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LOYOLA UNIVERSITY CHICAGO

PREDICTING SUITABLE HABITAT DECLINE OF MIDWESTERN UNITED STATES AMPHIBIANS AND QUANTIFYING THE CONSEQUENCE OF DECLINES USING POND-BREEDING SALAMANDERS

A THESIS SUBMITTED TO
THE FACULTY OF THE GRADUATE SCHOOL
IN CANDIDACY FOR THE DEGREE OF
MASTER OF SCIENCE

PROGRAM IN BIOLOGY

BY
BROCK PAUL STRUECKER
CHICAGO, IL
DECEMBER 2016

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ABSTRACT

With current declines of vertebrate taxa meeting or exceeding those of historic mass extinction events, there is a growing need to investigate the main drivers of declines. Amphibians are perhaps at greatest risk of global climate change and land-use changes than most other vertebrate classes and also have significant roles in ecosystem processes – combined, this creates a cause for concern. I designed a study that would investigate the effects of current and predicted climate change and land-use changes on amphibians using species distribution models and a field study to identify the potential consequences of amphibian species declines by investigating the role of larval pond-breeding salamanders in wetlands in the Midwestern U.S. My objectives were to: (1) quantify changes in suitable habitat space and species richness for amphibians from current to future predictions, (2) compare predictions based exclusively on climate with predictions based on both climate and land-use, (3) identify what factors influence density of biota in ephemeral wetlands in the Midwest and (4) determine if larval pond-breeding salamanders have a measurable role in shaping wetland biotic communities. Model results indicate climate, not land-use, is a primary factor driving predicted changes in suitable habitat for amphibians in the Midwest and the changing climate is predicted to result in an overall decline of amphibian species richness based on future predictions. Wetland investigations showed local level factors influence aquatic invertebrate density while landscape level factors influence larval pond-breeding salamanders. I did not find any significant effects of larval pond-breeding salamander densities on the density of aquatic invertebrates. However, larval salamanders showed a predation bias for certain taxa as well as for taxa within the predator functional group. Future research should center on the role larval ambystomatid salamanders have on whole-ecosystem processes within wetlands and further interpolate the relationships between current and predicted global climate change on the potential decline of ecosystem processes.

CHAPTER I

INTRODUCTION

Global Change

The collective global biodiversity declines in recent history has been labeled as the sixth mass extinction (Barnosky et al. 2011, Dirzo et al. 2014, Pievani 2014, Ceballos et al. 2015, McCallum 2015, Urban 2015) in which humans are thought to be the primary cause. For example, a recent study by Ceballos et al. (2015) found the modern extinction rate of vertebrates may be up to 100 times that of the expected background extinction rate, with recent extinctions within the past 114 years being equivalent to 5,000 years of background extinction. Anthropogenic changes to climate, land use and the overexploitation of resources are a few of the most threatening changes affecting global biodiversity (Sala et al. 2000, Dirzo et al. 2014) where these reductions are theorized to negatively impact ecosystem stability; altering the provision of ecosystem services (Hautier et al. 2015). Although declines in biodiversity in modern history have been substantial, there is evidence to suggest continued anthropogenic changes may result in further declines. For example, climate change is a burgeoning threat and may force a shift in the distribution of many species which will be a difficult or impossible adjustment for many sedentary species or those that have limited dispersal abilities. Along with climate change, land use changes will become an increasingly significant conservation issue because shifting distributions will require adequate habitat to traverse toward suitable areas (Sala et al. 2000). Therefore, it is important that we continue to work for conservation of biodiversity with anthropogenic threats in mind.

Modeling Global Change

Predicting future anthropogenic changes and their impacts on biodiversity will likely inform our current understandings of the relationships global taxa have with their environment and help scientists better grasp the potential consequences of future changes. Several studies have attempted to predict the impacts of future changes in climate (Araujo et al. 2006, Lawler et al. 2010, Matthews et al. 2011), land-use (Iverson et al. 2011, Barbet-Massin et al. 2012), invasive species (Worner and Gevrey 2006, Jones et al. 2010), and emerging diseases (Flory et al. 2012, James et al. 2015); in an effort to better-inform conservation efforts to their focal taxa. A popular tool used in these efforts is species distribution modeling (SDM). This technique is used to analyze the changes in predicted suitable habitat space over a user-defined study region, often using occurrence-only geographic locale points from historical museum record datasets along with current and predicted environmental data to build a predictive model based-on a current ecological envelope. Although SDMs can be useful for understanding the relationships between focal taxa and their environment and how predicted changes may affect those taxa, they are limited in their scope to build fully complete ecological envelopes. For example, many SDMs investigating the predicted effects of climate change do not incorporate the expansion or reduction in habitat space of competitors, predators or prey of their focal taxa; factors that could significantly affect the occurrence of any species. In addition, the foundation of these models is built on a correlative approach, meaning the occurrence data may not encompass the total ecological niche for a given species (e.g. minimum and maximum tolerance of mean annual temperature; Bocsi et al. 2016). Rather, occurrence data represent the synergy of a variety of factors that affect the distribution of a given species in space. Therefore, we are limited in our capacity to interpret the results of any SDM. Yet, these models provide a basis from which we can build our understanding of the relationships between taxa and their environments and the inclusion of predicted changes allows us to visualize changes from which we can then prepare for.

