SPECIES RICHNESS, SPECIES INCIDENCE AND TURNOVER OF AMPHIBIANS IN NORTHWESTERN ONTARIO: ASSESSING THE ROLE OF HABITAT CHARACTERISTICS

by:

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ABSTRACT

There has been recent global concern over the decline of some amphibian populations. The loss of amphibian species is of concern because they play a crucial role in ecosystem structure and are indicators of ecosystem health. Amphibians within the boreal forest, especially in Northern Ontario, have not been studied as extensively as in other parts of the world. The lack of knowledge concerning amphibians within the boreal forest is troubling because the boreal forest contains half of the world's wetlands and is facing increasing pressure from human activities such as forest harvesting. Therefore by investigating the patterns and distribution of amphibian species richness, species incidence and turnover and the effect habitat has on each of these, we can infer the status of a species, determine how communities and species' populations are structured and have a better understanding of how to manage and protect them. My goals were to investigate the patterns of amphibian species richness, turnover, and incidence over a 4-year period and compare these communities between northern and southern Ontario; to assess the role local habitat and landscape characteristics have on amphibian species richness and turnover; and to develop single-species habitat models for amphibian species of Northwestern Ontario.

I surveyed pond sites around the Thunder Bay region of Northwestern Ontario from 1999 to 2002. Multiple day and night surveys were used to generate species lists at all study sites. I mapped out each pond along with the surrounding habitat characteristics and estimated local habitat variables. Landscape variables were collected using a GIS (Geographical Information System). I found that ten amphibian species made up the pond communities in Northwestern Ontario. There was higher immigration than extinction among the pond sites and

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species incidence differed over time. Species incidence was significantly different between northern and southern Ontario. These differences were related to where northern and southern Ontario were located within each species' geographic range. Those species with high incidence were located near to the core of their range while those with a low incidence were near the periphery. Species richness was positively associated with distance to the closest stream, pH, area of agriculture and percentage of shrubs surrounding a pond site, and was negatively associated with conductivity. Turnover was positively associated with the proportion of substrate around the edge of a pond and negatively associated with bank slope. Thus richer amphibian communities occur at pond sites with high pH, a mosaic of complementary habitat surrounding the breeding site, gentle sloping banks and open areas which may promote juvenile recruitment. Species' habitat models depended on each species' natural history, and its distribution. As a result, each species was associated with different habitat variables.

From this study, we can see that there are many factors to consider when trying to conserve an amphibian community or population. When conserving a single species, we need to take into account each habitat component on both a local and regional scale and consider each species habitat requirements. From a community perspective, we can select a mosaic of habitats that are complementary to all species. Another very important point to keep in mind is where species are within their geographic range. Depending on the where a species is located within its range can determine whether is it common or rare. Because species habitat requirements appear to vary so greatly among species, I recommend including individual species habitat models in amphibian conservation strategies and not limiting our efforts to habitat restoration/creation.

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GENERAL INTRODUCTION

A central goal of ecology is to document and explain patterns of biological diversity and to understand why these patterns differ spatially and temporally. A variety of approaches are used to achieve this goal such as studying both populations and communities. Population ecologists are interested in, among other things, the variation of population densities and how they are spatially structured (Delibes et al. 2001; Campbell & Reece 2002) whereas community ecologists are interested in determining community composition, and how communities are affected by environmental factors and interspecific interactions (Begon et al. 1990; Smith 1996). Studies of ecological processes have provided insights into many factors responsible for community structure. These factors include local, regional, biotic, abiotic, current and historical processes (Ricklefs 1987; Dunson & Travis 1991; Cornell & Lawton 1992; Ricklefs & Schluter 1993).

In order to explain patterns in the distribution of populations and communities, we need to look at them on different spatial scales. What can be viewed as a disturbance at one scale can be unimportant at another. Local extinction processes can be determined on a smaller scale however the status of a species is determined at the regional scale by looking at metapopulations or metacommunity dynamics. Recently, studies have shown that some amphibian species display metapopulation spatial structure as a consequence of their reliance on aquatic habitat for breeding and terrestrial habitat for hibernation and foraging (Gill 1978; Sjögren 1991; Hecnar & M'Closkey 1996c; Sjögren-Gulve & Ray 1996; Skelly et al. 1999; Carlson & Edenhamn 2000). Metapopulations are groups of local populations, interconnected by dispersal and characterized by the opposing processes of colonization and extinction (Levins 1969; Hanski & Gilpin 1991).

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Regional species incidence is determined by the balance between local colonization and extinction. By investigating species incidence, we can determine if a species is common or rare within a region. Due to the dynamic nature of metapopulations, taking a metacommunity perspective may reveal changing species compositions. Turnover is the rate at which new species are colonizing and others are becoming extinct per unit time (Clark & Rosenzweig 1994; Gotelli 1998; McKinney & Drake 1998). Species with high turnover tend to go extinct sooner because they experience greater fluctuations in abundance which takes them to zero abundance more often than those species with lower turnover (McKinney & Drake 1998). However, this is dependent on the rates of colonization and extinction. If the rate of colonization exceeds the rate of extinction, there will be high turnover characterized by high species richness. Conversely if the rate of extinction exceeds the rate of colonization, there will be high turnover but a decline in species diversity causing species and communities to be more vulnerable to extinction (Gilinsky 1998). Thus explaining patterns of species richness, species incidence, turnover and spatial dynamics is an important step for amphibian conservation (Green 1997; Hecnar 1997) because it allows us to assess the status of populations and communities as well as providing insight into how they are structured.

There are a number of reasons why the loss of amphibians from ecosystems should be of concern. Amphibians constitute a major component of the biomass in some ecosystems. In the eastern deciduous forest more biomass is contributed by just one species of salamander than all bird species or about that amount equal to small mammals (Burton & Likens 1975). Being both predator and prey, amphibians play an important role in energy flow and trophic dynamics of both aquatic and terrestrial ecosystems (Dunson et al. 1992; deMaynadier & Hunter 1995;

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Murphy et al. 2000). For example, tadpoles convert a large amount of aquatic plant biomass, zooplankton, insect larvae, and other tadpoles into energy that can be transported to terrestrial environments via predation (Wassersug 1975; Murphy et al. 2000). Also, adults are able to exploit and convert small invertebrate biomass into energy that becomes available to larger vertebrates (deMaynadier & Hunter 1995; Murphy et al. 2000). Amphibians are important as prey to fish, snakes, small mammals, birds and other larger amphibians and they also act as middle to upper level predators. Therefore all phases of an amphibian's life cycle provide important food resources for many species from a number of trophic levels.

Since amphibians are an important link within the food chain, may act as "keystone" as well as "indicator" species (Vitt et al. 1991). A keystone species is one that's role in the ecosystem is so vital that it's disappearance or even reduction would cause changes throughout the community resulting in declines or extinctions of many dependent species (Morin 1983; Mills et al. 1993; Murphy et al. 2000). Experiments performed by Morin (1983) showed that slight alterations in the abundance of two predatory amphibians, *Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum*, significantly altered the abundances of the rest of the anuran community. In the absence of these predators, competitively inferior species did not survive well. At high predator densities, competitively superior species declined. Thus, these salamander predators acted as keystone species by mediating interspecific competition among larval anurans which allowed competitively inferior species to persist and promote community diversity. Hecnar and M'Closkey (1996a) studied the disappearance of bullfrogs from Point Pelee National Park, Ontario, Canada and the impact it had on the structured amphibian community. They reported a four-fold increase in green frog abundance and considered it a

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result of predatory release.

A number of biological and natural history traits of amphibians suggest that they make good indicators of ecosystem health. An indicator species is one that is very sensitive to changes in the environment and thus declines of these species could reflect declines in environmental quality (Murphy et al. 2000). Amphibians may be more sensitive than other vertebrates to anthropogenic changes because of their unique biological characteristics and habitat requirements (Vitt et al. 1991). Most amphibians have a biphasic life cycle and use both aquatic and terrestrial habitats (Wilbur 1984). Their permeable skin and eggs readily absorb substances from the surrounding aquatic and terrestrial environments (Vitt et al. 1991; Dunson et al. 1992; Blaustein 1994; deMaynadier & Hunter 1995). Amphibian skin also acts as a respiratory organ which increases vulnerability to drought and microhabitat drying (Vitt et al. 1991; deMaynadier & Hunter 1995; Murphy et al. 2000). Aquatic larvae have high growth rates in order to metamorphose before microhabitat drying (Dunson et al. 1992). Also, metamorphosis involves ontogenetic shifts with a change in habitat and /or a trophic level shift from herbivory to carnivory (Werner 1994; deMaynadier & Hunter 1995; Murphy et al. 2000). Amphibians have relatively poor dispersal abilities and strong site fidelity (Sinsch 1990, 1991) which hinders them in dispersing from disturbed environments (Ash 1988; Petranka et al. 1994; deMaynadier & Hunter 1995). Thus small-scale alterations to both aquatic and terrestrial habitats could affect amphibians much more than other organisms. Therefore amphibians may be useful for monitoring the effects of local environmental disturbances (Vitt et al. 1991; Blaustein 1994).

Recent global concern over the decline of some amphibian populations has increased interest in determining the causes and developing preventive conservation measures (Blaustein &

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Wake 1990; Wake 1991; Wake & Morowitz 1991; Blaustein et al. 1994; Pechmann & Wilbur 1994; Houlahan et al. 2000; Alford et al. 2001). Concerns are warranted because amphibians have survived for more than 350 million years in the wake of numerous pressures from predators and climate changes (Murphy et al. 2000). Recent evidence of large-scale die-offs and disappearances of numerous species suggest that rapid, widespread anthropogenic environmental changes are exceeding the ability of these survivors to adapt (Murphy et al. 2000). Anthropogenic causes of declines can be attributed to numerous factors including habitat destruction, pollution, UV radiation, disease, introduced predators or competitors, acid precipitation and climate change (Dunson et al. 1992; Blaustein et al. 1994).

The most important causes of amphibian declines are habitat destruction, fragmentation and degradation (Green 1997; Hecnar 2004). Most amphibians require more than one habitat for foraging, hibernation and breeding (Pope et al. 2000). Therefore loss or degradation of even one type of habitat could be detrimental to populations or communities. One way to prevent this is to determine and understand the role habitat components play in amphibian habitat selection. Since amphibians require both aquatic and terrestrial habitat, it would be beneficial to look at choice on both a local habitat and regional landscape level (Hecnar & M'Closkey 1998).

The loss of woodland habitat for agriculture or forestry and the increase in roads and highways have increased the fragmentation of forests (Vos & Stumpel 1995; Forman & Alexander 1998; Murphy et al. 2000). Fragmentation severs connections between local populations, decreasing the possibility for recolonization from other sites and increases the risk of extinction (Laan & Verboom 1990; Vos & Stumpel 1995; Green 1997). The increase in

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roads, highways, and their traffic volumes, increase road mortality of amphibians (deMaynadier & Hunter 1995; Findlay et al. 2001) as individuals cross during seasonal migrations (Fahrig et al. 1995). Roads also act as barriers reducing gene flow between populations (Reh & Seitz 1990). Since most amphibians use aquatic and terrestrial habitat, suppression of movements between these habitats may cause a substantial decline in amphibian species. However roads can also provide good habitat. Ditches can act as migration corridors and breeding sites for temporary pond species. Woodland surrounding a breeding site is important for salamanders, woodfrogs, gray treefrogs and spring peepers because they use these sites for foraging and hibernation (Hecnar & M'Closkey 1996c; Hecnar 1997; Conant & Collins 1998). Many studies have shown that some salamander species are negatively affected by forest harvesting practices and especially by clearcutting (Bury 1983; Petranka et al. 1993, 1994; deMaynadier & Hunter 1995). Timber harvesting practices modify the amount of cover, shade and moisture that is available to amphibians. Removal of coarse woody debris and understory vegetation, and lack of leaf litter, decreases the amount of microhabitat that amphibians rely on, decreases the amount of moisture and increases risk of desiccation (Pough et al. 1987; Petranka et al. 1994). Hecnar and M'Closkey (1998) found that amphibian species richness in southern Ontario was highly correlated with forest cover. Also, regional faunas now differ as a consequence of land-use history (Hecnar & M'Closkey 1996c). However Ash (1997) found that plethodontid salamanders began to return to clearcut sites four to six years after cutting occurred, and their return to clearcut sites was strongly correlated with the reformation and increase of the leaf litter layer.

At a breeding site, vegetation is used by many amphibians for calling and oviposition

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sites and as refuge from predators (Johnson 1989, Hecnar & M'Closkey 1996b; Baker & Halliday 1999; Carr & Fahrig 2001). The size of a pond may also be important to amphibians. In temporary ponds, hydroperiod is short and larvae run the risk of desiccation before they can metamorphose (Semlitsch 2000). Although some amphibians use larger ponds for hibernation, there is a higher risk of predation from fish species (Beebee 1981; Petranka 1983; Hecnar & M'Closkey 1997; Eason & Fauth 2001). Amphibians are also negatively affected by high acidity levels in aquatic habitats due to their permeable skin (Roudebush 1988; Dunson et al. 1992; Karns 1992; Eason & Fauth 2001). By determining the relationship between amphibians and their habitat, we can begin to explain local and regional patterns and aid in future conservation efforts such as habitat protection, habitat restoration, and repatriation programs.

Human activities have placed increasing pressures on the boreal forest ecosystem. As of 1995, about 10 million cubic metres of wood a year had been harvested from Northwestern Ontario's boreal forests. This is troubling because the boreal forest contains almost half of the world's wetlands (Schindler 1998). In addition, the ecology of amphibian populations within the boreal forest is poorly understood (Elmberg 1993), especially in northern Ontario (see maps in Oldham & Weller 1992).

My goal was to determine and to try to explain the patterns of species richness, incidence, and turnover in boreal amphibian communities. Specifically, I investigated the relative association of local habitat characteristics and regional landscape features in relation to amphibian species richness, incidence, and regional dynamics over a four-year period, and compared these communities to previously studied amphibian communities in Southern Ontario.

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GENERAL METHODS

Study Area

I conducted my study in the Thunder Bay region of northwestern, Ontario, Canada (Figure 1). Thunder Bay has been colonized by humans since the 1700's although the population did not start to boom until the logging industry started up in the early 20th century. Now two thirds of northern Ontario's communities rely on forests and forest industry. This region is situated on the Canadian shield and glacial scouring has resulted in minimal soil, and rolling topography. This area experiences brief warm, moist summers and long, cold, dry winters (Zoladeski & Maycock 1990). The Thunder Bay region is located within the Boreal Shield Ecozone and lies on the border of two major biomes, the Northern Boreal Forest Region and the Southern Great Lakes-St. Lawrence Forest Region (Wiken 1986; Wiken et al. 1993). Vegetation consists of a combination of coniferous and mixed forests comprised of black and white spruce (*Picea mariana, P. glauca*), jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) as well as trembling aspen (*Populus tremuloides*), and white birch *(Betula papyrifera)* (Baldwin & Sims 1989; Ecoregions Working Group 1989; Zoladeski & Maycock 1990). These tree species occur on humo-ferric podzols or brunisols that are often shallow and coarse-textured (Thompson 2000).

Pond Surveys

A set of 41 ponds had been previously surveyed by Stephen J. Hecnar from 1999 to 2000. I continued surveying these ponds from 2001 to 2002 and used the combined data for all four years to investigate the patterns of species richness, incidence, and turnover. In 2001, I increased my sample size to 69 ponds and surveyed these from 2001 to 2002. I used the 69

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ponds to look at the effects of local habitat and landscape characteristics on amphibian species richness, incidence and turnover. Pond sites were located by using topographic maps, information provided by private landowners, inquiring at conservation authorities and provincial parks, and by chance discovery.

Ponds were chosen because many amphibians use ponds for breeding, foraging, oviposition, and hibernation and ponds provide refuge for eggs and larvae from predators, such as fish, and exposure to extreme elements. Therefore all stages of an amphibian's life cycle can be sampled in pond habitats. I considered ponds to be small bodies of still water that ranged in depth from 0.5 to 7 m and 7.0×10^{-5} to 0. 04 km^2 in area.

I surveyed all ponds from late April to September each year. A minimum of four day and four night visits were made to each site, spread throughout the collection period, to account for seasonal phenology that exists in temperate-zone amphibian faunas. I conducted visual surveys around and within at least ten metres from the pond edge, searching underneath any woody debris that was found as well as wading and canoeing within the pond. The amount of time spent at each pond varied, depending on the size and the difficulty manoeuvring around it. I used dipnets to search for larvae through the submerged vegetation and along the edge. I identified larvae to species at the pond when possible or took specimens back to the lab to permit further development to facilitate species identification. Night surveys consisted of listening at each site for up to ten minutes for anuran breeding calls. I considered this sufficient as over 90% of breeding anuran species present at a site can be detected within the first three minutes of listening to calls (Shirose et al. 1997; Paton & Crouch 2002). Species were recorded as present if eggs, tadpoles, juveniles or adults were observed or calls were heard at any visit during the

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sampling year. The goal of the surveys was to construct accurate species lists for individual ponds that I could compare among sites and over time.

