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# Community Ecology Approaches to Amphibian Conservation

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COMMUNITY ECOLOGY APPROACHES TO AMPHIBIAN CONSERVATION

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A Thesis  
Presented to  
the Graduate School of  
Clemson University

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In Partial Fulfillment  
of the Requirements for the Degree  
Master of Science  
Wildlife and Fisheries Biology

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by  
Joanna Emily Hawley  
August 2010

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Accepted by:  
Robert F. Baldwin, Committee Chair  
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David W. Tonkyn

## ABSTRACT

Amphibian declines have been observed globally for several decades and populations continue to decline in many areas today. Through an extensive literature review of amphibian ‘impact studies,’ I evaluated the use of multiple species, multiple spatial and temporal scales in an effort to ascertain a more complete, community-wide perspective on the causes of amphibian declines as well as management and conservation implications aimed at reversing these declines. Additionally, I performed multivariate analysis of an amphibian community dataset from southern Maine, USA using a multi-species and scalar approach to identify potentially important environmental variables associated with high levels of amphibian reproductive effort. By taking a community perspective on amphibian conservation, I suggest that scientists can better assess how multiple species respond to environmental changes and how these changes affect communities at multiple levels of organization. The metacommunity framework can serve as an important starting point for assessing amphibian community dynamics across a landscape because many amphibian life histories have phases that are dependent on multiple spatial scales. Multivariate statistical techniques are useful for the analysis of community data because most ecological datasets are complex, highly-dimensional and are more often robust to the relaxed assumptions of multivariate analyses than to those of more predictive univariate methods. Multivariate techniques can aid in the initial description of the structure of community data as well as in the development of *a priori* hypotheses. By studying amphibians in their natural community context (i.e., considering their interaction with other abiotic factors) and by recognizing the potential for multiple

communities to interact across a landscape, researchers can better understand how and at what spatial and temporal scales amphibians are being impacted by environmental disturbance. My research suggests that amphibian conservation will be greatly served by community approaches because it is likely that communities as functional entities rather than individual species are better, more reliable indicators of environmental disturbance and biological stress. The utilization of a community theoretical approach coupled with multivariate analytical techniques will serve to further our knowledge of the processes contributing to amphibian declines as well as to inform us of the most optimal ways to both address and potentially reverse these declines.

## DEDICATION

This manuscript is dedicated to my remarkable grandmother, R.L. Hall who has loved and supported me through all of my various endeavors and has always encouraged me to follow my dreams.

## ACKNOWLEDGMENTS

I would like to thank Clemson University and the Department of Wildlife and Fisheries Biology as well as the Department of Forestry and Natural Resources for my funding and Research Assistantship. I am deeply grateful to Dr. Robert Baldwin, Dr. Bryan Brown and Dr. Dave Tonkyn for serving on my Masters committee and guiding me through this process. I would like to thank Dr. Amber Pitt and Amanda Hackney for their feedback, advice and encouragement. Lastly, I would like to thank Jenna Stanek for always lending a willing ear, a pair of sharp eyes and a set of helpful hands.

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## CHAPTER ONE

### AMPHIBIAN CONSERVATION AND THE METACOMMUNITY CONCEPT: A MULTI-SPECIES, MULTI-SCALE FRAMEWORK

#### INTRODUCTION

The metacommunity concept is a framework for the study of ecological communities which integrates spatial dynamics into studies of community ecology. Because of this spatial integration, the metacommunity framework possesses important implications for the study of community processes at both local and regional spatial scales. The framework holds that local communities frequently undergo extinctions that are mediated by dispersal and recolonization events from surrounding regional populations and in this sense, it expands upon the metapopulation concept (Hanski 1994). Like the metapopulation concept, the metacommunity framework relies heavily on the movement of individuals at the regional scale for long-term persistence making the theory an ideal framework for landscape-scale conservation of any given species and/or community.

While traditional community ecology has historically focused on local-scale processes (e.g., environmental habitat conditions), the metacommunity framework considers local dynamics as well as the processes occurring at the regional scale (e.g., dispersal, immigration) in structuring communities. The metacommunity framework integrates four theoretical paradigms to account for the structure of local communities: 1) patch-dynamic, 2) species-sorting, 3) mass effects and 4) neutral perspective, all of which differ in terms of the importance of local versus regional processes, including dispersal,

migration and environmental habitat conditions (Urban 2004). The patch-dynamic paradigm assumes that all habitat patches are homogeneous and that local processes dominate the structure of the metacommunity (Leibold 2004). The species-sorting model emphasizes the importance of patch heterogeneity and niche partitioning in determining dynamics of local communities within a metacommunity, where dispersal is less important to the system (Leibold 2004). The mass-effect paradigm strongly emphasizes the importance of dispersal, rather than environmental conditions, among local communities in determining metacommunity structure (Leibold 2004, Urban 2004). Finally, the neutral paradigm assumes that all species are equal in terms of competitive ability and that community structure is determined predominantly by regional processes which control the rates of species gains and losses in the local communities (Leibold 2004). By considering the effects of multiple temporal and spatial scales on community dynamics, ecologists are beginning to bridge some fundamental gaps in theory and practice which have plagued traditional community ecology (Holyoak et al. 2005).

The goal of this study was to assess to what degree the current body of amphibian ecological and conservation literature has considered the three major components of the metacommunity framework: multiple species, multiple spatial, and multiple temporal scales. Despite its relative novelty in community ecology, the metacommunity framework has proven to be a promising and informative approach for theoretical, empirical and conservation-based studies of ecological communities as defined by Davies et al. (2005) and may be beneficial to the conservation of amphibians as well as other taxonomic groups for which regional processes are believed to be of importance for persistence.

## **THE METACOMMUNITY FRAMEWORK AND AMPHIBIAN DECLINES**

Amphibians, along with many other taxa, are experiencing worldwide declines due to a number of potential environmental stressors, the greatest of which is likely physical habitat degradation (Gibbs 1999, Cushman 2006, Petranka et al. 2007, Hamer and McDonnell 2008). Habitat loss and degradation not only reduce the amount and quality of suitable habitat but also may compound the effects of other environmental stressors including disease, pollution and UV-B radiation (Blaustein and Kiesecker 2002, Boone et al. 2007). Because of the severe threat of habitat fragmentation to amphibians as well as the challenges these animals will likely face due to future habitat losses, it is vital to understand how and to what degree changes in land use and increases in urbanization affect amphibian communities. Amphibians are vulnerable to natural fluctuations due to environmental and demographic stochasticity and this variability makes amphibians even more susceptible to the amplifying effects of anthropogenic changes in land use; thus it is increasingly difficult to discern true, human-induced declines from natural oscillations (Pechmann et al. 1991, Gibbs 1999, Salvidio 2008, Todd et al. 2009). Amphibians are highly influenced by anthropogenic landscape conditions such as the presence and density of roads (Vos and Chardon 1998), levels of impervious surface cover (Simon et al. 2009), amount of agricultural activity (Gray et al. 2004) and isolation due to urban development (Parris 2006). Success at the regional scale for amphibian populations is limited by their abilities to migrate and/or disperse to suitable habitat and this task is further complicated in a fragmented landscape. Furthermore, the biphasic life cycles of many amphibians mean that they are dependent on water at some point in their life cycles

and thus may be more vulnerable to habitat loss because they require both aquatic and terrestrial habitats (Semlitsch 2000). These dual habitat requirements mean that degradation or loss of either habitat type or the connectivity between them can severely threaten amphibian populations.

Amphibians play important roles in many ecosystems in which they live, such as energy transfer through the food web, and may often constitute a significant proportion of animal biomass in forests (Burton and Likens 1975a, Hairston 1987, Wyman 1998). While current efforts have been focused on population and regions, future conservation efforts for amphibians must take into account their community interactions in both aquatic and terrestrial habitats and focus should be placed on the roles they play in these systems (Trenham and Shaffer 2005, Skidds et al. 2007). Terrestrial salamanders are the most abundant and important group of vertebrates in many temperate forests and they may also help to regulate the forest decomposer community (Burton and Likens 1975a). Some salamanders in particular may play a critical role in many forest ecosystems because they serve as prey for a number of other taxa (e.g., small mammals, birds, reptiles, macroinvertebrates) and also as predators of the macroinvertebrate and algal community, which in turn helps regulate community diversity of aquatic insects and plants (Wyman 1998). It has been demonstrated that amphibians are important contributors to ecosystem biomass and biodiversity and may be responsible for a significant amount of the energy transfer between aquatic and terrestrial ecosystems (Burton and Likens 1975b). Because of the important roles many amphibians play with regard to trophic and other interspecific interactions, they may exert strong influences in

both directions of the food web. Thus, their decline or extirpation has the potential to greatly threaten ecosystem dynamics and lead to alterations in trophic interactions and predator-prey dynamics.

The alarming rates of amphibian declines as well as global development, industrialization and urbanization have led to many ecological impact studies, in which species' responses to anthropogenic environmental changes are quantified and analyzed for the purposes of conservation and management (Petranka et al. 1993, Rothermel and Luhring 2005, Rittenhouse and Semlitsch 2007). These studies are relevant to amphibian conservation because they often consider human activity as a variable to potentially explain species distributions. Additionally, many studies have also recognized the importance of including multiple spatial scales. Much of this work has emerged from traditional and foundational ecological life history studies which aim to understand the ecosystem through the study of a single organism. In many ways, this organismal approach is somewhat broad because it entails studying the natural history and ecology of one species in great detail in order to extrapolate conclusions regarding the entire ecosystem. Therefore, many organismal studies focus on one or a few species of the same taxonomic group, often across a localized geographic area (local site or landscape level) over one or a few seasons. While this limited scope is also influenced by financial, time and biogeographical constraints, it is likely that realistic and effective solutions to amphibian declines need to take into account the responses of multiple species from several taxonomic groups over greater periods of time and space. Future amphibian conservation studies may benefit from further consideration of these important

dimensions: multiple species, temporal and spatial scales and that future studies should ascend the hierarchical chain of organization and examine the structure and function of the organism as seen from a community perspective.

The metacommunity framework has not been thoroughly discussed in the context of amphibian conservation yet offers a spatial and temporal framework for addressing many of the related issues. This framework provides key opportunities to examine the extremely understudied area of interactions between community biology and changing landscape structures (vanNouhuys and Hanski 2005), which may be of critical importance to amphibians. In the face of continued urbanization and changes in land use, successful conservation of ecological systems will likely require the examination of multiple species' responses to anthropogenic disturbance over multiple spatial and temporal scales (Forman and Godron 1981, Turner et al. 1989). Previous studies have revealed that amphibians are sensitive to processes occurring at different spatial scales, therefore, data collection over multiple spatial and, if possible, temporal scales is critical for understanding these effects (Ernst and Rodel 2005, Todd et al. 2009).

## **PREVIOUS WORK ON AMPHIBIAN COMMUNITIES AND THEIR DECLINES**

The past several decades of amphibian research have revealed widespread declines in amphibian populations across the globe. These observed decreases led to much research to elucidate the environmental causes contributing to declines. The past two decades of impact studies provided invaluable information regarding the effects of clearcutting and forest/canopy removal (Petranka et al. 1993, deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002, Perkins and Hunter 2006, Todd and Rothermel



2006), loss or modification of breeding and/or terrestrial habitat (Semlitsch and Bodie 1998, Gibbs 1999, Homan et al. 2004, Babbitt 2005, Cushman 2006, Gallant et al. 2007), road density and associated mortality (Findlay and Houlihan 1997, Vos and Chardon 1998, Findlay and Bourdages 2000, Carr and Fahrig 2001, Glista et al. 2008), increases in UV radiation (Blaustein et al. 1997, Blaustein and Kiesecker 2002) and environmental pollutants resulting from human activity (Kolozsvary and Swihart 1999, Guerry and Hunter 2002, Porej et al. 2004, Gray and Smith 2005, Mazerolle and Vos 2006). Many of the aforementioned works are life history and habitat selection studies which take an organismal approach. Clearly these studies have furthered our knowledge of how many amphibian species are affected by the numerous changes associated with anthropogenic activity. Furthermore, these studies have recognized that humans act as potential drivers of amphibian distributions. However, many of these studies have also demonstrated that different species may interact with and respond to the same environment in different ways and thus it is important to take a community-wide approach and develop strategies which will benefit the maximum number of species.