Amphibians and Global Change

Of all vertebrates, amphibians are one of the most imperiled taxonomic classes with some estimates of over 50% of species having gone extinct since the year 1500 (McCallum 2015). Amphibian populations have been declining across the globe wherein multiple factors such as expanding infectious diseases, land use changes, climate change, invasive species and excessive collection are thought to be responsible (Collins and Storfer 2003). However, it is often difficult to attribute any one factor directly to a documented population decline or extinction because often many of these factors act in synergy (Blaustein et al. 2011). For example, there is evidence to suggest climate change may exacerbate the effects of *Batrachochytrium dendrobatidis* (*Bd*), a type of chytrid fungus that affects amphibians (Bosch et al. 2007). In addition, overexploitation through pet trade may facilitate the spread of emerging diseases toward areas with high amphibian diversity (Richgels et al. 2016). The co-occurrence of climate change and land-use change may also have exponentially negative effects on amphibian populations because of the relatively strict habitat requirements for many amphibian species. Yet, provided links from historic climate changes to population declines have been infrequent and examination of impacts of climate and land-use changes on amphibians concurrently does not exist for many regions and species.

Amphibian Biology

Amphibian biological characteristics are unique from many other vertebrate organisms. Many amphibians exhibit biphasic life histories with an aquatic larval stage and a terrestrial adult stage, although some species are fully aquatic, fully terrestrial, and/or exhibit triphasic or direct development life histories (Lannoo 2005). In addition, amphibians are poikilothermic and rely on the external environment to regulate their body temperature and skin moisture (Feder and Burggren 1992). Skin moisture is important for amphibian physiology because of their ability for cutaneous respiration, facilitated by moist skin. Some amphibians use cutaneous respiration facultatively while others are lungless and rely solely on this method to respire while fully aquatic larvae (e.g. larval *Ambystoma* species) or neotenic species (e.g. Axolotls) use external gills for breathing. All amphibians have permeable skin, allowing elements to transfer from the external environment into their body. This attribute leaves amphibians susceptible to chemical pollution which can have significant effects on development (Taylor et al. 2005).

Because of their unique physiology and respiration requirements, amphibians inhabit areas with specific microclimates. So much so, moisture and temperature have been shown to dictate the distribution of amphibians at the landscape (Peterman and Semlitsch 2014) and regional levels (Qian 2010). Vegetative structure and land cover influence local climates and are important factors in determining suitable amphibian habitat (Semlitsch 1998, Roloff et al. 2011, Alix et al. 2014). For example, terrestrial lungless species are particularly limited to forested areas where the over story keeps conditions cool and humid underneath and clear cutting as well as roads have shown to impact the abundance of terrestrial salamanders (Marsh and Beckman 2004, Homyack and Haas 2009, Hocking et al. 2013). Other amphibians occur in close proximity to breeding habitats such wetlands and streams and use these habitats to breed, deposit eggs and for larval development. These species are affected by both aquatic and upland habitat characteristics (Semlitsch 1998, Semlitsch and Bodie 2003, Peterman et al. 2014). Furthermore, regional vegetation is highly correlated with large-scale climate patterns (Gong and Ho 2003). Therefore, it is important that research focuses not only on local factors but regional, or landscape factors that affect amphibian populations.

Modeling Amphibian Response to Global Change

Previous research has used SDMs to predict the changes in habitat space for amphibians across the globe, including the United States (Parra-Olea et al. 2005, Araujo et al. 2006, Lawler et al. 2010, Milanovich et al. 2010, Barrett et al. 2014, Sutton et al. 2015, Fong G et al. 2015). Amphibians are useful model organisms for correlative model approaches because amphibians are poikilothermic, meaning they are tied highly to their abiotic environments. Therefore, variables often used in SDM approaches (e.g. climate) are likely the most significant factors determining their occurrence; increasing the accuracy of SDM predictions. In addition, for the above reasons, amphibians are considered sensitive species wherein they are often most negatively affected by environmental changes (Welsh and Ollivier 1998, Zhou et al. 2008, Koprivnikar et al. 2012). Thus, by investigating the effects of future changes on amphibians we can assess the full scope of negative impacts. Global climate change is perhaps the most foreboding future environmental change and many SDM approaches have predicted large reductions in suitable habitat space as well as shifting distributions for multiple amphibian species, specifically, shifting distributions toward higher latitudes and elevations (Parra-Olea et al. 2005, Lawler et al. 2010, Milanovich et al. 2010, Sutton et al. 2015). However, there are many gaps in the context of geography in scientific literature on the effects of climate change on the distribution of amphibians; even within the United States. For example, the effects of future climate change on the distribution of amphibians in the Midwestern U.S. have yet to be investigated. This area may be important as it contains fairly low elevation habitats as well as containing a high degree of amphibian diversity.