Statistical Analyses

I report descriptive statistics as mean ± standard error of the mean (SE). I used $\alpha =$ 0.05 for minimal significance when interpreting test results, but used $p \leq 0.15$ when selecting variables for stepwise model building. I consulted Sokal & Rohlf (1994) and for most analyses I used SYSTAT 9 (Wilkinson 1990).
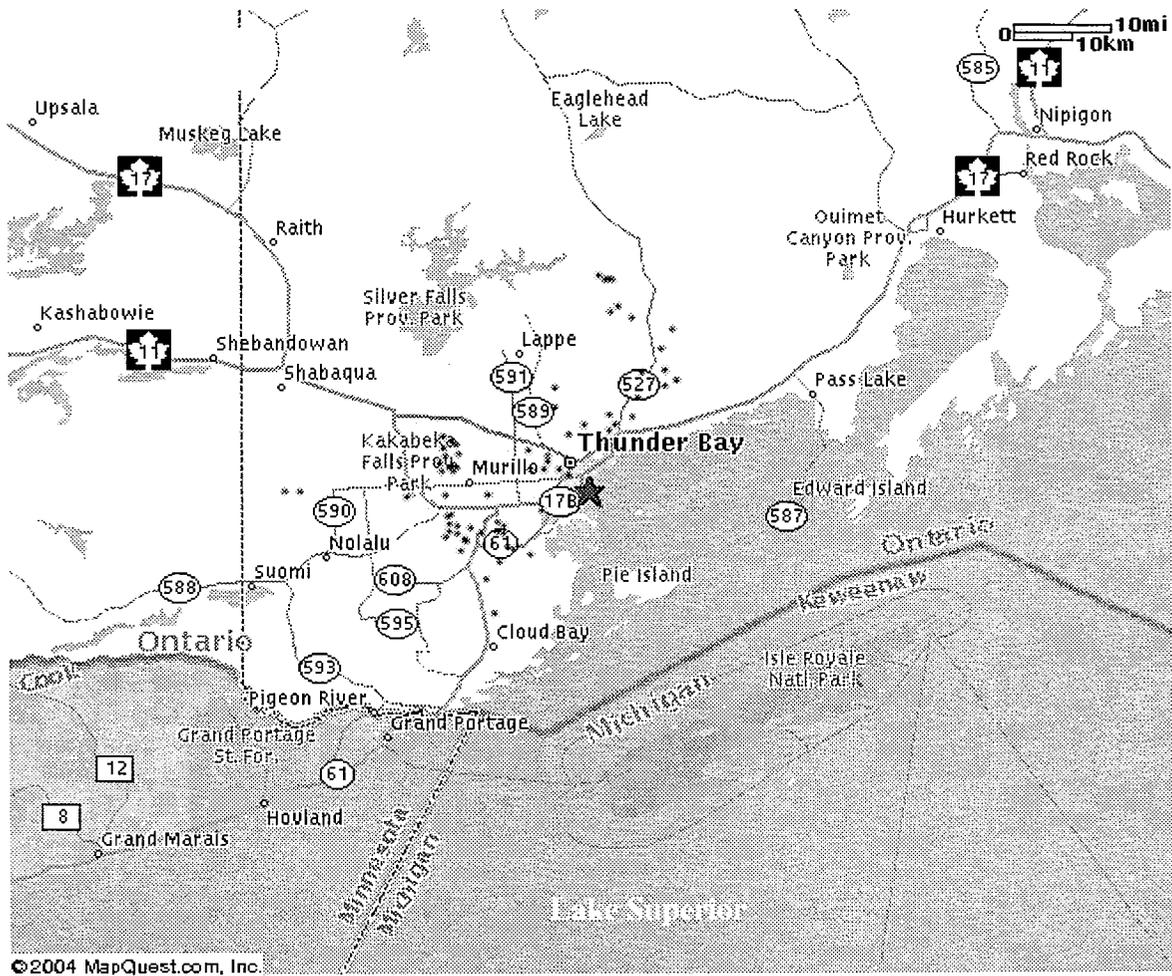
Figure 1. Map of study sites around and within the region of Thunder Bay, Ontario. Small black dots represent ponds.

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CHAPTER 1

Patterns of species richness, incidence, and turnover in amphibian pond communities of Northwestern Ontario

INTRODUCTION

A long-standing goal of ecology is to understand the dynamics of biological diversity. Ecological communities often undergo fluctuations in abundance and distribution among species as their environments change. Demographic changes in populations (i.e. immigration, emigration, birth and death rates) can result in replacements of species in communities over time. Much attention has focussed on turnover of species in ecology. Specifically, the topic of ecological succession (Wissinger & Whiteman 1992; Weitzel & Panik 1993; Rosenzweig 1995) and the debate regarding whether these changes are deterministic (Clementsian community) or stochastic (Gleasonian community) continues. Species turnover has also received much attention in the field of island biogeography (MacArthur & Wilson 1963, 1967; Diamond & May 1977; Hanski & Gilpin 1991; Nores 1995). Equilibrium theory models species richness and species turnover as a dynamic balance between immigration and extinction (MacArthur & Wilson 1963, 1967). Similarly, turnover is also an important factor in metapopulation or metacommunity theory being a product of local colonization and local extinction (Hanski & Gilpin 1991).

A metapopulation is a set of local populations connected by migration, gene flow, extinction and colonization (Levins 1969; Hanski & Gilpin 1991). Recent studies have started to take a metapopulation approach to amphibian ecology (Sjögren 1991; Sjögren-Gulve 1994; Hecnar & M'Closkey 1996c; Skelly et al. 1999). This is because amphibian breeding ponds form habitat patches of subpopulations between which individuals move and are open to

extinction and recolonization from other ponds (Marsh & Trenham 2001). Local extinctions at ponds can be frequent but recolonization allows amphibian species to persist on a regional scale. Metapopulation dynamics can be studied by investigating pond occupancy, extinction and recolonization from annual pond surveys. This can be done by looking at species richness, incidence and turnover. Species richness is an important component of biological diversity and can be measured at a variety of scales. Species incidence is the fraction of patches of habitat that are occupied by a species and this changes over time due to colonization of unoccupied patches and extinction of presently occupied patches (Mauer & Nott 1998). Therefore an increase in incidence of a species lowers the risk of extinction. Local extinction and recolonization are assessed by examining turnover. Turnover is the rate at which new species are colonizing and others are becoming extinct per unit time (Clark & Rosenzweig 1994; Gotelli 1998; McKinney & Drake 1998). There are many studies of species turnover in the literature (Diamond & May 1977; Hecnar & M'Closkey 1996b, 1996c, 1997; Caley & Schluter 1997; Skelly et al. 1999; Hanski & Singer 2001). Understanding turnover is important because it reflects the stability of communities. To assess community status, a minimum of one complete turnover is needed (Connell & Sousa 1983; Hecnar 1997). However, to avoid concluding that communities are stable (by only looking at one complete turnover) when they just may be composed of long-lived individuals, turnover should be observed throughout the entire lifespan of a species. Species with high turnover tend to go extinct sooner because they experience more fluctuations in their abundance which takes them to zero abundance more often then those populations with lower turnover (McKinney & Drake 1998). However if colonization exceeds extinction events, species will exhibit high turnover and high species diversity reducing risk of extinction (Gilinsky 1998).

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Some local populations may also be considered source populations while others may be acting as sinks (Pulliam 1988; Harrison 1991). Source populations produce excess individuals that emigrate to nearby sink populations while population sinks survive based on the continual immigration of individuals from the source populations. Thus the loss of the source population will cause losses to the surrounding populations that are dependent on the emigration of individuals from the source population (Holt 1985; Green 1997; Gotelli 1998). Continual local losses of species will eventually make them rare on a regional scale. Therefore these source/sink dynamics are important in determining whether loss is temporary or permanent. Furthermore, with the size and number of suitable patch habitats decreasing, the role of metapopulation dynamics becomes more crucial (Hanski et al. 1994) especially in predicting effects of future habitat loss and fragmentation (Marsh & Trenham 2001).

There has been little to no investigation on the status of amphibian species in Northwestern Ontario. However, extensive research has been conducted in Southwestern Ontario (Hecnar & M'Closkey 1996a, 1996b, 1996c, 1997, 1998; Hecnar 1997). Although climate, habitat and the nature of landscape modification differs between northern and southern Ontario, the species pool between is virtually the same (exceptions include *Rana palustris, Rana catesbeiana* whose ranges does not extend into northern Ontario and *Pseudacris maculata* whose range does not extend into southern Ontario). However, how rare or common these species are within northern Ontario is unknown. Habitat loss from forest harvesting and agriculture has not been as extensive and intense in the north where extensive forest regeneration has occurred and is not restricted by agriculture. Thus it is important to gain more knowledge about boreal forest species so we can assess the impact future forest harvesting may have on these communities.

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Species also vary in abundance throughout their geographic range, being numerous in some areas and scarce or absent in others. A pattern of spatial variation often emerges where the density of a species decreases and population patchiness increases from the centre towards the periphery of its geographic range (Whittaker 1956, 1965; Hengeveld & Haeck 1982; Brown 1984). Therefore, depending on where species are located within their ranges could effect how common or rare that species will be, possibly as a result of decreasing availability of niche requirements farther from the centre of the range (Brown 1984). Consideration of range position in ecological studies may provide insights into possible reasons why conservation efforts may not be working for some species. Many believe that when a species becomes endangered, its geographical range will shrink towards the centre and only the core population will persist until the end (Brown 1995). Efforts to try to protect, relocate, or reintroduce a species may be in vain when working with a population at or near the edge of their range (Griffith et al. 1989, Dodd & Seigel 1991). However a study by Channell & Lomolino (2000) found that 98% of endangered species maintained populations in a portion of their peripheral range and that 37% of those species had remnant populations occurring exclusively in the periphery of their historical range. Although this may prove insightful for maintaining and the possible discovery of new populations of endangered species, many of these populations may be sinks or isolated populations that will go extinct without a continual source of immigrants.

In this study, I assess the patterns of amphibian species richness, incidence and turnover over a four-year period. My objectives were 1) to construct a list of amphibian species that were present in Northwestern Ontario, 2) to evaluate and compare species richness, incidence and turnover among pond sites from year to year and 3) to compare the species

incidence findings to Southern Ontario. I expected to find low turnover, high species richness and high species incidence among my pond sites in Northwestern Ontario. I also expected to find differences in incidence between the two regions, with woodland species having higher incidence in Northern Ontario. Species were expected to have a higher incidence in either region if they are located close to the core of their geographic range.

METHODS

I surveyed 41 ponds between 1999 and 2002 in the Thunder Bay region of Northwestern Ontario to determine the presence of amphibian species. Amphibian species richness, and turnover was calculated for each pond and species incidence was calculated for the entire region.

Cumulative species richness, over all of the visits made to a site within a year, was used for analyses. I calculated species incidence by dividing the number of ponds in which each species occurred by the total number of ponds surveyed. I calculated annual turnover by estimating local extinction and colonization rates at pond sites and compared the presence or absence of a species between consecutive years using the following equation (Clark & Rosenzweig 1994; Hecnar 1997; McKinney & Drake 1998):

$$T = \left(\frac{C + E}{S_t + S_{t+1}} \right)$$

where T is the turnover rate, C is the number of new species that colonized a local site, E is the

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number of species that became locally extinct at the site, and S_t is the number of species at the site at time t.

I used the average species incidence over the four years to conduct comparisons between northern and southern Ontario. I also divided species for both regions into two categories, Core and Periphery, and compared their incidence. This was done by visual inspection of each species' range map (Conant & Collins 1998). I placed species in either category based on which area within their geographic range they were closest to. Core species were those located close to or in the middle of their geographical range and Periphery species were those that were located close to or along the edge of their range. I expected lower incidence for peripheral species relative to core species.

Statistical Analysis

I used F-max and One-sample Kolmogorov-Smirnov tests using Lillifor's distribution to check for homogeneity of variance and normality of data. Data that did not pass these tests were transformed accordingly (Sokal & Rohlf 1994).

I used one-way ANOVAs to determine if species richness and turnover differed among years and Tukey HSD Multiple Comparisons tests to determine which years differed. I also used correlation analyses to determine if a temporal trend existed. I used G-tests (William's Correction) to compare species incidence among years and between northern and southern Ontario. I used a two-sample t-test to compare species incidence between northern and southern Ontario for each species and between Core and Periphery species. A statistical significance of α = 0.05 was used. All analyses followed Sokal & Rohlf (1994) and were generated using SYSTAT 9 (Wilkinson 1990).

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RESULTS

I found nine amphibian species over the four years (Table 1.1). Mean species richness over the four years was 4.1 (±0.11) and ranged from 1.0 - 7.0. Mean species richness increased from 1999 to 2002 (Table 1.2) as values ranged from 3.8 (±0.22) in 1999 to 4.6 (±0.20) in 2002 (Figure 1.1). Mean species richness also differed among years ($F_{3,160} = 5.01$, df = 3, p < 0.05; Figure 1.1).

Mean overall turnover was 0.189 (± 0.015) and decreased over sample seasons from 0.24 (± 0.032) in 1999/2000 to 0.13 (± 0.020) in 2001/2002 (Figure 1.2). Mean turnover also differed among years ($F_{2,120} = 4.74$, df = 2, p < 0.05; Figure 1.2). The results from the correlations indicated species richness was increasing over time and that turnover was decreasing over time (Table 1.2).

No pond was inhabited by all species. Species incidence varied among species and among years (Figure 1.3). The overall incidence distribution was significantly different between 1999 and 2001 (G = 23.04, df = 7, p < 0.005), and 2002 (G = 25.57, df = 7, p < 0.001). There were no differences in incidence distribution between 1999 and 2000 (G = 12.71, df = 7, p = 0.080), 2000 and 2001 (G = 6.97, df = 6, p = 0.324), 2000 and 2002 (G = 8.50, df = 6, p = 0.204) and between 2001 and 2002 (G = 3.85, df = 6, p = 0.70). Most species incidence increased over time (Figure 1.3). *P. maculata* showed the most change in distribution by more than doubling it's incidence from 1999 to 2002. *R. sylvatica* also showed a high change in distribution among these years, increasing by nearly 50 %. Between 1999 and 2000, *R. septentrionalis* contributed the most to the change in incidence distribution even though I did not find a significant change between the rest of the years. *P. crucifer, B. americanus,* and *R. sylvatica* all increased to almost

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90% incidence over the four years while *R. pipiens* and *R. clamitans* varied between 5-10%. I found *A. laterale* only during the first year of surveying.

Species incidence differed significantly between northern and southern Ontario (G = 87.67, df = 5, p < 0.0001; Figure 1.4). There were four species that showed the largest differences in incidence between the two regions. *R. clamitans* (t = 28.83, df = 135, p < 0.001) and *R. pipiens* (t = 7.918, df = 135, p < 0.001) had a higher incidence in southern Ontario while *R. sylvatica* (t = 10.365, df = 135, p < 0.001) and *B. americanus* (t = 4.091, df = 135, p < 0.001) had a higher incidence in northern Ontario. There were no differences between regions for *Pseudacris crucifer* (t = 0.726, df = 135, p = 0.469) and *A. laterale* (t = 0, df = 135, p = 1.0). *Pseudacris maculata* and *R. septentrionalis,* were only found in northern Ontario and *N. viridescens* and *A. maculatum* were only present in southern Ontario and therefore were eliminated from the analysis.

Core species had higher incidence than peripheral species (t = 3.35, df = 17.2, p < 0.01; Table 1.3 & Figure 1.5). Mean species incidence was 58.2% for core species and 17.6% for peripheral species.

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Table 1.1. Amphibians encountered at study pond between 1999 and 2002.

Scientific Name	Common Name
Pseudacris crucifer	Spring Peeper
Pseudacris maculata	Boreal Chorus Frog
Hyla versicolor	Gray Treefrog
Rana sylvatica	Wood Frog
Rana clamitans	Green Frog
Rana septentrionalis	Mink Frog
Rana pipiens	Northern Leopard Frog
Bufo americanus	American Toad
Ambystoma laterale	Blue-spotted Salamander

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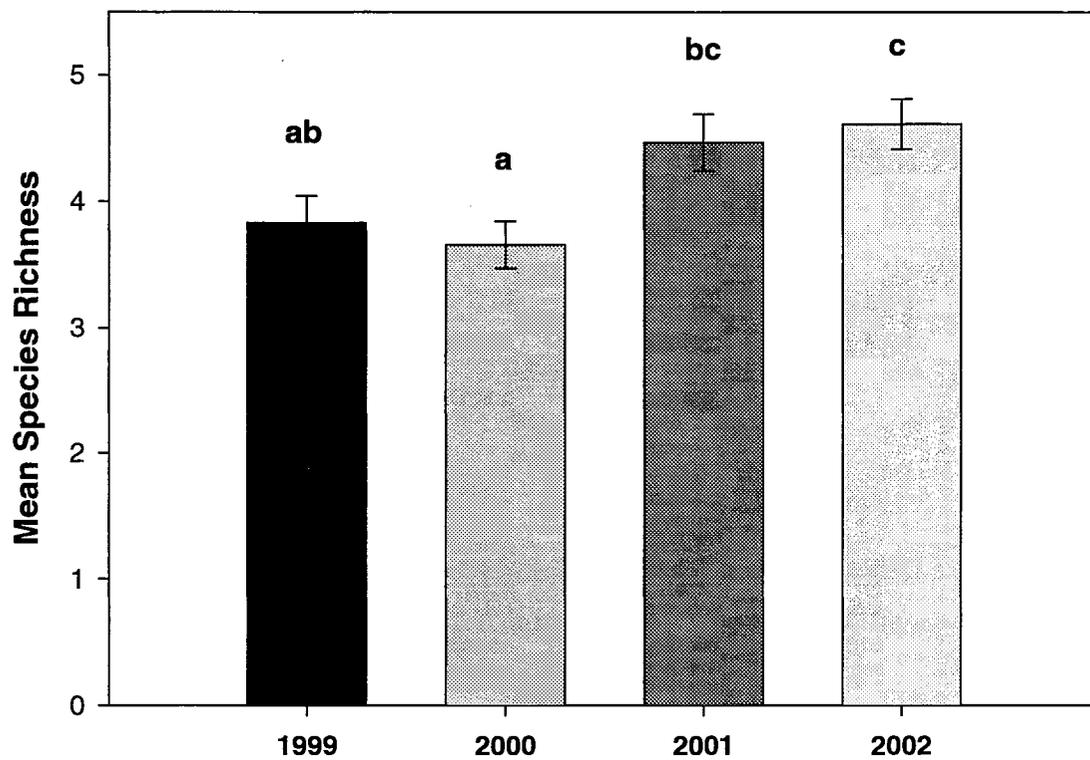
Figure 1.1. Mean amphibian species richness (± SE) among aquatic breeding sites in Northwestern Ontario from 1999 to 2002. Different letters represent significant differences (p ≤ 0.05).