Studies which consider the potential for amphibian populations to be part of a larger, regional metapopulation have taken an important step towards understanding the effects of human activity and fragmentation at multiple spatial scales. These studies have shifted the focus from single habitat patches to multiple patches across a landscape interacting through the exchange of individuals. Because the metapopulation framework deals directly with both spatial arrangement and connectivity of ponds and allows empirical evaluation of the relative importance of each, these studies are highly

significant and important in the context of global declines and have built the foundation for the next step in amphibian research, which is the examination of multiple interacting communities across a landscape (Marsh and Trenham 2001). While there is no shortage of controversy as to whether all amphibians exhibit metapopulation structure, it may be beneficial to assume they do until proven otherwise (R. Semlitsch, pers. comm.). The risk of failing to recognize metapopulation structure where it truly exists is likely much greater than erroneously assuming it. Failure to recognize metapopulation structure could lead to losses of source habitats, inhibition of movement between breeding and terrestrial habitat or leave large habitat patches totally isolated from the rest of the metapopulation, all of which may have dramatic consequences for long-term persistence.

### **AMPHIBIAN SPATIAL DYNAMICS AND THE METACOMMUNITY FRAMEWORK**

The influences of different spatial scales on different species' responses likely means that population dynamics change as spatial scale changes (Law and Amarasekare 2005). Some amphibians are typically considered to be small-bodied and relatively slow-moving, while other species (e.g., Anurans) have demonstrated astounding movement capabilities (Semlitsch and Bodie 2003, Smith and Green 2005), meaning that movement between patches is variable and dependent on the species of interest. Amphibians offer two reasonable ways in which to empirically study the metacommunity concept by examining 1) environmental heterogeneity between patches and 2) amount of interpatch movement (Cottenie and DeMeester 2005). Most amphibians are dependent on at least two different habitat types to complete their life cycle: habitats patches that are distinct

from the background habitat matrix (streams and wetlands) and those that exist with unclear boundaries (terrestrial habitats). In some cases, these habitats are segregated by life history needs as in “breeding versus non-breeding habitats” for pond-obligate amphibians; in other cases (e.g., some stream salamanders), the differences are not as clear. Because of the distinct life history stages, it is important to examine both aquatic and terrestrial population dynamics and the relative importance of each in determining if metacommunity structure applies (Smith and Green 2005, Berven 2009). Furthermore, it is not unreasonable to think that amphibian communities may exhibit metacommunity dynamics at different stages of their life cycles and these distinct life history stages as well as the biotic and abiotic requirements that accompany them may be used to empirically test assumptions of the metacommunity framework. This research endeavor is not without its challenges as it is not a simple task to incorporate multiple types of habitat and inevitably the connectivity between them. However, in order to make further progress towards amphibian conservation, researchers need to understand amphibian community dynamics in the context of the different spatial and temporal scales at which amphibians respond to as well as the other species with which they interact. These multiple considerations will serve to provide both ecologists and conservation biologists with a more complete picture of how, why and at what scales amphibians are declining as well as how to ameliorate these declines.

While the best paradigm for many communities will likely involve a synthesis of several of the metacommunity conceptual models (patch dynamic, mass effects, species-sorting and neutral), pond obligate amphibians may exhibit dynamics of species-sorting

and mass effects, both of which offer sound paradigms to begin research under (Cottenie and DeMeester 2005). Species-sorting describes a system in which dispersal is somewhat restricted (although not absent) and local community dynamics prevail in structuring the community whereas mass effects are presumed when dispersal is high and spatial dynamics are increasingly important to the community structure of the system (Medley and Havel 2007). It is possible that many amphibian communities lie somewhere in the middle of this continuum in terms of community-structuring dynamics and exhibit aspects of multiple paradigms (Mouquet and Loreau 2003). It has been shown that dispersal events, particularly juvenile dispersal, are critical for persistence of local populations through rescue effects and establishment of breeding populations at unoccupied sites (deMaynadier and Hunter 1999, Johnson and Semlitsch 2003). Species-sorting may be a realistic paradigm for amphibians because it is likely that local conditions are highly influential given amphibians' generally-limited dispersal capabilities (but see Berven 2009). For example, Werner et al. (2007) demonstrated that abiotic variables explained a significantly greater amount of variation in amphibian turnover than did biotic variables with the exception of fish. This and other studies have revealed the importance of variation of local habitat conditions in explaining species occurrences (Fahrig et al. 1995, Hodgkison et al. 2007, Werner et al. 2007). Conversely, some studies have shown that abiotic habitat variables explain relatively little variation and have inferred that dynamic population processes such as competition may play a larger role in structuring communities than previously thought (Schmidt and Pellet 2005). Other work has shown some amphibians respond to coarse-scale, landscape habitat

variation during migration and fine-scale, local variation following cessation of movement, meaning that the influential spatial scale may also depend upon the life history stage (Patrick et al. 2008). However, because levels of habitat fragmentation and anthropogenic disturbance are projected to increase well into the future (Brown et al. 2005), it is likely that both local and regional habitat conditions will be the primary determinants of amphibian community dynamics.

Gene flow is known to occur among local populations of amphibians, although it may not be a prevailing dynamic in all systems due to generally low rates of dispersal and high site fidelity (Johnson and Semlitsch 2003, Hamer et al. 2008). For example, in floodplain pond systems which experience fairly regular connection to large bodies of water via flood events, dispersal may be much more regular and thus have a greater influence on community structure of individual ponds (Cottenie and De Meester 2004). These flood-mediated dispersal events have been demonstrated to contribute to community structure of zooplankton and fish, both of which exhibit limited dispersal, in floodplain ponds in Missouri (Medley and Havel 2007). Additionally, juvenile dispersal generally spans greater distances than do typical adult movements (Berven and Grudzien 1990). It is difficult to quantify true maximum migration and dispersal distances because of biases in experimental design which may underestimate organisms' movement capacity (Semlitsch and Bodie 2003, Smith and Green 2005, Baldwin et al. 2006a). However, the importance of dispersal to long-term success of local populations through recruitment and recolonization and the ways in which amphibian movement may be compromised by changes in landscape permeability cannot be overstated.

When determining if metacommunity dynamics apply to a system, the often-ephemeral breeding ponds used by many amphibians pose interesting and complicating challenges because of high variation in flood regime through space and time (Medley and Havel 2007). However, freshwater pond systems are useful for studying metacommunity dynamics because they can be considered as distinct habitat patches and potentially host very different species assemblages with different levels of synchrony because of variation in hydroperiod and other abiotic variables (Trenham et al. 2003, Cottenie and DeMeester 2005, DeMeester et al. 2005). Some amphibians with complex life cycles lend themselves well to metacommunity studies because they exist in patchy distributions of often-ephemeral wetlands during their aquatic phase (Marsh and Trenham 2001). The discrete nature of their habitat combined with both intra-specific interactions and the specificity of some amphibians and their predators (i.e., fish, aquatic insects) may lead to metacommunity dynamics in the amphibian-fish-insect assemblages (Shurin and Allen 2001). The effects of predators on diversity of amphibian assemblages can vary, depending on the direct and indirect effects on prey and other species in the community (Shurin and Allen 2001). For example, fish have been demonstrated to play a significant role in turnover rates and regional coexistence in amphibian communities and thus, likely act as part of the metacommunity assemblage (Shurin and Allen 2001, Werner et al. 2007). Fish presence has been shown to inhibit the presence of many amphibians in breeding ponds, while facilitating the survival of others (Laurila et al. 1998, Monello and Wright 1999, Leibowitz 2003). The study of amphibian communities can benefit from the

study of other taxa, particularly fish, because these members of the community can potentially exert strong forces in structuring amphibian assemblages.

Habitat fragmentation at the landscape scale also has the potential to greatly reduce amphibian movement and likely serves as a community-structuring force. Amphibian communities found in areas experiencing landscape fragmentation have an increased risk of isolation and extinction and decreased chances of recolonization events (Hanski 1999). The effects of habitat fragmentation on amphibian metacommunities may depend largely on 1) the rates of extinction and colonization a local community experiences and 2) the level of synchrony among local communities (Trenham et al. 2003). Areas with high levels of urban or agricultural activity and/or road densities have been shown to pose high risks to the movement of many amphibians (Vos and Chardon 1998, Findlay and Bourdages 2000, Carr and Fahrig 2001). Furthermore, the threat these obstacles present for juveniles may be of greater consequence from a metacommunity standpoint because juveniles are heavily relied upon by local communities for breeding recruitment and rescue effects (Semlitsch 2000).

### **LITERATURE REVIEW OF TAXONOMIC DIVERSITY, TEMPORAL AND SPATIAL SCALES**

I conducted an extensive review of the amphibian “impact study” literature to assess to what degree multiple spatial, temporal scales and taxonomic diversity have so far been represented. This review focused on amphibian research studies which were intended to explain amphibian declines and/or offer conservation and management solutions; this review included but was not limited to studies which examined the

metacommunity framework. I included peer-reviewed articles that 1) are widely-cited (>50 citations) works in the research community on the topic of amphibian communities and/or amphibian declines and 2) are published in journals with a current impact factor of three or greater. The two methods of selection, while very admittedly arbitrary values, were chosen to eliminate any time-bias towards older papers which have had longer periods of time to gain notoriety and to make sure more recent, less widely-cited papers which fit the criteria were included. I used “amphibian declines” and “amphibian communities” as search terms and included papers published from 1985-2009, using two search engines: Cambridge Scientific Abstracts and Web of Knowledge. Each selected paper was assigned three separate scores on a scale of 1-10 (Table 1) based on their inclusion of the three critical components of metacommunities in their study: 1) multi-species and/or taxonomic groups, 2) multiple spatial scales and 3) multiple temporal scales. In some cases, the scores corresponding to certain studies were awarded an extra 0.5-1.0 point in instances where the analysis considered only one species of amphibian but the presence, absence and/or interaction with other species or taxonomic groups (e.g., fish, odonate larvae) was acknowledged, though not used explicitly in the analysis. Another example would be if a study only spanned one or two years but was based on previous work in the same area or used historic data in addition to their own collected data. This “extra points” system was used to give certain studies a higher weight in the overall analysis because they took into consideration multiple taxa, years and/or spatial scales and thus should be differentiated from those that did not.



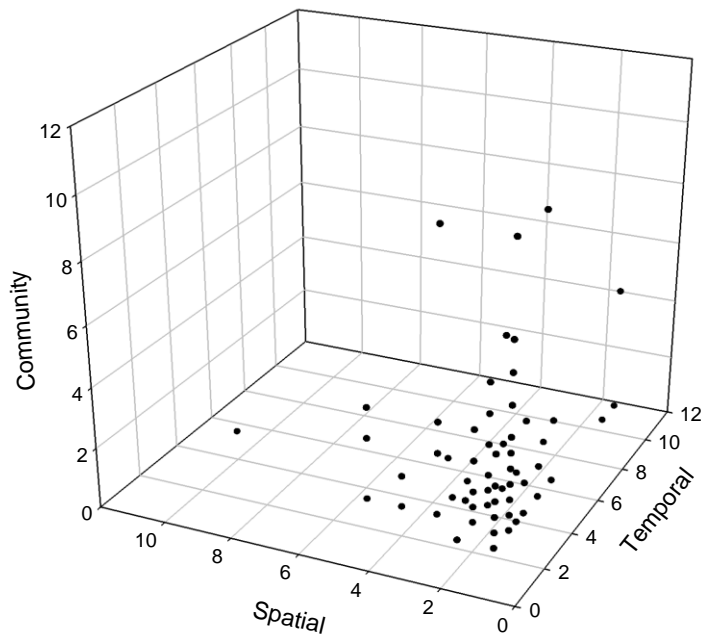
**Table 1.1.** Criteria for Triplet Score Assignment. Each paper reviewed was assigned an (x,y,z) triplet score based on its authors' inclusion of multiple species, temporal and spatial scales.

Axis Score	Years	Spatial Scales	Species
1	< 1	1	1 to 5
2	1 to 5	2	6 to 10
3	6 to 10	3	11 to 15
4	11 to 25	4	16 to 30
5	26 to 40	5	31 to 45
6	41 to 55	6	46 to 60
7	56 to 70	7	61 to 75
8	71 to 85	8	76 to 90
9	86 to 100	9	91 to 105
10	> 100	≥ 10	> 105

The set of three scores corresponding to each paper were then entered as (x,y,z) triplets and plotted to visually demonstrate the community considerations of each study along the three axes. All graphs were plotted using SigmaPlot Version 10.0 (Systat Software Inc, San Jose, CA, 2006). I did not include experiments which took place strictly in a laboratory setting. Although lab studies often score higher on the community axis for the consideration of multiple species or taxa, they very rarely encompass more than one spatial or temporal scale. This is not to discount the importance of laboratory studies and experiments rather we chose to place the focus of this review on impact studies which took place under more natural conditions. I did, however, include manipulative experiments which took place in field settings (e.g., outdoor mesocosms, in-pond exclosures) because they often include more realistic environmental variables and conditions and are more representative of natural field conditions.

