North America Editorial Committee (1993), Fleurbec (1993) and Bell, Lechowicz and Waterway (unpublished).

Representative families	**Representative genera**	**Number of species worldwide**	**Number of North American species**	**Number of species in Quebec**	**Number of species at Mont St. Hilaire**
Aspleniaceae		~ 700	28	-	-
	Asplenium	~ 700	28	5	1
Dennstaedtiaceae		~ 400	4	-	-
	Dennstaedtia	70	3	1	1
	Pteridium	1	1	1	1
Dryopteridaceae		>3000	79	-	-
	Athyrium	~180	2	2	1
	Cystopteris	~ 20	9	3	2
	Deparia	~ 50	2	1	1
	Diplazium	~ 400	3	3	1
	Dryopteris	~ 250	14	10	8
	Gymnocarpium	8	5	2	1
	Matteuccia	3	1	1	1
	Onoclea	1	1	1	1
	Polystichum	~ 180	15	4	2
	Woodsia	~ 30	10	6	1
Ophioglossaceae		~ 70-80	38	-	-
	Botrychium	50-60	30	8	6
Osmundaceae		16-36	3	-	-
	Osmunda	10	3	4	3
Polypodiaceae		500	25	-	-
	Polypodium	~ 100	11	1	1
Pteridaceae		~ 1000	90	-	-
	Adiantum	150-200	9	2	1
Thelypteridaceae		~ 900	25	-	-
	Phegopteris	3	2	2	2
	Thelypteris	~ 875	21	3	3
	Total	**>9747**	**462**	**60**	**36**

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Chapter 1

Environmental affinities of fern species present on Mont Saint-Hilaire

Introduction

Niche partitioning is reflected in species' preferences for different environments. The different environments are defined with respect to the scale considered. At continental scales, climatic tolerances may define the range of a species (e.g. Currie and Paquin, 1987) and at finer scales, topographical gradients may influence the occurrence of a species (e.g. Brown, 1994). The spatial coincidence between species distributions and the environment indicates that environmental factors are underlying spatial patterns. The presence of consistent environmental affinities implies that niche-assembly is influential in the patterns of species assemblages in a locality. In this chapter, I examine environmental preferences and thus, niche-partitioning, among the ferns of Mont Saint-Hilaire (MSH). Three sources describing environmental affinities at different scales are used: 1. North American fern range maps, 2. qualitative descriptions of fern environmental preferences within these ranges and 3. quantitative micro-environmental characterizations for a set of ferns from MSH.

Continental ranges of ferns present at Mont Saint-Hilaire

The continental ranges vary among the fern species present on MSH (see Appendix B). *Cystopteris fragilis* is found on most of the North American continent. *Dryopteris carthusiana*, *Botrychium virginianum*, *B. multifidum*, *Gymnocarpium dryopteris*, *Matteuccia struthiopteris* and *Phegopteris connectilis* extend from Canada's west to eastern coasts. *Dryopteris cristata* and *Polypodium virginianum* are found mostly in eastern Canada and northeastern United States but also have a "finger" extending into Canada's prairies. *Woodsia ilvensis* occurs in eastern Canada, just into northeastern United States and northwestern Canada. *Botrychium lanceolatum*, *Asplenium trichomanes* and *Polystichum braunii* have disjunct populations occurring in eastern North America and west of Alberta. The remaining ferns found at MSH cover more or less the eastern United States, with their northern limit just above the Canadian border (including *Thelypteris palustris*, *Thelypteris noveboracensis* and *Osmunda regalis*, whose distribution maps were not available through Flora of North America website (http://hua.huh.harvard.edu/FNA/), however, the distribution was confirmed by Fleurbec, 1993).

Many North American ferns co-occur in the east with similar ranges, which suggests a deterministic cause to species assemblages as opposed to a stochastic factor. The majority of MSH ferns belong to this eastern subset. The similarity in these ranges suggests that there is a common underlying control at the geographical scale. Species outside this subset, such as *Phegopteris connectilis,* also seem to be restricted by obvious climatic barriers, like the prairies and the northern tree line (see Appendix B). The common control underlying fern distribution at this scale is most likely climate related, similar to what has been found with trees (Iverson *et al.*, 1999) and plant species in Florida (Box *et al.*, 1993).

Environmental affinities of species may be affected by their location within their range. For example, the location of an individual, range-edge or range-core, may affect its distribution and abundance. This has been shown with many invertebrate species that occupy narrower niches within regions towards the northern edges of their ranges (Thomas *et al.*, 1999). At their northern limits, they are found in microsites that are substantially warmer than are typical for the latitude. Similarly for plants, the differences between plant communities on south and north facing slopes allows different regional vegetation to exist in close proximity under the same regional climate. For example, Piggot and Piggot (1993) found that different woodland communities existed on slopes with different aspects on the boundary of the Mediterranean zone in southern France. Species characteristic of central Europe were found on north facing slopes whereas Mediterranean species were found on south slopes.

The ferns of MSH, however, do not seem to show a connection between range patterns and their distribution on the mountain. Considering a comprehensive survey of ferns at MSH (Bell, Lechowicz and Waterway, unpublished), it is clear that ferns at their northern limit are not confined to southern slopes (e.g. *Deparia acrostichoides*, *Cystopteris bulbifera*, and *Dryopteris intermedia*), or conversely, ferns at their southern limit are not confined to northern slopes or even cooler microclimates on the mountain (e.g. ridge tops, valley bottoms) (e.g. *Cystopteris fragilis* and *Woodsia ilvensis*). In fact, there does not appear to be any consistency between range patterns and distribution of ferns at MSH (at the hectare level) and only that most ferns are found in localities with higher moisture availability (Figure 1-1). Most of the fern-rich hectares are found close to streams and where fern-rich hectares are found on a ridge top (i.e. the highest peak on the western side of the mountain), it is a site where impermeable rock has formed a closed basin with little water drainage.

Environmental preferences of ferns over their geographic ranges

Within species' ranges, there is habitat diversity. Species may prefer different habitats such as marshes, forests or swamps which reflect their environmental affinities. Environmental preferences have been well established for each of the MSH fern species (Table 1-1). Within their ranges, ferns appear to segregate to different parts of the environment. Broadly speaking, fern species vary in affinity for moisture, pH, fertility and light. Some ferns such as, *Cystopteris bulbifera* and *Asplenium trichomanes* prefer more alkaline areas compared to ferns like *Osmunda cinnamomea*, *Dennstaedtia punctilobula* and *Gymnocarpium dryopteris*. Other ferns, like *Adiantum pedatum* and *Deparia acrostichoides,* thrive in rich soils. *Onoclea sensibilis* and *Pteridium aquilinum* are tolerant of sunny conditions whereas most other ferns require shade.

An ordination of MSH ferns using the 1996 hectare survey data (Bell, Lechowicz and Waterway, unpublished; see Figure 1-2 for methods) suggests that ferns differ ecologically, but not necessarily in accordance with what is known about their differences in habitat preference. *Asplenium trichomanes* and *Cystopteris fragilis* are relatively close together in this ordination indicating they are found in similar hectares, and therefore may have similar environmental preferences. Indeed,

Figure 1-1: Elevation map of Mont Saint-Hilaire showing streams and hectares representing the top fifth percentile of fern richness based on 1996 comprehensive fern survey of presence of ferns in each hectare (1015 hectares in total) (Bell, Lechowicz and Waterway, unpublished data). Two places where ferns cannot occur are blacked out: Lac Hertel (middle) and a stone quarry (northern edge).

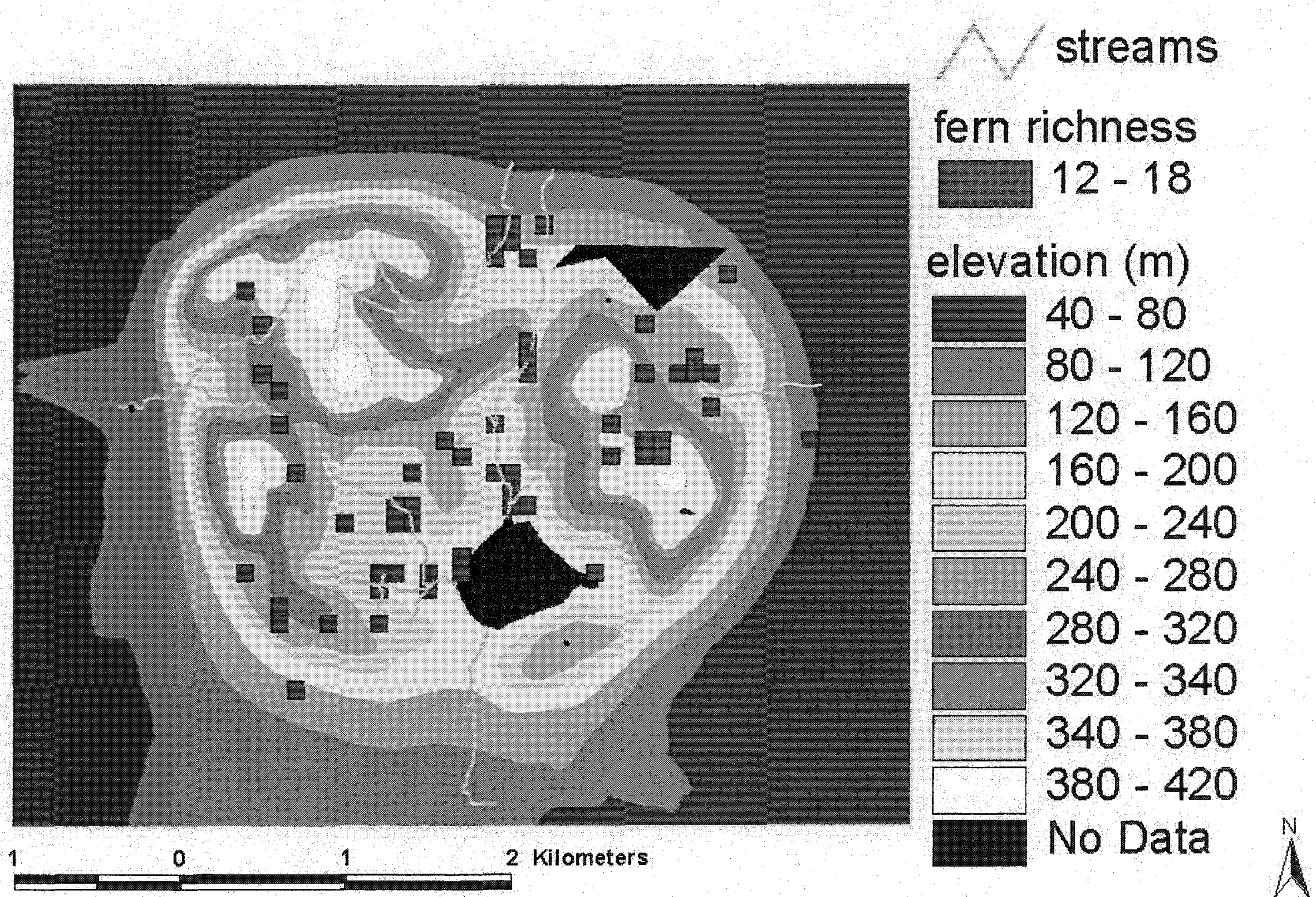
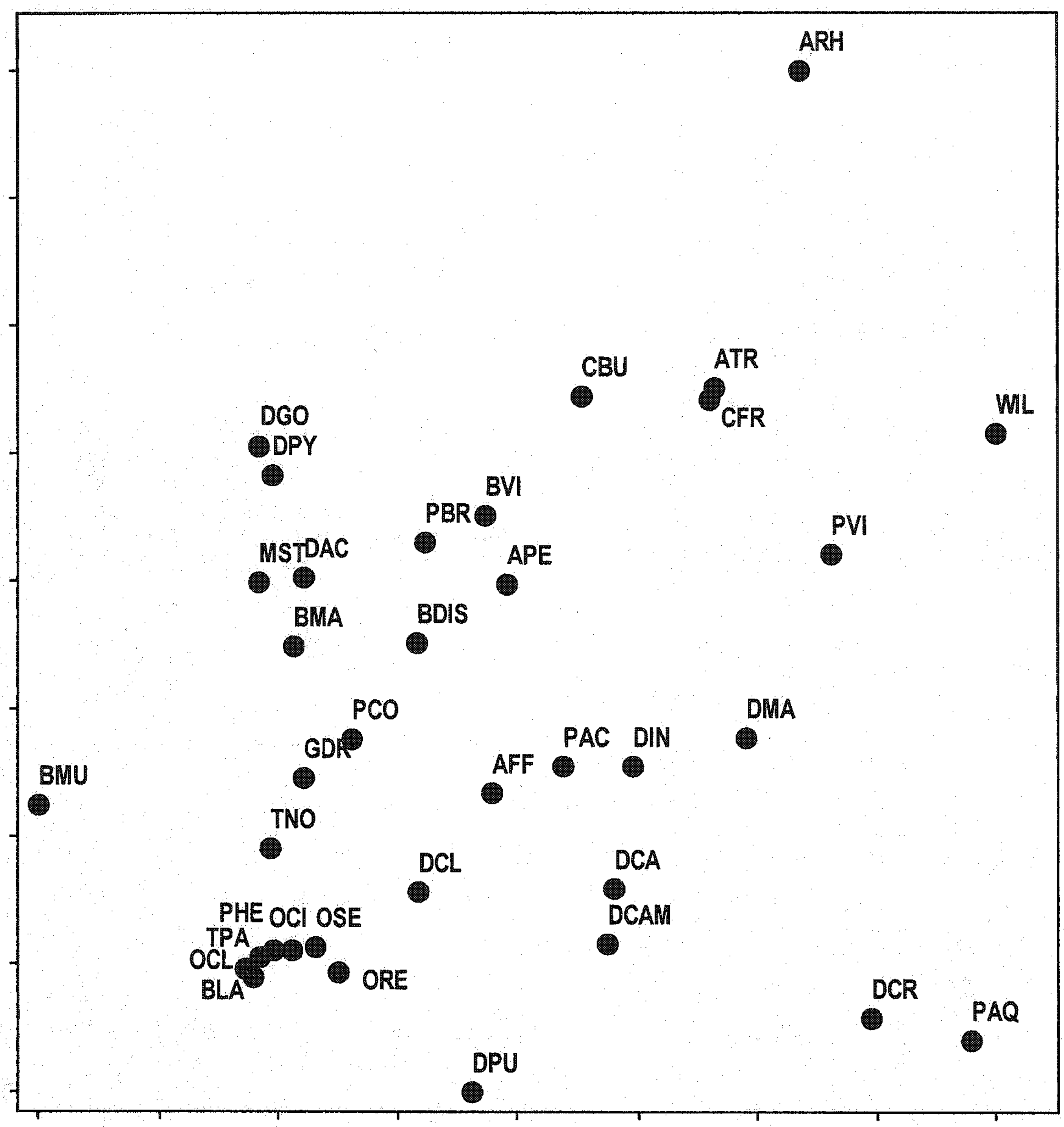

streams
fern richness
12 - 18
elevation (m)
40 - 80
80 - 120
120 - 160
160 - 200
200 - 240
240 - 280
280 - 320
320 - 340
340 - 380
380 - 420
No Data
N
1
0
1
2 Kilometers

Table 1-1: Habitats and environmental preferences of fern species present at Mont Saint-Hilaire, Quebec. Compiled from Flora of North America Editorial Committee (1993), Gleason and Cronquist (1991) and Wherry (1942).

Fern species	Habitat	Family
Asplenium trichomanes	moist sheltered places in rocks; calcareous substrates	Aspleniaceae
Asplenium rhizophyllum	shaded, usually moss-covered boulders and ledges, rarely on fallen tree trunks; usually on limestone or other basic rocks, but occasionally on sandstone or other acidic rocks	Aspleniaceae
Dennstaedtia punctilobula	rocky slopes, meadows, woods, stream banks and roadsides; acidic soils	Dennstaedtiaceae
Pteridium aquilinum	barrens, pastures, open woodland; moderate to strong acid soil	Dennstaedtiaceae
Athyrium filix-femina	moist woods, swamps, thickets	Dryopteridaceae
Cystopteris bulbifera	cracks and ledges on cliffs, rarely terrestrial; usually on calcareous substrates	Dryopteridaceae
Cystopteris fragilis	moist, mostly wooded slopes, mostly on cliff faces, also on thin soil over rock	Dryopteridaceae
Deparia acrostichoides	rich moist woodlands, often on slopes; soil often subacid	Dryopteridaceae
Diplazium pycnocarpon	moist woods and slopes; neutral soils	Dryopteridaceae
Dryopteris campyloptera	cool, rocky woods; soil acidic	Dryopteridaceae
Dryopteris carthusiana	swampy woods, moist wooded slopes, stream banks and conifer plantations	Dryopteridaceae
Dryopteris clintoniana	swampy woods	Dryopteridaceae
Dryopteris cristata	swamps, swampy woods or open shrubby wetlands	Dryopteridaceae
Dryopteris goldiana	dense moist woods, especially ravines, limey seeps or at edges of swamps	Dryopteridaceae
Dryopteris intermedia	moist rocky woods, especially hemlock hardwoods, ravines and edges of swamps; soil circumneutral or subacid	Dryopteridaceae
Dryopteris marginalis	rocky wooded slopes, and ravines, edges of woods, stream banks and road banks, rock walls; indifferent to reaction but often in subacid soil	Dryopteridaceae
Gymnocarpium dryopteris	cool, coniferous and mixed woods at base of shale talus slopes	Dryopteridaceae
Matteuccia struthiopteris	rich woods, often in alluvial or mucky swamp soil	Dryopteridaceae
Onoclea sensibilis	open swamps, thickets, marshes or low woods, sunny or shaded locations; thriving in circumneutral but tolerating moderate acidity	Dryopteridaceae
Polystichum acrostichoides	forest floor and shady rocky slopes, open thickets; indifferent to soil reaction	Dryopteridaceae
Polystichum braunii	moist places in boreal forests and interior moist woods, uplands and rock ledges; circumneutral soil	Dryopteridaceae
Woodsia ilvensis	cliffs and rocky slopes, found on a variety of substrates including serpentine	Dryopteridaceae

Fern species	**Habitat**	**Family**
Botrychium dissectum	open grassy areas to deep forest	Ophioglossaceae
Botrychium lanceolatum	shaded woods	Ophioglossaceae
Botrychium matricariifolium	old fields, humus-rich soil in woods and thickets; soil subacid or circumneutral	Ophioglossaceae
Botrychium multifidum	mainly in fields, open woods; acidic soils	Ophioglossaceae
Botrychium virginianum	shaded forests and shrubby secondary growth	Ophioglossaceae
Osmunda cinnamomea	moist areas, frequent in vernal seeps; soils mediacid	Osmundaceae
Osmunda claytoniana	open moist woods and margins of swamps; subacid or neutral soils	Osmundaceae
Osmunda regalis	swamps, bog-margins, moist woods and springy slopes; soils mediacid	Osmundaceae
Polypodium virginianum	cliffs and rocky slopes on a variety of substrates	Polypodiaceae
Adiantum pedatum	rich, deciduous woodlands, often on humus-covered talus slopes; indifferent to soil reaction but luxuriant in low acidities	Pteridaceae
Phegopteris connectilis	rocks in shaded, moist rock crevices; strongly to moderately acidic soil	Thelypteridiaceae
Phegopteris hexagonoptera	moist woods and thickets; soils usually subacid	Thelypteridiaceae
Thelypteris noveboracensis	terrestrial, in moist woods, especially near swamps, streams in vernal seeps of ravines; usually in subacid soils	Thelypteridiaceae
Thelypteris palustris	terrestrial in swamps, bogs and marshes also along riverbanks and roadside ditches and wet woods; thrives in soil of low acidity	Thelypterdiaceae

Figure 1-2: Detrended correspondence analysis ordination of Mont Saint-Hilaire fern species based on the 1996 survey for presence of ferns in each hectare (Bell, Lechowicz and Waterway, unpublished; extent = 1015 hectares; grain = 1 ha). See Appendix A, for species abbreviations. Ordination was performed using PC-ORD 4.0 (McCune and Mefford, 1995).