23
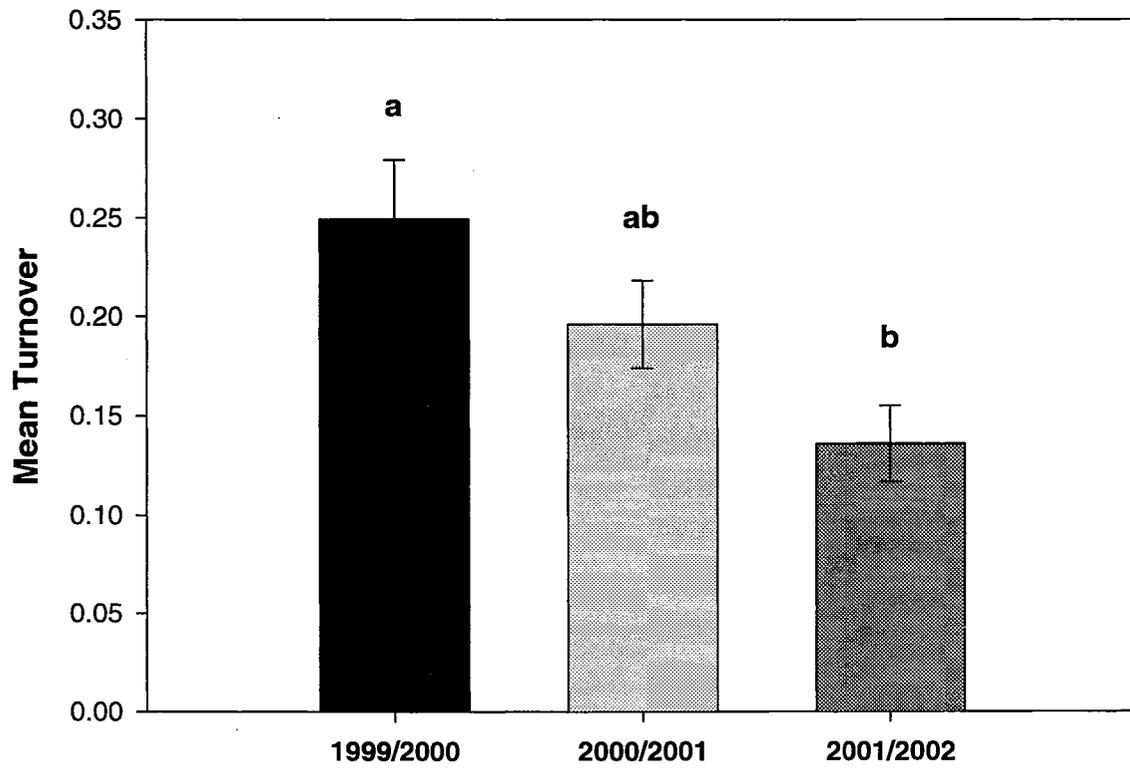
Figure 1.2. Mean turnover ($\pm$ SE) of species among aquatic amphibian breeding sites from 1999 to 2002. Different letters denote significance ($p \leq 0.05$).

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Table 1.2. Pearson correlations comparing mean species richness and mean turnover over time in years. Both variables were significantly correlated to year at $p \leq 0.05$. $N = 164$ (species richness), $N = 123$ (turnover)

Variable	Years
Species Richness	0.256
Turnover	-0.270

25
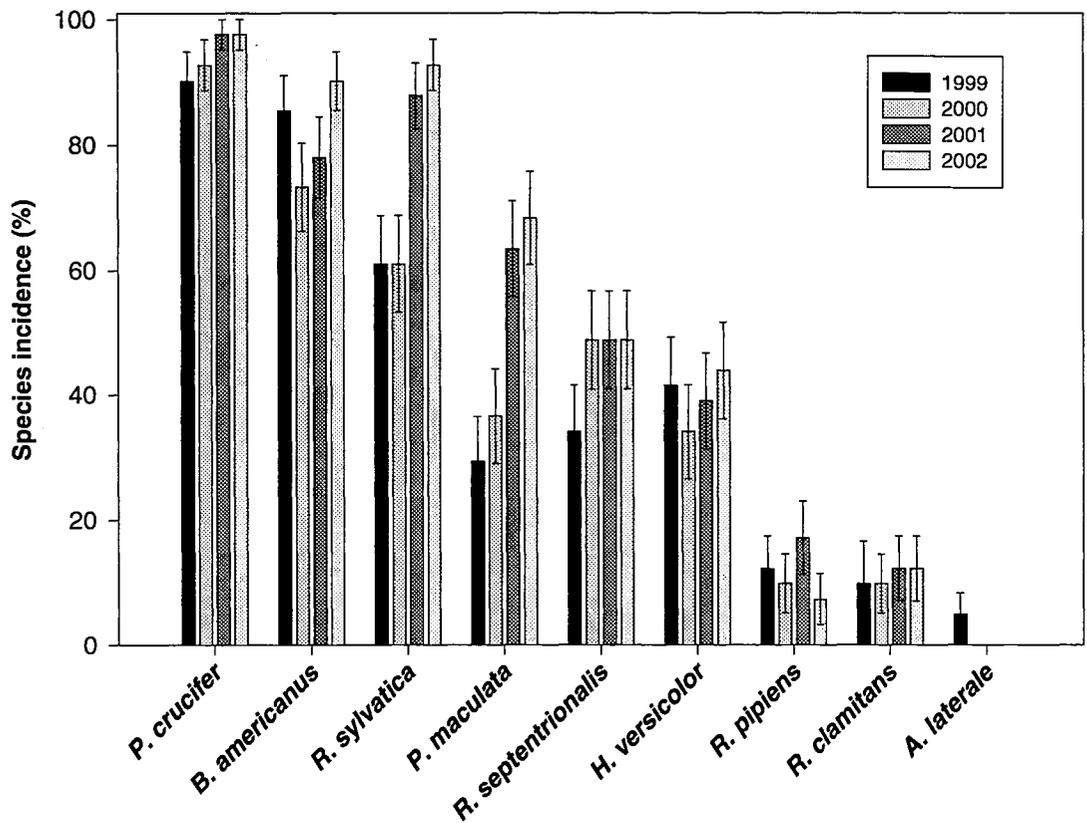
Figure 1.3. Percent amphibian species incidence (±SE) among aquatic breeding sites in Northwestern Ontario from 1999 to 2002. (N = 41)

26
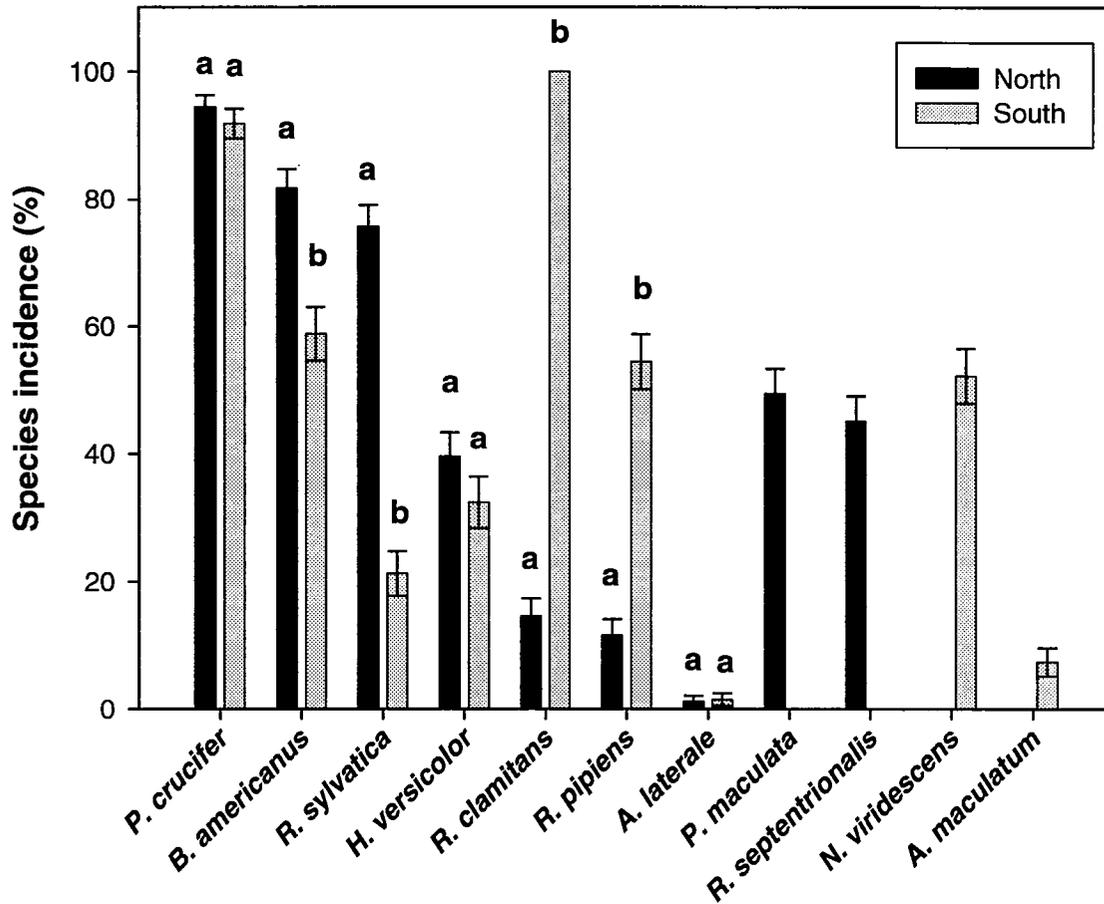
Figure 1.4. Comparison of mean percent species incidence (± SE) between Northern and Southern Ontario. Different letters represent significance (p≤0.05) between regions for each species.

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Table 1.3. Mean amphibian species incidence for Northern and Southern Ontario and categorized into core and/or peripheral areas within the geographical ranges of each species

Species	Ontario Location	Core/Periphery	Incidence
P. maculata*	North	Periphery	0.494
	South	Not in range*	-
P. crucifer	North	Core	0.945
	South	Core	0.919
H. versicolor	North	Periphery	0.396
	South	Periphery	0.324
R. sylvatica	North	Core	0.756
	South	Core	0.213
R. clamitans	North	Periphery	0.146
	South	Core	1.0
R. septentrionalis	North	Core	0.451
	South	Periphery	0
R. pipiens	North	Core	0.116
	South	Periphery	0.544
B. americanus	North	Core	0.817
	South	Core	0.588
A. laterale	North	Periphery	0.012
	South	Periphery	0.015
A. maculatum	North	Periphery	0
	South	Core	0.074
N. viridescens	North	Periphery	0
	South	Core	0.522

* P. maculata's geographical range does not extend into Southern Ontario

28
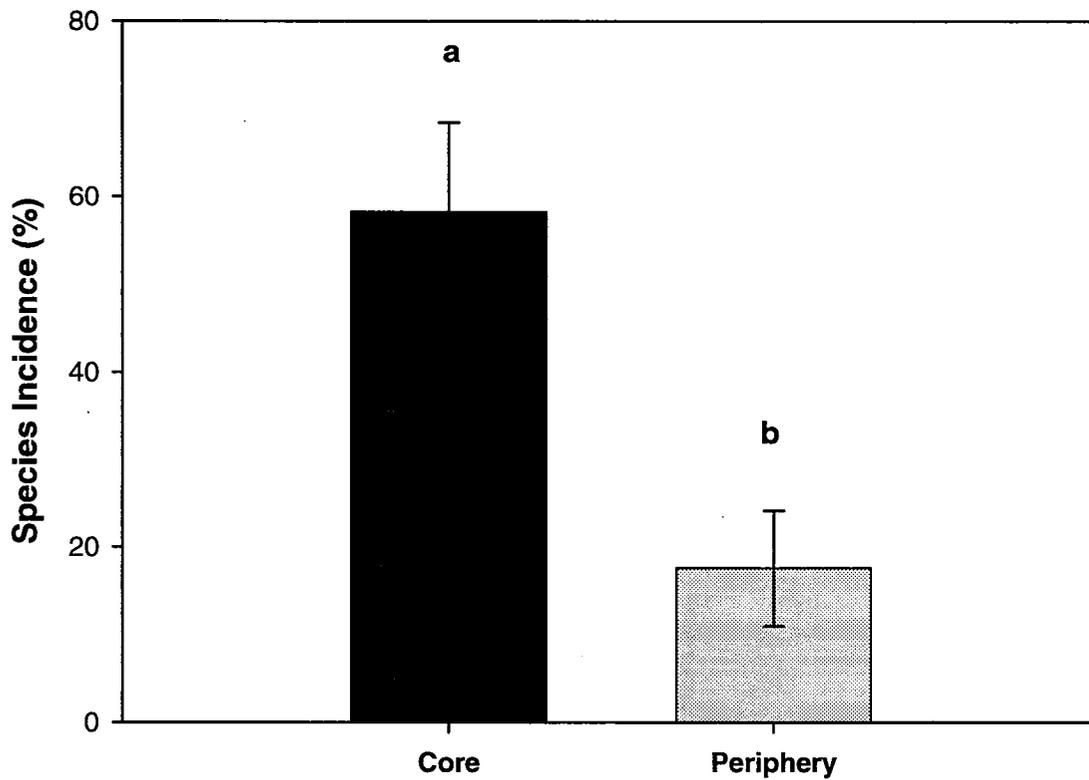
Figure 1.5. Comparison of species incidence ($\pm$SE) between species located either at or close to the core or periphery of their geographical ranges. Different letters represent significant differences ($p \leq 0.05$).

DISCUSSION

Diverse amphibian communities exist in ponds in Northwestern Ontario. Unfortunately, historical records for comparison are not available. My study also revealed that species richness and incidence increased and turnover decreased over the course of this study. This study suggests complex spatial dynamics with high population turnover and recolonization and stresses the importance of metapopulation processes. Similar results were found in a study by Hecnar & M'Closkey (1996c) who found high turnover within regions and at the individual species level. A study on pond populations of the tree frog, *Hyla arborea*, revealed the metapopulation consisted of a set of larger persistent populations mixed with smaller populations characterized by high turnover (Carlson & Edenhamn 2000). A possible reason for my observed patterns of species richness, incidence and turnover is that temporary pond species may be moving into semi-permanent pond sites, such as the ones I surveyed, due to the recent drought conditions in Northwestern Ontario. Annual snowfall was much lower (145 cm) than normal (196 cm) from 1999 to 2002 (t = -6.76, df = 3, p<0.01). Most amphibians in northern Ontario hibernate underground under a think blanket of insulating snow. Some of them are able to withstand temperatures of 0°C while others have antifreeze in their cells to allow them to survive to temperatures of -5°C to -7°C (Johnson 1989). Without a thick layer of snow, the ground can freeze and expose amphibians to much lower temperatures than they can withstand. Furthermore, melting waters help to fill wetlands especially temporary ponds. Without sufficient amount of water, amphibians are forced to move to more permanent wetlands. A recent study by Robinson (2004), looked at the importance of hydroperiod in amphibian communities in Northwestern Ontario. He found more species in permanent wetlands than in temporary and that

species richness peaked in semi-permanent wetlands.

There were four species of amphibians that I did not find that are known to occur in Northwestern Ontario. I was not surprised at the absence of *Plethodon cinereus* and *Necturus maculosus* at my pond sites. *Plethodon cinereus*, red-backed salamander, is a terrestrial salamander that lays its' eggs in water-soaked logs rather than in water bodies (Johnson 1989). *Necturus maculosus*, the mudpuppy, lives permanently in large lakes or rivers and therefore would not be found in semi-permanent sites (Johnson 1989). I was surprised, however, by the absence of *N. viridescens* and *A. maculatum* and the rarity of *A. laterale* at any of my pond sites even though the study area was within their ranges (Johnson 1989; Conant & Collins 1998). Although adult ambystomatid salamanders are only known to occupy ponds during the short breeding season and then migrate to surrounding woodland (Johnson 1989), I still expected to find larvae as they would persist longer within the pond sites. Ambystomatids are long lived iteroparous species that can skip breeding in unsuitable years by remaining underground (Conant & Collins 1998). They return to disturbed areas, such as cutovers, as long as there is no continued disturbance and there is a reformation of leaf litter (Ash 1997). The majority of my sites were located near residential and agricultural areas where logging and land clearance has been continuous and therefore there is no sufficient amount of forest or microhabitat left for salamanders. However most of the other amphibian forest species are still common. This could mean that salamanders are more sensitive to continual land clearance than other amphibian species. This may also explain why there was an absence of *N. viridescens*. Juveniles are terrestrial and can remain juvenile for 2 - 5 years (Johnson 1989; Conant & Collins 1998). If there is no habitat for hibernation and for juvenile newts to disperse into, there will be no

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recruitment at pond sites the following year. The adult stage of the Red-spotted newt is aquatic, only leaving aquatic sites to hibernate under rocks, logs and leaf litter (Helferty 2002). Therefore hydroperiod is also an important factor in determining where the red-spotted newt is found. Robinson (2004) found a high incidence of *N. viridescens* in lakes while finding none in temporary and semi-permanent wetlands.

There seemed to be an increase in species distribution over the years on both a community and population level. This may be indicative of species which can adapt to any type of habitat, regardless of land-use type (as I will explain in the proceeding chapters). For *P. crucifer* and *R. sylvatica*, this also could be because in Northern Ontario, the boreal forest has not undergone severe deforestation or other habitat disturbances for as long as in some other parts of it's range (eg. Southern Ontario). For example, Hecnar (1997) found that *P. crucifer, R. sylvatica, H. versicolor* and ambystomatid salamanders were rare in some parts of Southwestern Ontario due to the loss of woodland and wetland habitat. Historically humans have had a greater impact on habitat, and logging and land clearance has occurred longer and more often in southern Ontario than in northern Ontario (Moss and Davis 1989). This may explain the high incidence of species associated with woodlands (*P. crucifer, R. sylvatica, P. maculata,* and *H. versicolor*). Many of the species whose incidence increased over time were those that normally occupy temporary or spring ephemeral ponds (*R. sylvatica, P. maculata, B. americanus*). As previously mentioned, I may be seeing a shift in these species from temporary to more permanent aquatic habitat because of recent drought conditions.

Since my pond sites were situated in both woodland and agricultural areas, I was not surprised to find a low incidence of *Rana pipiens* among my sites. *Rana pipiens* is known to

migrate to grasslands and meadows after breeding where it spends the summer foraging (Johnson 1989; Conant & Collins 1998). Agricultural practices around these ponds could be too intense or perhaps there may not be enough meadow (open) habitat available for *R. pipiens* to survive.

Although I found nine amphibian species, some of these appear to be rare. *Rana clamitans* is one species that I found to be rare. *Rana clamitans* has been found more often in lakes than semi-permanent wetlands (Robinson 2004) mainly because its dependence on water for hibernation. Another reason for species to be common or rare in northwestern Ontario is higher incidences near the core of species geographic ranges as opposed to the periphery. In northern Ontario, *R. clamitans* is close to the periphery of it's range but is near to the core of it's range in southern Ontario. Those species that had less than 50% incidence were also found to be near the edge of their ranges (*P. maculata, H. versicolor,* and *A. laterale*). This may also explain the low incidence of *A. laterale* and the absence of *A. maculatum* and *N. viridescens* from my sites in northern Ontario and *R. septentrionalis* in southern Ontario.

In conclusion, species richness and incidence increased and turnover decreased over time most likely as a result of temporary pond species moving into more permanent ponds due to recent drought conditions. There seems to be more species at each pond and more ponds being occupied by the same species thus resulting in low extinction. However there are some species that are rare. Salamander species may be rare due to a combination of continual forest harvesting, lack of microhabitat and low dispersal ability. Other species with low abundance or in this case incidence, may not necessarily be a result of habitat destruction or alteration. Simply by looking at where these species occur within their geographic range could explain the reasoning for low or high incidence in a region. Considering range position in the context of

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abundance can provide important insight into assessing species status and explaining incidence

patterns we see among communities and populations. Conservation efforts may be better spent

on species declining near the centre of their range rather than declining peripheral populations.