## **MULTIPLE DIMENSIONS IN AMPHIBIAN RESEARCH**

This exercise resulted in a total of 244 papers which met the specific search criteria (Appendix A). Few studies have maximized all three axes in attempting to explain what factors influence amphibian communities and/or contribute to their declines (Figure 1.1). In particular, the majority of studies do not examine more than one or two spatial scales which may be especially detrimental to amphibian conservation because a number of amphibians are known to be influenced by different variables at different scales (Gibbs et al. 2005, Garner et al. 2007, Patrick et al. 2008). While several amphibian studies encompass a very large number of species (maximum = 132 species), the majority of studies (67.62 %) focus on fewer than five species. Natural biogeographical variation among regions may account for limited taxonomic focus; i.e., some areas of the world have naturally high levels of amphibian diversity (e.g., Brazil, 765 amphibian species) while others do not (e.g., Europe, 143 herpetofaunal species), (Duellman 1999, Araujo et al. 2007)



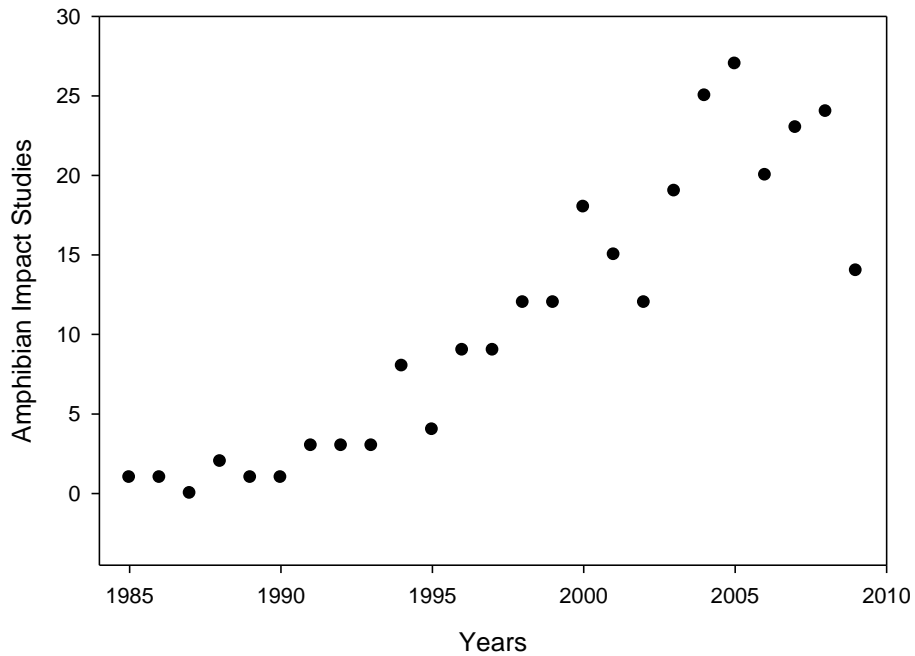
**Figure 1.1** Triplet Scores for Amphibian Impact Studies. Each study (N=244) was assigned a triplet score and plotted based on its inclusion of multiple species, multiple temporal and multiple spatial scales. Many studies do not maximize at least one axis, particularly spatial scale (mean =  $1.6 \pm 1.88$  scales), while the community (mean =  $7.8 \pm 16.3$  species) and temporal (mean =  $6.1 \pm 15.2$  years)

The fact that many studies did not examine a full complement of species over a long period of time across multiple spatial scales is likely due to practical constraints that simply do not allow all three dimensions to be equally and simultaneously incorporated. Many studies exhibit a trade-off between the three dimensions; that is, studies which focus on a single species or a single site are often balanced by long-term temporal considerations or vice versa. For example, Berven (2009) carried out a study spanning multiple spatial scales over a period of twenty one years on a single wood frog population in Michigan. Even studies which span long time periods are still subject to logistical difficulties that may require the study to focus on one or a few species, although one

notable exception comes from a fifteen-year study of sixteen amphibian species at a single Carolina Bay (Semlitsch et al. 1996). Conversely, other studies have been successful at incorporating many species while only covering one temporal and/or spatial scale (Vallan 2000, Johnson et al. 2002, Lips et al. 2004, Brooks et al. 2006, Barrett and Guyer 2008). For example, laboratory studies typically scored low on both the spatial and temporal axis but high on the community axis. This is likely because the study of actual community interactions in the larval/aquatic stage are best performed in controlled experiments and often do not run for more than one year or season. Thus the nature of laboratory studies necessitates that they fall on the lower end of both the temporal and spatial axes. However, laboratory experiments are highly useful for elucidating cause and effect relationships as well as understanding the mechanisms of competitive interactions within and among species (Relyea and Mills 2001, Blaustein et al. 2005, Relyea et al. 2005, Forson and Storfer 2006, Hoverman and Relyea 2008). While these limitations are practical, given the time, financial and biogeographical constraints of most scientific studies, there is a need for projects which consider communities as functional entities across multiple units of time and space rather than as disjunct groups of organisms which respond independently to disturbance or environmental changes. This highlights the importance of incorporating multiple study designs into amphibian conservation projects when possible (Diamond 1986). The utilization of different methods of observation (e.g., field, laboratory, manipulative experiments) under a unifying question related to amphibian conservation will likely encompass multiple species, temporal and spatial scales.

The wide range of temporal scales, particularly noticeable in the recent literature (discussed below), may reflect the scientific recognition that short-term, “snapshot” studies often do not always accurately reveal the condition of amphibian populations (Pechmann et al. 1991). I recognize that the time constraints associated with degree programs and funding cycles may contribute to the prevalence of short-term research studies. It is possible that the pressure to “publish or perish” encourages scientists to employ fairly rapid ecological studies which can be carried out in a reasonable amount of time in order to publish frequently (Cassey and Blackburn 2006, Pile 2009). Furthermore, the availability of funding for purely observational/exploratory research is limited and many ecological studies are funded in order to meet certain policy goals which are focused on a limited number of species and/or time frame (Lindenmayer et al. 2007).

The number of amphibian studies published per year increased markedly over the study period (Figure 1.2). We consider studies published from 2000 to the present “recent” from here onward and those from 1985-1999 “older” studies. Figure 2 clearly demonstrates a major increase in research interest on amphibian declines and/or communities from 2000 onward. Field work in recent studies spanned an average of 6.7 ( $\pm 17.5$ ) years while older studies spanned an average of 3.2 ( $\pm 5$ ) years. Because the data were often strongly skewed, non-parametric Wilcoxon Rank-sum tests were performed using recent vs. older studies to determine if there were significant differences between numbers of species, spatial and temporal scales.



**Figure 1.2** Number of Amphibian Impact Studies, 1985-2009. Number of studies which met the criteria published between 1985 and 2009 plotted against years.

I found evidence to suggest that recent studies did span significantly greater time lengths than older studies (*Wilcoxon test,  $p = 0.041$* ). This may be influenced by the fact that in many cases, only more recent publications have been able to report the findings of long-term studies begun years or even decades before. Additionally, recent studies used significantly greater numbers of spatial scales when compared to older studies (*Wilcoxon test,  $p = 0.01$* ). I did not find evidence, however, to suggest that there were significant differences between recent vs. older studies in terms of numbers of species used (*Wilcoxon test,  $p = 0.1478$* ). The increases in spatial and temporal scales employed by more recent studies may be a reflection of the conclusions of more recent amphibian studies, which have emphasized the highly fluctuating nature of amphibian populations

and the fact that they may be affected by different environmental factors at different spatial scales. Additionally, this trend may reflect the increased funding and interest for amphibian research as a result of reported global declines.

### **LIMITATIONS FOR TESTING THE METACOMMUNITY FRAMEWORK**

Although the metacommunity framework shows much promise for future research and conservation of amphibian communities, there are limitations associated with empirically testing its assumptions in the field. Logistically, studying a group of communities composed of many species interacting at the landscape scale may require large spatial scales as well as large amounts of money, man-power and time, depending on the organisms of study (vanNouhuys and Hanski 2005). Because of these logistical constraints, researchers are often unable to study a large number of habitat patches in sufficient taxonomic detail to determine if metacommunity dynamics apply to a system. The primary problem is balancing sampling intensity and number of sites a researcher is able to sample for inclusion in a study. Furthermore, most community studies carried out at great spatial scales only assess presence/absence or relative abundance of multiple species and infer rather than test for community dynamics. Thus, many studies which incorporate multi-species interactions must take place in laboratory settings and therefore their conclusions are suggestive as to what interactions *could* occur in the natural environment rather than what *does* occur.

The predominant empirical challenges encountered in metacommunity studies are 1) the lack of definite boundaries between some local communities 2) the fact that different species may respond to processes at different spatial scales and 3) the difficulty

of identifying parameters that can be measured in the field to test for metacommunity dynamics (Mouquet and Loreau 2003, Holyoak and Holt 2005). These challenges are of particular significance to the study of many amphibians because different species' vagilities lead to different perceived habitat boundaries for each species as well as different responses at various spatial scales to community processes. Furthermore, empirical testing of metacommunity assumptions is challenging because of the inherent difficulties associated with quantification of dispersal, colonization and extinction rates for not only one but multiple local communities. In order to quantify these processes, studies which span multiple seasons and/or generations are needed before a researcher can determine if metacommunity dynamics apply to a system.

Parris (2006) was able to circumvent the problem of quantifying dispersal empirically by testing for other general patterns that would be expected if metacommunity dynamics were exhibited in a system. This and other similar methods may be the most practical avenue for studying metacommunity dynamics without a long-term data source. Because of the logistical problems associated with long-term studies and lack of historical data, the metacommunity framework has yet to be rigorously tested in the field and lacks extensive empirical validation (Mouquet and Loreau 2003, Davies et al. 2005). Currently, the metacommunity framework has not yet been established as valid for understanding community dynamics of urban faunal assemblages (Parris 2006). This is likely due to the logistical difficulties associated with testing the assumptions of the metacommunity concept and the fact that urban faunal assemblages are often highly-fragmented and often confined to small geographic areas. A more complete theoretical



and empirical solidification of metacommunity theory will be limited by tradeoffs between feasible analytical methods and realistic biological complexity (Urban and Skelly 2006).

Historical data, or some other type of verified mechanism, are needed in to differentiate between temporal variability of amphibian populations and true, long-term declines which are of special interest to conservationists (Werner et al. 2007). Unfortunately, long-term historical data are typically unavailable for amphibians in North America and many other countries, likely due to biases in historical records towards larger, commercially-important or more visible species (e.g., mammals, birds, trees). Furthermore, the lack of long-term amphibian data begs for increased public education in order to bring about a more widespread and general interest in amphibians and their declines. To achieve this goal in part, the North American Amphibian Monitoring Program (NAAMP) has supported long-term amphibian monitoring projects since 1995 and emphasizes volunteer-based surveys. These volunteer-based surveys serve to both collect long-term data and to improve public knowledge and awareness regarding amphibian declines in North America (Nelson & Graves 2004). Additionally, Partners in Amphibian and Reptile Conservation (PARC) is an organization which seeks to promote herpetofaunal conservation of both endangered and common species through federal, state and local partnerships with citizens, professionals and organizations. Furthermore, certain areas of the U.S. (e.g. New England, the Southeast) have demonstrated major, regional interest in sustaining amphibian communities by dedicating time, and energy for the greater good of amphibian conservation.

## **IMPORTANCE OF THE METACOMMUNITY FRAMEWORK**

Consideration of metacommunity dynamics will be useful for conservation efforts of amphibians and other species for several reasons. In the face of dramatic habitat loss and alteration due to human activity, scientists need to recognize and conserve those habitat patches which serve as potential multi-species sources for the surrounding communities. Because the metacommunity framework integrates spatial dynamics into the study of ecological communities, it highlights the importance of dispersal and rescue effects for long-term community persistence, particularly for spatially-disjunct groups of organisms. Finally, the metacommunity framework is unique in that it allows as many species to be incorporated as are relevant in the particular ecosystem; that is, the application of the metacommunity concept is not limited to amphibians alone and can be extended to look at the structure and function of entire aquatic or terrestrial communities composed of many taxonomic groups.