ARH
CBU
ATR
CFR
WIL
DGO
DPY
BVI
PBR
PVI
MST
DAC
APE
BMA
BDIS
PCO
DMA
PAC
DIN
GDR
AFF
BMU
TNO
DCL
DCA
PHE
OCI
OSE
DCAM
TPA
OCL
BLA
ORE
DCR
PAQ
DPU

both species are noted to occur in sheltered crevices on rocks (see Table 1-1). Conversely, other species such as, *Dryopteris goldiana* and *Dryopteris clintoniana*, which would be expected to be close in ordination space based on their similar habitat descriptions, occur in different hectares and consequently are far apart. There is a group of seven species tightly clustered in ordination space (*Botrychium lanceolatum*, *Osmunda claytoniana*, *Osmunda cinnamomea*, *Osmunda regalis*, *Thelypteris palustris*, *Phegopteris hexagonoptera*, and *Onoclea sensibilis*). All of them, except *Botrychium lanceolatum* and *Phegopteris hexagonoptera,* could be loosely termed as preferring wet habitats, and at this scale it is not possible to ecologically separate them by ordination. Are they ecologically equivalent, or do we just need to adjust our focus (i.e. decrease the scale)?

At the hectare level, relationships of ferns and the environment can be shown, but they are not necessarily useful in explaining niche differences. For example, other research on MSH shows that fern species richness was negatively correlated with insolation and positively correlated with the mean and variance of an index for soil water retention (but, similar results were also generated by a neutral community model; Bell, Lechowicz and Waterway, submitted). When we turn to explain the distribution of each fern species, however, these variables will not necessarily predict the presence or absence of a fern species within a hectare. Within each hectare the environment is treated as homogenous, and the fern distribution within these hectares is not considered. In reality, the type of environment that each fern responds to, may not be representative of an environment "averaged" by an entire hectare (e.g. solar radiation of the hectare), but in fact may be at much smaller grains, such as at metres. Similarly, information on only the presence of a fern in a hectare may not be as useful in determining niche separation as information on where in the hectare the fern occurs (i.e. the type of environment). As well, differences within a single habitat (e.g. marshes) may prove to be important to detect niche differences among ferns.

Environmental preferences of ferns occurring on Mont Saint-Hilaire

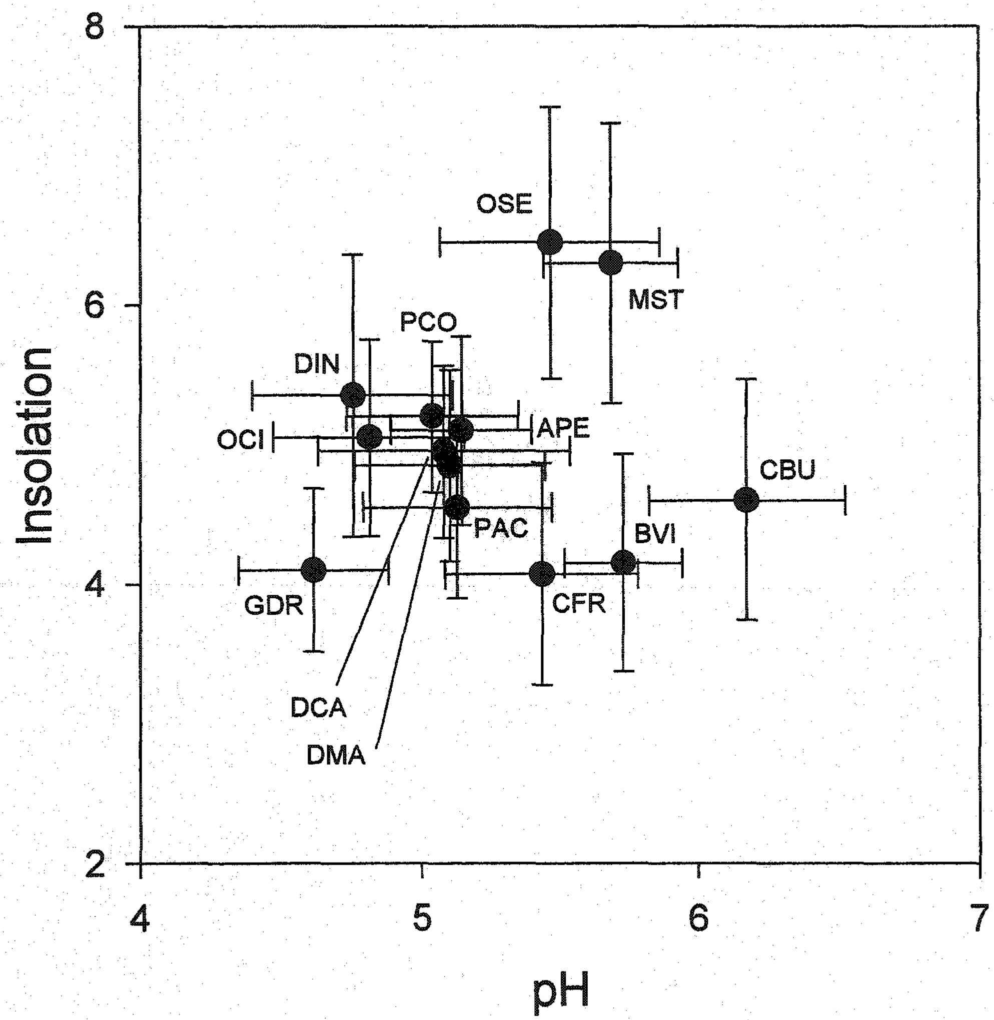
Distinct environmental affinities at the fine-scale for ferns of MSH are evident. In 2000, a characterization of the abiotic environmental conditions of selected ferns was performed (see captions on Figure 1-3 and 1-4 for methods). By incorporating different axes relating to soil conditions, niche partitioning was apparent. Fern species appeared to fall along pH and insolation gradients, with some niche overlap on each of the axes (Figure 1-3). *Cystopteris bulbifera* preferred the most alkaline soil and *Gymnocarpium dryopteris*, the least. *Onoclea sensibilis* and *Matteuccia struthiopteris* are found in areas of generally high insolation and *Cystopteris fragilis* in low light areas. Global radiation on north and south facing slopes of MSH has been found to lead to differential spring snow melt resulting in increased soil moisture on northern slopes (Rouse and Wilson, 1969). Therefore, insolation values may be related to soil moisture, but fine-scale topographical variability may discount this relationship for the fern habitats surveyed.

There is a cluster of four species (*Phegopteris connectilis*, *Dryopteris carthusiana*, *Adiantum pedatum* and *Dryopteris marginalis*) that seemingly occupy the same position in environmental space. However, when plotted against soil nitrate concentrations, the four species separate in their preferences (Figure 1-4). *Dryopteris marginalis* prefers the most nitrate-rich soils and *Phegopteris connectilis*, the least.

Some of the species environmental affinities agree with previous knowledge cited in floristic guides. For example, *Cystopteris bulbifera* was found on alkaline soil, which agrees with its tendency to be found at higher pH soils (see Table 1-1). *Onoclea sensibilis* has been noted to occur in sunny locations (see Table 1-1), which also agrees with these results. However, the environmental preferences shown for other species, such as *Matteuccia struthiopteris*, *Phegopteris connectilis*, and *Dryopteris marginalis* do not fit into the previous characterizations, only because the information is unavailable on their preferences for soil nitrate concentrations and

Figure 1-3: Mean and 95% confidence interval values of insolation and pH for common fern species of Mont Saint-Hilaire, Quebec[1]. APE= *Adiantum pedatum*, BVI= *Botrychium virginianum*, CBU= *Cystopteris bulbifera*, CFR= *C. fragilis*, DCA= *Dryopteris carthusiana*, DIN= *Dryopteris intermedia*, DMA= *D. marginalis*, GDR= *Gymnocarpium dryopteris*, MST= *Matteuccia struthiopteris*, PAC= *Polystichum acrostichoides*, PCO= *Phegopteris connectilis*, OCI= *Osmunda cinnamomea*, and OSE= *Onoclea sensibilis*

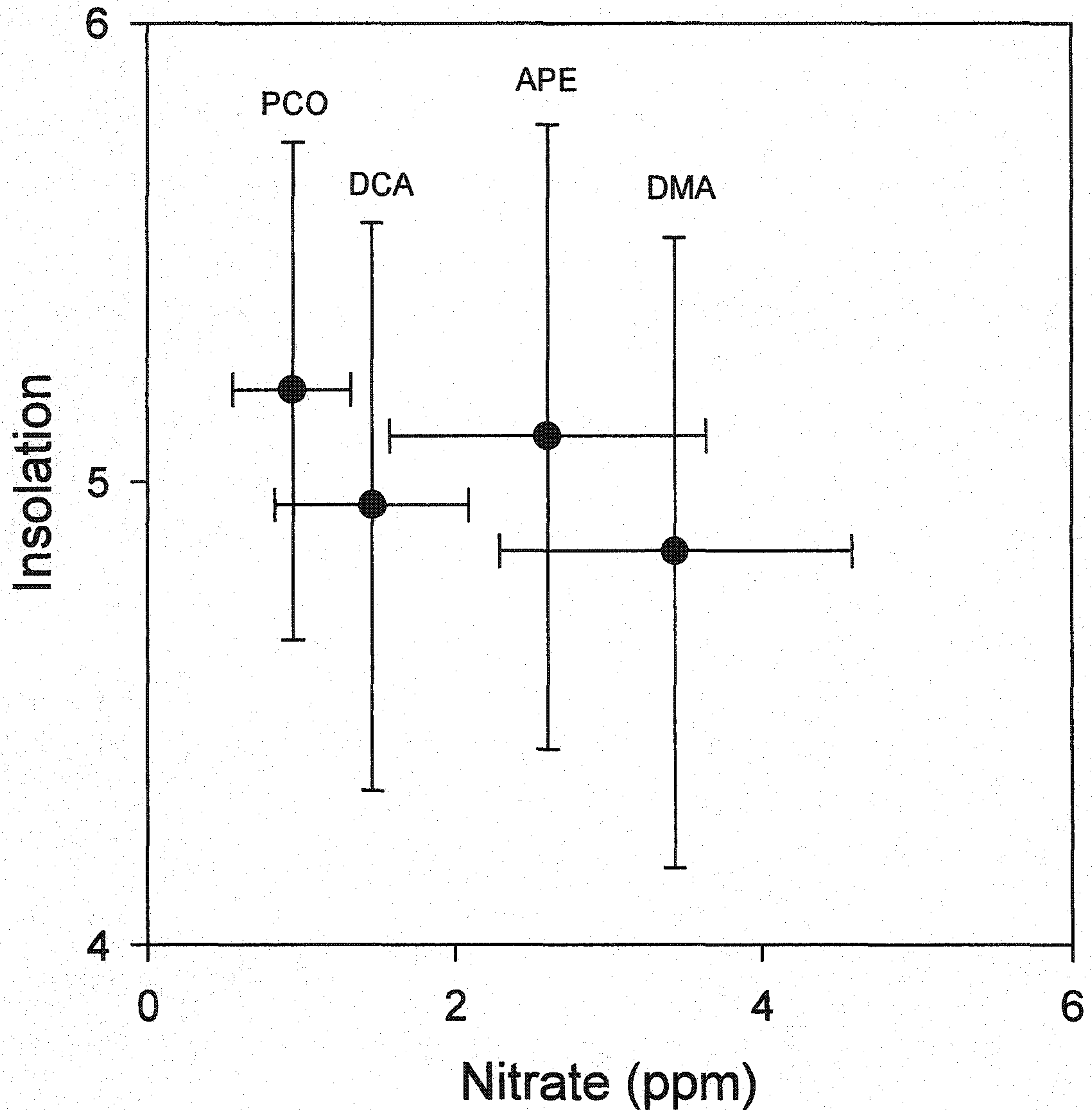
[1]In summer 2000, thirteen ferns were chosen based on their abundances on Mont Saint-Hilaire. Twenty randomly chosen sites for each species were characterized (fourteen for *Cystopteris fragilis*) with respect to environmental conditions. Sites among individuals within a species were at least 30 m apart. Soil pH was analyzed based on soil samples collected within 25 cm of the individuals. Soil samples were collected by removing leaf litter and taking approximately 500 ml of soil from the top 8 cm of the soil profile with a trowel. Soil samples were stored in Ziploc plastic bags and were refrigerated at 4 degrees Celsius until ion analysis. The soil was left unrefrigerated for 24 hours, mixed thoroughly and 20 ml of soil was added to 100 ml of distilled water and left for approximately thirty minutes. Soil pH was measured with a Fisher silver chloride pH probe connected to a Fisher AR 25 Ion meter. Insolation was estimated by two independent observers at each of the sites on a scale of 1-10, 10 being no canopy cover and 1 being closed canopy.



8
6
4
2
4
5
6
7
pH
Insolation
OSE
MST
PCO
DIN
APE
OCI
CBU
PAC
BVI
GDR
CFR
DCA
DMA

Figure 1-4: Mean and 95% confidence interval values of insolation and nitrate for common fern species of Mont Saint-Hilaire, Quebec showing evidence of four fern species (APE= *Adiantum pedatum*, DCA= *Dryopteris carthusiana*, DMA=*D. marginalis*, PCO= *Phegopteris connectilis*) separating on a soil nitrate gradient[1].

[1] See Figure four for description of methods used for sampling, collecting, storage and preparation of soil samples. Soil nitrate was measured with an Orion nitrate electrode (model 93-07) with an Orion Ag/AgCl double junction reference electrode (model 90-02), both connected to a Fisher AR 25 Ion meter. Two ml of Orion ionic strength adjuster (Orion catalogue number 13-641-850) was added to the sample and mixed for the duration the probes were immersed. Insolation was estimated by two independent observers at each of the sites on a scale of 1-10, 10 being no canopy cover and 1 being closed canopy.


PCO
APE
DCA
DMA
Insolation
6
5
4
0
2
4
6
Nitrate (ppm)

insolation. The separation on the environmental gradients shown here has not been examined, which reflects a need to better understand fern environmental tolerances.

Evidence suggests that some ferns do show consistent environmental preferences from one locality to another. The grain the environment is measured at may obscure these preferences, however. Are these demonstrated environmental preferences important in determining the community composition of ferns? Is there consistency between environmental affinities over scale? If fine-scale environmental heterogeneity can be mapped on to the distribution of ferns, niche partitioning would be concluded as underlying a community of ferns. A fine-scale survey will examine the role of microhabitats in fern species occurrence. In Chapter Two, further investigations on one fern-rich hectare, using more rigorous techniques, will more decisively answer if niche partitioning is evident within a community of ferns.

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Chapter 2

Fine-scale niche partitioning within a community of ferns

Introduction

Consideration of environmental preferences among fern species suggests that ferns partition resources in the environment (cf. Chapter One). At large spatial scales, the ranges of ferns differ, most likely reflecting broadly different climatic tolerances. Regional assemblages are discernible at the continental scale where groups of fern species share more or less similar ranges. An example is the set of eastern North American ferns, many of which occur at Mont Saint-Hilaire. Within any region there appears to be segregation among species with and among different habitats (e.g. forest versus marsh). In addition, evidence has shown that ferns have distinct environmental preferences (e.g. preferences for low versus high soil pH) that are species-specific and consistent from one locality to another.

With regards to the niche concept, species occurring together in an area should differ on at least one environmental axis in niche space. At a large spatial scale, fern species occurring in North America can be considered to differ on a niche axis representing climatic tolerances, but this is not the scale where competitive exclusion might lead to niche segregation. At the scale of a locality on Mont Saint-Hilaire, partitioning on niche axes representative of larger scale factors such as climate and history would be the same for different species. Niche-assembly rules only would dominate at finer-scales, where species in a locality may be engaged in competitive interactions. Species should differ on niche axes reflecting the fine-scale environment (e.g. soil moisture or chemistry).

Alternatively, species may be identical in niche space and their distribution and abundance may only reflect the chance arrival of one species in a locality before the next. The arguments for dispersal dominating community structure in this way are not trivial. According to the neutral theory of biodiversity (Hubbell, 2001; Bell, 2000), patterns in species distribution and abundance are disconnected from patterns in the environment. Random dispersal, chance and history are supposed to underlie patterns of species distribution and abundance in a dispersal-assembled community. If we can assume that in a locality, no species are dispersal limited, then the importance of niche-assembly rules alone can be tested directly. The spatial coincidence of numerous species with the environment would indicate species-specific adaptation, and suggest that the community is governed by rules of niche-assembly.

We in fact expect ferns to show patterns indicative of niche-assembly, i.e. they will respond to the environment in a way that reflects their distinct differences in performance along resource gradients. Within a locality, the high-dispersal capacity of fern spores (cf. Introduction) ensures that dispersal is unlikely to limit species distribution. The Botany Bay site itself is surrounded by many hectares that also contain species found in the study site, which further augment spore dispersal to and within the site (Bell, Lechowicz and Waterway, unpublished data). It is reasonable to set aside dispersal-limitations as an explanation of the distribution and abundance of ferns at this locality and to focus on a test of niche-assembly.

According to niche theory, ferns should segregate along resource gradients. In particular, at the community level, where all fern species potentially interact, each fern should occur in a microhabitat which reflects its environmental affinity. If the occurrence of many different fern species can be attributed to differences in the environment, it would be unlikely that this is due to mere chance. Such ecological separation between species on resource gradients can be quantitatively assessed by ordination methods (Jongman *et al.*, 1995), and GIS can evaluate the spatial coincidence of fern distribution with environmental variability. These are the approaches that will be used to evaluate the likelihood that niche-assembly rules organize the fern community in the Botany Bay hectare at Mont Saint-Hilaire.

Ordinations are a set of tools to segregate species into an ecological space of reduced dimensions. Indirect ordinations are based on the similarities of species distributions among plots; afterwards environmental measurements are correlated with the plot ordination scores to infer environmental gradients. Alternatively, the species (and site) scores can be constrained by a multiple regression of the environmental variables, as in the case of direct ordination methods. Results from both methods will yield species positioned in ordination space. Species that are farther apart are considered more ecologically different than species close together (Jongman *et al.*, 1995).

GIS is a tool to overlay maps describing different characteristics for a space. In doing so, the spatial coincidence of characteristics of the overlaid maps can be examined. In particular, the spatial coincidence of species occurrences with measurements of the environment can be demonstrated. This can provide two pieces of information; first, an indication that in fact, species distributions can be correlated with variability in the environment, and second, the environmental constraints of the species distribution.

Choice of scale will affect the interpretation of results from both ordination and GIS mapping, depending on the heterogeneity of the plots. Bellehumeur *et al.* (1997) found that when sampling grain was increased and extent remained constant, the variance of tree densities in 50 ha of tropical rain forest decreased, and the range of autocorrelation increased, "thus increasing the proportion of the spatially structured component with a range greater than the size of sampling units". The grain of plots also changed the relationship of plant abundances to soil environmental variables as reported by Palmer (1990), which found that although soil calcium was strongly related to variation in plant community compositions at larger scales (0.1 ha), the relationship did not hold for finer scales ($2m^2$). Similarly, Reed *et al.* (1993) showed that the results of vegetation analyses (ordinations) were dependent on scale. Indeed, the perception of species-richness itself, also changes with scale (Palmer and White, 1994), suggesting that many patterns seen in ecology are scale-dependent.

In this chapter, I will test for niche partitioning between fern species from a single locality using ordination techniques. Both indirect and direct ordinations will be used to show ecological differences between the ferns. Important environmental factors and their spatial structure will be identified. To test for niche partitioning between fern species at fine spatial scales, a comparison of the species associations from the two types of ordinations will be made to those reported in the existing literature. In addition, a series of ordinations run at different grains will assess if these associations are scale-dependent. Maps are the best medium to depict and to help understand spatial variation: therefore GIS also will be used to illustrate and confirm patterns suggested by the ordination results.