CHAPTER 2

The effect of local habitat and landscape characteristics on amphibian species richness and turnover in Northwestern Ontario

INTRODUCTION

Ecological communities are products or processes (either biotic or abiotic) that operate on different spatial and temporal scales. Arguably, ecologists have traditionally focussed more on biotic processes (i.e. competition, predation) than on abiotic factors (Dunson & Travis 1991). The nature of these structuring factors may differ among locations and their relative importance may change through time. Communities may also be affected by either contemporary or historical processes (Ricklefs & Schluter 1993). Former evolutionary or dispersal events, or human land use history, leaves a legacy on present day communities. Understanding the relative importance of these structuring factors are of interest to contemporary community ecologists (Connell & Sousa 1983; Ricklefs & Schluter 1993).

Patterns in the distribution of populations or communities, and their causal processes, may differ depending on scale of perception (Hecnar 1997). By investigating populations at the local scale, we can determine the causes of local extinction (Hecnar 1997). However it is not sufficient just to investigate populations at the local scale. The actual status of species is more accurately determined at the landscape or regional scale by considering metapopulation or metacommunity dynamics (Hecnar 1997). By considering the overall outcome of extinction and colonization processes at local sites, we can assess the overall status of species in a region and the cause of declines at the local scale (Hecnar 1997; Baker & Halliday 1999; Gill 1978; Sjögren-Gulve 1994).

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Metapopulation theory offers a useful way to understand, manage and conserve spatially isolated populations of species including amphibians (Sjögren-Gulve & Ray 1996; Hecnar 1997; Levins 1969; Hanski & Gilpin 1991). Many amphibian populations are thought to have a metapopulation structure due to the patchy nature of breeding habitat, restricted movement and strong site fidelity in many species (Sjögren-Gulve 1994). When living as metapopulations, amphibians are able to colonize new ponds as long as the distance between ponds is not too great (Baker & Halliday 1999). This allows for long-term persistence of local populations, a reduction in the risk of isolation resulting in local extinction (Reh & Seitz 1990; Hecnar 1997; Baker & Halliday 1999). Understanding metapopulation dynamics is important for amphibian conservation because it allows us to assess the structure and composition of amphibian communities as well as their persistence across all spatial scales (Gotelli 1998; Marsh & Trenham 2001). Studying a single taxon such as amphibians may provide us with information on community-level dynamics which may be much more effective than concentrating on a single species (McKinney & Drake 1998).

Recently much attention has focussed on declines of some amphibian populations (Wake & Morowitz 1991; Green 1997; Alford & Richards 1999; Houlahan et al. 2000; Carey et al. 2001). The primary causes of amphibian declines include: habitat destruction, fragmentation and degradation (Blaustein et al. 1994; Pechmann & Wilbur 1994; Green 1997; Hecnar 1997). Loss of habitat is mainly caused by anthropogenic disturbances such as timber harvesting, deforestation, road construction and drainage of wetlands (deMaynadier & Hunter 1995; Findlay et al. 2001). The loss of woodland habitat and the increase in roads and highways have increased habitat fragmentation (Vos & Stumpel 1995; Murphy et al. 2000). Fragmentation severs

connections between local populations, decreasing the possibility for recolonization from other sites or rescuing those populations that are going extinct (Laan & Verboom 1990; Vos & Stumpel 1995; Fahrig et al. 1995; Green 1997). Fragmentation is a problem for most amphibians as they require more than one habitat for foraging, hibernation and breeding (Pope et al. 2000). Although some species remain in or near aquatic sites all year round, others migrate to upland forest or meadow habitats to forage and overwinter (Reh & Seitz 1990; Sjögren-Gulve & Ray 1996; Baker & Halliday 1999). Therefore, suppression of movements between these habitats may cause a substantial decline in the number of amphibian populations.

Gaining more knowledge about the relationship between amphibians and their habitat will help us in our conservation efforts. One way to gain this knowledge is to determine what ecological features, on both a local and regional level, are important in structuring amphibian communities. On a landscape scale, woodland habitats are important because they provide most amphibians species with a place to forage and hibernate. Hecnar & M'Closkey (1996b, 1996c, 1998) examined the effects of forest fragmentation on amphibian communities and the importance of regional dynamics in assessing amphibian species. They found a difference in species richness among regions in southern Ontario and that as a result of large-scale deforestation, woodland species had become rare. Therefore they suggested using a regional approach to assess the status of amphibians. A study by Laan & Verboom (1990) also found that the presence of amphibians was positively influenced by the amount of woodland near a pond. On a local habitat scale, factors that have been found to be important are those that affect oviposition, and tadpole development such as aquatic vegetation and pH. Amphibians are very susceptible to water pollution because of their permeable skin (Vitt et al. 1990) and are known to

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be highly effected by acidity (Dunson et al. 1992). Amphibian sensitivity to pH has been observed by Eason & Fauth (2001) where anuran species richness declined with decreasing pH. Aquatic vegetation within a pond provides refuge from predators, places to call and bask on, and to attach eggs to (Johnson 1989). A study by Pavignano et al. (1990) revealed that amphibians selected ponds with abundant aquatic vegetation, low human disturbance and surrounded with terrestrial habitats consisting of gardens or woodlands.

The purpose of my study was to document and evaluate the association between amphibian species richness and turnover and local habitat and landscape characteristics. I hypothesize that species richness and turnover will be affected by a combination of local habitat and landscape characteristics due to different habitat requirements among species and I should see an overall effect of characteristics related to woodland.

METHODS

Habitat Characteristics

I examined the association of amphibian species richness and species turnover with local habitat and landscape characteristics at 69 pond sites (Table 2.1 and 2.2). At the local scale, I mapped each pond using optical range finders and compasses. Pond area and perimeter were calculated using image analysis of my hand drawn field maps (SigmaScan Pro 5.0). I calculated pond volume (V) using the following equation (Wetzel 2001):

$$V = 4.67 \times MaximumDepth \times Area$$

I divided dominant edge vegetation into four classes: substrate (no vegetation), grasses (including small herbaceous plants), shrubs and trees. Using the total perimeter found for each pond, I calculated the length (m) and the percent of each vegetation type. I divided vegetation within a pond into 2 categories: emergent and floating vegetation. For each category, I calculated the amount of cover (m^2) and the percentage cover for each category using my field maps and image analysis.

I classified bottom type as an index based on increasing particle size, where 1 = mud, 2 = sand, and 3 = gravel. The bank slope was measured at 4 randomly chosen locations. At each location, water depth was taken one metre from the edge. The slope angle was determined by using the formula:

$$\tan\theta = \frac{rise}{run}$$

$$\theta = \tan^{-1}\left(\frac{rise}{run}\right)$$

where rise is the depth of the water one metre from shore and run is one metre.

To determine habitat richness, I recorded the number of microhabitats occurring along the perimeter of each pond. A microhabitat could consist of a single habitat variable such as shrubs or could be a combination of different habitat variables such as trees, grass and emergent vegetation. The habitat variables that were used were emergent vegetation, substrate, grass, shrubs and trees. I calculated the proportions of each microhabitat occurring along the edge of a pond, and then calculated habitat diversity using the inverse of Simpson's Index:

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$$D = \frac{1}{\sum pi^2}$$

where p_i is the proportion of each microhabitat and D is habitat diversity.

I used two variables to represent turbidity, one measured and one categorical. I measured turbidity, given in Jackson's Turbidity Units (JTU), by using the LaMotte turbidity in water test kit and Fuller's Earth as the standard turbidity reagent. I also divided turbidity into 4 categories: 1 = transparent, 2 = translucent, 3 = moderate, and 4 = opaque. I measured conductivity and pH using Oakton pocket metres (TDSTestr 3 and pHTestr 2).

At the landscape scale, the variables were measured within a 2 km radius of each pond. I used a 2 km radius because most individuals in an amphibian population will not disperse more than 2 km (Semlitsch 1981; Sinsch 1990; Pechmann & Wilbur 1994; Hecnar & M'Closkey 1996b, 1996c). Furthermore *Rana pipiens*, considered to be the most vagile anuran in Ontario (Hecnar & M'Closkey 1997), has been known to migrate up to 1.5 km overland between habitats (Carr & Fahrig 2001). Therefore using 2 km could provide a guideline for measuring the effect of landscape variables on anuran populations in general.

Landscape variables were calculated using Environmental Systems Research Institute's (ESRI) ArcView Software package 3.2 (ESRI 1996). Global Positioning System (GPS) points of study sites (WGS84) were projected into the NAD83 CNT datum, with a Universal Transverse Mercator projection to match the Ontario Ministry of Natural Resources's (OMNR 2000) Natural Resource Values Information System (NRVIS). These points were then buffered with a 2 km radius to create a polygon centred around each point. The polygons were

used to clip and identify NRVIS data layers and to derive quantities within each polygon for each map feature. For streams, ArcView Spatial Analyst extension was used to process a 25 m digital elevation model (DEM) to generate a flow accumulation grid for the data extent. All flow accumulation cells with a value of > 150 were used to generate a vector coverage representing streams. Compared to the NRVIS stream layer, using flow accumulation cells with a value of > 150 increases the number of streams displayed across the extent because not all stream layers are digitized. The area and percent of wetlands, lakes, forest cover measurements including coniferous, deciduous and mixed forest, as well as agricultural and cutover areas were derived from provincial land cover data (OMNR 2000). Elevation was calculated as the average of all elevation points derived within each polygon at each site. The spatial heterogeneity or the variation in the landscape for each site was calculated by taking the covariance of all the elevation values within each polygon. I classified roads based on traffic flow into 3 categories: 1 = low use, 2 = moderate use, 3 = heavy use. Traffic flow was based on how many cars one would see per unit time. Roads with low use had $\leq$ 1 vehicle pass by/hour, moderate use had 1 vehicle pass by every 30 minutes to an hour and heavy use had 1 vehicle pass by every minute to 0.5 hour.

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Table 2.1. Local habitat variable abbreviations and their descriptions.

Local Habitat Characteristics	Description
Area	Total pond area (m^2)
Perimeter	Total pond perimeter (m)
Volume	Total pond volume (m^3)
Depth	Maximum water depth (m)
Floatm	Area of pond covered by floating vegetation (m^2)
Floatper	Proportion of pond covered by floating vegetation
Emergm	Area of pond covered by emergent vegetation (m^2)
Emergper	Proportion of pond covered by emergent vegetation
Subm	Length of substrate (m) on pond edge
Subp	Proportion of substrate on pond edge
Grassm	Length of pond edge consisting of grass (m)
Grassper	Proportion of pond edge consisting of grass
Shrubsm	Length of pond edge consisting of shrubs (m)
Shrubsper	Proportion of pond edge consisting of shrubs
Treesm	Length of pond edge consisting of trees (m)
Treesper	Proportion of pond edge consisting of trees
Bottom	Type of pond bottom (1, 2, 3, 4)
Slope	Average bank slope (°)
Richness	Number of microhabitats along perimeter of ponds
Diversity	Simpson's Diversity
Turb	Water Turbidity (JTU)
Turbcat	Turbidity (4 categories)
Cond	Conductivity (μs)
PH	pH

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Table 2.2. Landscape variable abbreviations and their descriptions.

Landscape Characteristics	Description
Woodp	Proportion of forest cover
Woodkm	Area of forest cover (km^2)
Coniferp	Proportion of coniferous forest
Coniferkm	Area of coniferous forest (km^2)
Deciduousp	Proportion of deciduous forest
Deciduouskm	Area of deciduous forest (km^2)
Mixedp	Proportion of mixed forest
Mixedkm	Area of mixed forest (km^2)
Wetlandp	Proportion of wetlands
Wetlandkm	Area of wetland (km^2)
Dwetland	Distance to nearest wetland (km)
Lakesp	Proportion of lakes
Lakeskm	Area of lakes (km^2)
Dlakes	Distance to nearest lake (km)
Streams	Total length of streams (km)
Dstream	Distance to nearest stream (km)
Roads	Total length of roads (km)
Roaduse	Traffic Flow (1, 2, 3)
Elevation	Elevation (m)
Spatial	Spatial Heterogeneity
Cutoverp	Proportion of cutovers
Cutoverkm	Area of cutover (km^2)
Agriper	Proportion of agricultural areas
Agrikm	Area of agriculture (km^2)

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Statistical Analyses

F-max and One-sample Kolmogorov-Smirnov tests using Lillifor's test distribution were performed on all of my data to check for homogeneity of variance and normality and non-normal data was transformed using either $\log_{10}$, square root or arcsine transformations (Sokal & Rohlf 1994). Correlations were used to rank the association between habitat variables and species richness and turnover. Only those variables with a probability of $p \leq 0.15$ were used in the stepwise regressions. A statistical significance of $\alpha = 0.05$ was used. All analyses followed Sokal & Rohlf (1994) and were generated using SYSTAT 9 (Wilkinson 1990).

I used stepwise multiple regression to examine the association of species richness and turnover with local habitat and regional landscape characteristics. I constructed three models; local variables only, regional variables only, and a combined model. If different results were obtained between the forward and backward regressions, I took those variables that were significant from both regressions and ran a complete regression. The local and landscape habitat variables found to be of significant importance to species richness, and turnover were then combined using multiple linear regressions. Principal Components Analysis (PCA) with a varimax rotation was used to determine if habitat variables could be separated into groups based on multiple collinearity between the habitat variables. The factor scores from each factor component were then used to run a stepwise multiple regression with species richness and turnover as the dependent variables.

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RESULTS

When I expanded the original 42 pond sites to 69, I found ten amphibian species. Mean species richness over all of the sites was 4.6 (± SE 0.14) (Figure 2.1) and the mean turnover was found to be 0.16 (± SE 0.016).

Species richness was correlated with thirteen local habitat and eight landscape characteristics (Table 2.3). Stepwise multiple regression with local habitat variables revealed that species richness was positively associated with Shrubsper, Richness and PH and negatively associated with Perimeter (Table 2.4). When I compared species richness to the landscape variables, I found a positive significant association with Woodkm, Wetlandkm, Dstream and Agrikm (Table 2.4). The final model included Shrubsper, Richness, Perimeter, Wetlandkm, Dstream, Agrikm (Table 2.4). The percentage of variance explained by the models was: 33.4% for local, 31.7% for landscape, and 53.4% for the combined model.

Turnover was correlated with seven local habitat and four landscape characteristics (Table 2.5). I found turnover to be negatively related to Slope and positively related to Perimeter and Subp (Table 2.5). When I compared the landscape variables to turnover, I found that turnover was negatively related to Deciduouskm, Woodp and positively related to Deciduousp (Table A6). I omitted case 11 and 68 because they were outliers and ran the stepwise multiple regression without Deciduouskm and Deciduousp because tolerance levels were close to zero. I found that turnover was negatively related to Woodkm (Table 2.5). The final model included Perimeter, Slope and Subp (Table 2.6). The percentage of variance explained by the models were: 11% for landscape, and 31% for local and the combined model.

The Principal Components Analysis resulted in twelve components (or factors)

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explaining a total variance of 83% (Table A2). I chose to use only the first nine factors in the stepwise multiple regressions because factors ten, eleven and twelve only explained 12% of the total variance. I found species richness to be positively related to Factor 3 and 7 (Table 2.7 & 2.8). I found turnover to be negatively related to Factor 1 (Table 2.7 & 2.8).

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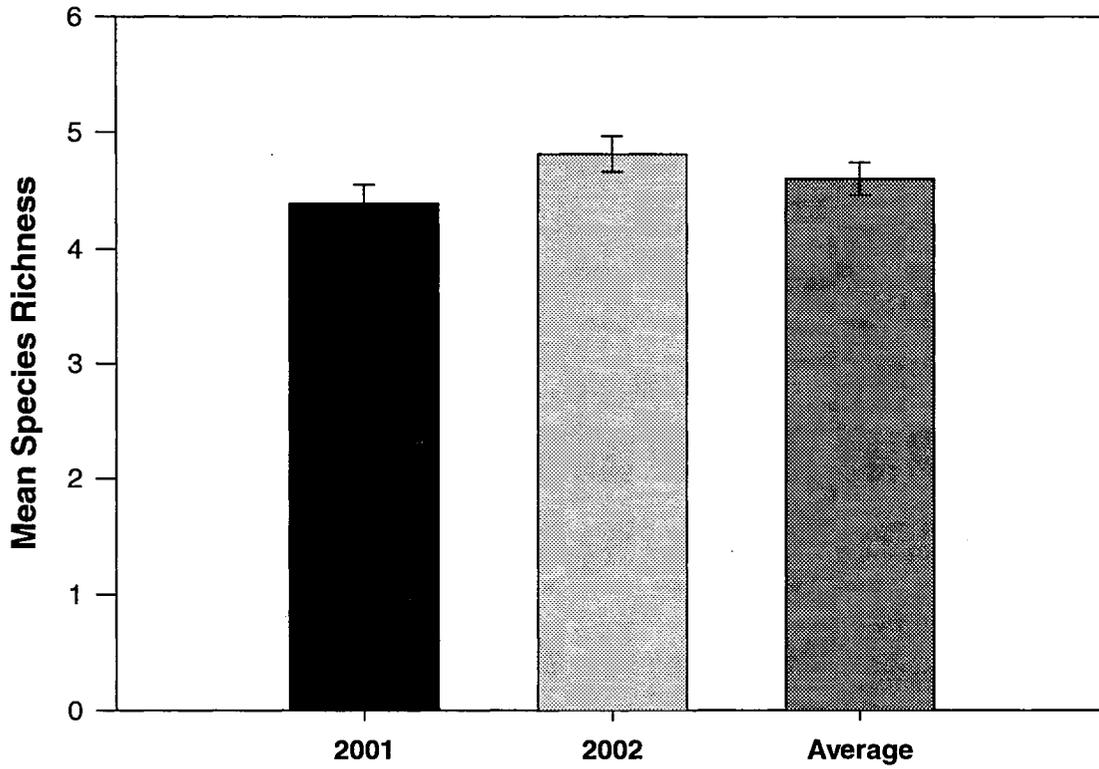
Figure 2.1. Mean amphibian species richness (±SE) at 69 aquatic breeding ponds in Northwestern Ontario during 2001 and 2002.

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Table 2.3. Pearson correlation matrix between amphibian species richness and local habitat and landscape variables. Those variables that had a correlation with p≤0.15 are highlighted.