Fragmentation is one of the most important reasons why conservation studies are improved by the integration of spatial dynamics into the study of ecological communities. Only by considering multiple spatial and temporal scales in the study of amphibians can we discover at what level of fragmentation or disturbance species' persistence is negatively affected (Vos and Chardon 1998, Jeffries 2008). Without the explicit consideration of space in conservation studies, researchers have no way to assess how much fragmentation amphibians can sustain before their populations begin to suffer (Homan et al. 2004). Because of the importance of spatial dynamics in ecological studies, the metacommunity framework may be exceedingly useful for conservation purposes as

well as for understanding factors contributing to long-term persistence of communities in dynamic and fragmented environments (Werner et al. 2007).

It has been suggested that traditional ecological theory, which tends to focus on local processes, may not be adequate to fully understand the consequences of urbanization on amphibians and the metacommunity concept may be a better framework to realize this goal (Parris 2006). One reason for this is because traditional ecological theory poorly explains dynamics of urban assemblages (Collins et al. 2000, Hepinstall et al. 2008). Much of traditional community ecology has intentionally excluded the presence and influence of humans despite overwhelming evidence of the degree of human influence on natural systems (Sanderson et al. 2002). Human-dominated areas are novel environments for many species and their study requires the inclusion of humans and their effects on the landscape. The growth of urban and exurban areas is the newest and likely the most rapid form of landscape alteration occurring in the last century; between 1950-2000 the percentages of urban, exurban and other human-maintained areas more than doubled in the coterminous United States (Brown et al. 2005). Urban development is an entirely unique form of disturbance in that humans are able to rapidly alter environmental conditions and fragment habitats for reasons largely independent of our biological requirements; that is, human-induced landscape alteration in urban environments involves a variety of political, institutional and economic interests which are totally separate from our biological requirements for survival (Collins et al. 2000, Polasky et al. 2005, Hepinstall et al. 2008). Additionally, urbanization is a unique form of disturbance in that it is often permanent and irreversible. In the past decade, researchers

have begun to document the effects of urban and exurban land uses and consequent habitat degradation on the surrounding and/or displaced wildlife, particularly for avian species (Vierling 2000, Bautista et al. 2004, Hansen et al. 2005, Horn et al. 2005, Lenth et al. 2006, Partecke et al. 2006, Loss et al. 2009, Nemeth and Brumm 2009). Many studies have shown wildlife to be negatively affected by urbanization from individual levels (Relyea 2005, Partecke et al. 2006) to population and community levels (Gibbs et al. 2005, Horn et al. 2005, Lloyd et al. 2005). While there are many challenges associated with integrating humans into wildlife and conservation biology, it will benefit these fields to consider humans and their impacts on ecosystems as potential explanatory variables rather than sources of unexplained variation.

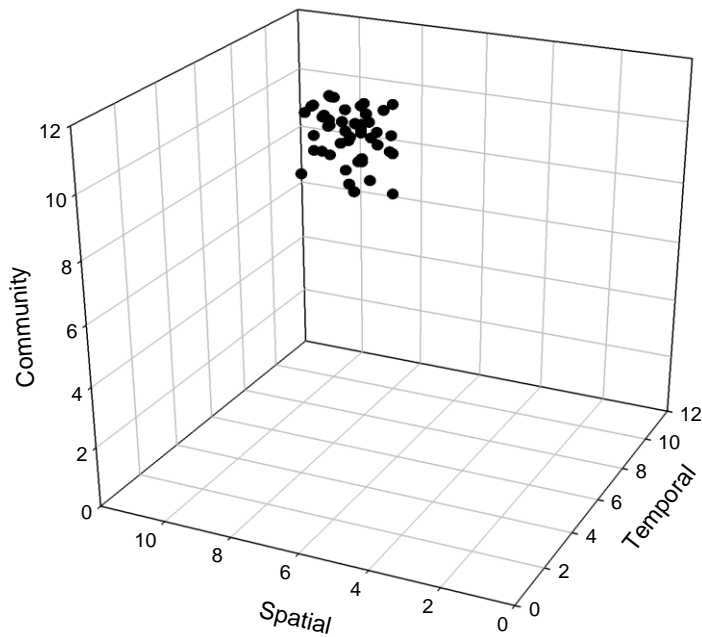
Maintaining regional biodiversity will likely require conserving entire complexes of ponds with a diverse array of hydroperiod and disturbance regimes over a large spatial scale so that different species with varying habitat preferences are considered (Semlitsch 2000, Snodgrass et al. 2000, DeMeester et al. 2005). Heterogeneity of habitat quality can actually increase regional biodiversity because heterogeneity increases the potential for persistent communities by creating refuges and habitat patches of different quality (Hoopes et al. 2005). Therefore, the metacommunity framework may allow both regional biodiversity and economic interests to coincide because the conservation of large, homogeneous tracts of undisturbed habitat may not necessarily be the best way to conserve regional biodiversity. Recent work has demonstrated that conserving clusters of ponds may be more effective at promoting both local species richness and regional diversity than single, larger ponds and complexes (Compton et al. 2007, Gamble et al.

2007, Jeffries 2008). In this way, ponds which occur in patchy distributions and the communities which inhabit them may be better indicators of environmental stress and ecosystem health than single focal areas which may not account for natural spatial variation in addition to differences in scale and intensity of disturbances. Furthermore, different amphibians have different successional preferences and not all species are able to persist in mature forest habitats or ponds with intermediate or long hydroperiods. For example, American toads (*Bufo Americanus*) and Leopard frogs (*Rana pipiens*) are known to persist in open and/or frequently-disturbed areas (Guerry and Hunter 2002). North American bullfrogs (*Rana catesbeiana*) may also persist in urbanized areas because they appear to be relatively unaffected by many environmental stressors associated with human activity (Gahl et al. 2009), and benefit from conversion of natural, temporary wetlands to permanently-inundated pools (Kupferberg 1997, Kiesecker and Skelly 2001).

The natural vulnerability of amphibians to stochastic events is magnified by losses of connectivity between habitats which often leads to hampered dispersal and migration processes. Anthropogenic barriers can affect dispersal dynamics either negatively or positively depending on pre-disturbance rates of movement and species characteristics (Rothermel and Semlitsch 2002, Mouquet and Loreau 2003). Regardless of how habitat conditions change, if connectivity between habitats is not maintained, urban amphibian communities may be drifting towards isolation and eventual extinction.

## CONCLUSION

The value of the metacommunity framework comes from the conservational and ecological benefits it offers to the fields of community ecology and conservation biology. Because testing for metacommunity dynamics in ecological systems necessitates the collection of data on population distributions and processes at multiple spatial and temporal scales, it is well suited for amphibian community and conservation studies. The value of spatial dynamics in metacommunity ecology serves to further highlight the importance of habitat connectivity (Gibbs 1993, Mouquet and Loreau 2003), which may be the most significant aspect of amphibian conservation biology in the future. By considering the dynamics and responses of multiple species or taxonomic groups, this framework allows researchers and managers to use a community approach in order to draw more realistic conclusions about the best ways to conserve habitat and connectivity among habitats in order to benefit as many organisms and their ecological functions, as possible. I suggest that the ideal form of amphibian conservation studies should maximize all three axes of consideration (Figure 1.3).



**Figure 1.3** Optimal Amphibian Impact Studies. Ideal representation of studies which maximize all three axes of the metacommunity framework by including multiple species, multiple temporal and spatial scales.

Although metacommunity dynamics may not strictly apply to all systems of interest, its principles can still be widely-applied to the conservation of many different communities and ecosystems. However, I acknowledge that it is rarely possible to maximize community, spatial and temporal axes simultaneously. Achieving the goal of reversal of species declines will likely involve accepting the fundamental truth that nature is a complicated web of multiple, dependent, interacting communities throughout space *and* time and applying this truth properly in the field, the laboratory and in management decisions will enable the ecological community to make great progress towards achieving this goal.

## CHAPTER TWO

### USING EGG MASS COUNTS TO PREDICT AND IDENTIFY ENVIRONMENTAL VARIATES OF HIGH REPRODUCTIVE EFFORT, MAINE, USA

#### INTRODUCTION

Amphibians are undergoing global declines due to interacting environmental stressors including climate change (Puschendorf et al. 2008, D'Amen and Bombi 2009, Rodenhouse et al. 2009), chemical contamination (Relyea and Diecks 2008, Jones et al. 2009, Relyea 2009), disease and pathogens (Murray et al. 2009, Voyles et al. 2009), invasive species (Brown et al. 2006, Cruz et al. 2008, Maerz et al. 2009) and commercial exploitation (Semlitsch 2000, Stuart et al. 2004, Wilson 2005, Lau et al. 2008). While the magnitude and interactive effects of such stressors remain unclear, the most salient mechanism contributing to amphibian declines is physical habitat loss and degradation associated with anthropogenic activity (Semlitsch 2000, Warren and Buttner 2008, Semlitsch et al. 2009).

Many amphibians have complex life cycles (CLC), requiring the use of both aquatic habitat for breeding and larval phases and terrestrial habitat for dispersal, foraging, overwintering and migration. Because of these habitat and movement requirements, CLC amphibians are even more vulnerable to habitat loss and fragmentation at multiple spatial scales (deMaynadier and Hunter 1999, Gamble et al. 2007, Baldwin and deMaynadier 2009, Greenwald et al. 2009). Therefore, the degradation of either their terrestrial or breeding habitat or the connectivity between them will likely compromise their population persistence (Semlitsch and Bodie 1998, Gibbs 1999, Blihovde 2006, Todd et al. 2009). In North America, a large number of CLC



amphibian species preferentially breed in seasonal wetlands. These temporary and often fishless ponds are likely optimal breeding habitat for CLC amphibians because of their ephemeral nature which inhibits the establishment of predators (Wellborn et al. 1996, Leibowitz 2003, Babbitt 2005). Small, ephemeral wetlands are particularly important to amphibian populations because they are often found in complex spatial configurations across the landscape and typically host high levels of species diversity (Semlitsch and Bodie 1998, Gibbs 1999, Semlitsch 2000, Leibowitz 2003, Babbitt 2005). The spatial configuration is critical to groups of amphibians exhibiting metapopulation dynamics because population persistence depends heavily on juvenile dispersal and recruitment processes as well as rescue effects (Semlitsch and Bodie 1998, Gibbs 1999, Monello and Wright 1999). Because of their small size, ephemeral nature and patchy configuration, these pools remain severely under-protected by most state and federal regulations and are essentially being lost at an unknown rate (Gibbs 1999, Calhoun et al. 2003, Leibowitz 2003, Babbitt 2005). While protection of vernal pools is critical to conservation of pond-breeding amphibians, it is vital to couple this effort with conservation of surrounding terrestrial uplands in order to protect multiple spatial scales of habitats upon which amphibians rely (Marsh and Trenham 2001, Porej et al. 2004, Berven 2009).

A large number of studies have sought to characterize the relationship between amphibians and their aquatic and terrestrial environments in order to better understand amphibian distributions and how terrestrial areas adjacent to breeding habitat function to sustain populations (reviewed in Semlitsch and Bodie 2003, Cushman 2006, Hamer and McDonnell 2008). Researchers often utilize known distributions, classic regression

methods and model selection techniques to reveal structure and relationships among environmental variables which determine species distributions (Porej et al. 2004, Babbitt 2005, Baldwin et al. 2006b, Skidds et al. 2007). These methods are advantageous for many reasons, particularly in terms of conservation and land management decisions because they simplify complex relationships and potentially allow for a certain level of predictability regarding amphibian distributions.

Because parsimony is critical for information theoretic approaches to model selection, the number of potential explanatory variables is often reduced *a priori* by the investigator to only what is deemed biologically relevant. Despite widespread use in ecology, this emphasis and validation of parsimony as critical to the selection process is questioned by some (Guthery et al. 2005, Wittingham et al. 2006). In almost all cases, the model with the fewest parameters and assumptions (i.e., the least amount of information explaining the greatest amount of variation) is awarded the greatest weight (Burnham and Anderson 2004, Wittingham et al. 2006). These techniques attempt to eliminate spurious results due to data-dredging because the researcher reduces the number of variables *a priori*; therefore it is reasonable to expect that the resulting conclusions may unintentionally overlook fine-scale sources of variation in the data. Moreover, if the system under study is not well-understood or well-studied, it may be difficult to put forth preconceived notions of what is ecologically important to the system (Eberhardt 2003).