Methods

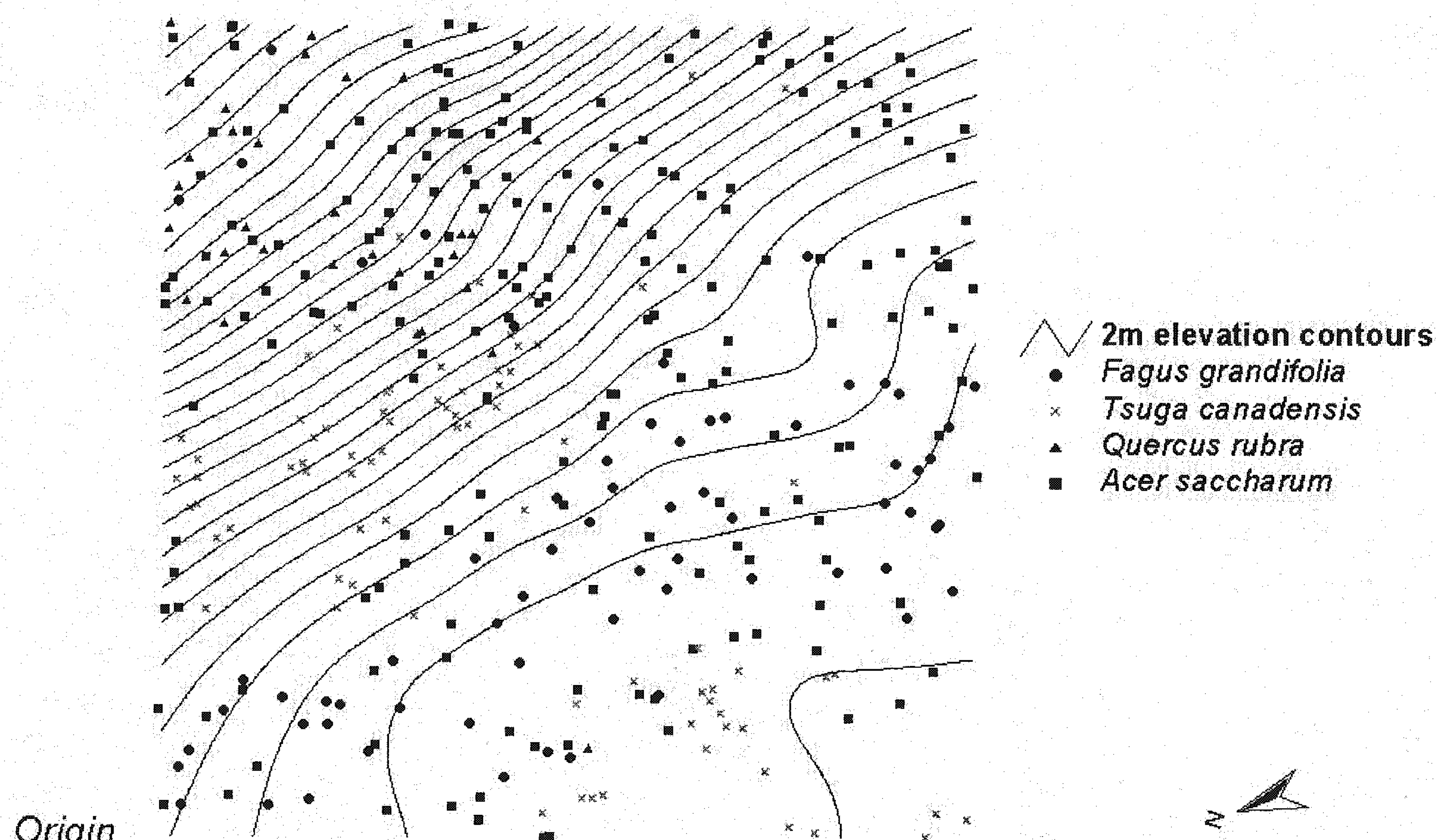
Survey

The survey took place in the summer of 2000, in the SI/MAB hectare (Botany Bay) located at Mont Saint-Hilaire (MSH) (45°32' N, 73°8' W), Quebec. The reader is referred to the thesis Introduction for a description of MSH. A mountain-wide survey in 1996 had found that Botany Bay was one of the most fern-rich hectares on MSH, with 18 of the 36 fern species found on the mountain in this single hectare (Bell, Lechowicz and Waterway, unpublished data; Figure 1-1). The hectare itself consists of wet, flat terrain in the west corner and a steep, rocky slope in the east corner (Figure 2-1).

The hectare had been previously divided into 100-10 x 10 m plots. These 100 m^2 plots were surveyed in projected map view, which resulted in somewhat irregular sized plots on the ground, as the topography is quite steep in places. The effective lengths of the plot sides varied from 9 to 12 m. To adjust for the irregularities of the plots, the north-south and east-west edges (the origin was taken at the north corner) were removed to form consistent 8 x 8 m plots as surveyed on the ground. The result was an array of 100-8 x 8m not quite contiguous plots within the hectare. This adjustment was performed on the data itself, and not at the time the hectare was being surveyed; the full record of ferns in each of the 10 822 square metres in the hectare are available in appendix C (file:2000survey.xls).

Similar to methods used by Richard *et al.* (2000), each square meter of the hectare was surveyed for percent cover of fern species and ground cover including

Figure 2-1: Topography of Botany Bay hectare (Mont Saint-Hilaire, Quebec) shown by 2m contour intervals. Also shown are stems of common tree species (*Acer saccharum*, *Fagus grandifolia*, *Tsuga canadensis* and *Quercus rubra*) (>10 cm dbh).


2m elevation contours
Fagus grandifolia
Tsuga canadensis
Quercus rubra
Acer saccharum
N
Origin

rock, woody debris (sticks and stumps), tip-up mounds, standing water, mud and path cover. Also within each square meter, soil depth was measured using a 50 cm probe hatched at one-centimetre intervals.

Each 8 x 8m plot was divided into four quarters. For each "quarter", three random soil samples were collected by removing leaf litter and taking approximately 500 ml of soil from the top 8 cm of the soil profile with a trowel. These samples were pooled to form one soil sample per quarter, for a total of 400 samples for the entire hectare. Soil samples were stored in Ziploc plastic bags and were refrigerated at 4 degrees Celsius until ion analyses. In preparation for the ion analyses, the soil was left unrefrigerated for 24 hours, and then combined thoroughly. Twenty ml of the soil was then mixed with 100 ml of distilled water and the mixture was left for approximately thirty minutes. Soil pH and nitrate concentrations were measured simultaneously; pH was measured with a Fisher silver chloride pH probe and nitrate was measured with an Orion nitrate electrode (model 93-07) combined with an Orion Ag/AgCl double junction reference electrode (model 90-02), all connected to a Fisher AR 25 Ion meter. Two ml of Orion ionic strength adjuster (Orion catalogue number 13-641-850) was mixed into each sample and mixed with a 1-cm stir bar for the duration in which the probes were immersed.

In addition to the soil sampling, soil moisture was measured in each "quarter" within the hectare. Soil moisture was measured twice in the season, once in early August, the other in mid-September using a Delta-T Devices theta probe (type ML2x, Cambridge, England). Due to the wet conditions in the west corner of the hectare, the voltage, rather than percent soil moisture was measured over the entire hectare (the relationship between voltage and soil moisture is non-linear at values greater than 1.0V). Voltage was measured in three random locations (including non-soil areas, which were considered to have 0% soil moisture) within a quarter which were then converted into percent soil moisture. Values below 1.0 V were converted using the formulae outlined by Delta-T Devices (1999). Voltage values above 1.0 were interpolated using the conversion Table provided in the "Theta probe-soil moisture sensor type ML2x User Manual". Mean soil moisture was calculated taken from the six readings (three random readings in August plus three random readings from September) for each quarter.

Ordination analysis: Direct ordination

All direct ordinations were performed using CANOCO 4.0 (ter Braak and Smilaurer, 1998). A canonical correspondence analysis (CCA) ordination was performed on data aggregated in the plot "quarters" ($16m^2$). Rare species were downweighted, and Hill's scaling, focusing on inter-species distances, was selected. In addition to performing a "standard" CCA, the spatial structure of environmental variables was measured. Recognizing spatial structure is important as the assumption of statistical independence can be violated due to spatial autocorrelation. As well, the identification of spatial structure in ecological data may detect underlying processes that are not easily measured (e.g. predation, competition and past disturbances; Borcard *et al.*, 1992). Borcard *et al.* (1992), using CCA, suggested a way to partition the variation in species abundance data into independent components. With this partitioning, the effect of the environment on species abundance can be obtained as well as that generated by spatial structure, spatially structured environmental variation, and undetermined processes. In this way, the proportion of species abundance variation that can be attributed to environmental effects (as opposed to neutral processes) can be determined. However, this undetermined component would also include missing environmental factors and/or more complex spatial structure. Three different matrices were required for the ordinations: a species data matrix comprised of the abundance of species in each of the quarters, an environmental data matrix, composed of measured environmental variables and a spatial data matrix, made up of geographical coordinates.

Four hundred quarters with percent cover for each of the fern species, comprised the species matrix (cover values of the square meters were summed). The environmental matrix was formed by the surveyed environmental variables for each

$16m^2$ quarter of the hectare (400 quarters in total) and included: log transformed mean soil moisture (LAVGH2O), the coefficient of variation of soil moisture within the quarter (based on the six measurements from August and September)(CVH2O), log transformed soil nitrate concentration (ppm) (LNO3), soil pH (pH), log transformed percent rock cover (LROCK), and log transformed median soil depth (up to 50 cm) (LDEPTH).

In addition to the ground level measurements of the environment, canopy conditions were also described. All trees and saplings had been surveyed in the hectare two years prior to the survey, providing a rich inventory of canopy conditions for the hectare after a catastrophic ice storm in 1998 (Duguay *et al.*, 2001). The 'inverse distance weighted interpolation' in the spatial analyst extension of ArcView 3.2 was used to calculate interpolated values of canopy conditions for each quarter. Using survey data collected in 1999, the second summer following the ice storm, the following variables were calculated: a tree canopy damage value based on a 1-5 scale (5 = most damage) of trees greater than 10 cm dbh (refer to Duguay *et al*, 2001 for details of survey), and dbh of each of the four most common tree species (*Acer saccharum*, (ACER) *Fagus grandifolia* (FAGUS), *Quercus rubra* (QUERCUS) and *Tsuga canadensis* (TSUGA)) (see Figure 2-1 for tree distribution within the hectare). The objective of interpolating tree canopy damage was to assess whether ferns respond to gap conditions created by the ice storm. Interpolation of dbh was to obtain an estimate for the canopy cover of tree species (it is assumed that a higher dbh will produce more canopy cover). Only common species were chosen under the assumption that the environmental conditions created by rare tree species would be unpredicTable and have an insignificant effect on the fern distribution. All environmental variables were tested for significance in explaining species abundance, using a forward selection procedure (based on Monte Carlo test, 999 permutations).

The spatial matrix was created from the geographical coordinates (x,y) of the centre of each quarter. It was completed by "adding all terms for a cubic trend surface regression of the form" (Borcard *et al.*, 1992):

Equation (1): $z = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$

Each of the terms was input as an interaction in CCA and 'forward selection of explanatory variables' was performed to extract the significant terms of Equation (1)(Monte Carlo test, 999 permutations). All terms, excluding 'b_6x^3', were retained and used in the spatial data matrix.

A preliminary detrended correspondence analysis (Hill and Gauch, 1980) ordination was run on the species data matrix to test for the length of gradients. Axis one was found to have a length of 4.89, which indicated that further ordinations should be run in a unimodal context (i.e. CCA as opposed to redundancy analysis (RDA)). To dissect the percentage of variation explained by the environmental variables into its components, the sum of all canonical eigenvalues (sum of all eigenvalues in the case of correspondence analysis) was obtained by the following five ordinations:

1. CCA of the species matrix constrained by the environmental matrix
2. CCA of the species matrix constrained by the environmental matrix, after removing the effect of the spatial matrix (pure environmental)
3. CCA of the species matrix constrained by the spatial matrix
4. CCA of the species matrix constrained by the spatial matrix, after removing the effect of environmental variables (pure spatial)
5. Correspondence analysis (indirect gradient analysis, unimodal context) of the species matrix (eigenvalue represents the total explained variation)

To obtain the spatially structured environmental variation, the difference between the canonical eigenvalues from ordinations 1 and 2 were used (note that the difference between the eigenvalues of ordinations 3 and 4 could have also been used). From these ordinations, the relative contributions to the variation in species data were obtained using steps outlined in Borcard *et al.* (1992). The global significance of

CCA ordinations was determined by a Monte Carlo permutation test (999 permutations).

Ordination analysis: Indirect ordinations

Each square meter was aggregated into larger units at three different grains: $4m^2$, $16m^2$ and $64m^2$. Detrended correspondence analysis ordinations using PC-ORD 4.0 (McCune and Mefford, 1995) were run on species abundance matrices for the three different grains. Rare species were downweighted in each case. This type of ordination was used as only information on the environment was collected at one of the scales (i.e.$16m^2$).

GIS analysis

Map layers were created based on the ordination results of correlation and significance between environmental axes with species abundance. Only fern species that represented greater than 0.05% total percent cover of the entire hectare were illustrated (AFF, APE, CBU, DAC, DCA, DMA, GDR, OSE, OCI and PAC (see Results)). This threshold also corresponds to a significant drop in observed species occurrence. Individual species abundance was depicted using the interpolated surface function in the spatial analyst extension of Arc View 3.2 to create contours of 2% cover intervals for all species (except AFF and DAC, where 5% cover intervals were used). The difference in the depicted contour intervals was chosen for graphical clarity. Interpolated surfaces for specific environmental variables were shown based on inverse distance weighted interpolation, using nearest neighbour data points at the resolution of a $4m^2$. No statistical analysis was performed, however the spatial coincidence of species distribution and abundance is apparent when overlaid with mapped environmental measurements.

Results

Survey

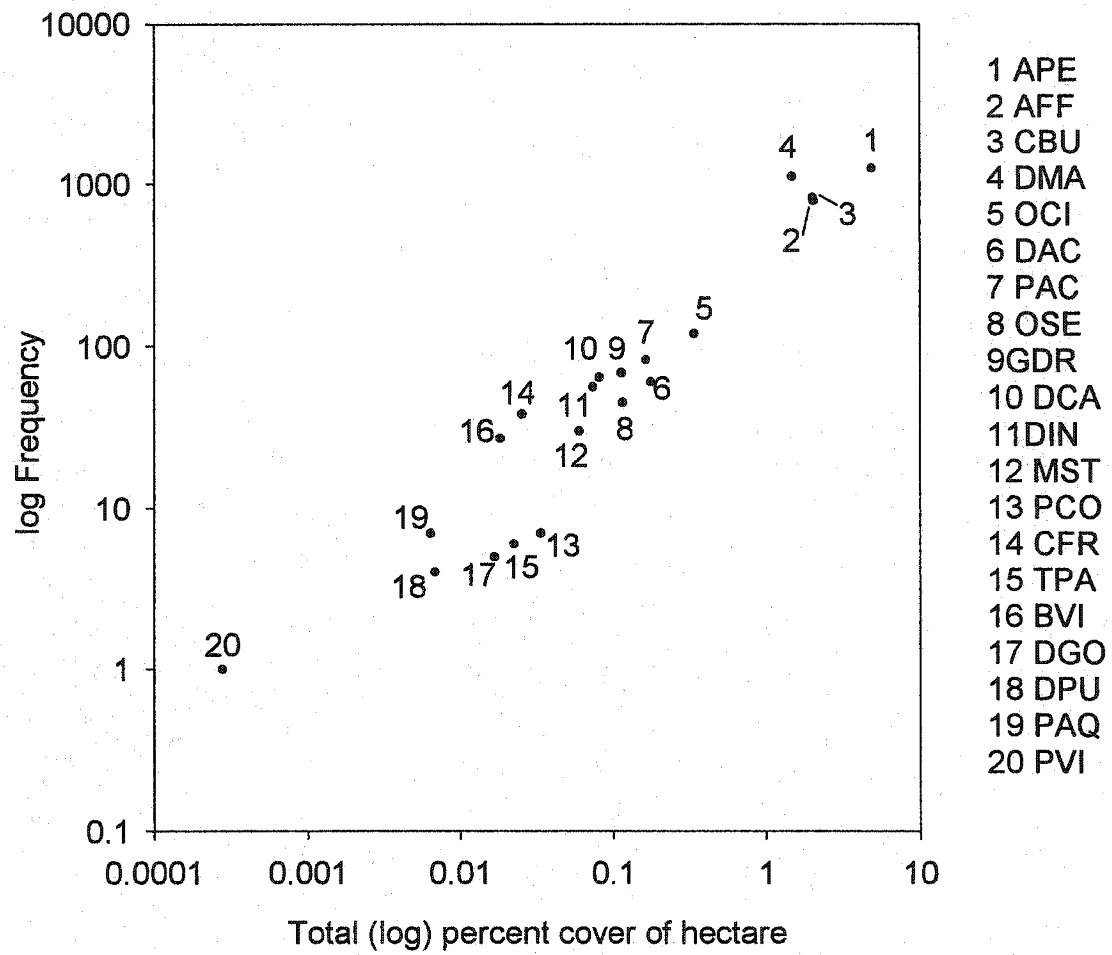
The total coverage of all the fern species in the Botany Bay hectare is approximately 11%. The following ferns were identified: *Athyrium filix-femina* (AFF), *Adiantum pedatum* (APE), *Botrychium virginianum* (BVI), *Cystopteris bulbifera* (CBU), *Cystopteris fragilis* (CFR), *Dennstaedtia punctilobula* (DPU), *Deparia acrostichoides* (DAC), *Dryopteris carthusiana* (DCA), *Dryopteris goldiana* (DGO), *Dryopteris intermedia* (DIN), *Dryopteris marginalis* (DMA), *Gymnocarpium dryopteris* (GDR), *Matteuccia struthiopteris* (MST), *Onoclea sensibilis* (OSE), *Osmunda cinnamomea* (OCI), *Phegopteris connectilis* (PCO), *Polypodium virginianum* (PVI), *Polystichum acrostichoides* (PAC), *Pteridium aquilinum* (PAQ) and *Thelypteris palustris* (TPA). Voucher specimens can be found in the McGill University herbarium. APE, DMA and CBU were the most abundant and PVI, DPU, DGO, PAQ and PCO were the least abundant (Figure 2-2). Fern species richness ranged from 0 to 6 species per quarter. Fern richness was highest in the west corner of the hectare with additional species-rich patches running from the south to north corners of the hectare (Figure 2-3).

Soil conditions in Botany Bay are heterogeneous. General descriptive statistics for each of the surveyed variables are given in Table 2-1. The heterogeneity within the hectare with respect to soil moisture ranged by 90.3 % (mean 31%) and the pH by 3.6 (mean 5.98). The soil nitrate concentration ranged by 25.3 ppm (mean 8.2 ppm). There was also heterogeneity at the plot level ($64m^2$); values for soil moisture, pH and nitrate ranged by 58.5%, 2.5, and 19.8 ppm, respectively.

"Standard" CCA ordination

The CCA ordination diagram shows species scores in 2-D space with the environmental variables represented by biplot arrows. Longer arrows indicate a stronger correlation with the ordination axes, and consequently a closer relation to the pattern of vegetation variation. Small angles between arrows may indicate a positive

Figure 2-2: Abundance (total percent cover) and frequency (number of occurrences) of fern species of Botany Bay, Mont Saint-Hilaire, Quebec.



10000
1000
100
10
1
0.1
log Frequency
0.0001
0.001
0.01
0.1
1
10
Total (log) percent cover of hectare
1 APE
2 AFF
3 CBU
4 DMA
5 OCI
6 DAC
7 PAC
8 OSE
9GDR
10 DCA
11DIN
12 MST
13 PCO
14 CFR
15 TPA
16 BVI
17 DGO
18 DPU
19 PAQ
20 PVI

Figure 2-3: Fern richness of Botany Bay (resolution = $16m^2$) (Mont Saint-Hilaire, Quebec).