Local Variables		Landscape Variables	
Perimeter	**-0.296**	**Woodp**	**-0.212**
Area	0.165	**Woodkm**	**-0.199**
Volume	**0.238**	Coniferp	0.029
Depth	**0.261**	Coniferkm	0.031
Floatm	-0.081	Deciduousp	-0.168
Floatper	**-0.210**	Deciduouskm	-0.163
Emergm	-0.080	Mixedp	-0.061
Emergper	-0.166	Mixedkm	-0.059
Subm	0.244	**Wetlandp**	**0.242**
Subp	**0.173**	**Wetlandkm**	**0.242**
Grassm	0.053	Dwetland	0.038
Grassper	-0.129	Lakesp	0.139
Shrubsm	**0.295**	Lakeskm	0.140
Shrubsper	**0.242**	Dlakes	0.039
Treesm	-0.110	Streams	-0.032
Treesper	-0.004	**Dstream**	**0.309**
Bottom	0.151	Roads	-0.018
Slope	0.013	Roaduse	0.033
Richness	**0.302**	Elevation	0.099
Diversity	**0.315**	**Spatial**	**-0.276**
Turb	0.033	Cutoverp	0.026
Turbcat	**-0.211**	Cutoverkm	0.027
Cond	**-0.214**	**Agriper**	**0.260**
PH	**0.253**	**Agrikm**	**0.259**

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Table 2.4. Stepwise multiple regression model of amphibian species richness (N=69).

Variable	Coefficient	Std Error	Tolerance	t	p
Local Habitat Variables ($F_{4,64} = 8.01$, $p < 0.001$, $R^2 = 0.334$)					
Constant	0.55	0.445	-	1.237	0.22
Perimeter	-0.079	0.026	0.961	-3.093	< 0.01
Shrubsper	0.295	0.09	0.945	3.285	< 0.01
PH	0.171	0.055	0.919	3.135	< 0.01
Richness	0.037	0.016	0.963	2.233	< 0.05
Landscape Variables ($F_{4,64} = 7.44$, $p < 0.001$, $R^2 = 0.317$)					
Constant	1.541	0.174	-	8.832	< 0.001
Wetlandkm	0.282	0.085	0.689	3.307	< 0.005
Dstream	0.599	0.20	0.93	2.992	< 0.005
Agrikm	0.075	0.02	0.31	3.718	< 0.001
Complete Model ($F_{7,61} = 10.0$, $p < 0.001$, $R^2 = 0.534$)					
Constant	0.91	0.403	-	2.258	< 0.05
Wetlandkm	0.147	0.069	0.749	2.126	< 0.05
Dstream	0.638	0.173	0.894	3.688	< 0.001
Agrikm	0.04	0.012	0.649	3.385	< 0.005
Shrubsper	0.255	0.082	0.825	3.107	< 0.005
Perimeter	-0.061	0.023	0.853	-2.604	< 0.05
Richness	0.049	0.014	0.93	3.425	< 0.005

Table 2.5. Pearson correlation matrix between amphibian turnover and local habitat and landscape variables. Variables having p <0.15 are highlighted.

Local		Landscape	
Perimeter	**0.211**	**Woodp**	**-0.199**
Area	-0.058	**Woodkm**	**-0.213**
Volume	-0.051	Coniferp	0.168
Depth	-0.056	Coniferkm	0.164
Floatm	0.153	**Deciduousp**	**-0.250**
Floatper	-0.061	**Deciduouskm**	**-0.255**
Emergm	-0.111	Mixedp	-0.005
Emergper	-0.112	Mixedkm	-0.014
Subm	**0.256**	Wetlandp	0.105
Subp	**0.441**	Wetlandkm	0.103
Grassm	-0.137	Dwetland	0.079
Grassper	**-0.227**	Lakesp	0.122
Shrubsm	0.084	Lakeskm	0.120
Shrubsper	0.018	Dlakes	0.020
Treesm	-0.054	Streams	0.051
Treesper	-0.071	Dstream	0.133
Bottom	**0.245**	Roads	-0.084
Slope	**-0.207**	Roaduse	-0.168
Richness	0.060	Elevation	-0.021
Diversity	0.098	Spatial	-0.050
Turb	0.028	Cutoverp	0.085
Turbcat	**-0.201**	Cutoverkm	0.080
Cond	0.118	Agriper	0.036
PH	-0.105	Agrikm	0.036

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Table 2.6. Stepwise multiple regression of amphibian turnover with local habitat and landscape variables (N=69).

Variable	Coefficient	Std. Error	Tolerance	t	p
Landscape Variables ($F_{1,65} = 7.891$, $p < 0.01$, $R^2 = 0.108$) *					
Constant	0.235	0.033	-	7.084	< 0.001
Woodkm	-0.001	0	1.0	-2.809	< 0.01
Local Variables and Complete model ($F_{3,65} = 9.681$, $p < 0.001$, $R^2 = 0.309$)					
Constant	0.243	0.066	-	3.688	< 0.001
Perimeter	0.032	0.012	0.984	2.566	< 0.05
Slope	-0.048	0.024	1.0	-2.004	< 0.05
Subp	0.452	0.099	0.984	4.583	< 0.001

* without outliers (N = 67)

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Table 2.7. Rotated loading components from the principal components analysis that were significantly associated with species richness and turnover. Factors 1, 3 and 7 explained 13.9%, 7.2% and 6.4% of the total variance respectively.

Variables	Factor 1	Variables	Factor 3	Variables	Factor 7
Woodp	0.95	Diversity	0.831	Shrubsm	0.888
Woodkm	0.949	Richness	0.807	Shrubsper	0.875
Agrikm	-0.833	Subp	0.627		
Agriper	-0.833	Bottom	0.626		
Elevation	0.653	Subm	0.56		
Mixedkm	0.597				
Mixedp	0.594				
Streams	-0.529				

Table 2.8. Stepwise multiple regression of species richness and turnover with the component loadings from the principal components analysis (N = 69).

Variable	Coefficient	Std Error	Tolerance	t	p
Species Richness ($F_{3,65}$ = 4.45, $p < 0.01$, $R^2 = 0.17$)					
Constant	2.128	0.031	-	69.06	< 0.001
Factor 3	0.066	0.031	1.0	2.121	< 0.05
Factor 7	0.074	0.031	1.0	2.397	< 0.05
Turnover ($F_{4,63}$ = 3.809, $p < 0.01$, $R^2 = 0.195$)					
Constant	0.147	0.013	-	11.383	< 0.001
Factor 1	-0.032	0.013	0.998	-2.455	< 0.05

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DISCUSSION

My analyses revealed complex associations of amphibian species richness and turnover with local and landscape characteristics. This was expected considering that local communities are products of processes operating on multiple scales (Caley & Schluter 1997; Hecnar & M'Closkey 1997, 1998). Mazerolle & Villard (1999) reviewed studies that included both landscape-scale and patch-scale effects to determine if landscape characteristics increased the prediction of species presence and distribution when local habitat variables were known. They found that including habitat variables at many scales improved models for vertebrate species. The results from Mazerolle & Villard's (1999) study were similar to what I found when I looked at the association between species richness and local habitat and landscape characteristics. My results revealed that species richness was associated with a diverse array of local habitat variables and landscape variables related to land-use and wetlands.

I found a positive association between species richness and the area of wetlands around a pond. Wetlands are important sources for sink habitats such as temporary ponds and some semi-permanent ponds that may be experiencing lower water levels due to lower snow fall as explained in Chapter 1.

I found that species richness was positively related to the distance to streams. One possible explanation for this association is that fish are present in streams and amphibians have been found to be negatively affected by fish predation (Hecnar 1997; Hecnar & M'Closkey 1997; Baker & Halliday 1999; Semlitsch 2000; Eason & Fauth 2001). Most amphibians are not able to cross streams due to fast flowing, cold waters and thus streams become barriers for movement between breeding sites and terrestrial habitat.

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Contrary to what I expected, species richness was positively related to the area of agriculture around a pond site. Similar results were found by Knutson et al. (1999), where relative anuran abundance was higher in areas with more agricultural land. Agriculture, especially mixed farm land, increases diversity of habitats that may support a variety of amphibians (Baker & Halliday 1999). Previous studies have suggested that amphibian presence in agricultural areas is determined by geology and the nature of adjacent terrestrial habitat to ponds, pond vegetation and age (Beebee 1985; Laan & Verboom 1990; Pavignano et al. 1990; Baker & Halliday 1999). Agricultural areas open up the landscape allowing more light and faster warming of pond waters. Increased water temperature shortens time to metamorphosis for larvae (Newman 1998). Agricultural areas can also provide excellent refuge for migrating adults or juveniles (Knutson et al. 1999). Lemckert (1999) found that species richness was higher in more disturbed areas as opposed to undisturbed forest. He also found that more recent disturbances increased the richness of generalist species at ponds. There are many species that prefer open canopy habitats such as *Pseudacris maculata*, *Rana pipiens* and *Bufo americanus* (Werner & Glennmeier 1999). The presence of agriculture in the predominately forested landscape of the study area promotes habitat heterogeneity by creating a 'mosaic' of complementary habitats (Pope et al. 2000).

Species richness increased with decreasing perimeter. Smaller ponds usually indicate shallower waters with no predators and are good substitutes for species that normally breed in ephemeral ponds.

I found a positive relationship between species richness and the percentage of shrubs surrounding a pond. Shrubs are important to amphibians because they are used for basking on,

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calling sites, and to provide protection from predators. Shrubs also help to stabilize the pond edge, decreasing erosion and sediment flow into ponds. Gomez & Anthony (1996) found that species richness was similar among forest types but greater in shrub stands. Shrubs could be complementing the needs of amphibian species who rely on woodland habitat more than agricultural.

I was not surprised to find that high habitat richness along the edge of a pond promotes high species richness. Having a variety of microhabitats within a pond complements each species' niche requirements allowing a diverse community of amphibians to exist together.

The regression models for turnover showed a negative relationship with slope and a positive relationship with perimeter and the percent of substrate around a pond. The presence of substrate indicates disturbance along the edge of the pond that is affecting edge habitat. Without any edge vegetation, all stages of an amphibian's life cycle cannot survive leading to an increase in local extinction and an increase in species moving out of the ponds. Steep banks prevent species from dispersing in or out of the pond, resulting in low turnover. The positive relationship with perimeter coincides with the negative relationship found between species richness and perimeter. This supports the theory that high turnover is caused by extinction or migration out of the pond and not colonization into the pond. If turnover was high because of high colonization, then we would see a positive relationship with species richness and perimeter which is not the case.

Local habitat and landscape characteristics play an important role in determining species richness and turnover in amphibian pond communities. Specifically smaller ponds situated in heterogeneous landscapes that are open with diverse microhabitat along the edge and local

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habitat characteristics promote high species richness and low turnover. In order to conserve on a community level we must provide adequate habitat, at the local and regional level, to meet all of the species needs within that community.

CHAPTER 3

Single-species habitat models for amphibian species in Northwestern Ontario

INTRODUCTION

The local distribution of species is fundamentally determined by the availability habitats

and how characteristics of a species' habitat satisfy its natural history requirements (Campbell &

Reece 2002). The amounts, quality and juxtaposition of essential habitats can affect fitness of

individuals and population persistence (Walters et al. 2002). The factors or processes affecting

species presence can also be either abiotic or biotic and operate on different spatial scales

(Ricklefs & Schluter 1993; Smith 1996).

The regional distribution of a species is ultimately determined by the balance between

colonization and extinction of local populations that together make up a metapopulation (Levins

1969; Hanski & Gilpin 1991; Clark & Rosenzweig 1994; Gotelli 1998; McKinney & Drake

1998). In order for a species to persist and to reduce the risk of extinction, there must be

multiple populations between which individuals are able to migrate or be within a large,

continuous population (Sjögren-Gulve 1994). Many amphibian populations form

metapopulations as a consequence of their reliance on ponds (Marsh & Trenham 2001) and

surrounding terrestrial habitats for breeding, larval development, hibernation and foraging (Pope

et al. 2000). If we can understand the regional dynamics of these amphibian populations, then

we will be able to determine the status of species (Hecnar & M'Closkey 1996c). Using presence

and/or absence of a species at a breeding site is a better indicator of the present state of a

population than using population size because amphibians are viviparous and thus it is hard to

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determine population size when surveying at multiple times during the year. Besides with no previous population density data to compare populations to, it makes it hard to determine if the species is declining.

Determining the status of species is crucial because of recent concerns over the decline of amphibian populations (Wake & Morowitz 1991; Green 1997; Alford & Richards 1999; Houlahan et al. 2000; Carey et al. 2001). This has lead to a search for the causes of these declines and to determine which populations are declining. The major factor affecting amphibians is habitat loss (Wake & Morowitz 1991; Blaustein et al. 1994; Pechmann & Wilbur 1994; Green 1997). Because most amphibians use both aquatic and terrestrial habitat, loss or degradation of these habitat components could be damaging to populations and communities.

In order to conserve both amphibians and their habitats, we must determine what components within each habitat are both important for, and detrimental to, amphibian survival (Semlitsch 2002). It is also important to consider habitat characteristics at both local and regional landscape scales because amphibians migrate between breeding sites and terrestrial habitats. At the local scale, vegetation within a pond (i.e. emergent vegetation) acts as important refuge from predators and is used for calling and oviposition sites (Johnson 1989; Hecnar & M'Closkey 1996b; Baker & Halliday 1999; Carr & Fahrig 2001). On the other hand, acidity has been found to negatively affect amphibians (Roudebush 1988; Dunson, et al. 1992; Karns 1992; Eason & Fauth 2001). At the local and regional scale, woodland surrounding a breeding site is important for salamanders, woodfrogs, gray treefrogs and spring peepers because they use these sites for foraging and hibernation (Hecnar & M'Closkey 1996b; Hecnar 1997; Conant & Collins 1998). However, roads can be detrimental to amphibians. Roads act as physical barriers to

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amphibian movement (Reh & Seitz 1990; Carr & Fahrig 2001) and dissect the landscape creating small patches of habitat that may lead to population isolation (Sjögren-Gulve 1994; Carr & Fahrig 2001) or high traffic mortality as a result of migration between seasonal habitats (deMaynadier & Hunter 1995; Fahrig et al. 1995; Carr & Fahrig 2001; Findlay et al. 2001). However roads can be beneficial for amphibian species. Ditches along roads act as migration corridors and breeding sites for temporary pond species. Thus the survival and movement of individuals between the aquatic and terrestrial environments is the crucial process that ensures successful dispersal and recolonization among metapopulations (Semlitsch 2002).

The importance of assessing relationships between amphibians and habitat features may help explain local and regional patterns of species incidence, and aid in future conservation efforts. Information gained by assessing habitat quality will help in translocation/reintroduction programs, habitat restoration, environmental impact assessments, and determining species status (Griffith et al. 1989; Beebee 1997; Helferty 2002; Semlitsch 2002). For example, Griffith et al. (1989) found that the success rate of translocations of birds and mammals was higher in good quality habitat compared to those in poor habitat. Assessing habitat quality is an important aspect in conservation in addition to determining a species' habitat requirements. Hamer et al. (2002) investigated the habitat requirements of the endangered green and golden bell frog (*Litoria aurea*) in order to create and manage wetland habitats. The study revealed that the diversity of vegetation on the banks of water bodies, including three plant species, were significant predictors of the presence of *Litoria aurea*. Hamer et al. (2002) recommended that to create successful habitat for the green and golden bell frog, the wetlands need to be placed close to existing populations and contain those predictors mentioned previously. Habitat quality

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information can allow us to assess the probability of each individual species occurring at a site depending on what habitat and landscape variables are present.

The purpose of my study was to document and explain the patterns of amphibian species incidence in terms of local and landscape characteristics within the boreal forest biome in northwestern Ontario. The distribution patterns of boreal amphibians are poorly understood despite potential threats to populations by human activities such as forestry (Elmberg 1993; Constible et al. 2001). My objectives were to create single species habitat models based on species incidence and habitat characteristics. Due to differences in habitat preferences between species, I expected unique habitat models to emerge.

METHODS

I sampled 69 ponds for the presence and absence of amphibian species in 2001 and 2002. I considered an amphibian as present at a site if it was found there in either of the two years.

Habitat Characteristics

Local habitat and landscape characteristics were measured using the same methods discussed in Chapter 2.

Statistical Analyses

I used stepwise logistic regression analysis to examine the effects of the habitat variables (Table 2.1 & 2.2) on individual species. If results differed between the forward and backward stepwise regressions, I took those variables that were significant from both regressions and ran a complete regression.

I performed F-max and one-sample Kolmogorov-Smirnov tests using Lillifor's distribution to check for homogeneity of variance and normality and non-normal data was

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transformed using either $\log_{10}$, square root or arcsine transformations. MANOVA was used to narrow down the habitat variables to those that were most associated with each individual species among all sites. Only those variables with a probability of $p \leq 0.15$ were used in the logistic regressions. I used a statistical significance of $\alpha = 0.05$. All analyses followed Sokal and Rohlf (1994) and were generated using SYSTAT 9 (Wilkinson 1990).

RESULTS

I found 10 amphibian species during pond surveys (Figure 3.1). By expanding the number of ponds to 69, I found one more species of amphibian, *Ambystoma maculatum*. This may be attributed to the addition of ponds located within more forested habitat giving me study sites within a variety of different landscapes. *Pseudacris crucifer, Rana sylvatica* and *Bufo americanus* occurred at over 90% of the sites whereas *Rana pipiens, Ambystoma maculatum* and *Ambystoma laterale* were found at less than 15% of sites (Figure 3.1). Logistic regression revealed complex patterns of species association with habitat characteristics (Table 3.1).

Pseudacris crucifer

There were no correlations for *P. crucifer* with any of the habitat variables because it was found at all of my pond sites.

Pseudacris maculata

Pseudacris maculata presence was negatively related to Woodp, Woodkm, Mixedp, Mixedkm, Streams, Roaduse, Elevation, Spatial, Cutoverp, Cutoverkm and positively related to Agriper, Agrikm, Dstream and Roads. When I compared *P. maculata* to the local habitat variables, I found that Area, Volume, Depth, Emergm, Shrubsm, PH, Cond and Turb were positively correlated.

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Logistic stepwise regressions revealed a positive association with *P. maculata* and

Shrubsm, PH and Turb (χ^2_4 = 23.744, Rho^2 = 0.270, p < 0.001). When I compared incidence to

the landscape characteristics, I found *P. maculata* to be positively related to Dstream and Agrikm

and negatively related to Mixedp, Streams, and Cutoverp (χ^2_5 = 67.463, Rho^2 = 0.768, p <

0.001). The final model included PH, Cutoverp, Agrikm, Mixedp, and Streams and the

probability of finding *P. maculata* at pond sites with these characteristics was 84% (χ^2_5 = 50.437;

Table 3.1).