While the utility of regression and model selection in ecology is well-understood, it is possible that these methods may be complemented by a number of multivariate techniques. Multivariate analyses seek to study the joint relationships of variables

simultaneously and reveal relationships and patterns in large community data sets (Gauch 1982, James and McCulloch 1990). Because large sets of ecological data are often more robust to multivariate assumptions and restrictions than those of univariate techniques (as defined by Sokal and Rohlf 1994), multivariate analyses may expand upon those conclusions reached by univariate analytical methods. While the limitations of multivariate techniques are well-established (reviewed in James and McCulloch 1990), particularly their descriptive rather than predictive nature, they are an important first step to describing and analyzing community structure and may offer important opportunities to improve and further develop our knowledge of the ecosystems and habitats we study (Guthery et al. 2005). Although most multivariate methods are considered descriptive and exploratory, good knowledge of their functions and appropriate uses are not only beneficial but may be essential in order to gain a full understanding of ecological entities under study (James and McCulloch 1990). In many cases, the use of multivariate statistics allows the researcher to analyze ecological data with minimal reduction of information. Thus for analyses of rich and highly-dimensional datasets, multivariate statistics offer a set of alternative methods for examining the relationship between a species and its environment which may be complementary and informative to traditional model selection methods.

The goal of this study was to identify environmental variables which characterized areas with high amphibian breeding effort in a mostly forested landscape in central New England. By utilizing a multivariate analytical method, we examined the interactions between amphibian breeding efforts and a broad range of environmental

conditions. Using an unconventional method of matrix assignment, our species distributions served as predictors of suitable environmental variables which, in turn, contributed to optimal breeding effort of CLC amphibians. This approach was employed to explain the distributions of amphibian reproductive effort in relation to a large dataset of environmental variables describing pond, forest and landscape structure and composition at multiple spatial scales. This is the same dataset previously analyzed using negative binomial regression and model selection (Baldwin et al. 2006b), therefore a secondary goal was to understand how multivariate techniques may reveal more information than univariate analyses. Because we used habitat composition and structure as the dependent variable, issues with multicollinearity were avoided and no initial reduction of the data was necessary. We are not currently aware of any other ecological study which has employed this variant of a multivariate statistical analysis.

## **METHODS**

### *Study Area and Data Set*

Data was collected according to Baldwin et al. (2006b) in a mostly-forested landscape in three townships of southern Maine, USA. This region has a high density of vernal pools, (~ 516 pools/ 5751 ha) which provide critical breeding habitat for a number of amphibian species (Calhoun et al. 2003). Similar to many other forested areas in the northeast, this part of Maine is undergoing high rates of development often coupled with habitat loss and/or fragmentation and may pose a serious threat to many resident amphibian populations (Baldwin and deMaynadier 2009). The two focal species for this study, the wood frog (*Rana sylvatica*, LeConte, 1825) and the spotted salamander

(*Ambystoma maculatum*, Shaw, 1802), have broad ranges throughout eastern North America and are generally representative of many CLC amphibians in their habitat and life cycle requirements (Madison 1997). Environmental variables used in the original analysis were collected at three spatial scales: within-pool, local (within 150 m of the pool) and landscape-scale (within 500 m of the pool) at a total of 87 randomly-selected ephemeral pools. Adjacent forested areas were subdivided into three to nine forest plots per pool, depending on the area of upland forest (total number of plots = 310). Egg masses of both species were counted over two consecutive breeding seasons in order to obtain an index of amphibian breeding effort. Because many CLC amphibians exhibit high levels of philopatry, reproductive output (i.e., egg masses) can be considered a measure of success in that populations were able to return and successfully oviposit in the same areas for consecutive years (Baldwin et al. 2006b). The purpose of this study was to explore how two species of CLC amphibians respond to both small and large-scale variation within their terrestrial and aquatic habitats at multiple spatial scales (Baldwin et al. 2006a).

Baldwin et al. (2006b) reduced forest composition data using a principal components analysis and then input the scores of the first two principal components into a multiple regression analysis. The egg count data were fit using a negative binomial distribution which is appropriate for ecological data because it allows for modal values of zero and overdispersion in the data (White and Bennetts 1996). The egg count data were then used as the response variable in the regression analyses and model weighting and selection were performed using AIC.

In contrast to Baldwin et al. (2006), I performed a multivariate regression technique, inverting the response and predictor matrices, and then compared these findings to the original results which were generated using multiple regression and model selection based on Akaike's Information Criterion (AIC). By using the same dataset analyzed by Baldwin et al. (2006b) in the current study, I hope to directly compare the results and explore the advantages and disadvantages of each analytical method. I hypothesized that the use of a multivariate technique would reveal additional complexity of environmental influences that were potentially overlooked by the original regression analysis.

#### *Current Analysis*

In order to keep the conclusions of the current analysis comparable with those from the original analysis, I did not add or subtract any information from the dataset. In an effort to study the general relationships between egg count data and the environmental structure (i.e., linear vs. unimodal), I generated simple plots to visually examine how egg mass counts were related to collected environmental variables to determine whether canonical correspondence or redundancy analysis were more appropriate for the data. Canonical correspondence analysis is appropriate when assuming unimodal relationships between variables whereas Redundancy Analysis (RDA) is appropriate for linear models of species response (McCune and Grace 2002). I used Redundancy Analysis (Stewart and Love 1968), a method of constrained linear ordination, to examine the relationships among amphibian breeding effort and environmental composition and structure at the

within-pond, local and landscape scales. All environmental variables (Table 1) were standardized to a mean of zero and a variance of one.

**Table 2.1** All Environmental Variables. Habitat variables included in the original analysis by Baldwin et al. (2006b). Data were collected across three spatial scales, within-pond, local (150 m) and landscape (500 m), to characterize aquatic and terrestrial habitat structure.

Habitat variables
Within Pond
Hydroperiod
Pool Area
Pool Depth
Percent Canopy Cover
Local scale (<150m)
Resistance Factor
Number of surrounding vernal pools
Area of surrounding forested wetlands
Percent canopy cover
Mean DBH
Tree species richness
Litter depth
Slope
Percent shrub cover
Rocky outcrops
Macropores
Total basal area
Number of cuts
Class 1 coarse woody debris
Class 2 coarse woody debris
Class 3 coarse woody debris
Class 4 coarse woody debris
Landscape scale (<500m)
Resistance Factor
Number of surrounding vernal pools
Area of surrounding forested wetlands

For both years of egg count data, separate analyses were performed using the matrix of egg mass counts as the predictor matrix and the environmental variables as the response, such that the ordination of the environmental variables was constrained by the

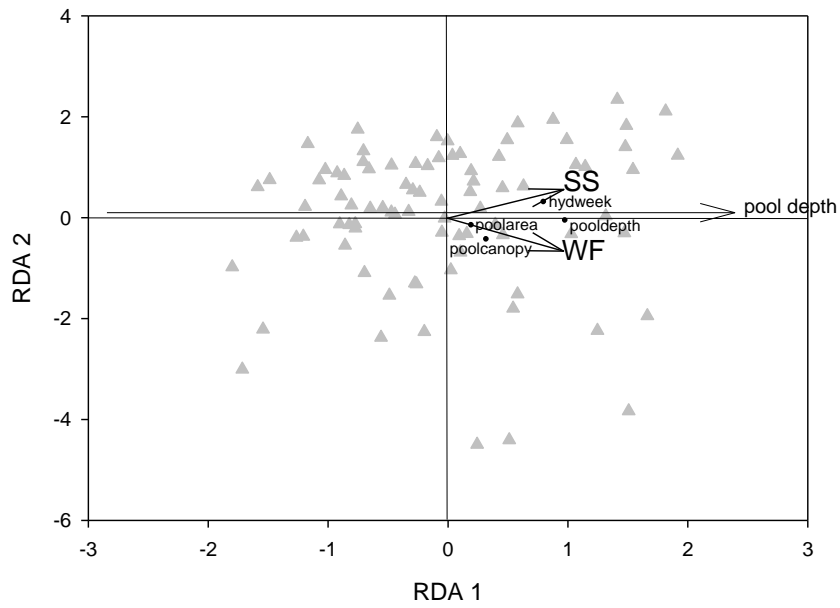
multiple linear regression of the egg mass counts. I performed the RDA in this way in order to use egg mass counts as a predictor of optimal or important environmental conditions which may contribute to higher amphibian reproductive effort. For each year of egg mass counts, four separate RDA's were performed using count data and environmental variables at 1) the within-pond scale, 2) the local scale, 3) the landscape scale and 4) all spatial scales together. Following each analysis, Monte Carlo tests (permutations = 500) were run to determine robustness of solutions reached by RDA compared to those generated by random chance. Lastly, in an effort to examine the relationship between tree species richness and other variables, I calculated both Simpson's D and Shannon H' diversity indices for each of the 87 plots.

## **RESULTS**

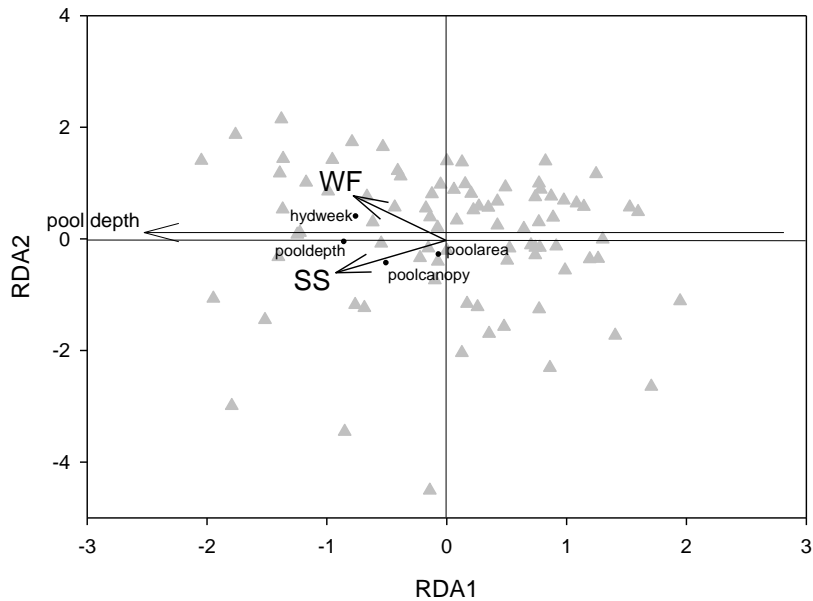
I found that solutions reached using RDA were significantly more robust than those generated randomly for all analyses except those of only landscape-scale variables (*Monte Carlo permutation tests, year one,  $p = 0.484$ , year two,  $p = 0.266$* ). Thus, within-pond and local scale factors had the most significant impacts on amphibian egg mass counts. For the first year of egg count data, within-pond variables explained 11 % of constrained variation in egg count data with local-scale variables explaining 5.6 % constrained variation and all variables (i.e., within pond + local + landscape variables) together explaining 0.7 % constrained variation. In examining the second year of egg count data, within-pond variables explained 10.77 % constrained variation, local-scale variables accounted for 5.82 % and all variables analyzed together accounted for 5.27 % of constrained variation.



For both species during both years of egg count data, hydroperiod and pool depth were the most strongly-predicted environmental variates for both species' reproductive effort at the within-pond scale (Figure 2.1).