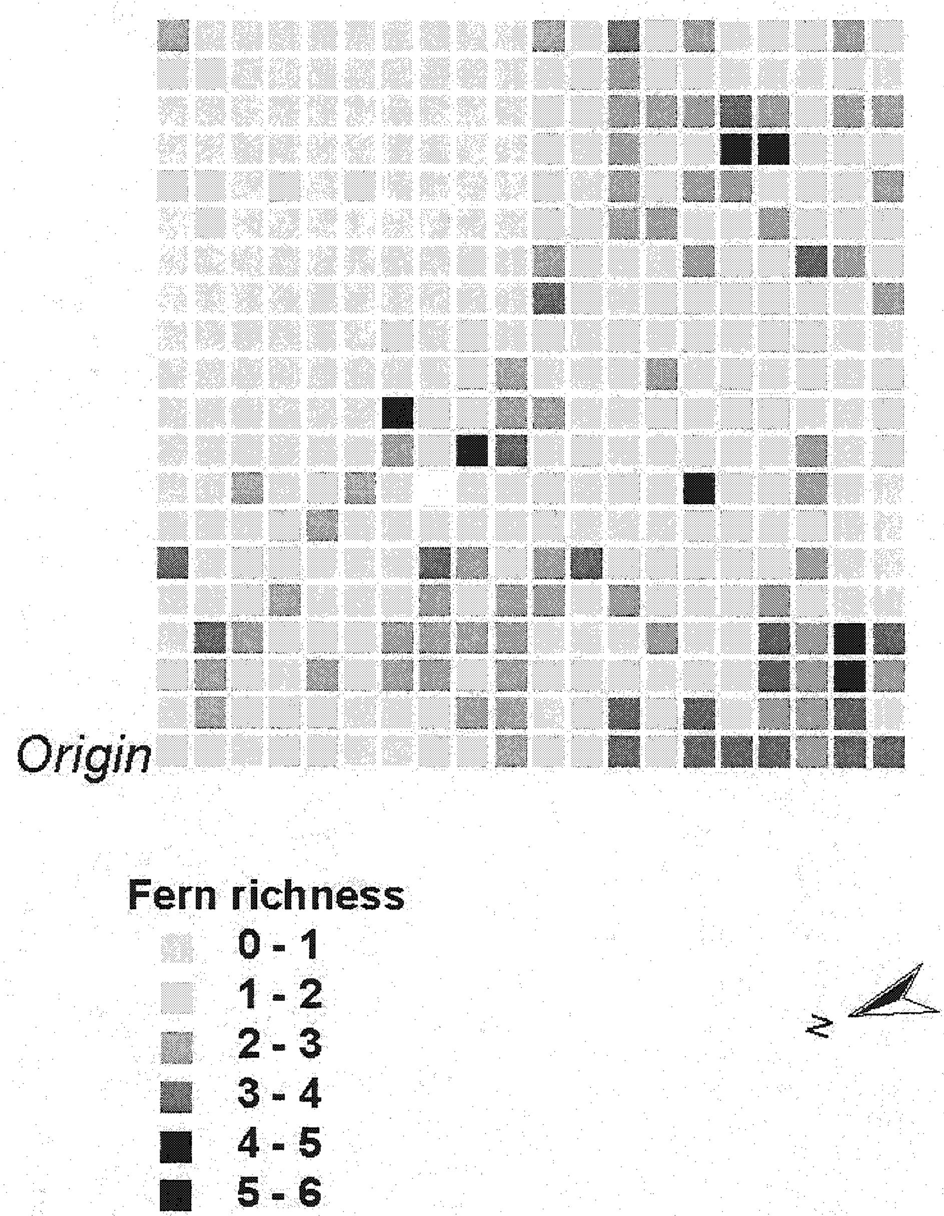

Origin
Fern richness
0 - 1
1 - 2
2 - 3
3 - 4
4 - 5
5 - 6
N

Table 2-1: Summary statistics for Botany Bay hectare (Mont Saint-Hilaire, Quebec) plots ($16m^2$) for ground cover and soil conditions.

Environmental variable	Mean	Maximum	Minimum	Median
Mean soil moisture (%)	30.8	96.1	5.8	26.0
Coefficient of variation of mean soil moisture	37.5	99.3	2.5	35.0
Soil pH	6.0	7.5	3.9	6.0
Soil nitrate concentration (ppm)	8.2	25.5	0.2	8.1
% rock cover	17	98	0	7
% wood cover	13	67	0	11
% path cover	1	25	0	0
% mud cover	2	57	0	0
% tip-up cover	0	22	0	0
% cover of standing water	1	49	0	0
Soil depth (cm)(up to 50 cm)	10	40	0	8

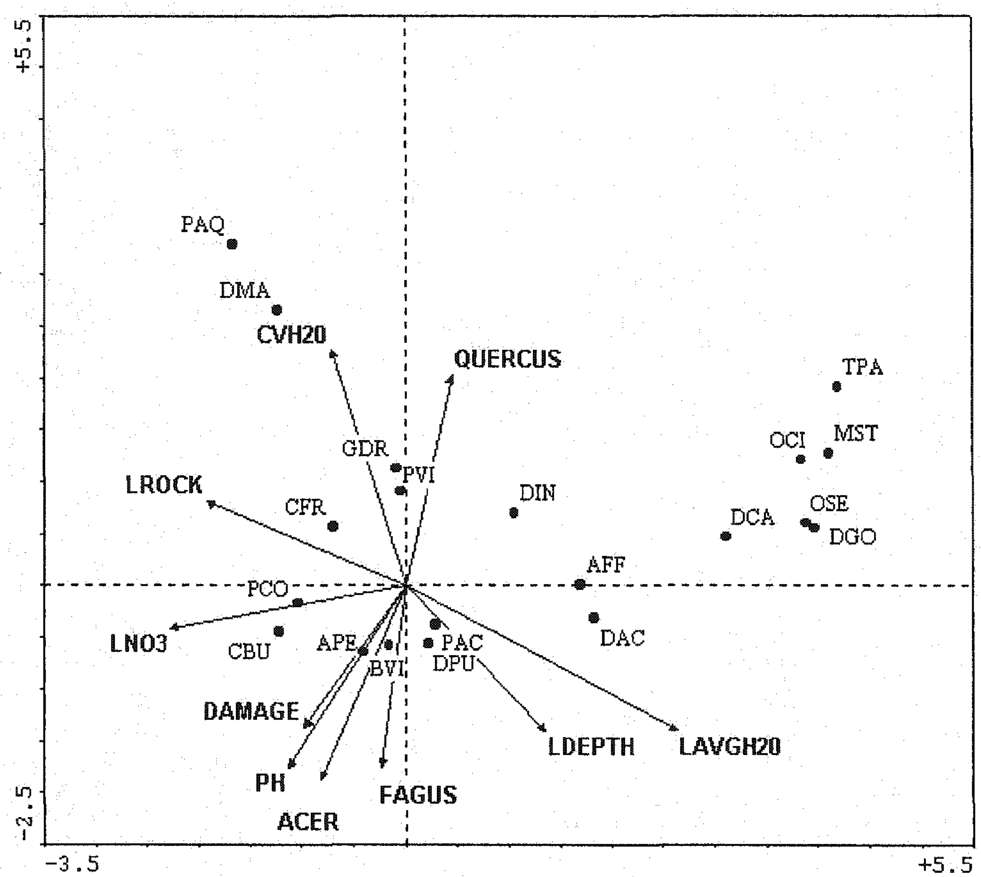
correlation and arrows meeting at right angles may suggest a correlation close to zero between the respective environmental variables (ter Braak and Smilaurer, 1998).

Globally, the available environmental variables are significant (P= 0.001) and they explain 37% of the variance in the species data (Figure 2-4). With respect to axis one, LAVGH2O is the most highly correlated, followed by LNO3. CVH2O is most correlated with axis two, followed by QUERCUS. Tip-ups, path cover, wood and TSUGA were excluded from the analysis as they explained a negligible amount of variance. Standing water and mud were also removed, as it was believed that average soil moisture reflected these values (correlation values of 0.46 and 0.61, respectively).

There are three main groupings of species (Figure 2-4). The first cluster, comprising TPA, OCI, MST, DCA, OSE and DGO occupies soils that are wet, deep, non-rocky and with low nitrate concentration. The second cluster, PAQ and DMA appears at the opposite end of the previous cluster and is related to drier soil, higher soil nitrate concentrations and greater rock cover. The third cluster, CBU, APE, BVI, PAC, DPU, GDR, PVI, CFR, PCO, AFF, DIN and DAC is loosely assembled in the central part of the diagram. CBU, APE and BVI are characterized by relatively higher pH; GDR, DIN, PVI and CFR occupy areas with relatively lower pH and higher QUERCUS cover. AFF and DAC are represented more in the wetter and lower soil nitrate concentration area of the diagram but are not connected with the first cluster of predominantly wet species. Species that prefer rocky sites are PAQ, DMA, CBU, CFR, PCO and PVI. These same species are also in areas of higher soil moisture variability (CVH2O) and QUERCUS cover. The QUERCUS biplot arrow points in the opposite direction of ACER and FAGUS, indicating a negative correlation with coverage by these species.

With consideration of intrageneric differences, DMA, DIN and DCA appear to separate on the LAVGH2O axis, with DMA occupying the very driest areas of the hectare, DIN occupying intermediate areas and DCA occupying the wettest areas. DGO also is situated in the wetter areas, but only has two occurrences in the hectare.

Figure 2-4: Canonical correspondence analysis ordination of Botany Bay ferns (Mont Saint-Hilaire, Quebec). Eigenvalues for axis one and two are, 0.632 and 0.523 respectively. Environmental measurements taken for each of 100-16m^2 plots comprising the hectare. See text for species and environmental variable abbreviations.



Weighted correlation matrix

Variable	Axis 1	Axis 2
LAVGH2O	0.7754	-0.3284
CVH2O	-0.20852	0.5349
PH	-0.3298	-0.4154
LNO3	-0.6658	-0.0985
LROCK	-0.5621	0.1916
LDEPTH	0.3995	-0.3320
DAMAGE	-0.2835	-0.3247
FAGUS	-0.0676	-0.4162
QUERCUS	0.1340	0.4783
ACER	-0.2353	-0.4432

CBU and CFR are also separated, but because they lie in the central portion of the ordination diagram, the dominant environmental gradient that ecologically differentiates them is unclear.

Spatial structure of environment: "partitioned" CCA ordination

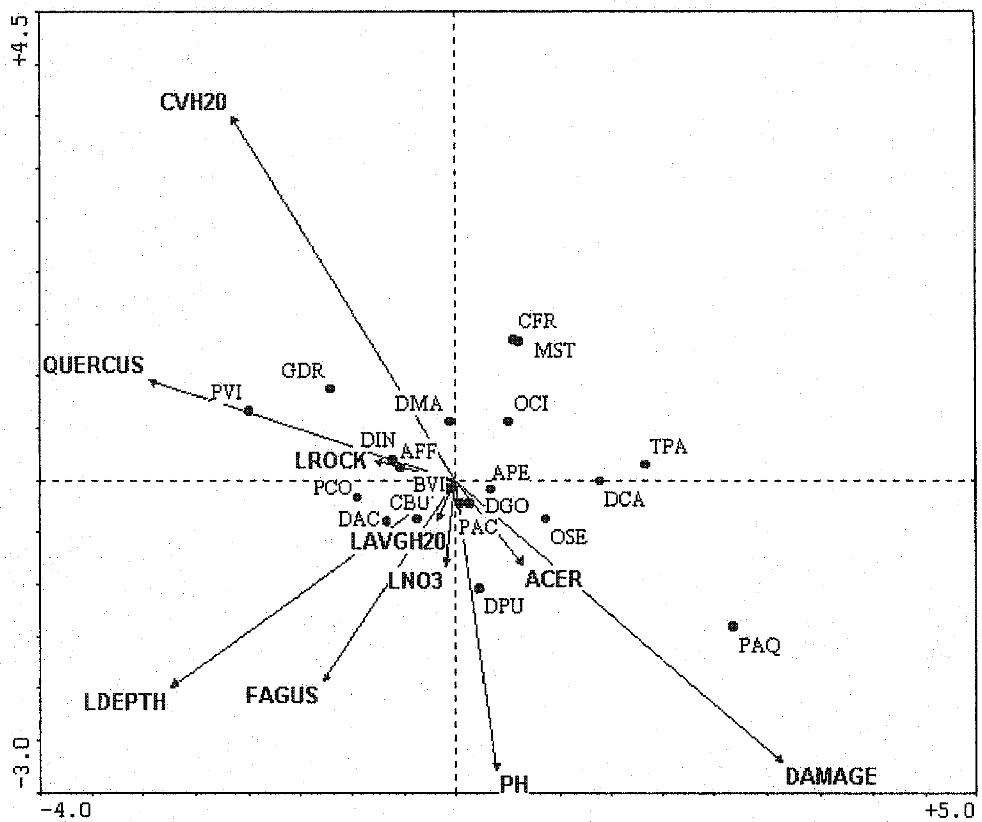
The partitioning or partialling of the total explained variance in the species abundance data is calculated by the sum of all canonical eigenvalues for ordinations 1, 2, 3, and 4, which are 1.569, 0.372, 1.763 and 0.566, respectively (sum = 4.27). The sum of all eigenvalues in the correspondence analysis of the species matrix (ordination 5 in methods)) is 5.768. The undetermined component accounts for the largest percentage of variation (63%) followed by combined spatial and environmental structure (20%) and nearly equal percentages of pure spatial (10%) and pure environmental structure (7%).

The effect of removing the globally significant (P=0.001) spatial structure is shown graphically in Figure 2-5. LAVGH2O and LNO3, which were influential in the standard ordination, have now become less important correlates of species distribution. QUERCUS has become most highly correlated with the distribution of species, followed by pH along the first axis and again, CVH20 most correlated with axis two. The relative species positions stay more or less constant, except that PAQ and DMA have separated.

Scale-dependence of species associations: detrended correspondence analysis ordinations

The greatest species separation along both axes occurs at $64m^2$ and $16m^2$; species differentiation is less apparent along axis two in the $4m^2$ ordination (Figure 2-6 a, b and c). For all ordinations TPA, MST, OCI, OSE, DGO, DCA and ATH are found on one side of the axis while AFF is found close to the center. For ordinations at $16m^2$ and $64m^2$, trends along axis one are similar: CBU and TPA are at opposite ends of axis one, and PVI and PAC are at opposite ends of axis two. PVI and GDR

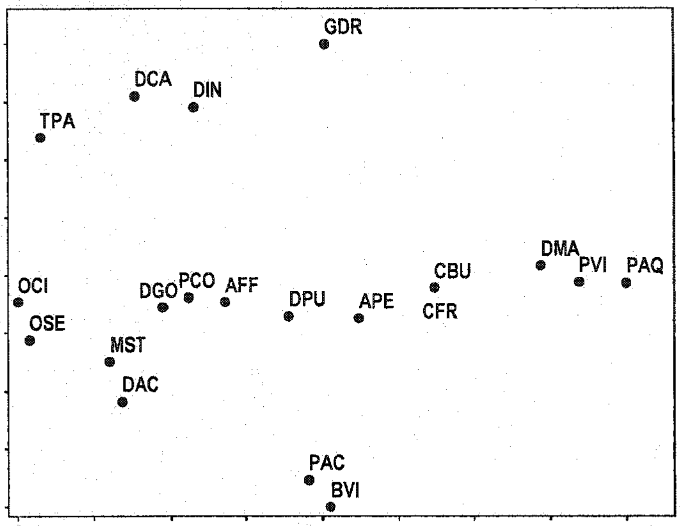
Figure 2-5: Partial canonical correspondence analysis ordination of Botany Bay ferns (Mont Saint-Hilaire, Quebec) (i.e. controlled for spatial structure of environmental factors). Eigenvalues for axis one and two are, 0.144 and 0.079 respectively. Environmental measurements taken for each of 100-16m^2 plots comprising the hectare. See text for species and environmental variable abbreviations.



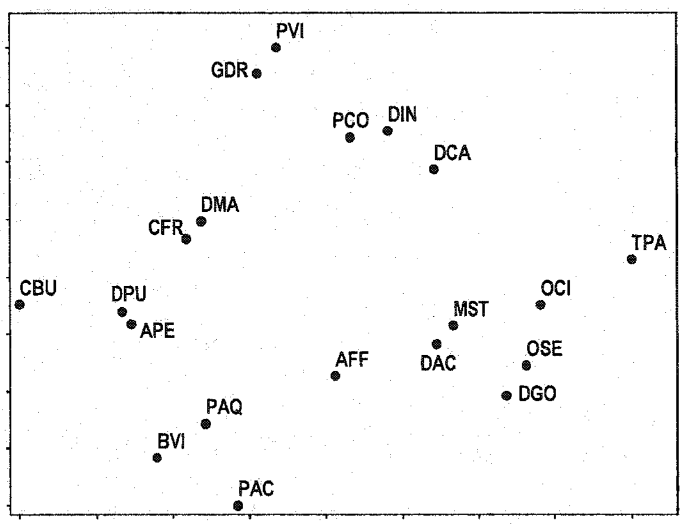
Weighted correlation matrix

Variable	Axis 1	Axis 2
LAVGH20	-0.0234	-0.0521
CVH20	-0.1901	0.2975
PH	0.0371	-0.2525
LNO3	-0.0105	-0.0882
LROCK	-0.1013	0.0242
LDEPTH	-0.2950	-0.2075
LDAMAGE	0.2461	-0.2043
FAGUS	-0.1280	-0.1850
QUERCUS	-0.3148	0.0985
ACER	0.0597	-0.0713

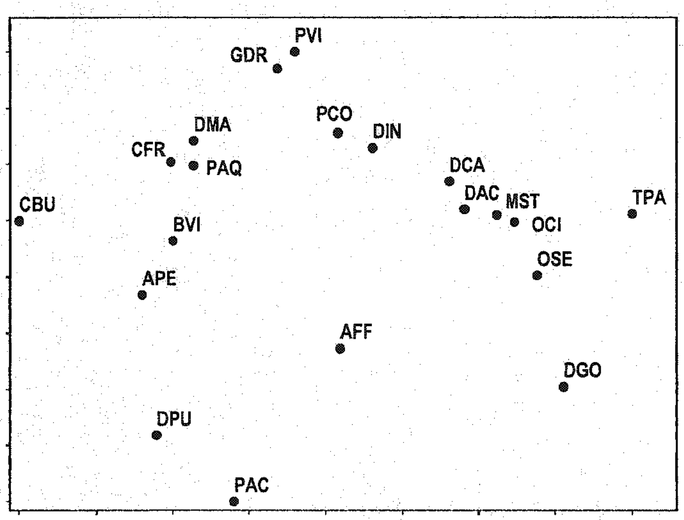
Figure 2-6: Detrended correspondence analysis ordination of Botany Bay ferns (Mont Saint-Hilaire, Quebec). The hectare m^2 were aggregated into plots of a.) $4m^2$, b.) $16m^2$ and c.) $64m^2$ and ordinations were run. See text for species abbreviations.



a. $4m^2$



b. $16m^2$



c. $64m^2$

are found close together in both ordinations. At the smallest grain ($4m^2$), the species found at the extremes of axis one and two are interchanged. OCI and PAQ are found at either ends of axis one, and GDR and BVI are polarized on axis two. As well, GDR and PVI are no longer found together. CBU and CFR are indistinguishable with respect to their positions in ordination space at the smallest grain.

Spatial coincidence of fern species and the environment: GIS Analysis

GIS overlays sets the ordination results into a spatial perspective as well as giving an overall impression of the environmental heterogeneity within the hectare. Based on the environmental gradients generated from the ordinations, the spatial coincidence of common (> 0.05% cover of the hectare) fern species with different interpolated surfaces is shown. The primary environmental gradient of the standard CCA ordination is one of wet to dry. Spatially, the primary wet to dry gradient extends from the dry and rocky slope of the east corner of the hectare to the moisture-saturated, lower west corner. The CCA identified wet habitat species, OCI, OSE and DCA, fall almost exclusively in the wettest portion (Figure 2-7). DCA has some outlying occurrences, but is still within wetter areas of the plot. Compared to the other common *Dryopteris* species in Botany Bay, DCA occurs in the wettest areas, followed by DIN and DMA (Figure 2-8). The next two species on the wet-dry ordination gradient, AFF and DAC also occur in the wet corner of the plot but their occurrence extends further up into less wet areas, up to the foot of the rocky slope (Figure 2-9). AFF has an outlying occurrence also in the center of the hectare on a small wet pocket of soil.

Nitrate concentration is the second most highly correlated variable with the CCA ordination axis one. Soil nitrate concentrations are generally lowest in the wet parts of the hectare with pockets of high concentration situated in the upper part (Figure 2-10). The spatial nitrate gradient is patchier than that of soil moisture. DMA is the species represented at the highest end of the nitrate gradient (as evidenced by the CCA) and it is also found on the more nitrate-rich areas of the hectare (Figure 2-

Figure 2-7: Interpolated mean soil moisture (resolution $4m^2$) of Botany Bay hectare (Mont Saint-Hilaire, Quebec). Abundance of OCI (*Osmunda cinnamomea*), OSE (*Onoclea sensibilis*) and DCA (*Dryopteris carthusiana*) shown with 2% cover contour intervals.