Hyla versicolor

The MANOVA narrowed down the landscape variables to Woodp, Woodkm, Mixedp,

Mixedkm, Roaduse, Cutoverp, Cutoverkm which were negatively correlated and Dwetland,

Dlakes, Dstream, Agriper and Agrikm which were positively correlated. When I compared *H.*

versicolor to all of the local habitat variables, I found Area, Volume, Depth, Subm, Emergm,

Grassm, Shrubsm and Turb to be positively correlated.

Logistic regression revealed that Depth, Shrubsm and Turb were significantly different

(χ^2_3 = 19.379, Rho^2 = 0.203, p < 0.001). I also found a significant difference with Dstream (χ^2_3 =

26.467, Rho^2 = 0.277, p < 0.05). When all of these significant variables were placed together in

one final model, only Shrubsm, Depth, and Turb were significant (χ^2_4 = 23.07; Table 3.1).

Rana pipiens

When comparing *R. pipiens* with landscape variables, I found Woodp, Woodkm,

Coniferp, Coniferkm, Mixedp, Mixedkm, Elevation, Cutoverp, and Cutoverkm to be negatively

correlated and Dwetland, Streams, Agriper and Agrikm to be positively correlated. I also found

R. pipiens to be positively correlated with Volume, Depth, Subp, Subm, Grassm, Richness,

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Diversity and PH.

I found significant differences with Volume, Depth, Subm ($\chi^2_3 = 24.534$, $Rho^2 = 0.459$, p < 0.001) and Agrikm ($\chi^2_1 = 22.35$, $Rho^2 = 0.418$, p < 0.001). A complete regression of all of the significant variables revealed only Agrikm was significantly different ($\chi^2_1 = 22.350$; Table 3.1).

Rana clamitans

Rana clamitans was negatively associated with Deciduousp, Dlakes, Agrikm and Agriper and was positively associated with Woodkm, Mixedp, Mixedkm, Wetlandp, Wetlandkm, Lakesp, Lakeskm and Elevation. Similarly R. clamitans was negatively correlated with Floatper, Emergper and Turbcat and positively correlated with Subm, Richness and Diversity.

Logistic regression revealed significant differences with Floatper ($\chi^2_1 = 7.814$, $Rho^2 = 0.099$, p < 0.005) and Dlakes ($\chi^2_4 = 20.865$, $Rho^2 = 0.263$, p < 0.001). These results were also found to be significant when they were both placed into a complete regression ($\chi^2_2 = 15.738$; Table 3.1).

Rana septentrionalis

Rana septentrionalis incidence was negatively correlated with Roads, Floatper, Emergper, Cond, and Turb and positively correlated with Volume, Depth, Subm, Subp, Bottom, Richness, Diversity, Slope, and PH.

Logistic regressions revealed significant differences with Richness, Turb ($\chi^2_3 = 12.898$, $Rho^2 = 0.143$, p < 0.01) and Roads ($\chi^2_1 = 4.753$, $Rho^2 = 0.053$, p < 0.05). In the final regression model, all of these variables were significant ($\chi^2_2 = 18.204$; Table 3.1).

Rana sylvatica

I did not find *Rana sylvatica* to be correlated with any of the landscape variables however

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I did find negative correlations with Grass and Cond. However when I ran the logistic regression, I did not find any significant results between *R. sylvatica* and any of the habitat variables.

Bufo americanus

I found negative correlations with Coniferp, Coniferkm, Wetlandp, Wetlandkm, and Roads and positive correlations with Deciduousp, Deciduouskm, Lakeskm and Lakesp. I also found negative correlations with Shrubsper, and positive correlations with Perimeter, Area and Volume.

Stepwise logistic regression revealed significant associations between *B. americanus* and Area ($\chi^2_1 = 6.179$, $Rho^2 = 0.152$, $p < 0.05$; Table 3.6), Deciduousp, and Lakesp ($\chi^2_2 = 10.504$, $Rho^2 = 0.258$, $p < 0.005$). After combining these latter variables in a complete regression, I found only Area and Lakesp to be significant ($\chi^2_2 = 10.922$; Table 3.1).

Ambystoma maculatum

I found *Ambystoma maculatum* to be negatively correlated with Deciduousp, Deciduouskm, Dwetland, Roads, Spatial, Agriper, Agrikm and positively correlated with Coniferp, Coniferkm, Mixedp, Mixedkm, Wetlandp, Wetlandkm, Lakesp, Lakeskm, Dstream, Elevation, Cutoverp and Cutoverkm. When I compared *A. maculatum* to the local habitat variables, I found positive correlations with Shrubsper, Shrubsm, Bottom and negative correlations with Perimeter, Area, Volume, Depth, Floatper, Grassm, Grassper, Slope, PH, Cond and Turbcat.

Logistic regression revealed that Slope, Cond ($\chi^2_3 = 31.552$, $Rho^2 = 0.637$, $p < 0.001$), and Dstream, and Cutoverkm ($\chi^2_2 = 38.63$, $Rho^2 = 0.78$, $p < 0.001$) were significant. A complete

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regression revealed that only Dstream and Cutoverkm were significantly different to incidence ($\chi^2_2 = 38.63$; Table 3.1)

Ambystoma laterale

Correlations revealed negative relationships with Deciduousp, Deciduouskm, Dwetland, Spatial, Agriper, Agrikm and positive relationships with Coniferp, Coniferkm, Mixedp, Mixedkm, Wetlandp, Wetlandkm, Lakesp, Lakeskm, Dstream, Roaduse, Elevation, Cutoverp and Cutoverkm. *A. laterale* was also negatively correlated with Area, Volume, Depth, Floatper, Emergm, Grassm, Slope, PH, and Cond and positively correlated with Shrubsper, Shrubsm, and Bottom.

I found significant differences with Area, Slope and Cond ($\chi^2_3 = 38.74$, $Rho^2 = 0.725$, p < 0.001), as well as Wetlandp and Lakesp ($\chi^2_6 = 18.728$, $Rho^2 = 0.35$, p < 0.001). The final model revealed that Area, Slope and Conductivity were the only variables to be significant ($\chi^2_3 = 38.74$; Table 3.1).
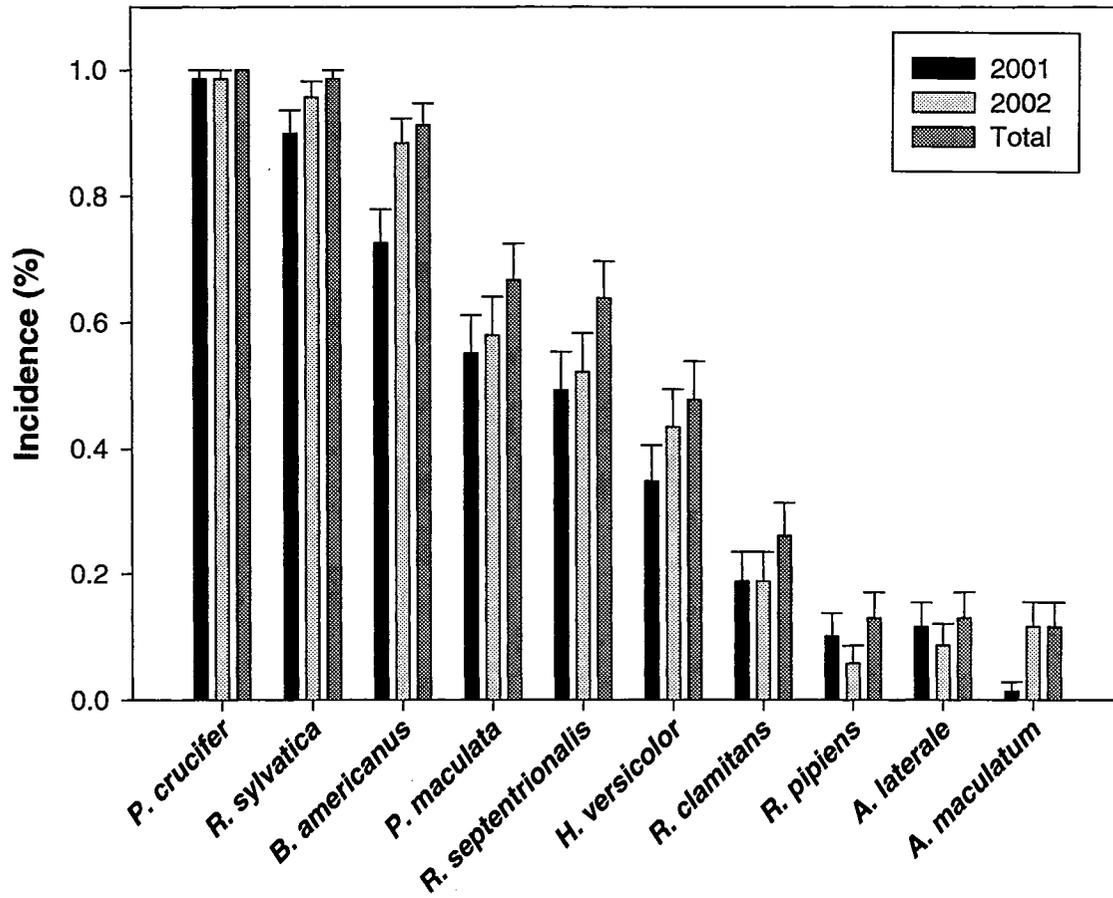
Figure 3.1. Percent amphibian species incidence (SE$\pm$) for 2001 to 2002 in aquatic breeding ponds in Northwestern Ontario (N = 69).

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Table 3.1. Final logistic regression models for each amphibian species. Number of presence and absences are indicated in parentheses in each species model respectively.

Species	Variable	Estimate	Std. Error	t-ratio	p
P. maculata	Constant	-15.275	10.037	-1.522	0.128
	PH	3.391	1.443	2.350	0.019
	Mixedp	-13.263	5.295	-2.505	0.012
	Streams	-0.314	0.101	-3.120	0.002
	Cutoverp	38.091	12.537	3.038	0.002
	Agrikm	1.353	0.575	2.354	0.019
	Full Model	(46, 30)	$Rho^2 = 0.840$		< 0.001
H. versicolor	Constant	-4.982	1.493	-3.337	0.001
	Shrubsm	0.015	0.006	2.567	0.010
	Depth	1.40	0.624	2.243	0.025
	Turb	1.025	0.495	2.072	0.038
	Dstream	3.957	2.127	1.861	0.063
	Full Model	(33, 36)	$Rho^2 = 0.242$		<0.001
R. pipiens	Constant	-5.386	1.385	-3.888	< 0.001
	Agrikm	0.814	0.239	3.410	0.001
	Full Model	(9, 60)	$Rho^2 = 0.418$		<0.001
R. clamitans	Constant	0.555	0.508	1.091	0.275
	Floatper	-7.366	3.424	-2.152	0.031
	Dlakes	-2.824	1.105	-2.556	0.011
	Full Model	(18, 51)	$Rho^2 = 0.199$		<0.001
R. septentrionalis	Constant	7.456	3.601	2.484	0.013
	Richness	0.438	0.199	2.202	0.028
	Turb	-1.174	0.474	-2.477	0.013
	Roads	-1.953	0.825	-2.366	0.018

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	Full Model	(44, 25)	$Rho^2 = 0.201$		<0.001
B. americanus	Constant	-2.967	3.560	-0.833	0.405
	Area	1.335	0.582	2.294	0.022
	Lakesp	0.660	0.315	2.094	0.036
	Full Model	(63, 6)	$Rho^2 = 0.268$		<0.005
A. maculatum	Constant	-25.778	11.184	-2.305	0.021
	Dstream	45.275	20.505	2.208	0.027
	Cutoverkm	4.807	2.009	2.393	0.017
	Full Model	(8, 61)	$Rho^2 = 0.780$		<0.001
A. laterale	Constant	38.374	17.810	2.155	0.031
	Area	-3.056	1.48	-2.065	0.039
	Slope	-5.06	2.386	-2.12	0.034
	Cond	-0.763	0.373	-2.048	0.041
	Full Model	(9, 60)	$Rho^2 = 0.725$		<0.001

DISCUSSION

Pseudacris crucifer & *Rana sylvatica*

Pseudacris crucifer and *Rana sylvatica* are woodland species that require woodland

habitat for foraging and hibernation. Despite current forestry and agricultural practices, finding

no relationship between P. crucifer and R. sylvatica and any of the habitat variables suggest there

is still a sufficient amount of forest habitat left. Logging and land clearance has not been as

extensive and intense as in other parts of the country where these species occur, such as Southern

Ontario. Hecnar & M'Closkey (1996) found the decline of *R. sylvatica* from most regions in

southern Ontario was related to loss of forest cover, however there was still sufficient amount of

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woodlots that sustained *P. crucifer* populations. Gibbs (1998) found that wood frogs were absent from areas where forest cover was reduced to below 30%. However northern spring peepers were able to occupy any type of available habitat regardless of forest fragmentation.

Pseudacris maculata

The presence of *Pseudacris maculata* at ponds was positively related to pH, area of agriculture and the percent of cutover and negatively related to the percent of mixed forest and the total length of streams surrounding a pond. Most amphibians are very sensitive to their aquatic environment thus it was no surprise to find that *P. maculata* may prefer ponds with high pH. Amphibians are known to be negatively affected by high acidity due to the nature of their skin (Pierce et al. 1984; Roudebush 1988; Dunson et al. 1992; Karns 1992; Eason & Fauth 2001). Low pH also inhibits fertilization and development of eggs and larvae (Dunson et al. 1992). Species sensitivity differs along the pH gradient. The range of pH detected in my study was not a large enough change to detect an effect with all species. This may indicate that *P. maculata* is more sensitive to slight changes in pH than other amphibian species.

Pseudacris maculata forages in open woodlands and open areas such as meadows and fields and prefers breeding in shallower ephemeral ponds including flooded fields (Johnson 1989) which is why I found a positive relationship with the area of agriculture. Agricultural areas provide a variety of vegetated habitats including grasses from which *P. maculata* call. This, in turn, explains why I found a positive relationship with the percentage of cutover. Although I should have found a negative relationship with woodland, I did find a negative relationship with mixed forest which was positively correlated with woodland.

In addition, I found that *P. maculata* prefers ponds that do not have a lot of streams/rivers

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within 2 km of them. Streams and rivers contain fish which have been shown to negatively affect amphibians especially the boreal chorus frog (Johnson 1989; Hecnar & M'Closkey 1997). *Pseudacris maculata* has no anti-predator defence which requires them to seek out temporary ponds that won't contain predatory fish. Also, the boreal chorus frog is a poor swimmer and fast flowing streams/rivers may become a barrier for *P. maculata* when migrating between habitats.

Hyla versicolor

I found that *Hyla versicolor* will select deep, turbid ponds with shrubs along the edge and are far away from streams. *Hyla versicolor* forage in and call from small trees and shrubs along the edge of the water (Johnson 1989; Hecnar & M'Closkey 1996b; Conant & Collins 1998). Metamorphs also forage and hide under bushes along the edge before migrating to woodlands (Johnson 1989). Thus it was not surprising to find that *H. versicolor* prefers wetlands or ponds that are surrounded by shrubs.

I found positive relationships with *H. versicolor* and depth and turbidity. This was puzzling because some amphibians are known to avoid deep breeding sites due to fish predation (Beebee 1981; Baker & Halliday 1999; Eason & Fauth 2001). With drought-like conditions occurring in the Thunder Bay region over the past few years, the decrease in hydroperiod may be forcing *H. versicolor* to breed in deeper ponds to avoid dessication. Richardson (2002) found that Hylidae frogs had higher growth rates in more permanent ponds than vernal ponds. However there has been recent concern over the effects of UV-B radiation on amphibians (Blaustein et al. 2001; Blaustein & Kiesecker 2002). A recent study by Kiesecker et al. (2001) found that hatching success of *Bufo boreas* was significantly lower in shallow waters due to the exposure of UV-B radiation which in return resulted in infection by *Saprolegnia ferax*, a

pathogenic oomycete. Kiesecker et al. (2001) also observed that UV-B flux decreased with increasing water depth, with almost 50% less UV-B radiation in just 50 cm of water compared to 10 cm of water. This may also explain why the gray treefrog may prefer more turbid waters. An increase in turbidity cuts down the amount of light penetrating the water column (Moore 1999), reducing the amount of UV-B radiation. Alternatively, *H. versicolor* could be occupying more turbid breeding sites because of the likelihood that fish will be present in deeper, more permanent ponds. The more turbid the water is, the easier it is for the tadpoles to hide from visually oriented predators.

Rana pipiens

Rana pipiens migrate after breeding to surrounding fields, meadows and moist grasslands to spend the summer foraging (Johnson 1989; Pope et al. 2000). Leopard frogs prefer dense terrestrial vegetation and use open fields more often than other species (Werner 1992). Werner (1992) also found that leopard frog tadpoles had higher growth and survivorship in open canopy ponds. Thus agricultural fields provide prime summer habitat for northern leopard frogs explaining the positive relationship I found with agriculture.

Rana clamitans

Since *Rana clamitans* hibernate at the bottom of ponds or lakes, it is dependent on permanent deep water bodies (Johnson 1989; Hecnar & M'Closkey 1996b; Hecnar 1997). As I previously mentioned, Thunder Bay has been experiencing drought-like conditions in recent years thus reducing hydroperiod. Therefore *R. clamitans* may be selecting ponds based on how close they are to lakes in the event that they will have to hibernate in a nearby lake. As a result of this, ponds may be sink populations in relation to lakes that are acting as sources. This may

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explain why I found a negative correlation with the distance to a lake. *Rana clamitans* tadpoles are more dependent on permanent water bodies because they overwinter 1-2 years as tadpoles before reaching maturity. Semi-permanent ponds may not be prime breeding sites for *Rana clamitans* in this particular region. This is supported by a study by Robinson (2004) who found higher incidences of *R. clamitans* in lakes than in semi permanent wetlands.

I found a negative relationship with *R. clamitans* and the percent of floating vegetation within a pond. Adult green frogs spend most of their time near the edges of fresh water calling from the banks, and foraging within the dense vegetation (Johnson 1989; Conant & Collins 1998). *Rana clamitans* will lay its eggs on the surface, supported by submergent and emergent vegetation, within the warmest shallow water of the pond (Johnson 1989; Carr & Fahrig 2001). Green frogs also inhabit the littoral zone of water bodies that consist of a combination of open water and herbaceous vegetation. Too much floating vegetation will fill in any open water areas within a pond, thus reducing preferred habitat of the green frog. *Rana clamitans* also prefer warm water (Johnson 1989). Therefore, floating vegetation along the edge may filter out the sunlight that is needed to warm the shallow areas of the pond which helps speed up metamorphosis.

Rana septentrionalis

I found a positive relationship between *R. septentrionalis* and habitat richness. Thus *R. septentrionalis* may prefer ponds with a mixture of different types of habitat along the edge of a pond providing more resources and microhabitats.