(a)

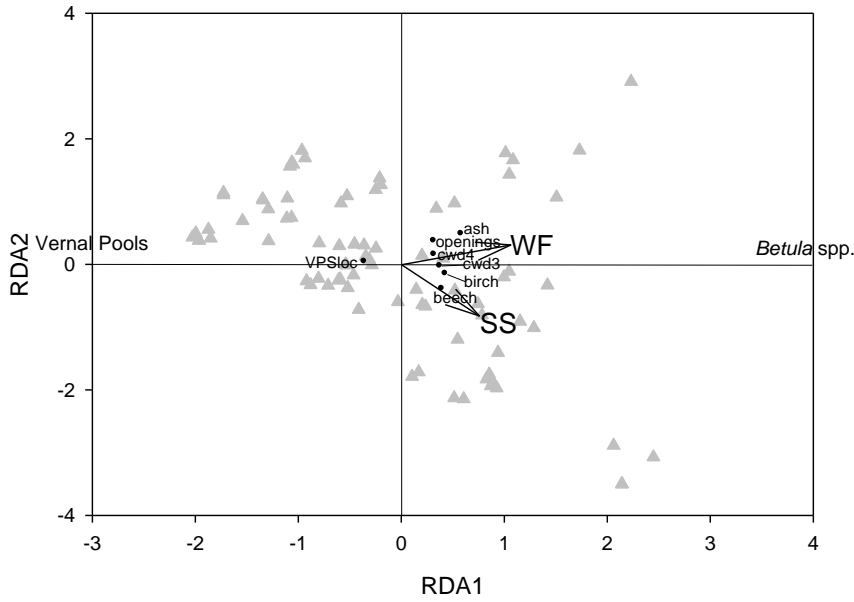


(b)

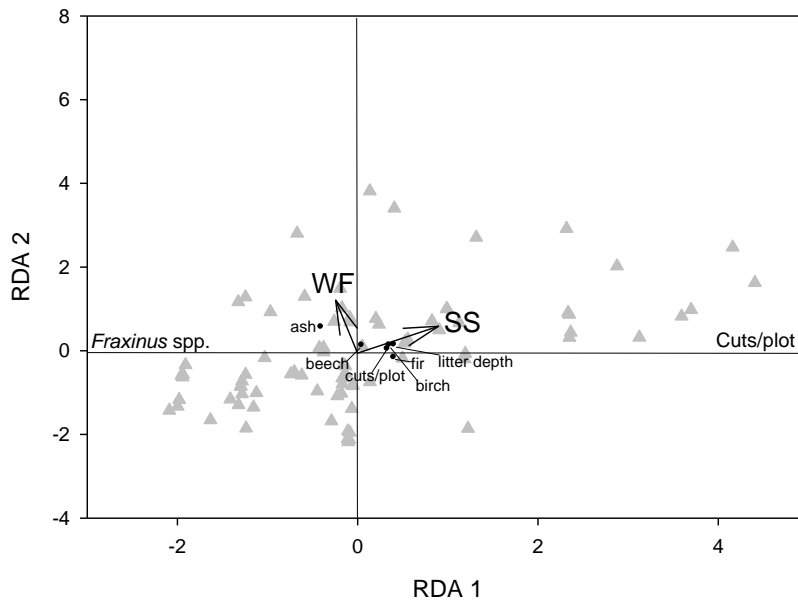
**Figure 2.1** Redundancy Analysis biplots of within-pond variables for (a) year one (b) year two of egg count data. (a) In year one, both species are influenced by hydroperiod (0.3737) and pool depth (0.4567) along RDA 1. Along RDA 2, spotted salamanders are driven in the positive direction by hydroperiod (0.1391) and wood frogs are driven in the negative direction by pool canopy cover (-0.2054). (b) In year two, both species are influenced by hydroperiod (-0.3508) and pool depth (-0.3965) along RDA 1. Along RDA 2, spotted salamanders are driven to the positive end by hydroperiod (0.1819) while wood frogs are driven in the negative direction by pool depth (-0.2074).

At the local scale, it was demonstrated that for both years, reproductive effort of both species predicted pools with a greater degree of canopy openness (Figure 2.2). The presence of birch (*Betula sp.*) species at the local scale was also predicted to be important to breeding effort of both species during both years. Additionally, at the local scale, high reproductive effort was observed at sites with a greater degree of canopy openness in the adjacent forest. For both years, I found that maximum numbers of both wood frog and spotted salamander eggs were found in areas with intermediate levels of tree species richness. Further exploration using Simpson's and Shannon indices of diversity revealed that forest community evenness was predicted strongly by amphibian reproductive effort

in this context. Therefore, in communities with intermediate levels of species richness and higher degrees of community evenness, amphibian reproductive effort may be greater.



(a)



(b)

**Figure 2.2** Redundancy Analysis biplots of local scale variables of (a) year one and (b) year two of egg count data. (a) In year one, both species are driven to the positive end of RDA 1 by *Fraxinus* spp. (0.4538), *Fagus grandifolia* (0.3166) and class-three woody debris (0.3013). (b) In year two, wood frogs and spotted salamanders diverge along RDA 1 with presence of *Fraxinus* spp. (-0.3266) driving the negative end and *Populus grandidentata* spp. (0.3247) and cuts/plot (0.2837) driving the positive end. Along RDA 2, both species are driven to the positive end by presence of and litter depth (0.14309).

For both years of wood frog egg count data, the presence of Ash (*Fraxinus* spp.) trees was predicted to be an important environmental variate for amphibian breeding effort. A lower percent canopy cover above the breeding pool was also found to positively correlate with wood frog breeding effort during both years of egg count data. The presence of beech (*Fagus* spp.) and ash species were predicted as important to the breeding effort of both species during the first year and the importance of ash species was predicted only for wood frogs during the second. The number of historic cuts on trees and stumps per plot as well as the levels of class-three coarse woody debris (more advanced decay) were strongly predicted for egg counts of both species during the second year but not the first. Furthermore, increased litter depth was found to positively contribute to both species' reproductive effort during the second year but not the first.

The presence of Balsam fir (*Abies balsamea*) and Big-toothed aspen (*Populus grandidentata*) as well as the number of surrounding vernal pools at the local scale were important environmental variates for spotted salamanders only during the second year of egg count data. Pool area and percent shrub cover were found to contribute to wood frog reproductive effort during the first year only.

## DISCUSSION

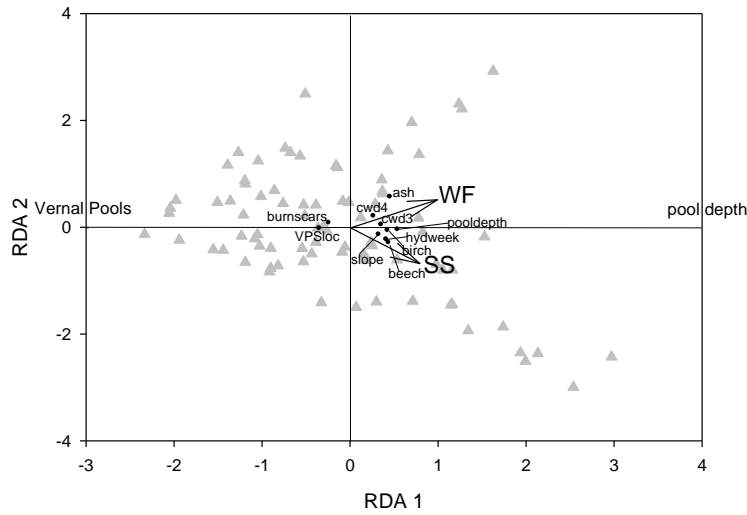
Our analysis revealed that hydroperiod was the most strongly predicted environmental variate contributing to greater amphibian breeding effort, with both

species exhibiting preference for intermediate to long periods of inundation. The significance of both hydroperiod and pool depth as important variables for amphibian breeding effort has been documented in previous studies (Skidds et al. 2007, Karraker and Gibbs 2009) and the tight relationship observed between these two variables concurs with results of the original analysis (Baldwin et al. 2006b). In this study, variables collected at the within-pond scale explained the highest percentage of constrained variation relative to other spatial scales examined. As such, my results agree with previous studies which have demonstrated that amphibians are strongly influenced by local habitat conditions (Skelly et al. 2002, Richter-Biox et al. 2007). These findings differ from a similar study on the relationship between wood frog and spotted salamander breeding effort and the surrounding environment in southern Rhode Island, where urbanization is more prevalent (Skidds et al. 2007).

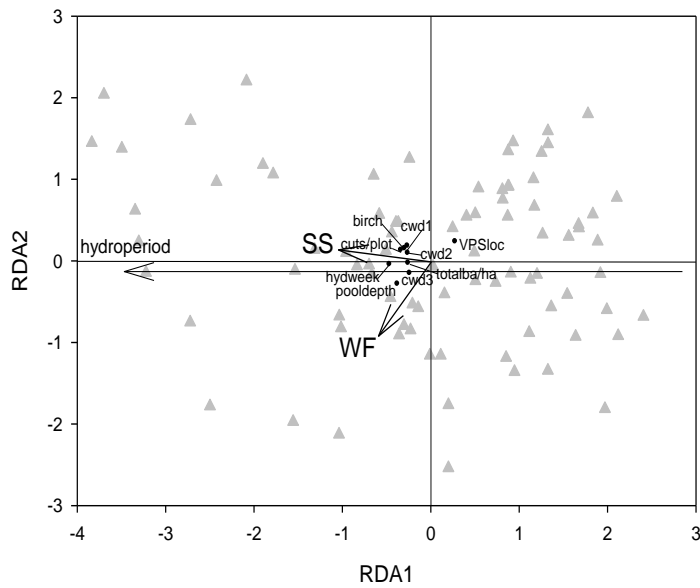
As the scale of analysis shifted from the smallest to the largest spatial area, I found substantial variation in the influence of environmental variables. Between the within-pond and landscape distances (500 m), I found notable differences in the amount of constrained variation explained. I suspect that combining environmental variables into one spatial scale (1 km<sup>2</sup>) (e.g., Skidds et al. 2007) may have unintentionally ignored important sources of fine-scale variation occurring at smaller scales, which may have more direct impact on amphibians. Given these contrasts, I suggest that there should be more consistent terminology across studies, both in experimental design as well as in the literature. What is considered by one study as “local” may be another study’s “landscape” scale and thus, it is difficult to compare different studies and draw general conclusions

about the effects of multiple spatial scales on amphibians because there is no predetermined or standard distance corresponding to “local” and “landscape” scales (Wu 2004).

The RDA results emphasized the importance of the surrounding terrestrial habitat through strong and consistent prediction of several tree species, litter depth and more advanced classes of coarse woody debris. The importance of litter depth for both amphibian species at the local scale is supported by previous work which has documented the importance of un-compacted, well-decayed leaf litter in contributing to moist terrestrial environment, all of which is conducive to amphibian movement and foraging activities (deMaynadier and Hunter 1999, Baldwin et al. 2006a, Semlitsch et al. 2007). Even when I included all variables at all three spatial scales in the analysis, several local-scale variables associated with the surrounding terrestrial habitat were consistently predicted to be important to reproductive effort (Figure 2.3). This and other work has demonstrated the primary importance of terrestrial habitat conditions for both species as well as conditions of the breeding habitat (deMaynadier and Hunter 1999, Berven 2009). For both species during both years the presence, and perhaps volume, of Black birch (*Betula lenta*) and American beech (*Fagus grandifolia*) trees were strongly predicted by egg mass counts. This clearly demonstrates the importance of a moderately moist, mature terrestrial environment for the juvenile and adult stages of both species.



(a)



(b)

**Figure 2.3.** Redundancy Analysis biplots of all spatial scales combined for (a) year one and (b) year two of egg count data. (a) In year one, both species are driven to the positive end of RDA by pool depth (0.4560) and presence of both *Fraxinus* spp. (0.3845) and American beech (0.3706) and to the negative end of RDA primarily by number of surrounding vernal pools at the local scale (-0.2927). Along RDA 2, spotted salamanders are driven to the negative end by *Fagus grandifolia* (-0.2455) and wood frogs are driven to the positive end by *Fraxinus* spp. (0.4765). (b) In year two, both species are driven to the negative end of RDA 1 by hydroperiod (-0.3933), cuts/plot (-0.2830) and *Betula* spp. (-0.2852). Along RDA 2, spotted

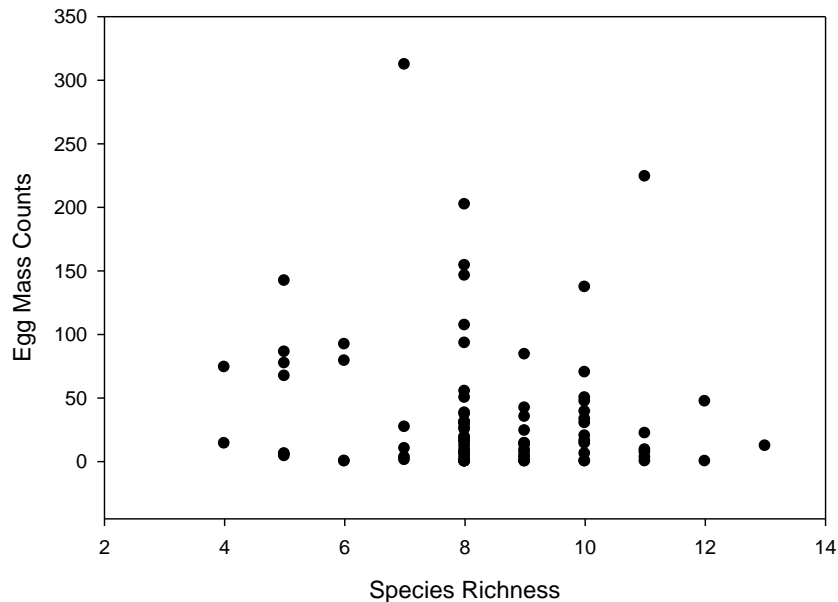
salamanders are driven in the positive direction by *Betula* spp. (0.1530) and wood frogs are driven in the negative direction by pool canopy cover (-0.3007).