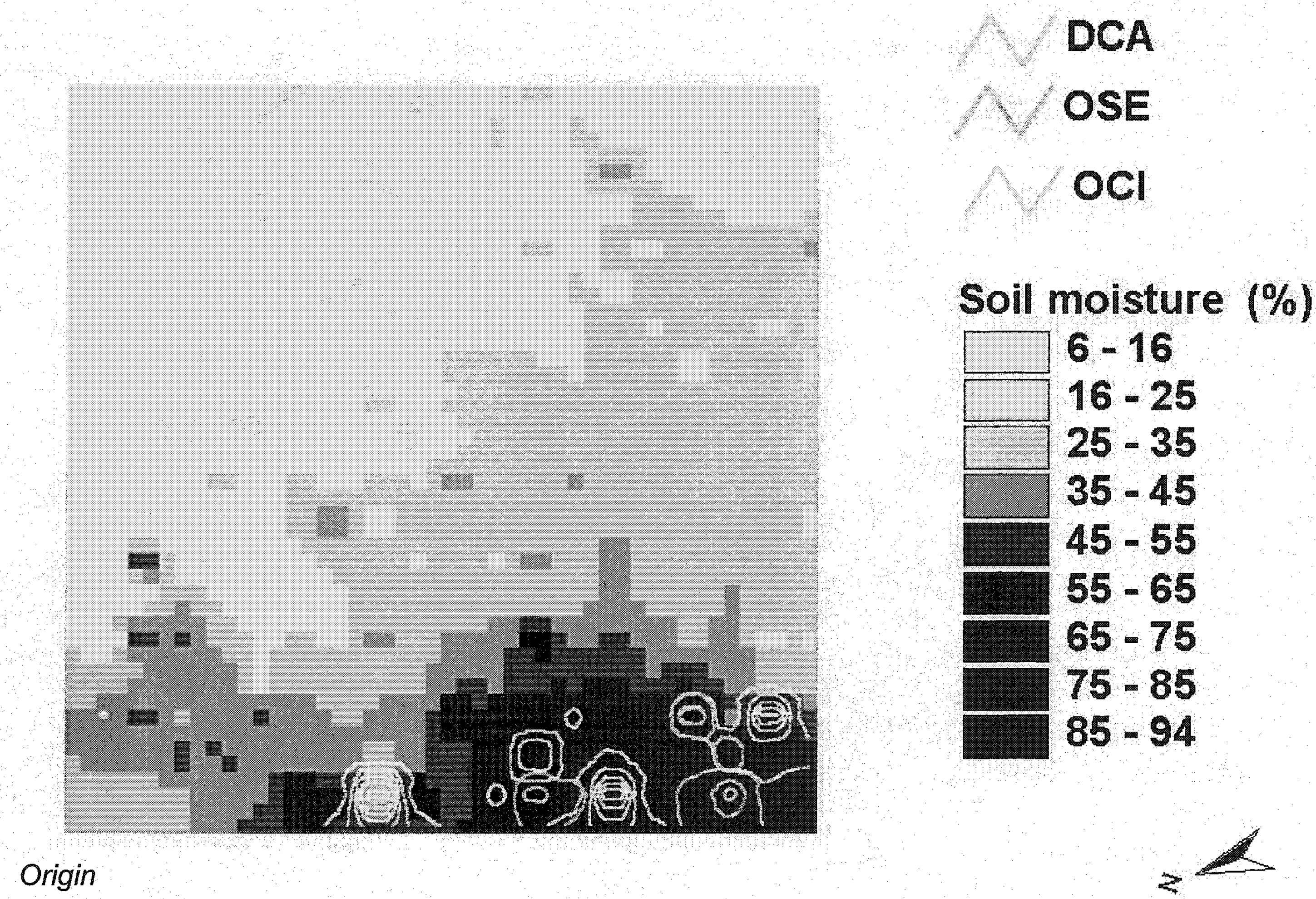
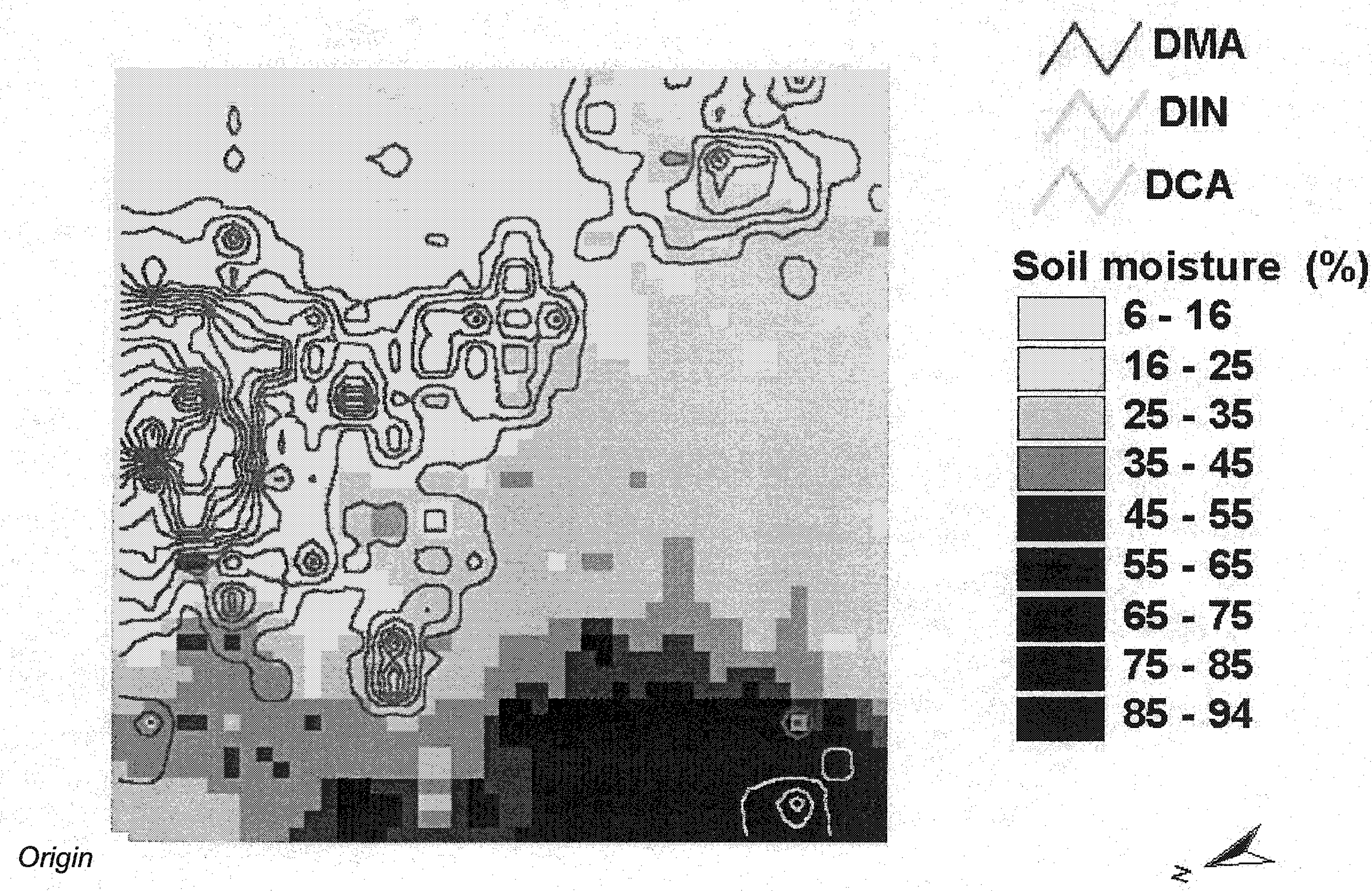

DCA
OSE
OCI
Soil moisture (%)
6 - 16
16 - 25
25 - 35
35 - 45
45 - 55
55 - 65
65 - 75
75 - 85
85 - 94
Origin
N

Figure 2-8: Interpolated mean soil moisture (resolution $4m^2$) of Botany Bay hectare (Mont Saint-Hilaire, Quebec). Abundance of DMA (*Dryopteris marginalis*), DIN (*Dryopteris intermedia*) and DCA (*Dryopteris carthusiana*) shown by 2% contour intervals. Note the spatial difference of the congeneric species over varying soil moisture.



Origin
DMA
DIN
DCA
Soil moisture (%)
6 - 16
16 - 25
25 - 35
35 - 45
45 - 55
55 - 65
65 - 75
75 - 85
85 - 94
N

Figure 2-9: Interpolated mean soil moisture (resolution $4m^2$) of Botany Bay hectare (Mont Saint-Hilaire, Quebec). Abundance of AFF (*Athyrium filix-femina*) and DAC (*Deparia acrostichoides,* previously known as *Athyrium thelyptroides*) shown by 5 % cover contour intervals. Note apparent clonal growth shown by DAC.

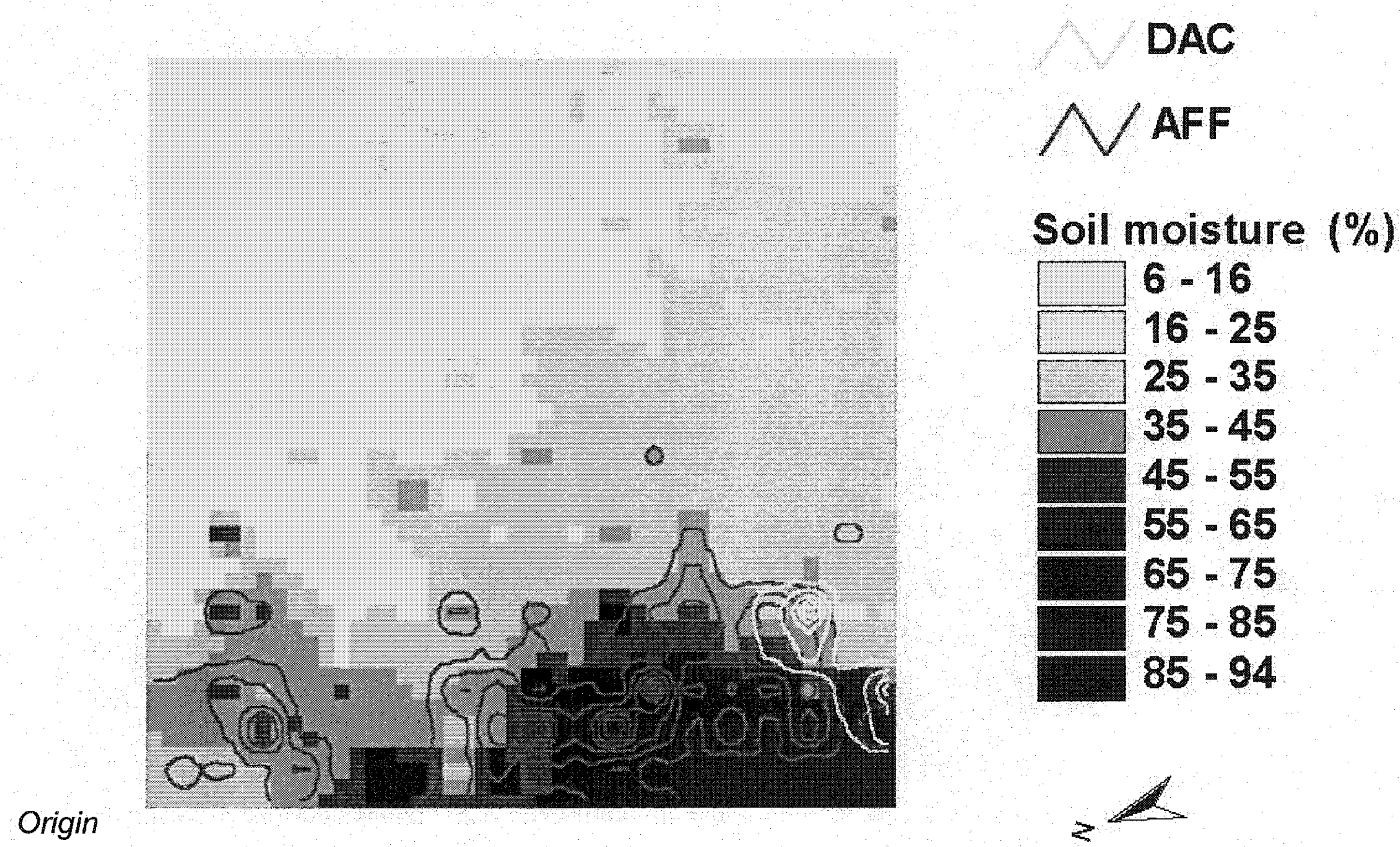
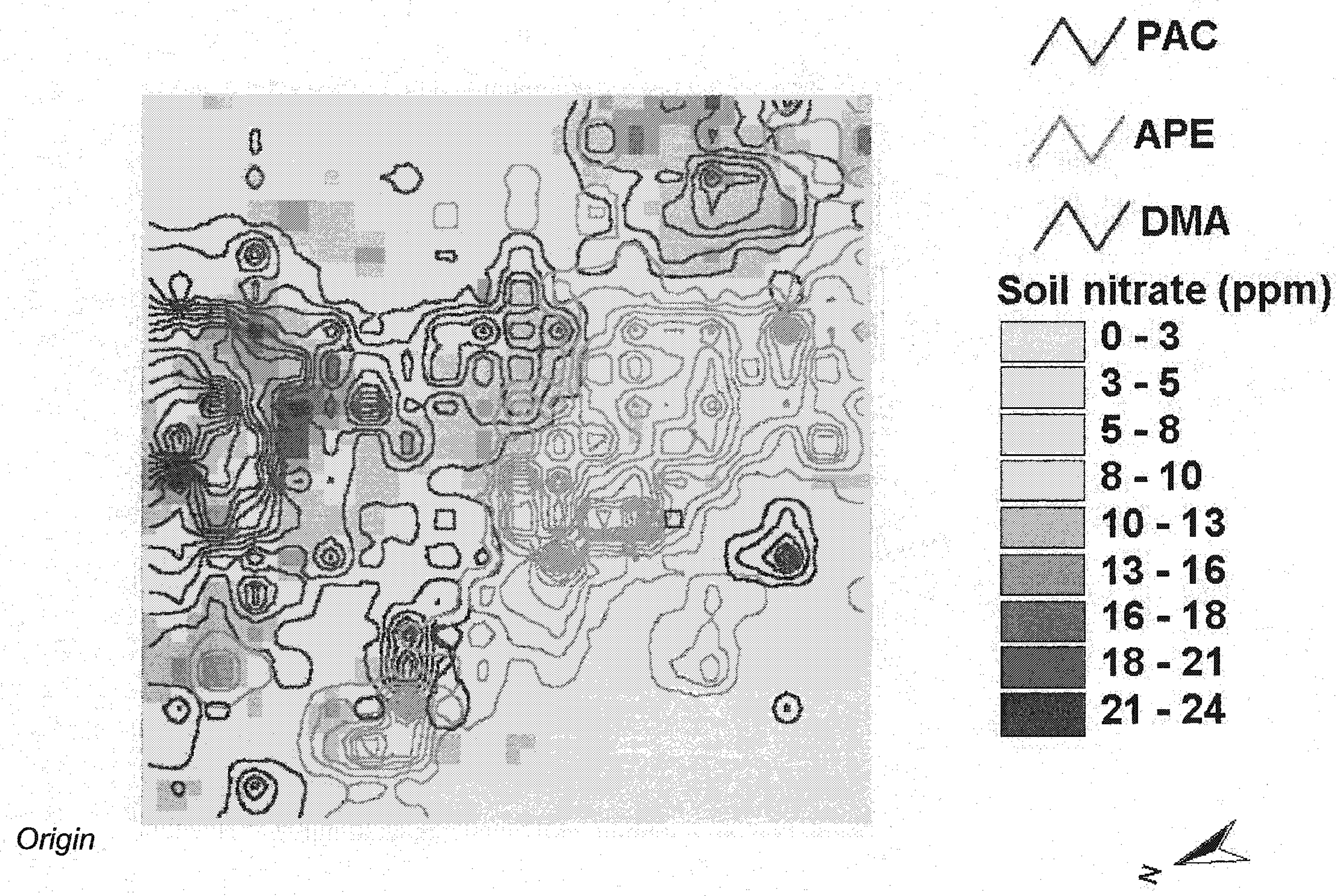

Origin
DAC
AFF
Soil moisture (%)
6 - 16
16 - 25
25 - 35
35 - 45
45 - 55
55 - 65
65 - 75
75 - 85
85 - 94
N

Figure 2-10: Interpolated soil nitrate concentrations (ppm) of Botany Bay hectare (Mont Saint-Hilaire, Quebec). Abundance of DMA (*Dryopteris marginalis*) and APE (*Adiantum pedatum*) and PAC (*Polystichum acrostichoides*) shown by 2% cover contour intervals.


PAC
APE
DMA
Soil nitrate (ppm)
0 - 3
3 - 5
5 - 8
8 - 10
10 - 13
13 - 16
16 - 18
18 - 21
21 - 24
Origin
N

10). Although pH was not found to be strongly correlated with the ordination axes, it has been cited as a dominant control on fern distribution. An old calcareous channel runs diagonally through the south side of the hectare; the corresponding pH values for quarters lying in the channel are circumneutral. Relatively more acidic areas occur in pockets on the other north half of the hectare as well as in the wet areas (Figure 2-11). GDR exists primarily on the acidic areas, and CBU is restricted to the most alkaline areas of the hectare, both results agreeing with ordination patterns (Figure 2-11). However, CBU does not exist in all alkaline areas; it is absent in an area adjacent to its main area of occurrence.

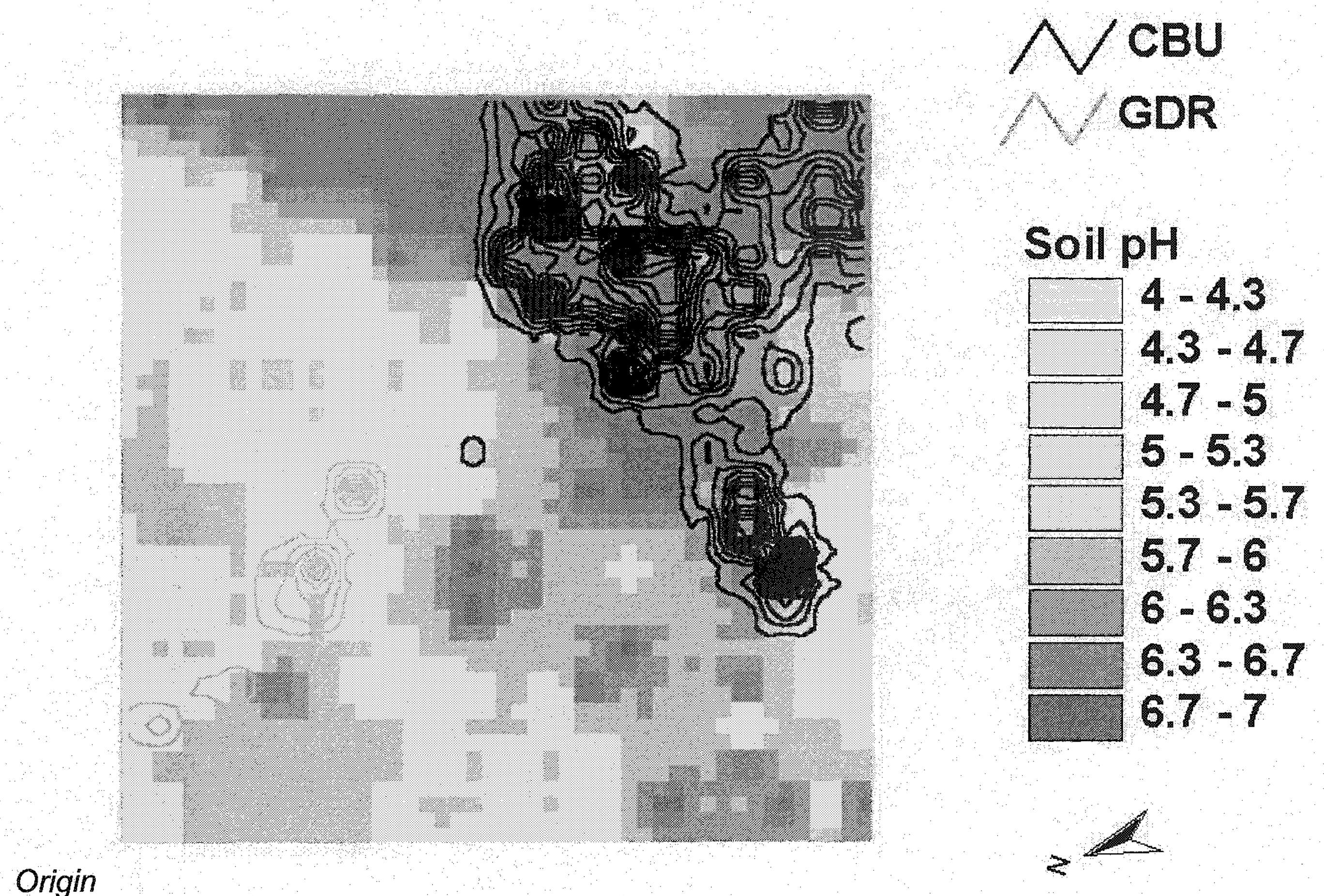
The distribution of APE and PAC is less clear with respect to environmental gradients than the previously illustrated species. Both species are also central in ordination space. APE is found at the foot of the talus, where the slope grades into a flatter area. It is not found in the wettest soils at the bottom west corner (Figure 2-10), nor overlapping with DMA. PAC appears to be similar to APE, following the diagonal of the hectare (Figure 2-10).