I found a negative relationship between *R. septentrionalis* and turbidity. Turbidity prevents sunlight from penetrating the water column causing the water to remain cooler which

inhibits tadpole development (Johnson 1989). Lack of sunlight also restricts the growth of aquatic vegetation. The mink frog uses aquatic vegetation for basking, cover, during foraging and to attach egg masses to (Johnson 1989; Conant & Collins 1998).

I also found a negative relationship between the mink frog and the amount of roads near a pond. Studies have shown that there is a high road mortality amongst amphibian species trying to migrate between habitats or water bodies (Fahrig et al. 1995; Findlay & Houlahan 1997; Vos & Chardon 1998; Semlitsch 2000; Carr & Fahrig 2001; Findlay et al. 2001). In this case, *R. septentrionalis* may need to cross roads as a dispersing juvenile or as an adult seeking more permanent water bodies if semi-permanent ponds begin to dry up due to recent drought conditions.

Bufo americanus

I found a positive relationship with *Bufo americanus* and area and the percentage of lakes surrounding a pond. American toad may prefer larger ponds or lakes because breeding in shallow ponds have a higher risk of desiccation. Recent dry conditions are turning temporary ponds into sink habitats. Lakes and larger ponds act as source populations supplying temporary ponds with individuals. The American toad is known to breed in more temporary ponds however toads also have been found to use shallow areas of large, more permanent water bodies as breeding areas (Johnson 1989; Conant & Collins 1998). Both adults and tadpoles have anti-predator defences that allow them to occupy permanent ponds that contain fish (Watt et al. 1997). The adults contain poison glands behind their eyes and the tadpoles congregate together and fan their tails to stir up food particles from the substrate to confuse predators (Johnson 1989). Plus with a high fecundity, they increase their chances of tadpoles surviving in areas of high predation

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or drought conditions by breeding in permanent water bodies.

Area was also found to be positively correlated with all of the vegetation types both around and within the pond and habitat richness. This could mean by choosing larger ponds, it provides itself with more of a variety of vegetation to meet all of it's life cycle needs (Conant & Collins 1998). For example, toads lay their eggs by wrapping them around submerged vegetation, and they call from vegetation along the shore or within the pond (Johnson 1989).

Ambystoma maculatum

Ambystoma maculatum breeds in temporary waters or shallow areas of permanent woodland ponds in early spring and during the summer can be found under logs, rocks, boards or even underground in tunnels when it is dry (Johnson 1989; Conant & Collins 1998). As a result, *A. maculatum* has no need to use streams or ditches as migration corridors or for breeding sites. Streams are usually too fast flowing for salamanders to cross and contain fish, which is a predator to the salamander. Thus streams can hinder movement between habitats and could explain why there was a positive relationship between incidence and the distance to the nearest stream. However, Dupuis et al. (1995) found no differences in salamander densities with distance from streams in both managed and old growth forests. I was surprised to find that the yellow spotted salamander was positively related to the area of cutover around the pond considering many papers have shown the opposite (Bury 1983; Petranka et al. 1993; Petranka et al. 1994; deMaynadier & Hunter 1995; Pough et al. 1987; Ash 1997; Brooks 2001). However deMaynadier et al. (1995) suggested that clearcuts have only a short-term negative impact on salamanders and these impacts can be lessened with regeneration practices that leave adequate microhabitat intact. Ash (1997) also reported that salamanders returned to clearcuts 4-6 years

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after cutting and their numbers increased rapidly with the reformation of litter layer. Thus the area of clearcuts around my study sites could either be older cuts in which the salamanders have returned to or could be recent clearcuts but possess adequate microhabitat and leaf litter for salamander survival. As long as there are plenty of logs and rocks to hide or burrow under and sufficient vegetative cover to conserve moisture (deMaynadier & Hunter 1995), the spotted salamander should be able to survive in logged forests.

Ambystoma laterale

I found that *Ambystoma laterale* favoured small ponds with low conductivity and gentle sloping banks. This is consistent with it's natural history in that it prefers to breed in temporary or small ponds (Johnson 1989; Conant & Collins 1998), and after the breeding season, it migrates to nearby woodlands. Thus steep banks can become a barrier to a salamander, preventing it from migrating out of the pond. Also the relationship with conductivity tells us that there is a high amount of ionic activity in the pond and indicating that there may be some chemical in those ponds that is negatively affecting the salamanders. However further chemical testing should be done in order to correctly determine this.

Caveat

Interpretation of results should be done with caution as I found low incidence in *Rana pipiens, Ambystoma maculata* and *Ambystoma laterale* as well as high incidence in *Pseudacris crucifer, Rana sylvatica* and *Bufo americanus*. Therefore associations found between the latter species and local and landscape variables may be coincidental.

Conclusion

I found significant differences in preference between most amphibian species and their

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habitat. I also discovered that amphibians rely on both local habitat and regional landscape variables for selection of breeding ponds and adjacent terrestrial habitat. Specifically, single-species habitat models appeared to differ with each other at the local scale but there were similarities at the landscape scale. There was a general preference for ponds situated in agricultural landscapes with larger water bodies nearby and no streams. In order to conserve more than one species of amphibian, we have to take into account each species own habitat preference in our conservation plans. Stable amphibian populations require habitat that provides basic resource requirements for all life history stages (Waldick 1997). Thus conserving amphibian habitat is complex in that not only do you have to take into account local breeding sites but you also have to consider what is happening on a landscape scale. Recolonization of a breeding site depends on landscape characteristics (distance between habitat patches), barrier effects (roads) and species characteristics (dispersal ability) (Laan & Verboom 1990). A species' population may be doomed if isolated from other populations. Waldick (1997) suggested that ponds act as stepping stones which ease recolonization of suitable habitats by allowing dispersal across patches of unfavourable habitat.

I also found that my models may be affected by low incidence of species studied. Thus using presence/absence data for habitat models may only be advantageous when a species is not rare. This may not be a problem if there is a distinct separation of differences between ponds however in this case there was not. Thus it may prove difficult to try to determine habitat preference of a species that is rare everywhere. By expanding this study into different areas where these species occur may provide more solid models for species that may be rare in northwestern Ontario but not elsewhere.

GENERAL CONCLUSION

Based on a four year study of amphibians in northwestern Ontario, I found an increase in species richness, a decrease in turnover and a difference in species incidence over time. *Pseudacris crucifer, B. americanus, R. sylvatica* occupied most ponds whereas, *R. pipiens, R. clamitans* and *A. laterale* occupied few. I also found species incidence to differ between northern and southern Ontario. These differences in incidence of species within and between regions can be explained by where species are located within their geographic range and the difference in land-use patterns. Species incidence was found to be higher near the core of a species' range than near the periphery. Thus species that had a low incidence in either region were located near the edge of their ranges. Exceptions to this rule were *A. maculatum* and *R. sylvatica*, which were affected by the intense habitat destruction in Southern Ontario, and *R. pipiens*, where the lack of meadow and grassland habitat in northern Ontario could be the cause.

I found interesting results when I looked at the role local habitat and landscape characteristics play in determining species richness and turnover at ponds sites. I found species richness to be positively affected by the distance to nearby streams, the area of agriculture and wetlands, habitat richness and the percent of shrubs surrounding a pond. I also found it to be negatively affected by perimeter. Turnover was found to be positively correlated with the percent of substrate and perimeter and negatively correlated to slope. This shows that generally, amphibian species in Northwestern Ontario prefer smaller aquatic habitats that are situated in landscapes with a good mixture of habitat types adjacent to them, are open but with sufficient amount of vegetation cover and microhabitat within and around them.

I also looked at individual amphibian species and established species habitat models. I

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found that each species preferred ponds that satisfied its own niche requirements. *Pseudacris crucifer & Rana sylvatica* were found at almost all of my pond sites thus suggesting that northwestern Ontario still has a sufficient amount of forested habitat left. *Pseudacris maculata* was associated with sites having high pH, surrounded by agriculture, and had little to no streams close to it. *Hyla versicolor* may prefer sites that are deep, murky and surrounded by shrubs. *Rana clamitans* was found to be negatively associated with the distance to nearby lakes and the amount of floating vegetation within a pond. *Rana septentrionalis* were found at pond sites where the water was low in turbidity, was surrounded by different habitat types and no roads. *Bufo americanus* was associated with large ponds that were surrounded by lakes. Although I found a low incidence of *Rana pipiens, Ambystoma maculatum* and *Ambystoma laterale*, I still managed to find variables that were highly correlated with each species. It was no surprise to find that *R. pipiens* was associated with ponds that were within areas of agriculture since this species spends most of the summer foraging in nearby meadows. I actually found a positive relationship with the presence of *A. maculatum* and the area of cutover and the distance to the nearest stream. *Ambystoma laterale* was negatively associated with conductivity and bank slope.

Single-species habitat models differed at the local scale but were similar on the landscape scale. These results were similar to Chapter 2 when I looked at the association between species richness and local habitat and landscape characteristics. In both cases, there was a general preference for ponds in agricultural landscapes, near larger water bodies and far away from streams. However they differed in local preferences with ponds containing variables that represent each species local habitat preferences. Therefore it is important to take into account each species habitat preferences when making conservation plans to protect all species within a

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community. We should also keep in mind that we shouldn't limit our conservation efforts to habitat restoration/creation. In order for a species to colonize a pond, the pond needs to be close to other existing populations. Therefore the placement of habitat is crucial. On a geographical scale, populations located close to the periphery of a species' range may always show a low incidence and conservation efforts may be in vain because rarity may not be related to a simple solution such as habitat restoration.

I recommend incorporating habitat models into amphibian conservation strategies keeping in mind that it is habitat destruction and not something else that is causing amphibians to decline. For future work, I would suggest expanding on my habitat analysis to try to include more habitat variables such as the actual types of vegetation within and around the aquatic sites, invertebrates in the pond, types of microhabitat that may be used for hibernation within their terrestrial habitat. I would also suggest testing my species models on the same or different amphibian species in different parts of their geographic ranges to see if this could work as a potential method for amphibian conservation. I would like to look at different types of aquatic habitat such as wetlands, swamps, bogs to see if there is a difference between them and the pond habitats I studied.

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APPENDIX 1: Additional Pond Information

Table A1. Species richness from 1999 to 2002 at 69 pond sites.

Sites	SR 99	SR 00	SR 01	SR 02	SR 01-02
A1	-	-	4	4	4
A2	-	-	3	6	4.5
A3	-	-	5	5	5
A4	-	-	4	4	4
A5	-	-	5	7	6
A6	-	-	3	4	3.5
A7	-	-	3	4	3.5
A8	-	-	5	5	5
A9	-	-	4	3	3.5
A10	-	-	6	4	5
A11	-	-	3	4	3.5
AL1	-	-	5	6	5.5
AL5	-	-	5	7	6
AL6	-	-	7	6	6.5
AL7	-	-	5	8	6.5
B1	-	-	7	7	7
G1	3	5	3	3	3
G2	5	4	3	4	3.5
N1	3	2	3	3	3
N2	4	3	3	4	3.5
N3	2	4	3	2	2.5
O1	4	4	5	5	5
O2	5	5	4	5	4.5
O3	3	4	5	5	5
O4	5	4	6	6	6
O5	5	5	7	6	6.5
O6	2	3	4	5	4.5
O7	5	5	4	5	4.5
O8	-	-	5	4	4.5
O9	-	-	3	5	4
O11	-	-	4	6	5
O12	-	-	3	5	4
P1	2	1	3	5	4
P2 a/b	5	3	4	5	4.5
P3	3	4	5	4	4.5
P4	3	5	7	6	6.5
P5	5	5	7	6	6.5
P6	5	5	6	7	6.5
P7	5	5	6	5	5.5
P8	1	2	5	3	4

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P9	3	4	5	5	5
P10	6	3	5	6	5.5
P12 a/b/c	3	4	5	3	4
P13	4	4	7	7	7
P14 a/b	3	3	5	6	5.5
P15	2	2	5	6	5.5
P16	4	3	6	5	5.5
P17	4	2	3	3	3
P18	5	3	5	7	6
P19	-	-	6	6	6
P20	-	-	3	5	4
P21 a/b/c	-	-	4	5	4.5
P23 a/b	-	-	3	5	4
P24	-	-	3	4	3.5
S1 A/B	6	5	5	5	5
S2	6	3	4	4	4
S3	-	-	5	4	4.5
S4	-	-	5	5	5
TB1	4	4	4	4	4
TB2	3	4	2	4	3
TB3 a/b/c/d	5	3	5	5	5
TB4	5	3	4	4	4
TB5	2	5	3	2	2.5
TB6	1	2	2	4	3
TB7 a/b	4	5	4	4	4
TB10	2	1	1	3	2
TB11	5	4	5	4	4.5
TB12	5	5	4	4	4
TB14	-	-	5	5	5

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APPENDIX 2: Principal Components Analysis and Pearson Correlation Matrix

Table A2. Results of the principal components analysis using varimax rotation comparing local habitat and landscape characteristics. Each numbered column represents a different factor loading.

Variables	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
ARSWOODPER	0.950	0.155	0.030	0.171	-0.086
SQWOODKM2	0.949	0.169	0.044	0.157	-0.082
AGRIKM2	-0.833	0.250	0.043	0.109	0.118
AGRIPER	-0.833	0.249	0.044	0.108	0.117
LOGELEVATION	0.653	-0.284	-0.030	0.253	-0.168
MIXEDKM2	0.597	-0.529	0.054	0.247	-0.257
MIXEDPER	0.594	-0.529	0.057	0.250	-0.259
STREAMSKM	-0.529	-0.013	-0.156	0.437	0.070
DECIDUOUSPER	0.321	0.864	-0.052	-0.003	0.145
DECIDUOUSKM2	0.317	0.864	-0.054	-0.008	0.150
CONIFERPER	0.386	-0.752	0.127	-0.254	0.035
CONIFERKM2	0.386	-0.751	0.126	-0.258	0.036
WETLANDPER	0.144	-0.666	-0.199	0.033	0.153
WETLANDKM2	0.143	-0.665	-0.200	0.031	0.153
CUTOVERKM2	0.195	-0.513	-0.039	0.107	-0.009
CUTOVERPER	0.193	-0.512	-0.038	0.108	-0.009
LOGDIVERSITY	-0.000	0.031	0.831	0.023	-0.190
HABITATRICH	0.088	0.078	0.807	-0.015	-0.140
SUBSTRATEPER	-0.175	-0.047	0.627	0.216	0.207
BOTTOMTYPE	0.286	-0.334	0.626	0.024	0.221
SUBSTRATEM2	-0.300	-0.048	0.560	-0.012	0.114
LOGROADS	-0.095	-0.073	-0.100	-0.781	0.143
LOGPERM	-0.132	-0.219	-0.080	-0.634	-0.072
SQRTCOND	-0.440	0.066	0.034	-0.589	0.096
TREESP	0.253	-0.084	0.122	0.087	-0.820
TREESM	0.147	-0.070	0.040	0.130	-0.815
SQRTEMERPER	0.014	0.116	-0.386	-0.171	-0.594
GRASSPER	-0.233	0.157	-0.394	-0.137	0.509
LOGAREA	-0.104	0.075	0.172	-0.024	-0.128
LOGVOL	-0.190	0.142	0.198	0.075	-0.078
SQRTGRASSM	-0.294	0.145	-0.091	-0.038	0.337
LOGEMERGM2	-0.105	0.240	-0.133	-0.184	-0.471
SHRUBSM	-0.001	-0.094	0.132	-0.048	-0.077
SHRUBSPER	0.095	-0.174	-0.023	0.067	0.022
LOGLAKEKM2	0.112	-0.069	0.089	0.054	-0.090
LOGLAKEPER	0.112	-0.070	0.090	0.055	-0.092
ROADUSE	0.149	0.173	0.224	0.322	0.111
FLOATINGPER	-0.146	0.277	-0.097	-0.122	0.038
FLOATINGM2	-0.047	0.071	-0.116	0.018	0.028
SQRTDSTREAM	0.078	-0.175	0.030	-0.107	-0.140
LOGTURB	-0.127	0.166	0.021	0.240	0.039
LOGTOPOGRAPH	0.197	0.176	-0.040	-0.106	0.180
DISTWETLAND	-0.394	0.127	-0.008	-0.167	0.006
LOGDISTLAKE	-0.447	0.049	-0.351	0.255	-0.228
LOGSLOPE	-0.183	0.132	-0.040	0.186	0.066
LOGDEPTH	-0.298	0.211	0.136	0.203	0.056
AVGPH	-0.325	0.088	0.148	-0.270	0.176
TURBCATEGORY	-0.005	0.031	-0.380	0.293	-0.057

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Variables	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10
ARSWOODPER	-0.081	0.012	0.015	0.017	0.006
SQWOODKM2	-0.081	0.012	0.012	0.031	0.021
AGRIKM2	0.192	-0.078	0.097	0.315	0.007
AGRIPER	0.192	-0.079	0.097	0.316	0.007
LOGELEVATION	-0.160	0.175	-0.103	-0.233	0.044
MIXEDKM2	-0.212	0.036	-0.151	-0.202	0.097
MIXEDPER	-0.212	0.038	-0.154	-0.204	0.095
STREAMSKM	0.006	-0.160	0.316	-0.249	0.070
DECIDUOUSPER	0.165	-0.028	0.164	0.156	-0.102
DECIDUOUSKM2	0.165	-0.028	0.167	0.156	-0.100
CONIFERPER	-0.170	0.088	0.067	0.070	-0.006
CONIFERKM2	-0.169	0.086	0.070	0.072	-0.005
WETLANDPER	0.102	0.271	0.002	-0.253	0.032
WETLANDKM2	0.103	0.269	0.004	-0.251	0.032
CUTOVERKM2	-0.094	0.104	-0.072	-0.751	0.027
CUTOVERPER	-0.093	0.110	-0.074	-0.751	0.026
LOGDIVERSITY	-0.036	0.114	0.010	-0.125	0.101
HABITATRICH	0.211	-0.006	0.073	-0.100	0.051
SUBSTRATEPER	0.084	0.001	-0.414	0.228	0.006
BOTTOMTYPE	-0.034	0.135	-0.139	0.093	0.078
SUBSTRATEM2	0.381	0.034	-0.342	0.201	0.047
LOGROADS	0.036	0.125	0.098	0.142	0.090
LOGPERM	-0.260	-0.056	-0.063	-0.027	-0.039
SQRTCOND	0.110	-0.352	0.187	0.138	-0.037
TREESP	-0.007	0.057	-0.006	-0.003	0.038
TREESM	0.165	-0.109	-0.179	0.097	0.013
SQRTEMERPER	0.108	0.285	0.056	-0.103	-0.210
GRASSPER	0.156	-0.498	0.245	0.085	-0.042
LOGAREA	0.906	0.012	-0.095	0.079	-0.026
LOGVOL	0.894	-0.060	0.041	0.049	0.101
SQRTGRASSM	0.684	-0.391	0.131	0.136	-0.120
LOGEMERGM2	0.645	0.160	0.083	-0.007	-0.161
SHRUBSM	0.131	0.888	0.101	-0.018	0.049
SHRUBSPER	-0.241	0.875	0.077	-0.060	0.059
LOGLAKEKM2	-0.038	-0.041	-0.932	-0.093	0.093
LOGLAKEPER	-0.038	-0.040	-0.932	-0.094	0.093
ROADUSE	-0.232	0.088	-0.118	-0.617	0.182
FLOATINGPER	-0.101	-0.200	0.235	0.136	-0.711
FLOATINGM2	0.494	0.006	0.075	0.151	-0.591
SQRTDSTREAM	-0.221	0.010	-0.029	0.074	0.132
LOGTURB	0.196	-0.160	0.217	-0.144	-0.468
LOGTOPOGRAPH	0.126	-0.088	0.064	-0.075	0.085
DISTWETLAND	-0.027	0.195	-0.094	0.331	0.022
LOGDISTLAKE	0.001	-0.006	0.206	-0.021	0.055
LOGSLOPE	0.041	-0.457	0.224	0.394	0.347
LOGDEPTH	0.468	-0.173	0.357	0.069	0.315
AVGPH	0.127	-0.185	0.136	0.245	0.488
TURBCATEGORY	-0.024	-0.421	0.221	0.160	-0.429