Ash (genus *Fraxinus*) trees were an important contributor to high reproductive effort for both years of wood frog egg count data when all variables were analyzed together and for both species both years when local-scale variables only were analyzed. Because Ash trees are facultative wetland species they are typically, but not always, indicative of moist breeding conditions and may also indicate appropriate upland habitat for amphibians. This echoes the importance of high quality forested wetland and terrestrial habitat composed of mature forest stands to optimal breeding effort of amphibians. Furthermore, the consistent prediction of class-three coarse woody debris for both species during both years may be an indicator of forest structure and even stand maturity (Fraver et al. 2002) as well as the importance of a cool, moist forest floor with adequate refugia.

The discovery of high egg mass counts and thus, reproductive effort, in areas with intermediate levels of tree species richness is perhaps the most unique finding in this endeavor (Figure 2.4). I explored whether evenness or abundance of tree communities was influencing the reproductive effort of these two amphibian species. The importance of evenness in the tree community may emphasize amphibians' need for high diversity in terms of three-dimensional structure of the microhabitats and interstitial spaces within the forest floor (as in Madison 1997, Regosin et al. 2003a); high community evenness may allow for a greater degree of diversity in terms of litter input and structure, both in the pond as well as in the surrounding upland habitat (Regosin et al. 2003b, Baldwin et al. 2006b). Greater diversity of leaf litter mixtures have been demonstrated to initially



contribute to higher levels of productivity in manipulative experiments and thus may be more conducive for non-breeding amphibians (King et al. 2002).



**Figure 2.4** Combined egg mass counts plotted against tree species richness for both species across both years of data collection. This demonstrates the consistent unimodal relationship where high numbers of egg masses were found in areas with intermediate levels of species richness.

Additionally, it is possible that species richness may relate to historic burning and logging regimes of the area. Baldwin et al. (2006b) found that forest maturity was related to site history where sites were not burned in the massive 1947 fire in southern Maine (Butler 1979). While I did not find any evidence that burn history directly influenced breeding effort, the number of historic cuts per plot did contribute significantly to constrained variation for both species when all variables at all spatial scales were included in the analysis of the second year of egg count data. This demonstrates the importance of considering both current and historic landscape conditions when examining the relationship between species and their environment, particularly the effect

of historical burn regimes on current stand characteristics (Foster 1992, Findlay and Bourdages 2000, Foster et al. 2003). Additionally, other work has shown maximum number of salamander catches took place in intermediate-aged forest stands (Petranka et al. 1993). This intermediacy of tree species richness and/or stand age, may relate to canopy cover levels and possibly productivity and structure of the forest floor (Pollock et al. 1998). Areas with optimal levels of productivity clearly benefit amphibian populations by providing greater amounts of certain habitat resources (e.g., cool, moist refugia) and thus may alleviate levels of inter- and intra-specific competition of some organisms.

Intermediate levels of tree species richness and stand age may also indicate variable canopy structure which can greatly influence processes occurring in the breeding pond and on the forest floor. A completely closed canopy may reduce productivity, both in the breeding pond as well as the upland forest, which may negatively impact certain amphibian species (e.g., wood frog and other grazing larvae). Several studies have documented the negative effects of complete canopy closure on larval development as well as the absence of many amphibians from closed canopy ponds (Werner and Glennemeier 1999, Skelly et al. 2002, Werner et al. 2007).

While the effects of canopy openness have been well-documented in the breeding pool, the ramifications of canopy cover in the adjacent terrestrial area are less understood (but see Homan et al. 2004). Amount of canopy cover is documented to affect various understory conditions such as soil moisture, soil temperature, soil evaporation, air temperature and amount of solar radiation, the diurnal contrasts of these variables as well as the abundances of some amphibians (Martens et al. 2000, Homan et al. 2004, Lemenih

et al. 2004). A completely closed forest canopy is beneficial to amphibians in some respects (e.g., moist microclimate, lower risk of desiccation, higher levels of soil moisture and subsequent reduced water stress) however it may also reduce the amount of three-dimensional structure of the understory because less solar radiation is allowed to reach the forest floor. Furthermore, dominance of the canopy by one or a few species often reduces the diversity of litter input on the ground which, depending on the species of dominance (e.g., pines) can be detrimental to amphibians such as wood frogs who require leaf cover or other structurally diverse microhabitats (Gibbs 1999, Baldwin et al. 2006b). Levels of leaf litter can greatly influence soil moisture, amount of available refugia as well as soil chemistry, all of which can have dramatic consequences for amphibians (reviewed in Semlitsch et al. 2009).

In the current analysis, landscape scale variables do not significantly contribute to the constrained variation explained by the RDA. This is not to say that landscape processes do not influence or impact local amphibian dynamics; however, in this continuous, intact, mostly-forested area of southern Maine, within-pond and local scale variables explain the majority of constrained variation and may be the primary drivers of this system. Contrary to this observation, other work has found that landscape composition is a significant driver of amphibian populations in predominantly agricultural landscapes of Ohio (Porej et al. 2004). These differing results may be indicative of the vastly different landscapes in which the studies were performed. Perhaps in intensively farmed areas, the amount of suitable habitat remaining for amphibians is reduced to the point that local scale processes no longer have an effect; because the areas

of suitable habitat are so few and far between, they are much more influenced by processes occurring at the landscape scale. In Maine, the study area is mostly forested and generally connected at the landscape scale. In comparison to the Ohio study, the amount of suitable habitat is likely significantly greater, more densely distributed and may be driven primarily by local processes. This concurs with other work in Maine which revealed that wetlands occurred at high densities ( $2.17/\text{km}^2$ ) and that inter-wetland distances were often small ( $<300$  m) and within dispersal capabilities of many animals in this undisturbed landscape (Gibbs 1999). Furthermore, this finding supports the conclusion that the spatial scale of influence may change depending on the level of landscape connectivity and disturbance. The observed influence of the number of vernal pools at the local scale on spotted salamander breeding effort is likely a reminder of their lower dispersal and migratory capabilities and thus their critical need for habitat connectivity and permeability, both of which can be influenced by landscape scale processes such as urban development and road building (Vos and Chardon 1998, Porej et al. 2004).

In terms of broad patterns, my conclusions were quite similar to those reached in the original analysis by Baldwin et al. (2006b), that hydroperiod and pool depth had the greatest influence on amphibian reproductive effort during both years of data collection. However, further exploration of the original dataset using a multivariate analytical technique revealed additional structural complexity of the data that were not elicited from the original analysis.

Amphibian populations are known to display particular sensitivity to the synergistic effects of multiple stressors (Semlitsch 2000, Blaustein and Kiesecker 2002, Boone et al. 2007). Moreover, human-induced environmental stressors are currently so pervasive throughout many ecosystems in North America that it may be more realistic to assume that amphibians must cope with synergistic effects of multiple stressors simultaneously as opposed to just one at a time. Because the various factors working in tandem to impact amphibian populations are not always necessarily obvious or explicit, multivariate analyses may serve as an important exploratory first step which compliments traditional methods of model selection and hypothesis generation.

When examining the relationship between amphibians and their environments, it is important to take into account the potential for complex interactions among biotic and abiotic factors which have been demonstrated to negatively impact amphibian populations (reviewed in Findlay and Houlihan 1997, Cushman 2006, Mann et al. 2009), highlighting the need for descriptive analytical techniques of equal dimensionality. Because multivariate techniques are often more accommodating to complex datasets with many variables, it is useful to employ these methods in conjunction with prediction-based methods in order to fully understand the structure and relationships which exist in the data (James and McCulloch 1990). Furthermore, my analysis demonstrates the utility of multivariate analysis in that the broad conclusions of a univariate and multivariate analytical technique are markedly similar. With good knowledge of the system and a rich and carefully-collected data set, it is possible to analyze environmental variables which contribute to optimal amphibian breeding effort using a multivariate technique that is

accommodating, rather than punitive, towards complex and dimensional data collection. Moreover, techniques which are able to describe factors influencing amphibian distributions and can examine a large number of variables without any *a priori* truncation of data may be complementary to those techniques traditionally utilized for conservation and land management decisions.



## APPENDICES



Appendix A

Authors Included in Metacommunity Review

Author	Years	Spatial Scales	Species	X (temporal)	Y (spatial)	Z (community)
Berven (2009)	21	2	1	5	2	1
Vonesh et al. (2009)	<1	1	2	1	1	2
Keller et al. (2009)	1	1	27	2	1	6
MacNalley et al. (2009)	2	1	2	2	1	2
Teacher et al. (2009)	12	1	1	4	1	1
Wu et al. (2009)	<1	1	1*	1	1	1.5
Maerz et al. (2009)	<1	1	2*	1	1	2.5
Schloegel et al. (2009)	6	1	1	3	1	1
Werner et al. (2009)	11	2	2	5	2	2
Garner et al. (2009)	2	1	1	2	1	1
Todd et al. (2009)	4	2	8	3	2	4
Mattfeldt et al. (2009)	3	1	13	2	1	5
Denoel et al. (2009)	35	2	3	6	2	2
Collins & Russell (2009)	1	1	5	2	1	3
Crossland et al. (2008)	7	1	21	4	1	6
Johnson et al. (2008)	<1	1	3	1	1	2
Rudolf (2008)	<1	1	2	1	1	2
McCoy & Bolker (2008)	<1	1	1*	1	1	1.5
Church (2008)	5	1	14	4	1	5
Hoverman & Relyea (2008)	<1	1	1*	1	1	1.5
Boone et al. (2008)	<1	1	4*	1	1	2.5
Urban (2008b)	3	1	2	2	1	2
Urban (2008)	2	1	3	2	1	2
Pope et al. (2008)	4	1	1	3	1	1
Picco & Collins (2008)	3	1	1	2	1	1
Gahl & Calhoun (2008)	6	3	4	3	3	2
Sanchez et al. (2008)	2	1	17	2	1	5
Barret & Guyer (2009)	3	1	38	2	1	7
Patrick et al. (2008)	2	5	1	2	5	1
Patrick et al. (2008b)	3	4	1	2	4	1
Relyea & Diecks (2008)	<1	1	2	1	1	2
Pillsbury & Miller (2008)	1^	2	7	2.5	2	3
Ryan et al. (2008)	7	2	1	4	2	1
Pope et al. (2008b)	6	2	5*	3	2	3.5
Delgado-Acevedo & Restrepo (2008)	1	1	2	2	1	2
Witte et al. (2008)	17	2	6*	5	2	3.5
Gamble et al. (2007)	7	15	1	4	10	1