Discussion

Environmental gradients underlying fern distributions

All three methods of detecting niche partitioning at a fine-scale (indirect and direct ordinations, and GIS mapping), show that most fern species in the community studied are distributed differentially according to environmental preferences. Direct ordination analysis reveals both the amount of soil moisture and the soil nitrate concentration ecologically separates fern species. The soil moisture gradient appears to separate fern species at all grains in both direct and indirect ordinations. A study in southeastern Ohio at a grain of 78.5m^2 found similar separation along gradients (soil moisture and nitrate) using detrended correspondence analysis (Greer *et al.*, 1997). As well, fern composition differences were attributed to variation in soil drainage of plots in Amazonian rain forests (100m^2 and 25m^2) (Tuomisto and Poulsen, 2000). Niche

Figure 2-11: Interpolated soil pH of Botany Bay hectare (Mont Saint-Hilaire, Quebec). Interpolated abundance of CBU (*Cystopteris bulbifera*) and GDR (*Gymnocarpium dryopteris*) shown by 2% cover contour intervals.


CBU
GDR
Soil pH
4 - 4.3
4.3 - 4.7
4.7 - 5
5 - 5.3
5.3 - 5.7
5.7 - 6
6 - 6.3
6.3 - 6.7
6.7 - 7
N
Origin

separation according to soil moisture conditions are not limited to ferns; soil hydrological conditions were found to separate English meadow plant species at a fine-scale in absence of any obvious topographic variation (Silvertown *et al.*, 1999). The strong and phylogenetically robust relationship found in the trade-off between drought and water-logging tolerance reflects a general physiological constraint (Silvertown *et al.*, 1999).

Many fern species are characterized as preferring wet habitats, but by using ordination and GIS, different tolerances to soil moisture were identified. The wet habitat affinities shown by *Osmunda cinnamomea*, *Dryopteris carthusiana* and *Onoclea sensibilis* agree with previously identified habitat preferences (Table 1-1). *Athyrium filix-femina* and *Deparia acrostichoides* also occurred in relatively wet areas of the hectare. All these species are characterized as preferring wet sites. However, the difference in distributions between *Athyrium filix-femina* and *Deparia acrostichoides* and the previously identified wet habitat species is most likely due to a lower tolerance of water-saturated soil. The western portion of the hectare has standing water as well as a small stream. Wet habitat species may be able to tolerate soil saturation whereas the other two species, *Athyrium filix-femina* and *Deparia acrostichoides*, prefer less saturated sites. The results of GIS mapping also support this. *Athyrium filix-femina* and *Deparia acrostichoides* are found in the wettest areas, but are most abundant in areas with slightly less soil moisture. Within the saturated sites, *Athyrium filix-femina* and *Deparia acrostichoides* were growing on the hummocks of drier areas. Distinct preferences for hummocks have also been shown for plants of wetland communities (Vivian-Smith, 1997). The pattern of occurrence for *Deparia acrostichoides* could also reflect limited dispersal; it is spreading outwards from only one point in the hectare.

Soil nitrate concentrations were also important in separating fern species in the hectare. Another study using larger plots (0.25 – 1.00 ha), found that fern species composition was correlated with a soil fertility gradient (Tuomisto and Poulsen, 1996). Floristic compositions in western Amazonia correlated with differences in the soils; two-thirds of the species were restricted to either poor, intermediate or rich soils. In Botany Bay, *Dryopteris marginalis* in particular, showed a preference for areas of relatively high nitrate concentrations. *Dryopteris marginalis* is found on rocky and wooded slopes, edges of woods, stream banks and road banks (Table 1-1). Although *Dryopteris marginalis* prefers a generally rocky area, in the study hectare it grows in nutrient-rich pockets of humus among the rocks. Greer *et al.* (1997) also noted that *Dryopteris marginalis* occurred in high-nutrient soils, but in wet areas. Perhaps the grain of their survey (78.5 m^2) obscured fine-scale differences in soil moisture, which were apparent here. It is interesting that *Dryopteris marginalis* is found in nutrient-rich areas, because its wintergreen leaves were theorized to conserve nutrients and enable the species to live in low-nutrient areas (Moore, 1984; van Buskirk and Edwards, 1995). In this case, the production of wintergreen frond structure may require relatively more nitrogen than other fern species, since these leaves are in fact shed annually.

It is uncertain what environmental factors underlie the distribution of *Adiantum pedatum*, the most abundant fern in the hectare. *Adiantum pedatum* is known to exist in nutrient-rich areas, in Botany Bay, it was observed to occur mainly at the bottom of the slope, but not in wet areas. Perhaps this placement is generally more fertile from nutrients percolating down the slope. *Adiantum pedatum* may require soil of higher fertility not necessarily represented only by nitrate levels. It is clear however, that *Adiantum pedatum* and *Dryopteris marginalis* have almost mutually exclusive preferences for the areas within the hectare. *Adiantum pedatum* may be constrained to flatter areas with deeper soil than *Dryopteris marginalis* due to its colonial nature; it requires room to spread. *Dryopteris marginalis* grows as individuals and can propagate itself in the islands of nutrient-rich pockets amidst the rocky talus.

There is some ambiguity whether soil chemical composition is inherent to the soil or plant induced. For example, *Pteridium aquilinum* has been found to change the soil chemical composition to facilitate its own existence (Johnsson-Maynard *et al.*, 1997). Sollins (1998), described reasons for failures to detect clear trends between soil and plant occurrence. They included statistical problems (e.g. lack of correlation from insufficient range in the independent variable, and confounding factors) and methodological problems (measuring availability of nutrients to plants that is ecologically representative, and how to account for soil variability).

Whether soil conditions are inherent or plant-altered, the ordination results, in conjunction with the spatial coincidences shown by the GIS, suggest that abiotic controls do exert a strong influence on fern distribution, at least for the common species. It is difficult to tell what factors are truly influencing rare species in the hectare. While environmental preferences are noted for the rare species of Botany Bay (*Dennstaedtia punctiloba*, *Dryopteris goldiana*, *Phegopteris connectilis*, *Pteridium aquilinum* and *Thelypteris palustris*)(Table 1-1), their environmental affinities cannot be accurately judged based on a few samples within the hectare. Nonetheless, it is noteworthy that *Pteridium aquilinum* was found in the driest, rockiest sites, and *Dryopteris goldiana* and *Thelypteris palustris* were both found in the wet area of the hectare, which agrees with previous accounts. *Dryopteris intermedia*, also less common, was found to occur above the wettest area and has also been noted to have reciprocal allelopathy with *Osmunda cinnamomea* (Petersen and Fairbrothers, 1980). This chemical inhibition was found between the gametophytes of the two species. No gametophyte surveys were performed in this study; however, *Osmunda cinnamomea* and *Dryopteris intermedia* were separated in ordination space, perhaps reflecting this allelopathic mechanism.

There is clear segregation of the common fern species between wet and relatively dry habitats of the hectare. Although the exact environmental gradient may not be clear for all of the common fern species of Botany Bay, there are preferences to different spatial locations of the hectare, reflecting ecological separation. As well, there does seem to be consistency with what is known of the species, indicating that the for some Botany Bay ferns niche-assembly rules are important. Within the habitats, some segregation is also apparent, but it is not as obvious. A finer-scaled survey may reveal micro-site preferences or only random dispersal.

Spatial structure of environmental gradients

The ordination results indicate that of most of the environmental influence on the variation of fern abundance, just over half is spatially structured (21% / 37%). Environmental variation in this case, is most likely related to the topography of the plot and thus classified as spatially structured variation; a value for soil moisture or nitrate concentration can be predicted by its spatial position in the hectare. Statistically, it is important to identify spatial autocorrelation to meet the assumption of independence among samples. Biologically speaking, the spatial structure of the environment obscures the presence of niche-partitioning. It can represent either dispersal limitations and/or the finer-scaled environment not described by the trend surface (Equation 1). Spatial autocorrelation in species occurrences may reflect real environmental similarity between sites or alternatively, dispersal from a parent plant. Pure environmental and pure spatial structure accounts for a small percentage of the total variation in species abundance data. The pure environmental component does suggest that some patterns in fern distribution are exclusively connected to the environment, thus reflecting niche-partitioning. However, spatial and environmental control in interaction, representing approximately one-fifth of the variation, indicates that of most of the environmental control, it is spatially structured (total explained variation is 37%). Two of the most abundant ferns of the hectare, *Adiantum pedatum* and *Cystopteris bulbifera*, both spread by clonal propagation. Their high abundance and clonal growth characteristic may explain why the variation explained by spatially structured environment is higher than that of pure environment. In any case, it is difficult to interpret whether the species locations are due to environmental preferences or only to nearby dispersal.

Once the effects of topography were removed (i.e. controlling for spatial structure), other environmental gradients, not associated with topography, became apparent. Contrary to most published research and qualitative observations, in the unpartitioned ordination, pH did not have much weight in controlling fine-scale fern distribution. Calcareous conditions in general have been cited as an important factor contributing to high fern richness of a site (Gaddy, 1990). However, when environmental variation was controlled for spatial structure, the effects of soil pH became more apparent. *Cystopteris bulbifera,* the second most abundant species of the hectare, most likely was dominating the pH gradient. *Cystopteris bulbifera*'s environmental specificity in combination with its high abundance caused pH to appear as a significant factor (with minor weighting) in the ordination results. Environmental gradients detected may be frequency-dependent; common and rare species reacted differently and independently to environmental variation in a study on Senegalese vegetation (Lawesson, 1997). When *Cysopteris bulbifera* is removed from the ordination, the weight of pH on controlling the fern distribution diminishes from –0.3298 to 0.0686 on the first axis, reflecting that the pH gradient is frequency-dependent. *Cystopteris bulbifera* was restricted to alkaline areas of the hectare, in agreement with other findings (e.g. Wherry, 1920), but it was not found in all high-pH areas. It was absent from the upper rocky slope and the wettest area of the hectare. Either soil moisture in conjunction with soil pH appears to be influential in affecting *Cystopteris bulbifera* in the hectare, or the species is dispersal limited and has not yet arrived to those sites.

Tree canopy effects, particularly *Quercus rubra* cover, also became more apparent after the effect of spatial structure had been controlled for in the ordination. Mixed tree canopies have been found to influence forest floor microsite properties, with the effects depending on the tree species (Pelletier *et al.*, 1999). Soil microsite conditions can be affected directly by the forest canopy (e.g. nutrient and organic inputs through above-ground litter decomposition, changes in local precipitation flows, and fine root turnover and exudates) or indirectly through modification of abiotic and biotic components (e.g. changes in understorey density and composition, mycorrhizal communities, soil moisture and soil microbial communities) (Pelletier *et al.*, 1999). It was surprising that despite the steep slope that existed throughout most of the field site, which most likely causes much litter movement, canopy effects were found to be important. As well, *Qurecus rubra* only occurs in the east corner on the steep rocky slope, coincidental with few fern species (e.g. *Dryopteris marginalis*). Perhaps only the absence of *Q. rubra* was correlated with the fern distribution, as opposed to variation in the abundance of the tree.

Spatial structure accounted for a great percentage of the variation in species abundance, but the greater proportion remained unexplained. This is not unusual and has been noted in other methodologically similar terrestrial studies (i.e. Heikkinen and Birks, 1996; Rydgren, 1996 and Borcard *et al.* 1992). Environmental heterogeneity within the quarters suggests that there may likely be microscale relationships at a grain slightly smaller than $16m^2$. The scale of plots will influence perceived associations for species. In larger plots that combine many habitat types, positive associations might occur with species, which at a finer scale have different environmental demands and would be negatively associated. In very small plots "stochastic effects, due to few individuals and/or large random variation in abundance estimates may restrict the ability to detect significant association among species" (Jonsson and Moen, 1998). Scale will have an effect on what environmental factors are most highly correlated with the vegetation composition (Reed *et al.*, 1993) and likely even the presence of significant environmental factors.

By controlling for spatial structure, the difference in importance of environmental gradients became evident. Spatial autocorrelation was present within the gradients, yet species still partitioned the environment in a consistent manner when spatial effects were controlled for. The species positions along ordination axes remained relatively constant, suggesting niche differentiation is underlying fern distribution and abundance. However, from this analysis it is not clear whether dispersal processes or finer-scale heterogeneity would explain more of the variation in fern species abundance patterns.

Consistency of species associations with changing grain

The variability of species associations in ordinations may indicate that patterns of distribution exist at a finer scale. The CCA ordination (grain of $16m^2$) showed *Polypodium virginianum, Phegopteris connectilis* and *Gymnocarpium dryopteris* as ecologically similar. Survey results showed that *Polypodium virginianum* and *Phegopteris connectilis* were found within the same quarter. However, *Polypodium virginianum* was found on a small crevice on a large boulder (*Polypodium virginianum* is well known to be able to grow on cliffs and rocky slopes (Table 1-1) and *Phegopteris connectilis* on the forest floor. Two distinct habitats were thus combined into one "homogenous" quarter ($16m^2$). *Gymnocarpium dryopteris* never physically occurred with *Phegopteris connectilis* in the same quarter even though they were placed together in ordination space. *Gymnocarpium dryopteris* and *Phegopteris connectilis* both prefer similar acidities, however (*Gymnocarpium dryopteris* mean pH = 4.6, *Phegopteris connectilis* mean pH = 5.0, see Figure 1-4) *Gymnocarpium dryopteris* is an indicator of low-pH soils and will occur on limestone only if the surface is locally acidified (Gartmann, 1988). Using a direct ordination method where species placement is constrained from environmental variables, the two species, *Gymnocarpium dryopteris* and *Phegopteris connectilis*, were viewed as ecologically similar. In the ordination, *Gymnocarpium dryopteris*'s association with *Phegopteris connectilis* caused the close proximity to *Polypodium virginianum*, which was not necessarily a true representation of its environmental affinity. When the grain was decreased to $4m^2$ (using detrended correspondence analysis), the true heterogeneous environmental response of the ferns became evident, as seen by the separation of *Polypodium virginianum, Phegopteris connectilis* and *Gymnocarpium dryopteris* in ordination space. An even finer-scaled inventory of the environment may identify further relationships between ferns and the environment and reduce the unexplained portion of variation in fern abundance.

As well, artifacts in the ordination resulting from the choice of grain, change the positions of extreme dry species. Only at the smallest grain, does *Dryopteris* *marginalis* appear to prefer the driest sites versus *Cystopteris bulbifera* (excluding *Pteridium aquilinum* and *Polypodium virginianum*, which are rare in the hectare). To obtain the plots used in the detrended correspondence analysis ordinations, abundance of one species is based on the summed abundance for each square meter within the plot. The variation in abundance within the plot is diluted as only the total sum is taken. By breaking the plot into smaller plots, the subtle variation of abundance over the same area is revealed and is detected by the ordination. It is only at the smallest grain that the subtle differences of species abundances moving down the slope (dry to wet) are noticed. At larger grains, the two species take on different ecology compared to what is found at a more fine-scaled inventory.

Species that fall on the extremes of resource gradients are consistent in their environmental preferences but species falling between these points are less consistent. In general, results from the previous environmental characterization (Figures 1-3 and 1-4) and CCA ordinations agree on the identity of species that occur at the extreme ends of gradients, whether it is in soil moisture, nitrate or pH (e.g. *Dryopteris marginalis* and *Cystopteris bulbifera*). Species that fall along mid-gradients may exhibit much overlap in their preferences, or the axes on which these other species would be found at extreme positions along other resource gradients were not incorporated. Alternatively, the scale of the sample sizes in the Botany Bay survey is so large that each quarter represents a region of environmental conditions, rather than a point (Palmer and Dixon, 1990). Considering the amount of variation shown by the range of soil nitrate concentrations, heterogeneity exists within the quarter. Comparable variation has been found at similar scales: for example Jackson and Caldwell (1993) found nitrate concentrations varied by two or three orders of magnitude within a $120m^2$ plot, however as much variability occurred in a $1m^2$ plot as in the whole $120m^2$ sites. Two to ten-fold differences were found at the scale of 20 cm in a British deciduous forest in addition to the temporal variation present in these values over the period of one growing season (Farley and Fitter, 1999). In a study performed close to Botany Bay, points separated up to 2m were homogenous in terms of pH, K+ and NO_{3-} (Lechowicz and Bell, 1991).

Choice of grain impacts the perceived species associations. There is some evidence that a finer-scaled inventory would clarify the instability of some species associations. However, this runs the risk of having too few individuals in a plot to perceive associations and the effects of random dispersal processes may obscure environmental preferences. With respect to accurately describing fern species environmental preferences, focal point sampling may provide more information.

Ecological separation of congeneric species

Congeneric species are thought to experience more competition because of their ecological and taxonomic similarities (Harper *et al.*, 1961), which would imply that species within a genus should show especially strong niche-partitioning. The opposite conclusion has also been argued in that phylogenetic relatedness should be correlated with ecological similarity (Webb, 2000). In Botany Bay, the species in the genus *Dryopteris*, were consistently separated on a soil moisture gradient. Carlson (1979) also observed that Michigan *Dryopteris* species followed a gradient from dry, upland forest to wet meadows, marshes, bogs or standing open water. For example, *Dryopteris marginalis* was associated with dry upland sites, and in places where soil moisture increased, the abundance of *Dryopteris marginalis* decreased and *Dryopteris intermedia* increased. In the lower regions, where the soil became wetter and richer, *Dryopteris goldiana* appeared. The Botany Bay GIS overlays support this *Dryopteris* separation as well. *Dryopteris marginalis* was found at the top of the slope, replaced by *Dryopteris intermedia* at mid-slope, and *Dryopteris carthusiana* was found in the wettest areas, with some intermingling *Dryopteris intermedia* and *Dryopteris goldiana*.

Other species within genera did not show clear ecological separation, but this may be due to scale. *Cystopteris bulbifera* and *Cystopteris fragilis* appear identical in environmental preference at the smallest grain in detrended correspondence analysis ordinations. At larger grains, *Cystopteris fragilis* co-occurs with more species and it becomes less similar to *Cystopteris bulbifera*. *Cystopteris bulbifera* and *Cystopteris* *fragilis* are both found in rocky areas (Table1-1) and the coincidence that most of the rock in the Botany Bay hectare is calcareous influences the similar pattern of distribution of the two species.

The evidence for niche partitioning among congeneric species remains equivocal. Again, similarly to investigating the instability of species along gradients over different scales, focal point sampling may prove more useful in detecting ecological differences among closely related species.

Conclusion

Within the Botany Bay hectare some fern species clearly showed preferences to their environment, most notably soil conditions. Distinct environmental preferences were shown for some of the fern species such as, *Dryopteris marginalis* which preferred dry, high-nitrate soils compared to *Osmunda cinnamomea*, which preferred wet sites, consistent with previous accounts. There were also parallel accounts for environmental preferences cited from other localities to the ferns of Botany Bay. The clear segregation for some species and their consistency with other reports suggests that environmental preferences are important in structuring fern communities. Within a habitat found in the hectare, there was also some evidence that species were ecologically differentiated at the fine-scale. *Athyrium filix-femina* and *Onoclea sensibilis* are both considered to prefer wet habitats (e.g. marshes, swamps, etc.) but there was a gradient in their tolerances to soil moisture within the habitat. The steep topography and the resulting high habitat heterogeneity of the plot, most likely allows for ecologically different species to co-exist and thus explains the high fern richness of the site.