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Variables	Factor 11	Factor 12
ARSWOODPER	-0.040	0.037
SQWOODKM2	-0.043	0.036
AGRIKM2	-0.068	0.141
AGRIPER	-0.070	0.141
LOGELEVATION	0.204	0.312
MIXEDKM2	-0.119	0.075
MIXEDPER	-0.120	0.074
STREAMSKM	-0.148	-0.071
DECIDUOUSPER	0.073	-0.018
DECIDUOUSKM2	0.074	-0.018
CONIFERPER	0.043	-0.032
CONIFERKM2	0.043	-0.031
WETLANDPER	0.355	0.263
WETLANDKM2	0.355	0.264
CUTOVERKM2	0.068	0.104
CUTOVERPER	0.065	0.102
LOGDIVERSITY	-0.096	0.154
HABITATRICH	-0.019	0.030
SUBSTRATEPER	0.190	-0.040
BOTTOMTYPE	0.050	-0.196
SUBSTRATEM2	0.142	-0.060
LOGROADS	0.010	-0.138
LOGPERM	0.028	-0.528
SQRTCOND	-0.125	-0.021
TREESP	0.029	0.111
TREESM	-0.011	0.077
SQRTEMERPER	0.227	-0.048
GRASSPER	-0.023	0.107
LOGAREA	-0.086	-0.071
LOGVOL	-0.017	0.006
SQRTGRASSM	-0.109	0.038
LOGEMERGM2	0.074	-0.040
SHRUBSM	-0.063	0.023
SHRUBSPER	0.032	-0.032
LOGLAKEKM2	-0.039	0.009
LOGLAKEPER	-0.039	0.009
ROADUSE	-0.144	-0.131
FLOATINGPER	0.055	0.155
FLOATINGM2	-0.125	-0.014
SQRTDSTREAM	0.709	0.090
LOGTURB	0.618	-0.017
LOGTOPOGRAPH	-0.116	-0.822
DISTWETLAND	0.015	-0.644
LOGDISTLAKE	0.307	-0.279
LOGSLOPE	-0.011	-0.160
LOGDEPTH	0.129	0.160
AVGPH	0.085	0.042
TURBCATEGORY	0.057	-0.007

"Variance" Explained by Rotated Components

1	2	3	4	5	6	7
6.664	5.524	3.451	2.674	2.989	3.928	3.084

8	9	10	11	12
2.918	2.765	1.980	1.611	1.998

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Percent of Total Variance Explained

1	2	3	4	5	6	7
13.883	11.507	7.190	5.571	6.226	8.184	6.425

8	9	10	11	12
6.080	5.760	4.126	3.356	4.162

Table A3. Pearson Correlation Matrix for all of the landscape variables (N = 69)

	ARSWOODPER	SQWOODKM2	CONIFERKM2	CONIFERPER	DECIDUOUSKM2
ARSWOODPER	1.000				
SQWOODKM2	0.996	1.000			
CONIFERKM2	0.207	0.205	1.000		
CONIFERPER	0.209	0.206	1.000	1.000	
DECIDUOUSKM2	0.399	0.410	-0.498	-0.500	1.000
DECIDUOUSPER	0.405	0.416	-0.497	-0.499	1.000
MIXEDKM2	0.601	0.586	0.482	0.486	-0.468
MIXEDPER	0.600	0.583	0.482	0.486	-0.470
WETLANDKM2	-0.003	-0.019	0.505	0.505	-0.491
WETLANDPER	-0.003	-0.018	0.506	0.506	-0.493
DISTWETLAND	-0.407	-0.396	-0.193	-0.195	0.015
LOGLAKEKM2	0.095	0.104	0.057	0.060	-0.227
LOGLAKEPER	0.096	0.105	0.058	0.061	-0.228
LOGDISTLAKE	-0.350	-0.364	-0.299	-0.297	-0.049
STREAMSKM	-0.394	-0.408	-0.333	-0.332	-0.139
SQRTDSTREAM	0.062	0.055	0.228	0.229	-0.173
LOGROADS	-0.250	-0.240	0.235	0.231	-0.014
ROADUSE	0.232	0.230	-0.020	-0.015	0.010
LOGELEVATION	0.645	0.638	0.367	0.369	-0.149
LOGTOPOGRAPH	0.120	0.123	-0.039	-0.040	0.268
CUTOVERPER	0.109	0.088	0.375	0.378	-0.517
CUTOVERKM2	0.109	0.089	0.375	0.378	-0.516
AGRIKM2	-0.753	-0.746	-0.498	-0.499	0.057
AGRIPER	-0.752	-0.746	-0.498	-0.499	0.056

	DECIDUOUSPER	MIXEDKM2	MIXEDPER	WETLANDKM2	WETLANDPER
DECIDUOUSPER	1.000				
MIXEDKM2	-0.462	1.000			
MIXEDPER	-0.464	1.000	1.000		
WETLANDKM2	-0.493	0.398	0.395	1.000	
WETLANDPER	-0.495	0.400	0.397	1.000	1.000
DISTWETLAND	0.011	-0.411	-0.412	-0.282	-0.283
LOGLAKEKM2	-0.224	0.302	0.303	0.034	0.035
LOGLAKEPER	-0.226	0.304	0.306	0.034	0.036
LOGDISTLAKE	-0.048	-0.246	-0.243	-0.030	-0.030
STREAMSKM	-0.142	-0.206	-0.205	-0.060	-0.059
SQRTDSTREAM	-0.172	0.183	0.183	0.238	0.239
LOGROADS	-0.018	-0.302	-0.304	-0.019	-0.020
ROADUSE	0.016	0.261	0.266	-0.061	-0.058
LOGELEVATION	-0.147	0.766	0.762	0.489	0.490
LOGTOPOGRAPH	0.265	-0.133	-0.136	-0.253	-0.254
CUTOVERPER	-0.516	0.589	0.590	0.583	0.586
CUTOVERKM2	-0.516	0.589	0.590	0.586	0.589
AGRIKM2	0.053	-0.753	-0.751	-0.347	-0.349
AGRIPER	0.052	-0.752	-0.749	-0.348	-0.349

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	DISTWETLAND	LOGLAKEKM2	LOGLAKEPER	LOGDISTLAKE	STREAMSKM
DISTWETLAND	1.000				
LOGLAKEKM2	-0.030	1.000			
LOGLAKEPER	-0.031	1.000	1.000		
LOGDISTLAKE	0.235	-0.241	-0.241	1.000	
STREAMSKM	0.034	-0.319	-0.319	0.384	1.000
SQRTDSTREAM	-0.013	0.053	0.054	0.142	-0.125
LOGROADS	0.343	-0.159	-0.160	-0.028	-0.291
ROADUSE	-0.206	0.249	0.251	-0.095	0.163
LOGELEVATION	-0.494	0.214	0.215	-0.224	-0.276
LOGTOPOGRAPH	0.455	-0.061	-0.062	0.037	-0.017
CUTOVERPER	-0.441	0.186	0.188	-0.073	0.058
CUTOVERKM2	-0.442	0.185	0.186	-0.076	0.056
AGRIKM2	0.317	-0.223	-0.224	0.321	0.431
AGRIPER	0.316	-0.223	-0.224	0.321	0.430

	SQRTDSTREAM	LOGROADS	ROADUSE	LOGELEVATION	LOGTOPOGRAPH
SQRTDSTREAM	1.000				
LOGROADS	0.100	1.000			
ROADUSE	-0.131	-0.309	1.000		
LOGELEVATION	0.296	-0.303	0.183	1.000	
LOGTOPOGRAPH	-0.217	0.145	0.095	-0.274	1.000
CUTOVERPER	0.128	-0.130	0.403	0.602	-0.126
CUTOVERKM2	0.129	-0.130	0.401	0.605	-0.126
AGRIKM2	-0.184	0.030	-0.245	-0.718	-0.178
AGRIPER	-0.184	0.031	-0.245	-0.719	-0.179

	CUTOVERPER	CUTOVERKM2	AGRIKM2	AGRIPER
CUTOVERPER	1.000			
CUTOVERKM2	1.000	1.000		
AGRIKM2	-0.546	-0.547	1.000	
AGRIPER	-0.546	-0.548	1.000	1.000

Table A4. Pearson correlation matrix for all of the local habitat variables.

	LOGPERM	LOGAREA	LOGVOL	LOGDEPTH	FLOATINGM2
LOGPERM	1.000				
LOGAREA	-0.200	1.000			
LOGVOL	-0.290	0.925	1.000		
LOGDEPTH	-0.333	0.375	0.666	1.000	
FLOATINGM2	-0.085	0.459	0.390	0.066	1.000
FLOATINGPER	-0.007	-0.039	-0.066	-0.049	0.416
LOGEMERGM2	-0.047	0.616	0.551	0.183	0.363
SQRTEMERPER	0.118	0.032	-0.048	-0.174	0.077
SUBSTRATEM2	-0.088	0.467	0.445	0.187	-0.004
SUBSTRATEPER	-0.126	0.195	0.199	0.101	-0.080
SQRTGRASSM	-0.142	0.604	0.653	0.472	0.507
GRASSPER	-0.000	0.004	0.102	0.285	0.170
SHRUBSM	0.001	0.171	0.122	-0.033	0.048
SHRUBSPER	0.058	-0.262	-0.297	-0.246	-0.169
TREESM	-0.086	0.246	0.187	-0.014	-0.006
TREESP	-0.122	0.111	0.059	-0.046	-0.071
BOTTOMTYPE	0.023	0.036	-0.032	-0.160	-0.167
HABITATRICH	-0.129	0.277	0.304	0.201	0.009
LOGDIVERSITY	-0.134	0.092	0.137	0.098	-0.186
LOGSLOPE	-0.020	0.025	0.155	0.400	-0.044
AVGPH	0.108	0.168	0.210	0.235	-0.059
SQRTCOND	0.392	0.157	0.174	0.202	0.121
LOGTURB	-0.146	0.122	0.194	0.255	0.293
TURBCATEGORY	-0.127	-0.098	-0.044	0.087	0.221

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	FLOATINGPER	LOGEMERGM2	SQRTEMERPER	SUBSTRATEM2	SUBSTRATEPER
FLOATINGPER	1.000				
LOGEMERGM2	0.136	1.000			
SQRTEMERPER	0.114	0.717	1.000		
SUBSTRATEM2	-0.148	0.197	-0.167	1.000	
SUBSTRATEPER	-0.175	-0.134	-0.365	0.730	1.000
SQRTGRASSM	0.237	0.324	-0.208	0.252	0.027
GRASSPER	0.386	-0.057	-0.223	-0.138	-0.253
SHRUBSM	-0.213	0.192	0.174	0.081	-0.019
SHRUBSPER	-0.265	-0.105	0.170	-0.141	-0.097
TREESM	-0.120	0.318	0.343	-0.008	0.009
TREESP	-0.094	0.209	0.360	-0.126	-0.154
BOTTOMTYPE	-0.285	-0.272	-0.339	0.394	0.477
HABITATRICH	-0.147	0.099	-0.184	0.363	0.352
LOGDIVERSITY	-0.200	-0.078	-0.246	0.357	0.349
LOGSLOPE	-0.028	-0.035	-0.194	0.074	0.011
AVGPH	-0.077	0.040	-0.196	0.270	0.146
SQRTCOND	0.260	0.167	-0.088	0.202	-0.002
LOGTURB	0.382	0.226	0.214	0.051	0.047
TURBCATEGORY	0.381	0.013	0.115	-0.287	-0.272

	SQRTGRASSM	GRASSPER	SHRUBSM	SHRUBSPER	TREESM
SQRTGRASSM	1.000				
GRASSPER	0.696	1.000			
SHRUBSM	-0.285	-0.480	1.000		
SHRUBSPER	-0.533	-0.500	0.815	1.000	
TREESM	-0.186	-0.411	0.005	-0.103	1.000
TREESP	-0.424	-0.575	0.112	0.021	0.705
BOTTOMTYPE	-0.254	-0.390	0.192	0.181	-0.076
HABITATRICH	0.049	-0.286	0.103	-0.044	0.170
LOGDIVERSITY	-0.158	-0.414	0.245	0.138	0.172
LOGSLOPE	0.326	0.360	-0.313	-0.333	-0.067
AVGPH	0.319	0.286	-0.108	-0.220	-0.161
SQRTCOND	0.445	0.453	-0.201	-0.372	-0.158
LOGTURB	0.265	0.187	-0.109	-0.136	-0.031
TURBCATEGORY	0.257	0.334	-0.410	-0.262	0.105

	TREESP	BOTTOMTYPE	HABITATRICH	LOGDIVERSITY	LOGSLOPE
TREESP	1.000				
BOTTOMTYPE	0.044	1.000			
HABITATRICH	0.162	0.327	1.000		
LOGDIVERSITY	0.237	0.310	0.842	1.000	
LOGSLOPE	-0.195	-0.130	-0.012	-0.075	1.000
AVGPH	-0.288	0.084	0.129	0.048	0.423
SQRTCOND	-0.330	-0.140	-0.069	-0.115	0.253
LOGTURB	-0.089	-0.126	0.012	-0.077	0.115
TURBCATEGORY	-0.077	-0.412	-0.287	-0.320	0.305

	AVGPH	SQRTCOND	LOGTURB	TURBCATEGORY
AVGPH	1.000			
SQRTCOND	0.397	1.000		
LOGTURB	-0.114	0.004	1.000	
TURBCATEGORY	-0.226	0.015	0.443	1.000

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APPENDIX 3: Full Regression Models

Table A5. Stepwise multiple regression model of amphibian species richness (N=69).

Variable	Coefficient	Std Error	Tolerance	t	p
Local Habitat Variables ($F_{4,64} = 8.01$, $p < 0.001$, $R^2 = 0.334$)					
Constant	0.55	0.445	-	1.237	0.220
Perimeter	-0.079	0.026	0.961	-3.093	0.003
Shrubsper	0.295	0.09	0.945	3.285	0.002
PH	0.171	0.055	0.919	3.135	0.003
Richness	0.037	0.016	0.963	2.233	0.029
Landscape Variables ($F_{4,64} = 7.44$, $p < 0.001$, $R^2 = 0.317$)					
Constant	1.541	0.174	-	8.832	0
Woodkm	0.002	0.001	0.355	1.763	0.083
Wetlandkm	0.282	0.085	0.689	3.307	0.002
Dstream	0.599	0.20	0.93	2.992	0.004
Agrikm	0.075	0.02	0.31	3.718	0
Complete Model ($F_{7,61} = 10.0$, $p < 0.001$, $R^2 = 0.534$)					
Constant	0.91	0.403	-	2.258	0.028
Wetlandkm	0.147	0.069	0.749	2.126	0.038
Dstream	0.638	0.173	0.894	3.688	0
Agrikm	0.04	0.012	0.649	3.385	0.001
Shrubsper	0.255	0.082	0.825	3.107	0.012
Perimeter	-0.061	0.023	0.853	-2.604	0.003
Richness	0.049	0.014	0.93	3.425	0.001
PH	0.086	0.052	0.74	1.658	0.102

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Table A6. Stepwise multiple regression of amphibian turnover with local habitat and landscape variables (N=69).

Variable	Coefficient	Std. Error	Tolerance	t	p
Landscape Variables $(F_{3,63} = 4.713, p < 0.01, R^2 = 0.183$					
Constant	0.248	0.044	-	5.709	0
Woodkm	-0.001	0	0.788	-2.437	0.018
Deciduouskm	-0.844	0.403	0	-2.092	0.04
Deciduousp	10.482	5.059	0	2.072	0.042
Landscape Variables $(F_{1,65} = 7.891, p < 0.01, R^2 = 0.108)$ *					
Constant	0.235	0.033	-	7.084	0
Woodkm	-0.001	0	1.0	-2.809	0.007
Local Habitat Variables and Complete Model $(F_{3,65} = 9.681, p < 0.001; R^2 = 0.309)$					
Constant	0.243	0.066	-	3.688	0
Perimeter	0.032	0.012	0.984	2.566	0.013
Slope	-0.048	0.024	1.0	-2.004	0.049
Subp	0.452	0.099	0.984	4.583	0

* without outliers (N = 67) and Deciduouskm and Deciduousp

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Table A7. Stepwise multiple regression of species richness and turnover with the component loadings from the principal components analysis (N = 69).

Variable	Coefficient	Std Error	Tolerance	t	p
Species Richness ($F_{3,65}$ = 4.45, $p < 0.01$, R^2 = 0.17)					
Constant	2.128	0.031	-	69.06	0
Factor 1	-0.055	0.031	1.0	-1.763	0.083
Factor 3	0.066	0.031	1.0	2.121	0.038
Factor 7	0.074	0.031	1.0	2.397	0.019
Turnover ($F_{4,63}$ = 3.809, $p < 0.01$, R^2 = 0.195)					
Constant	0.147	0.013	-	11.383	0
Factor 1	-0.032	0.013	0.998	-2.455	0.017
Factor 2	-0.026	0.013	0.998	-1.976	0.053
Factor 3	0.02	0.013	0.996	1.546	0.127
Factor 4	-0.021	0.014	0.994	-1.580	0.119