Garner et al. (2007)	2	1	53	2	1	8
Werner et al. (2007b)	7	2	17	4	2	5
Richter-Biox et al. (2007)	5	2	6	3	2	3
Hodgkison (2007)	3	3	110	2	3	10
Werner et al. (2007)	7	2	15	4	2	5
Crawford et al. (2007)	<1	1	12	1	1	5
Kruger et al. (2007)	1	1	1	2	1	1
Woodhams et al. (2007)	2	1	1	2	1	1
Finlay & Vredenburg (2007)	3	1	1*	2	1	1.5
Davidson & Knapp (2007)	6	2	1	3	2	1
Crawford & Semlitsch (2007)	1	8	4	2	8	2
Stevens et al. (2007)	2	3	3	2	3	2
Noonan & Gaucher (2006)	1	1	1	2	1	1
Ernst et al. (2006).	5 <sup>^</sup>	1	30	3.5	1	6
Brooks et al. (2006)	1	1	75	2	1	9
Lehtinen & Skinner (2006)	1 <sup>^</sup>	1	1	2.5	1	1
Rudolf (2006)	1	1	2	2	1	2
Scott et al. (2006)	1 <sup>^</sup>	1	132	2.5	1	10
Gomez-Mestre et al. (2006)	1	1	3	2	1	2
Todd & Rothermel (2006)	<1	2	1	1	2	1
Gibbons et al. (2006)	1	2	24	3	2	6
Puschendorf et al. (2006)	2	1	35	2	1	6
Denoel & Lehmann (2006)	4	3	1	3	3	1
Rachowicz et al. (2006)	2	1	1	2	1	1
Bank et al. (2006)	65	2	1	8	2	1
Weyrauch & Grubb (2006)	<1	1	1	1	1	1
Cruz et al. (2006)	2	2	13	2	2	5
Muths et al. (2006)	12	2	1	5	2	1
Chelgren et al. (2006)	1	2	1	2	2	1
Beard & O'Neill (2005)	1	1	1	2	1	1
Briggs et al. (2005)	150	1	1	10	1	1
Scherer et al. (2005)	11	1	1	5	1	1
Daszak et al. (2005)	35	1	15	6	1	5
Riley et al. (2005)	3	2	4*	2	2	3
Ouellet et al. (2005)	110	1	43	10	1	7
Relyea (2005)	<1	1	25	1	1	6
Schmidt et al. (2005)	20	1	1	5	1	1
Resetarits (2005)	1	2	1	2	2	1
deSolla et al (2005)	12	1	8	5	1	4
Vonesh (2005)	2	1	1	2	1	1
Woodhams & Alford (2005)	2	1	4	2	1	2
Gibbs et al. (2005)	30	4	5	6	4	3
Relyea (2005b)	1	1	3	2	1	2
Relyea et al. (2005)	1	1	6	2	1	3
Rohr & Crumrine (2005)	1	1	11*	2	1	5.5

Trenham & Shaffer (2005)	1	5	1	2	5	1
Stoddard & Hayes (2005)	2	4	3	2	4	2
Schmidt & Pellet (2005)	1	2	4	2	2	2
Rodriguez-Prieto & Fernandez-Juricic (2005)	1	2	1	2	2	1
Rubbo & Kiesecker (2005)	1	2	11	2	2	5
Pearman & Garner (2005)	<1	1	1	1	1	1
Reeder et al. (2005)	110	1	1	10	1	1
Denoel et al. (2005)	12	1	2	5	1	2
Funk et al. (2005)	3	2	1	2	2	1
Knapp (2005)	3	1	6	2	1	3
Pellet et al. (2004)	2	20	1	2	10	1
Davidson (2004)	17	1	5	5	1	3
Bell et al. (2004)	25	1	2	5	1	2
Hanselmann et al. (2004)	1	1	1	2	1	1
Crochet et al. (2004)	1^	2	11	2.5	2	5
Lips et al. (2004)	1	1	39	2	1	7
Gray et al. (2004)	2	1	7	2	1	3
Lecis & Norris (2004)	2	1	1	2	1	1
Mills & Semlitsch (2004)	2	1	2*	2	1	2.5
Burns et al. (2004)	3	1	1	2	1	1
Pineda & Halffter (2004)	3	3	21	2	3	6
Lecis & Norris (2004)	2	1	1*	2	1	1.5
Hoffman & Blouin (2004)	2	1	2	2	1	2
Curtis & Taylor (2004)	1	1	1	2	1	1
Ficetola & de Bernardi (2004)	1	2	7	2	2	3
Lowe et al. (2004)	1	1	1*	2	1	1.5
Boone et al. (2004)	<1	1	2	1	1	2
Richter-Boix et al. (2004)	<1	1	2	1	1	2
Boone et al. (2004)	<1	1	4	1	1	2
Rissler et al. (2004)	1	1	2	2	1	2
Rubbo & Kiesecker (2004)	3	2	3	2	2	2
Baber et al. (2004)	2	1	42*	2	1	7.5
Weldon et al. (2004)	35	1	3	6	1	2
Retallick et al. (2004)	4	1	6*	3	1	3.5
Vredenburg (2004)	8	1	1	4	1	1
Little et al. (2003)	2	1	2	2	1	2
Crawford (2003)	2	1	4	2	1	2
Knapp et al. (2003)	3	1	1	2	1	1
Richter et al. (2003)	14	1	1	5	1	1
Bradford et al. (2003)	3	3	1	2	3	1
Jansen & Healey (2003)	2	1	6	2	1	3
Martinez-Solano et al. (2003)	7	1	9	4	1	4
Wheeler et al. (2003)	25	1	1	5	1	1
Mazerolle (2003)	2	4	6	2	4	3
Boone & James (2003)	<1	1	4	1	1	2

Binckley & Resetarits (2003)	<1	1	1*	1	1	1.5
Chalcraft & Resetarits (2003)	<1	1	10	1	1	4
Chalcraft & Resetarits (2003b)	<1	1	10	1	1	4
Adams et al. (2003)	3	1	1*	2	1	1.5
Vonesh & Osenberg (2003)	<1	1	1*	1	1	1.5
Houlahan & Findlay (2003)	4	16	17	3	10	5
Lips et al. (2003)	18	1	116	5	1	10
Muths et al. (2003)	11	1	1	5	1	1
Hayes et al. (2003)	1	1	1	2	1	1
Kiesecker (2002)	1	1	2	2	1	2
Toral et al. (2002)	2^	1	12	2.5	1	5
Boone & Semlistsch (2002)	<1	1	6	1	1	3
Skelly et al. (2002)	<1	1	2	1	1	2
Skelly (2002)	1	1	2	2	1	2
Corn & Muths (2002)	15	1	1	5	1	1
Palen et al. (2002)	4	1	4	3	1	2
Hamer et al. (2002)	2	2	1*	2	2	1.5
Johnson et al. (2002)	1	1	9	2	1	4
Blaustein et al. (2001)	18	1	4	5	1	2
Matthews et al. (2001)	3	2	1	2	2	1
Gillespie (2001)	3	1	1	2	1	1
Parris (2001)	5	1	1	3	1	1
Newman & Squire (2001)	3	1	1	2	1	1
Beebee & Rowe (2001)	2	1	1	2	1	1
Corser (2001)	10	1	1	4	1	1
Fellers et al. (2001)	2	1	1	2	1	1
Knapp et al. (2001)	3	1	1	2	1	1
Carr & Fahrig (2001)	1	12	2	2	10	2
Sparling et al. (2001)	<1	1	1	1	1	1
Davidson et al. (2001)	26	2	1	6	2	1
Bosch et al. (2001)	1	2	1	2	2	1
Boone & Semlitsch (2001)	<1	1	3	1	1	2
Kiesecker & Skelly (2001)	<1	1	1*	1	1	1.5
Naughton et al. (2000)	3	1	1	2	1	1
Sower et al. (2000)	1	1	2	2	1	2
Bridges & Dorcas (2000)	1	1	9	2	1	4
Broomhall et al. (2000)	1	1	2	2	1	2
Adams (2000)	2	1	2*	2	1	2.5
Shaffer et al. (2000)	1	1	1	2	1	1
Starnes et al. (2000)	1	1	4	2	1	2
Crossland (2000)	<1	1	3	1	1	2
Peacor & Werner (2000)	<1	1	3*	1	1	2.5
Snodgrass et al. (2000)	1	1	20	2	1	5

Relyea (2000)	<1	1	2	1	1	2
Kiesecker & Skelly (2000)	<1	1	1*	1	1	1.5
Lips et al. (2000)	<1	1	2	1	1	2
Vallan (2000)	2	1	28	2	1	6
Bridges & Semlitsch (2000)	3	1	9	2	1	4
Pope et al. (2000)	1	3	1	2	3	1
Knapp & Matthews (2000)	2	1	1	2	1	1
Knutson et al. (1999)	4	1	14	3	1	5
Blaustein et al. (1999)	1	1	2	2	1	2
Lawler et al. (1999)	1	1	1*	2	1	1.5
Johnson et al. (1999)	2	1	1*	2	1	1.5
Lips (1999)	6	1	35	3	1	6
Pounds et al. (1999)	19	1	50	5	1	7
Bunnell & Zampella (1999)	1	1	10	2	1	4
Fauth (1999)	2	1	12	2	1	5
Wissinger et al. (1999)	<1	1	1*	1	1	1.5
Berger et al. (1998)	2	1	19	2	1	5
Meyer et al. (1998)	28	1	1	6	1	1
Welsh & Ollivier (1998)	1	1	3	2	1	2
Bardsley & Beebee (1998)	<1	1	2	1	1	2
Van Buskirk & Yurewicz (1998)	<1	1	1*	1	1	1.5
Hecnar & M'Closkey (1998)	3	2	13	2	2	5
Gibbs (1998)	3	1	5	2	1	3
Kurzava & Morin (1998)	<1	1	6*	1	1	3.5
Dodd & Cade (1998)	5	1	16	3	1	5
Laurila et al. (1998)	<1	1	2*	1	1	2.5
Corn (1998)	1	1	1	2	1	1
Lips (1998)	6	1	6	3	1	3
Vos & Chardon (1998)	1	6	4	2	6	2
Peacor & Werner (1997)	<1	1	2*	1	1	2.5
Laurila & Aho (1997)	<1	1	1*	1	1	1.5
Hacnar & M'Closkey (1997)	3	3	15	2	3	5
Hecnar & M'Closkey (1997b)	3	1	13*	2	1	5.5
Beachy (1997)	<1	1	2	1	1	2
Kiesecker & Blaustein (1997)	1	1	3	2	1	2
Pounds et al. (1997)	5	1	60	3	1	8
Blaustein et al. (1997)	1	1	1	2	1	1
Kupferberg (1997)	6	2	3	3	2	2
Fisher & Shaffer (1996)	11	1	6	5	1	3
Hecnar & M'Closkey (1996)	3	1	12	2	1	5
Drost & Fellers (1996)	1^	2	7	2.5	2	3
Raxworthy & Nussbaum	1	1	15*	2	1	5.5

(1996)						
Blaustein et al (1996)	1	1	1*	2	1	1.5
Blaustein et al. (1996b)	1	1	1	2	1	1
Blaustein & Margalit (1996)	<1	1	1*	1	1	1.5
Gamradt & Kats (1996)	2	1	1*	3	1	1.5
Garber & Burger (1995)	20	1	1	5	1	1
Skelly (1995)	<1	1	2*	1	1	2.5
Morin (1995)	<1	1	5	1	1	3
Blaustein et al. (1995)	1	1	1	2	1	1
Blaustein et al. (1994a)	1	1	1	2	1	1
Bradford et al. (1994)	2	1	3	2	1	2
Pounds & Crump (1994)	<1	1	2	1	1	2
Blaustein et al. (1994b)	<1	1	10	1	1	4
Petranka et al. (1994)	<1	1	2	1	1	2
Holomuzki et al. (1994)	<1	1	1*	1	1	1.5
Blaustein & Margalit (1994)	1	1	1*	2	1	1.5
Burkett & Thompson (1994)	1	2	25*	2	2	6.5
Semlitsch et al. (1993)	12	1	1	5	1	1
Warner et al. (1993)	<1	1	2	1	1	2
Fellers & Drost (1993)	1^	1	1	2.5	1	1
Diaz-Paniagua (1992)	7	1	9	4	1	4
Sredl & Collins (1992)	1	1	2	2	1	2
Crump et al. (1992)	3^	1	1	3.5	1	1
Fauth & Resetarits (1991)	1	1	7	2	1	3
Magnusson & Hero (1991)	3^	1	35	3.5	1	6
Pechmann et al (1991)	12	1	4	5	1	2
Berven & Grudzien (1990)	7	3	1	4	3	1
Laan (1990)	1	2	7	2	2	3
Resetarits & Wilbur (1989)	1	1	7	2	1	3
Kats et al. (1988)	1	1	15*	2	1	5.5
Vanbuskirk (1988)	1	1	4*	2	1	2.5
Morin (1986)	1	1	2	2	1	2
Ranta & Nuutinen (1985)	1	1	1*	2	1	1.5

Table A-1: Amphibian impact studies (N=244) which met the aforementioned criteria published from 1985-2009 and their respective assigned scores on temporal (x), spatial (y) and community (z) axes. Year, spatial scales and species represent the raw number of each included by their respective study. X (temporal), Y (spatial) and Z (community) represent the scores assigned to each aspect of individual studies.

\* denotes studies which considered effects of other taxonomic groups on amphibians while not explicitly using them in analyses

^ denotes studies which took into account historical considerations and/or historical data



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