Clear segregation and underlying environmental gradients were not evident for all species. Some species that fell in between easily discerned habitats (e.g. wet versus upland sites) did not show clear and consistent preferences to their environment. The occurrence of some species could not be linked to environmental variation (e.g. *Adiantum pedatum*) or did not occur in all sites where they would be expected to be found (e.g. *Cystopteris bulbifera*). Spatial autocorrelation was a factor in explaining some of the variation in species abundance, but whether it represented true environmental similarities or dispersal limitation between spatially close sites, could not be discriminated. As well, there was a large proportion of unexplained variation in species distribution, of which finer-scale heterogeneity, random dispersal or unknown processes may be identified. Dispersal limitation is impacting patterns of fern distribution, but the scale at which it would be deemed most influential is unclear.

The measurements taken on environmental variation were not exhaustive, there may be other environmental axes not represented that species' distributions would correlate with. Perhaps by measuring more of the environment and at a finer-scale, this may clear up some of the uncertainties of niche separation among ferns in Botany Bay. Focal-point sampling may also better define fern niches, and minimize the discrepancies scale can cause in the interpretations of niche separation. This type of sampling may negate the benefits of studying a fern-rich site; competition among functionally similar species that potentially interact because of high dispersal is a strong test for niche partitioning. However, if the assumption of high dispersal among ferns is invalid, their occurrences may be due to dispersal rather than niche-mediated processes.

To decisively answer whether fern communities are adapted or neutral, ordinations based on neutral models of species placement should be tested. Models such as the neutral community model developed by Bell (2000) where the diversity of a community is comprised of equivalent species with identical probabilities of immigration, birth, death and density regulation could be used. If a neutral model generated similar patterns of species-environment relationships, the dominant factor influencing fern species assemblages would have to be re-evaluated in the context of dispersal limitation.

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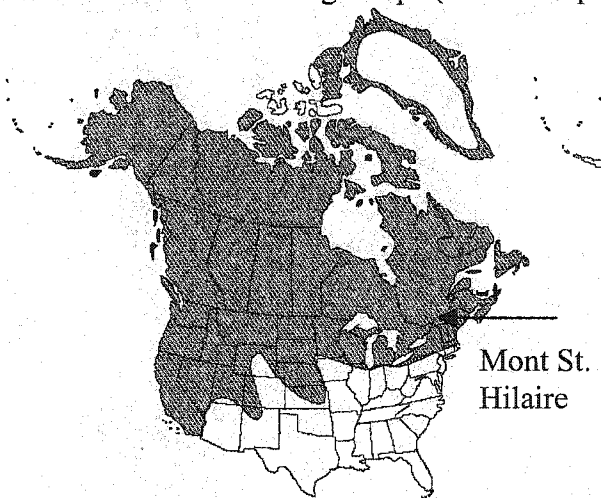
Appendix A: Mont Saint-Hilaire fern species nomenclature

Fern species nomenclature (according to Flora of North America Editorial Committee, 1993 (http://hua.huh.harvard.edu/FNA/)

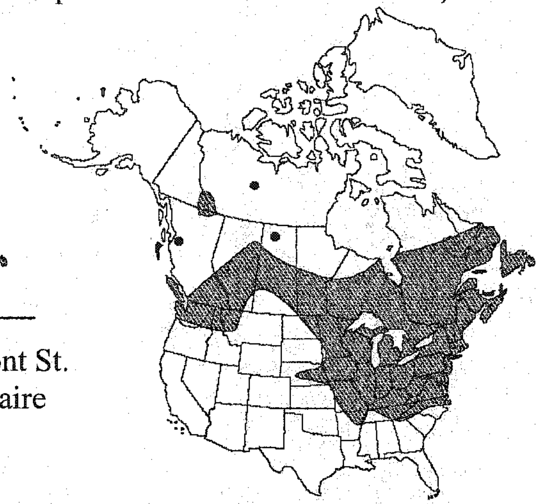
APE: *Adiantum pedatum* Linnaeus
ARH: *Asplenium rhizophyllum* Linnaeus
ATR: *Asplenium trichomanes* Linnaeus
AFF: *Athyrium filix-femina* variety *angustum* (Willendow) G. Lawson
BIS: *Botrychium dissectum* Sprengel
BLA: *Botrychium lanceolatum* subspecies *angustisegmentum* (S.G. Gmelin) Angström
BMA: *Botrychium matricariifolium* (Döll)A. Brown exW.D.J. Koch
BMU: *Botrychium multifidum* (S.G. Gmelin) Ruprecht
BVI: *Botrychium virginianum* (Linnaeus) Swartz
CBU: *Cystopteris bulbifera* (Linnaeus) Bernhardi
CFR: *Cystopteris fragilis* (Linnaeus) Bernhardi
DPU: *Dennsteadtia punctilobula* (Michaux) T. Moore
DAC: *Deparia acrostichoides* (Swartz) M. Kato
DPY: *Diplazium pycnocarpon* (Sprengel) M. Brown
DCAM: *Dryopteris campyloptera* (Kunze) Clarkson
DCA: *Dryopteris carthusiana* (Villars) H. P. Fuchs
DCL: *Dryopteris clintoniana* (D.C. Eaton) Dowell
DCR: *Dryopteris cristata* (Linnaeus) A. Gray
DGO: *Dryopteris goldiana* (Hooker exGoldie) A. Gray
DIN: *Dryopteris intermedia* (Muhlenberg exWillendow) A. Gray
DMA: *Dryopteris marginalis* (Linnaeus) A. Gray
GDR: *Gymnocarpium dryopteris* (Linnaeus) Newman
MST: *Matteuccia struthiopteris* variety *pensylvanica* (Willendow) C.V. Morton
OSE: *Onoclea sensibilis* Linnaeus
OCI: *Osmunda cinnamomea* Linnaeus
OCL: *Osmunda claytoniana* Linnaeus
ORE: *Osmunda regalis* variety *spectabilis* (Willendow) A. Gray
PAC: *Polystichum acrostichoides* (Michaux) Schott
PBR: *Polystichum braunii* (Spenner) Fée
PVI: *Polypodium virginianum* Linnaeus
PCO: *Phegopteris connectilis* (Michaux) Watt
PHE: *Phegopteris hexagonoptera* (Michaux) Fée
PAQ: *Pteridium aquilinum* variety *latiusculum* (Desvaux) L. Underwood exA. Heller
TNO: *Thelypteris noveboracensis*
TPA: *Thelypteris palustris*
WIL: *Woodsia ilvensis*(Linnaeus) R. Brown

Appendix B: North American fern range maps

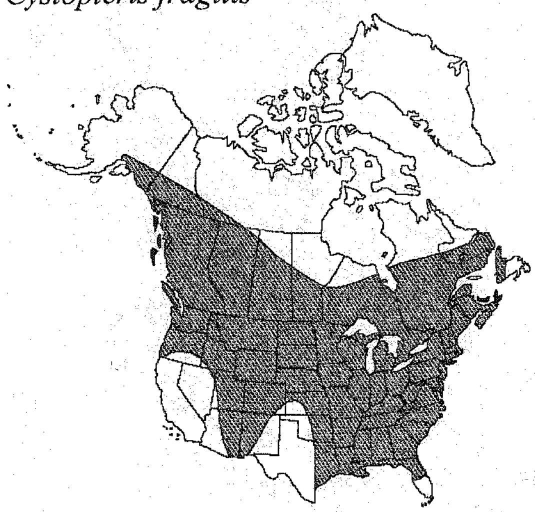
North American fern range maps (source: http://hua.huh.harvard.edu/FNA/)



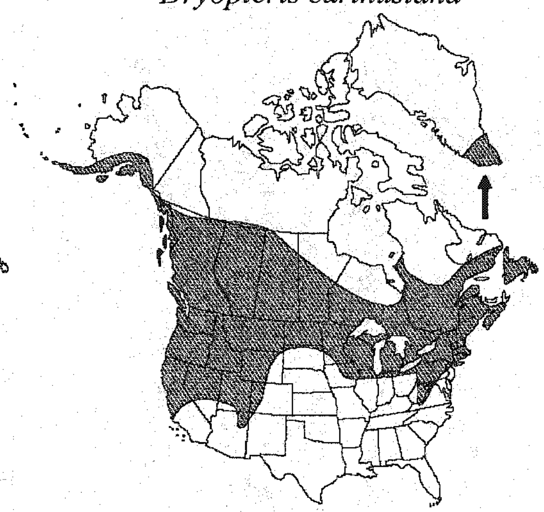
Cystopteris fragilis



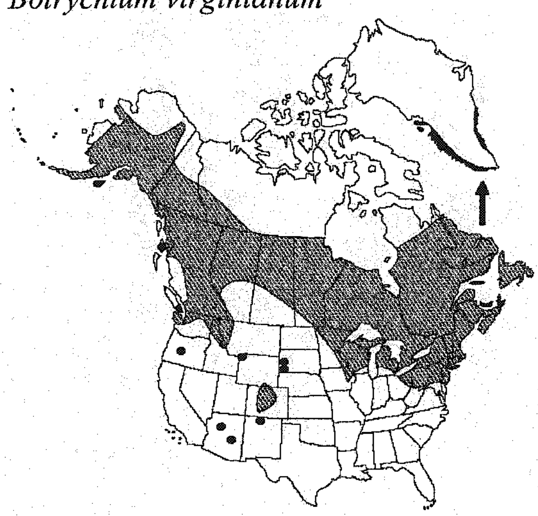
Dryopteris carthusiana



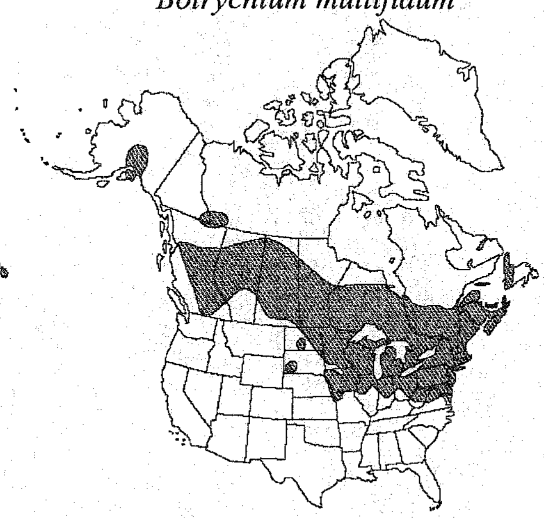
Botrychium virginianum



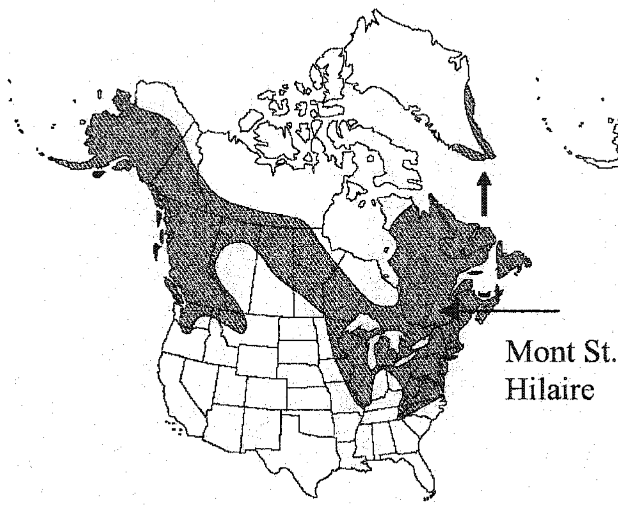
Botrychium multifidum



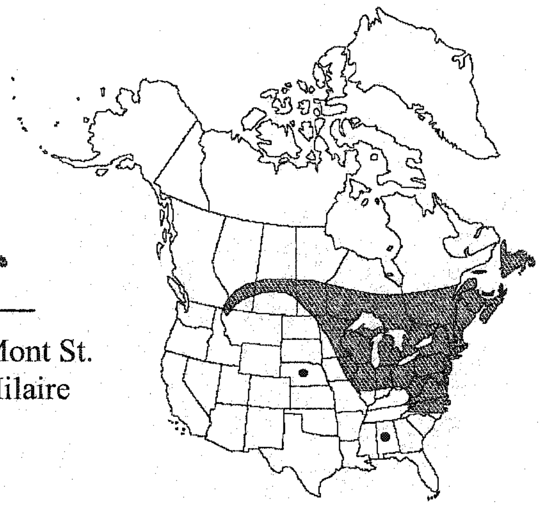
Gymnocarpium dryopteris



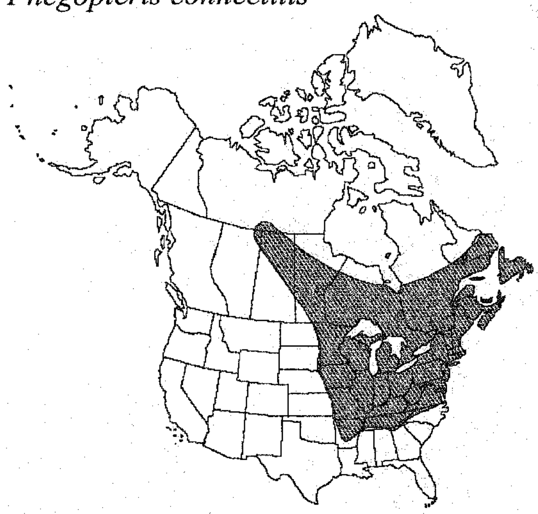
Matteuccia struthiopteris



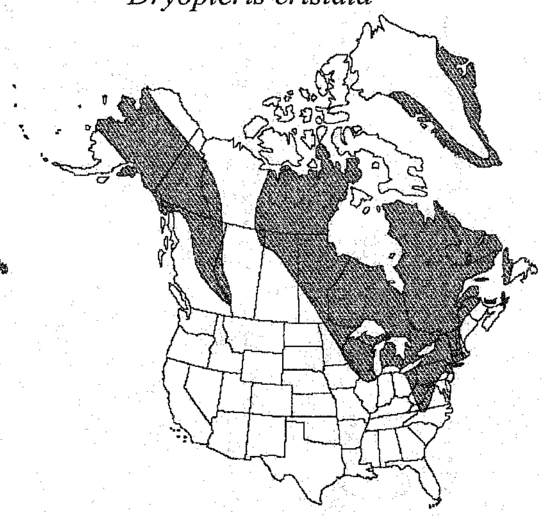
Phegopteris connectilis



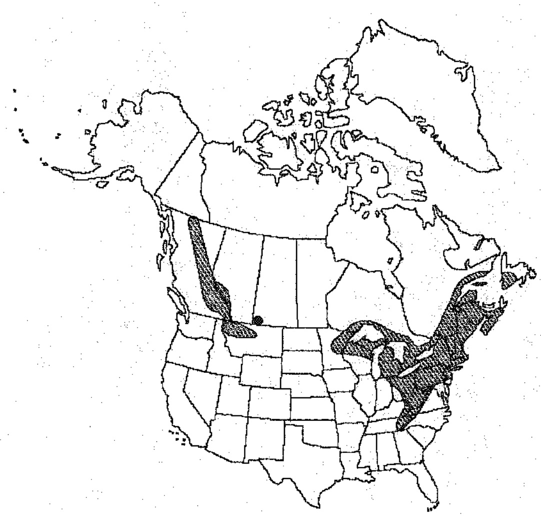
Dryopteris cristata



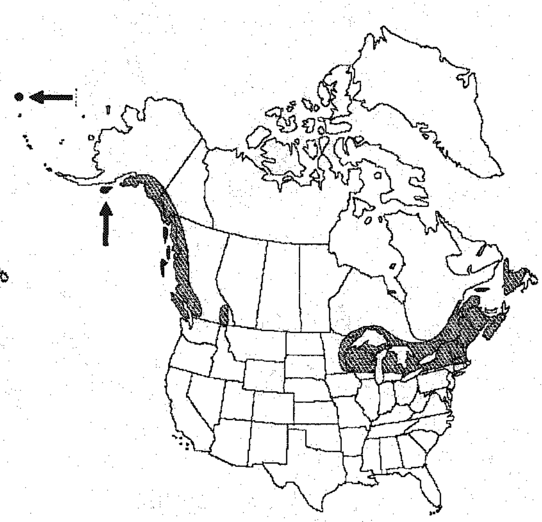
Polypodium virginianum



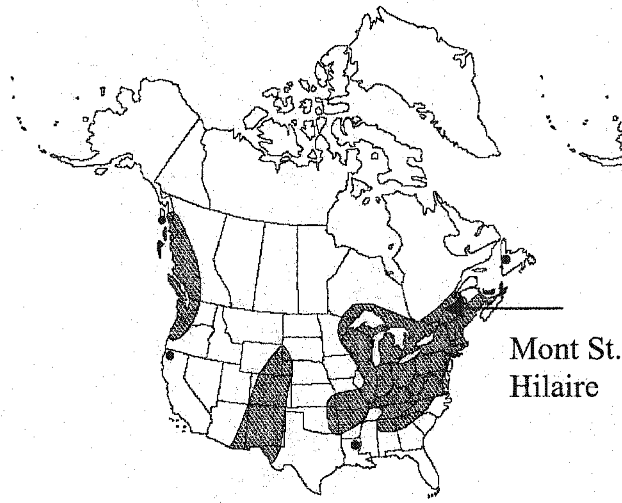
Woodsia ilvensis



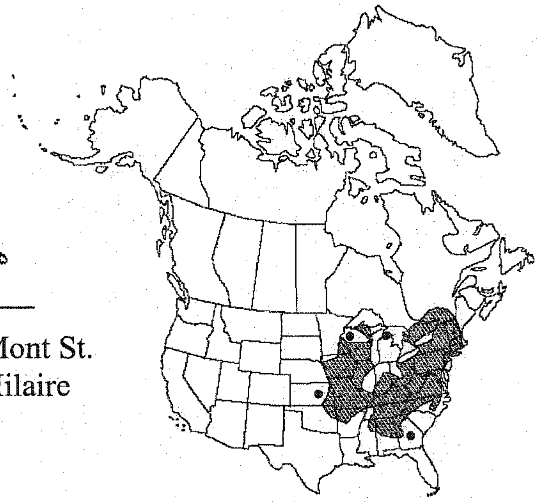
Botrychium lanceolatum



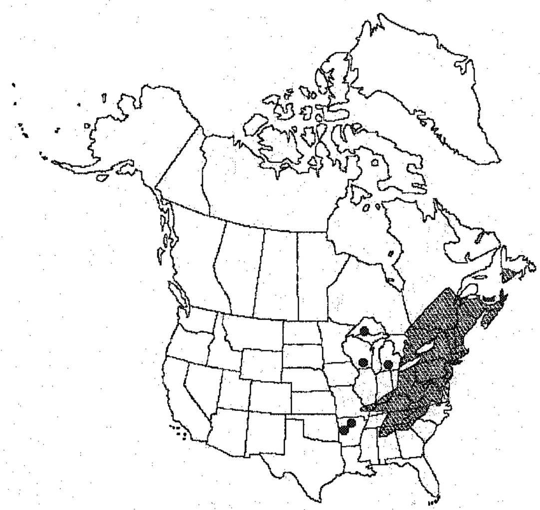
Polystichum braunii



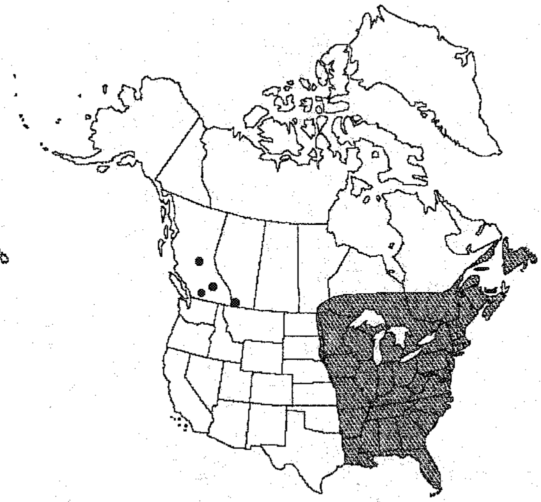
Asplenium trichomanes



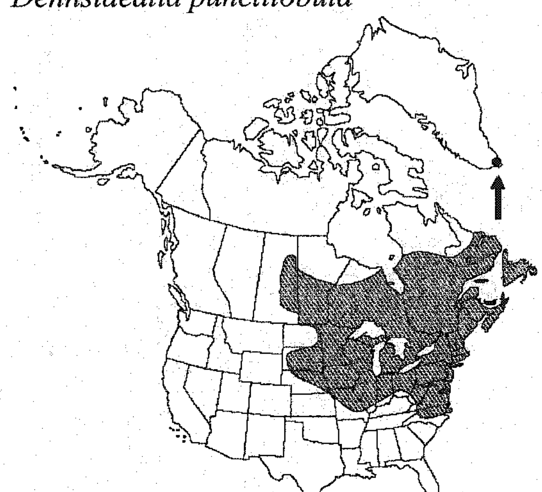
Asplenium rhizophyllum



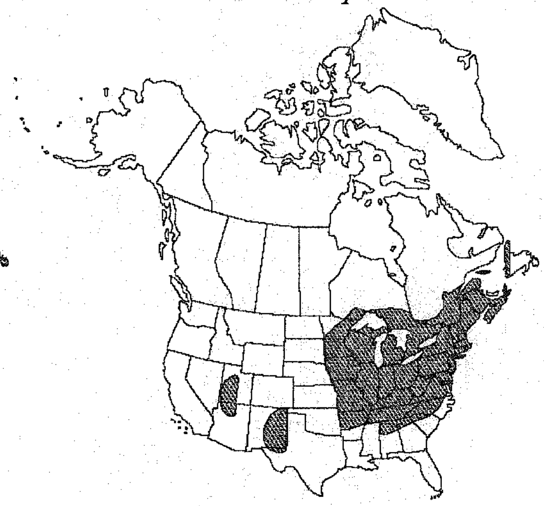
Dennstaedtia punctilobula



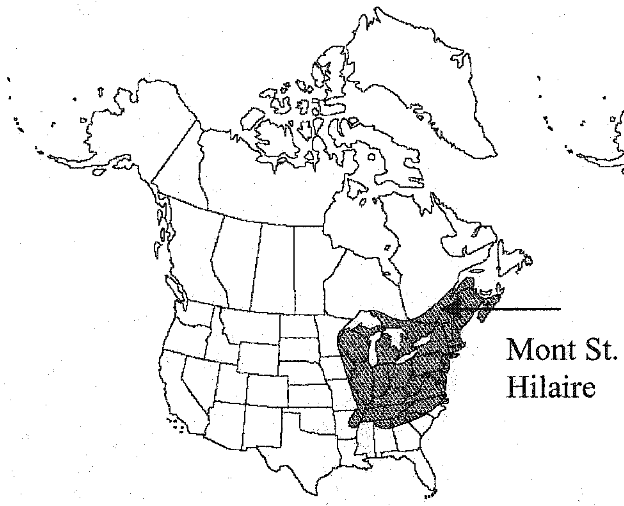
Pteridium aquilinum



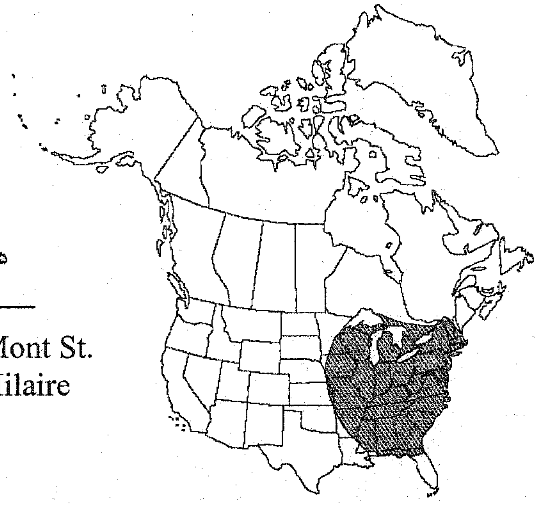
Athyrium filix-femina



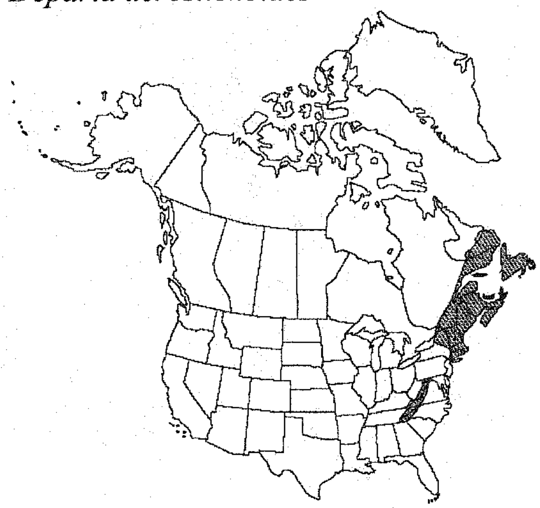
Cystopteris bulbifera



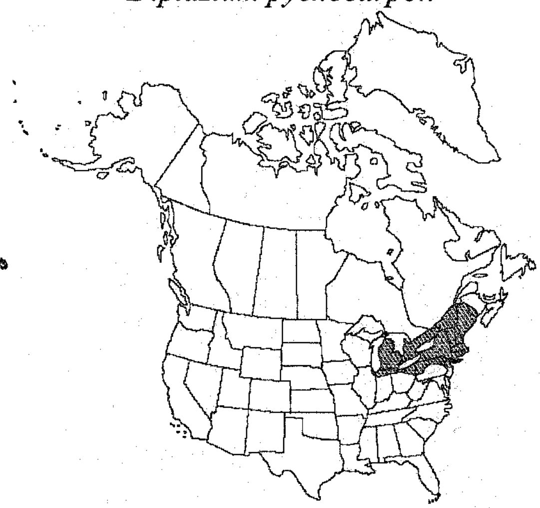
Deparia acrostichoides



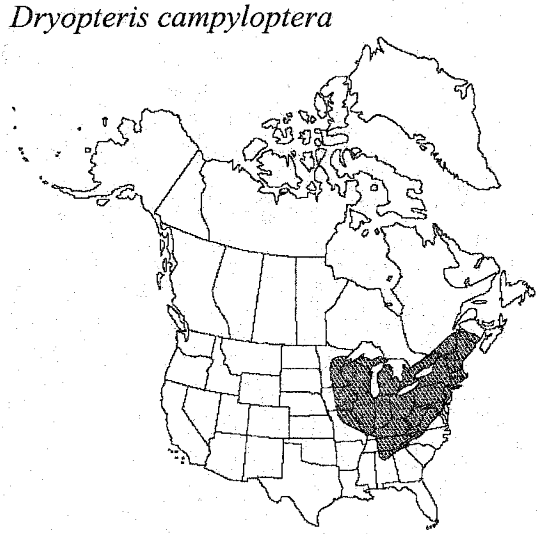
Diplazium pycnocarpon



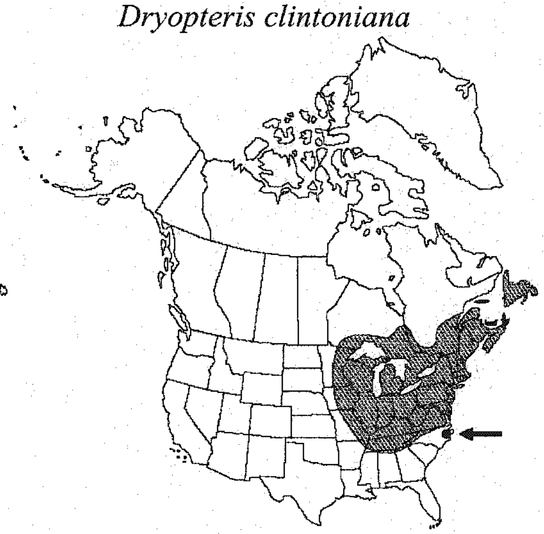
Dryopteris campyloptera



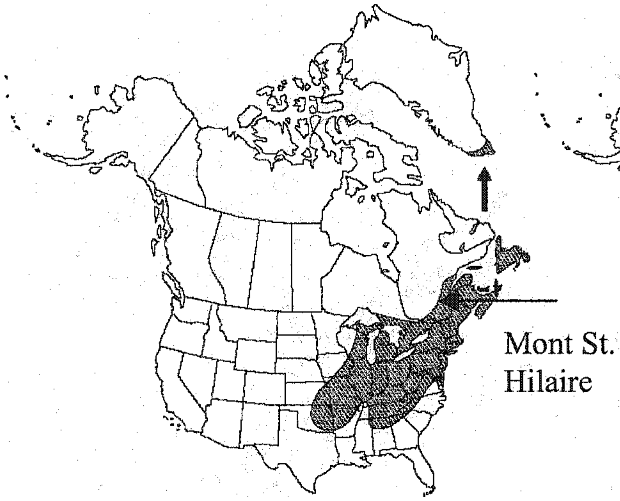
Dryopteris clintoniana



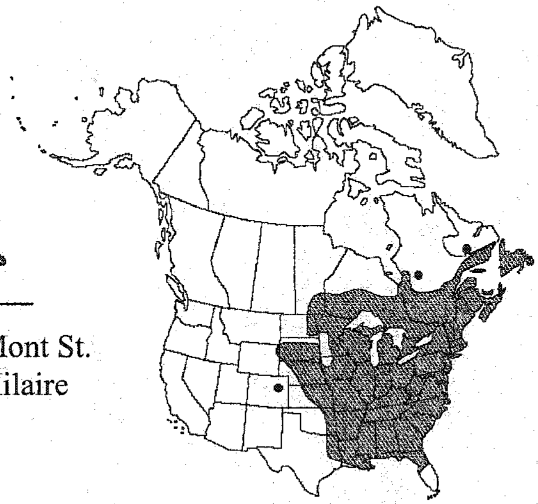
Dryopteris goldiana



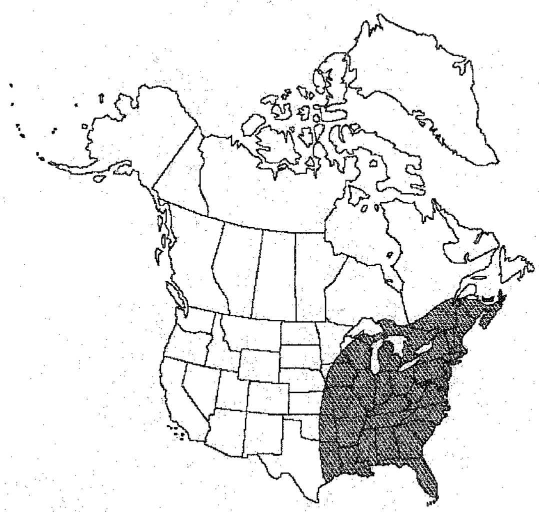
Dryopteris intermedia



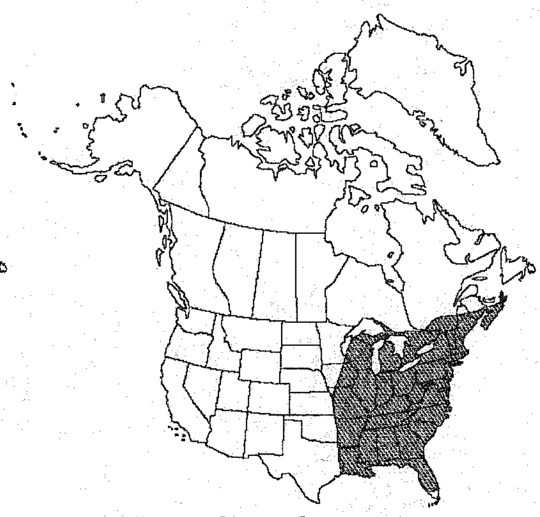
Dryopteris marginalis



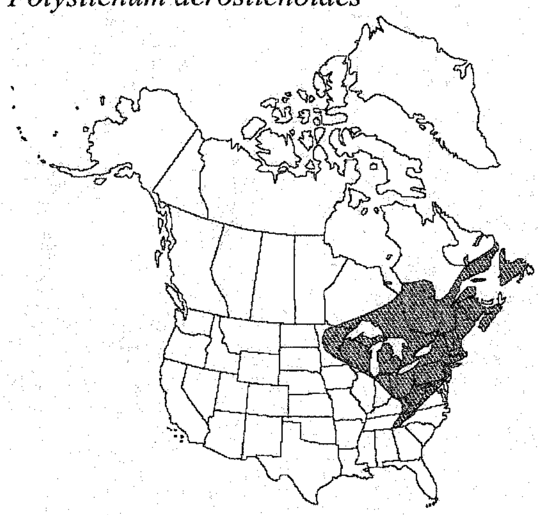
Onoclea sensibilis



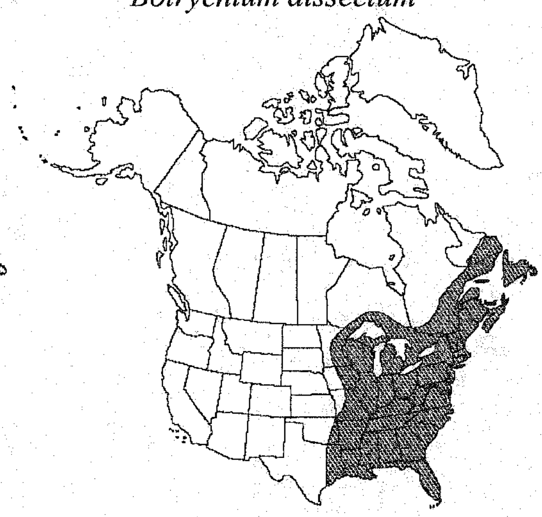
Polystichum acrostichoides



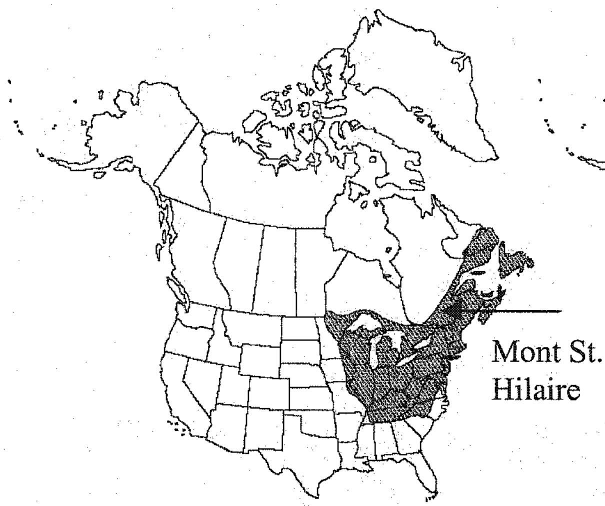
Botrychium dissectum



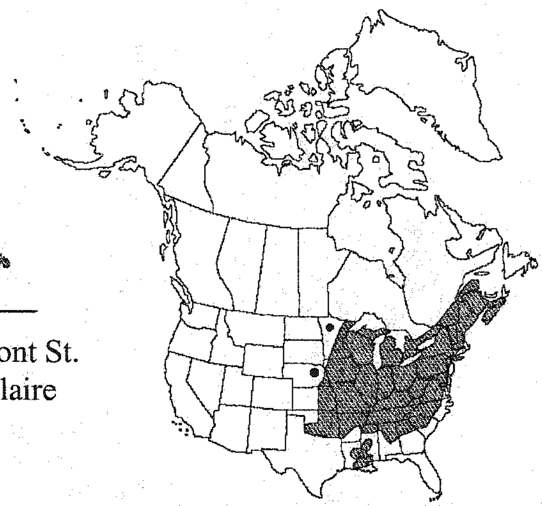
Botrychium matricariifolium



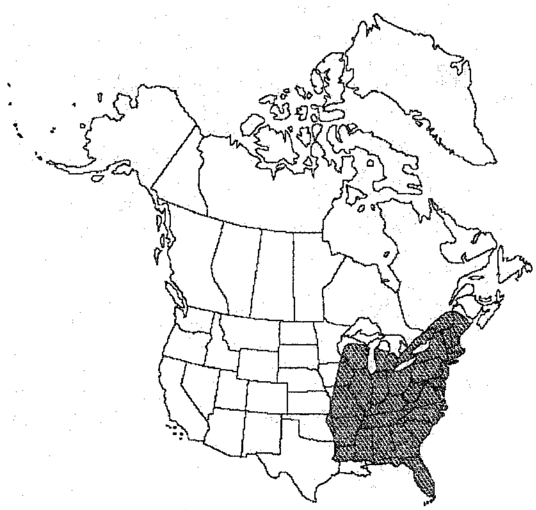
Osmunda cinnamomea



Osmunda claytoniana



Adiantum pedatum



Phegopteris hexagonoptera

Appendix C: File directory

File Directory

Data Files (note that all data files have an associated word document (*.doc) explaining contents of data file)

File name	Brief description
2000survey.xls	Raw data collected for each square metre of the hectare (fern and ground cover, soil depth)
2000surveyadj.xls	Information on square metres aggregated into 400-16m^2 quarters. Soil and canopy data also included.
Augustmoisture.xls	Data collected on soil moisture of 400 quarters in August (grain=16m^2).
Septembermoisture.xls	Data collected on soil moisture of 400 quarters in September(grain=16m^2).
moist.xls	Summary statistics of soil moisture readings for each of 400 quarters (grain=16m^2)
CANenv.xls	Environmental matrix used in CCA (grain=16m^2)
CANspa.xls	Spatial matrix used in partialled CCA (grain =16m^2).
CANspp.xls	Species matrix used in CCA (grain=16m^2)
MSHfern.xls	Raw data collected on 20 fern sites across MSH.
MSH.xls	Soil pH, nitrate concentrations and insolation for each fern site across MSH
2x2.wk1	Square metres aggregated into 4m^2 plots, used in DCA ordination.
4x4.wk1	Square metres aggregated into 16m^2 plots, used in DCA ordination.
8x8.wk1	Square metres aggregated into 64m^2 plots, used in DCA ordination.
msh.wk1	Presence/absence data collected from 1996 hectare survey of MSH, used in DCA ordination.

Files of Figures, tables and appendices used in thesis

File Name	Description
Fig.x.1.doc	Fern species richness of North America
Fig.x.2.JNB	Dominance-diversity curve for fern species of MSH
Fig.1.1.doc	Elevation map of Mont Saint-Hilaire showing streams and hectares representing the top fifth percentile of fern richness.
Fig.1.2.doc	Detrended correspondence analysis ordination of MSH fern species based on the 1996 survey for presence of ferns in each hectare
Fig.1.3.JNB	Mean and 95% confidence interval values of insolation and pH for common fern species of MSH
Fig.1.4.JNB	Mean and 95% confidence interval values of insolation and nitrate for common fern species of MSH
Fig.2.1.jpg	Topography of Botany Bay hectare shown by 2m contour intervals. Also shown are stems of common tree species.
Fig.2.2.JNB	Abundance (total percent cover) and frequency (number of occurrences) of fern species of Botany Bay.
Fig.2.3.jpg	Fern richness of Botany Bay
Fig.2.4.doc	Canonical correspondence analysis ordination of Botany Bay ferns.
Fig.2.5.doc	Partial canonical correspondence analysis ordination of Botany Bay ferns (i.e. controlled for spatial structure of environmental factors).
Fig.2.6.doc	Detrended correspondence analysis ordination of Botany Bay ferns.
Fig.2.7.jpg	Interpolated mean soil moisture (resolution $4m^2$) of Botany Bay hectare. Abundance of OCI (*Osmunda cinnamomea*), OSE (*Onoclea sensibilis*) and DCA (*Dryopteris carthusiana*) shown with 2% cover contour intervals.
Fig.2.8.jpg	Interpolated mean soil moisture (resolution $4m^2$) of Botany Bay hectare.Abundance of DMA (*Dryopteris marginalis*), DIN (*Dryopteris intermedia*) and DCA (*Dryopteris carthusiana*) shown by 2% contour intervals.

Fig.2.9.jpg	Interpolated mean soil moisture (resolution $4m^2$) of Botany Bay hectare. Abundance of AFF (*Athyrium filix-femina*) and DAC (*Deparia acrostichoides*, previously known as *Athyrium thelyptroides*) shown by 5 % cover contour intervals.
Fig.2.10.jpg	Interpolated soil nitrate concentrations (ppm) of Botany Bay hectare. Abundance of DMA (*Dryopteris marginalis*) and APE (*Adiantum pedatum*) and PAC (*Polystichum acrostichoides*) shown by 2% cover contour intervals.
Fig.2.11.jpg	Interpolated soil pH of Botany Bay hectare. Interpolated abundance of CBU (*Cystopteris bulbifera*) and GDR (*Gymnocarpium dryopteris*) shown by 2% cover contour intervals.
Tablex.1.doc	Representative fern families and genera of Mont Saint-Hilaire, Quebec and their counts at continental, regional and local scale.
Table1.1.doc	Habitats and environmental preferences of fern species present at MSH.
Table2.1.doc	Summary statistics for ground cover and soil conditions of Botany Bay.
AppendixA.doc	MSH fern species nomenclature
AppendixB.doc	North American fern range maps
AppendixC.doc	file directory