Ecological Importance of Amphibians

Amphibians play important roles within the multiple ecosystems in which they inhabit. First, amphibians typically occur at high densities and represent significant vertebrate biomass in many ecosystems. For example, Gibbons et al. (2006) found densities of larval anurans across decades at the Savannah River Ecology site in South Carolina was $3.7/m^2$, and showed a single wetland could produce a metric ton of amphibian biomass from metamorphic individuals. Second, high densities of amphibians often show their impact on nutrient cycles is prominent – especially when considering that many assimilate a high percentage of their diet into tissue (Fitzpatrick 1973, Davic and Welsh 2004, Semlitsch et al. 2014, Milanovich et al. 2015). Studies by Semlistch et al. (2014) and Milanovich and Peterman (2016) found that terrestrial salamanders occurred in high densities in forested ecosystems of the Midwestern United States and suggest their role in forest ecosystems nutrient dynamics is under-represented. The biphasic life history of some amphibians facilitates their impact on nutrient cycling and energy transfer within and between aquatic ecosystems (Regester et al. 2006, Schriever et al. 2014, Capps et al. 2015). For example, pond-breeding amphibians (e.g., *Ambystoma* spp.) deposit high amounts of biomass via eggs in wetlands by terrestrial adults and their decomposition and large energy inputs into wetland systems is significant (Regester and Whiles 2006). However, much is to be examined regarding amphibians role in ecosystem-level nutrient cycles.

Another aspect of amphibian ecology currently under-explored is their impact as predators. In many ecosystems, amphibians represent top predators, such as larval plethodontid salamanders in headwater streams (Keitzer and Goforth 2013). Larval pond-breeding salamandres, genus *Ambystoma*, also act as top predators within ephemeral wetlands (Benoy 2008). Pond-breeding salamanders are terrestrial as adults and aquatic as larvae. Adults breed in ephemeral wetlands to avoid predation by fish and as larvae are fully aquatic and predate on a variety of zooplankton and macroinvertebrate prey. However, there is discrepancy in the relationships in which larval predatory

Ambystoma have with invertebrates in aquatic systems. Previous research show varied effects of larval ambystomatids on aquatic invertebrates in wetland systems (Holomuzki and Collins 1987, Holomuzki et al. 1994, Blaustein et al. 1996, Benoy 2008, Urban 2013). Therefore, there is a need to further investigate the potential influence of larval ambystomatid salamanders on aquatic invertebrate communities in wetland ecosystems.

Experimental Design: Modeling the predicted impact of global change and quantifying the ecological role of pond-breeding salamanders in ephemeral wetlands located in the Midwestern United States

My research investigates the abiotic factors that influence the regional distribution of amphibians in the face of future climate change and land-use changes in the Midwestern United States (chapter 2). In addition I assess the local and landscape level factors that affect larval pond-breeding salamanders and their role in regulating ephemeral wetland communities (chapter 3). These investigations are aimed at untangling the relationships amphibians have with their environment and how that may affect their occurrence in the face of anthropogenic change and how those changes may affect ecosystems in which they live in.

The modeling portion of my study included modeling the changes in suitable habitat space for amphibian species in the Midwestern United States under future climate change and land-use changes. I used occurrence data of 33 amphibian species with known current distributions within an eight-state boundary in the Midwestern U.S. and eleven bioclimatic variables to model the ecological niche of each species. I employed an ensemble model design to model the distribution of amphibians for current, 2050 and

2070 predicted climate time periods, in which I used two general circulation models, two relative concentration pathways and three thresholds. I then quantified the change in suitable habitat space from current to future predictions. Next, I used current and predicted land-use to clip out unsuitable land-use area from the predicted suitable habitat area predicted by models and compared predictions from only climate (Climate-only) and predictions with unsuitable land-use removed (Climate + land-use). In addition, I quantified the changes in amphibian species richness from current to future predictions. I predicted declines in suitable habitat for all amphibians, land-use to have an increasingly negative effect on percent changes in suitable habitat and for overall species richness to decline. To better understand the consequences of changes in habitat space I wanted to further investigate the ecological role of amphibians in the Midwestern U.S.

The field portion of the study was conducted in both the Cincinnati, OH and Chicago, IL metropolitan areas. I designed a study to investigate the effects larval pond-breeding salamanders have on wetland communities. To do this, I extensively sampled five wetlands in Lake County, IL for larval pond-breeding salamanders (genus *Ambystoma*) and aquatic invertebrates. I also measured multiple wetland metrics such as dissolved oxygen, wetland area, days with water and percent urbanization of the adjacent landscape in an effort to understand which factors may be influencing the density of larval pond-breeding salamanders as well as aquatic invertebrate density. In addition I collected samples of both aquatic invertebrates as well as larval pond-breeding salamanders to identify the taxa in the water column of wetlands and the diets of larval *Ambystoma* species. Further, I analyzed previously collected data from a study conducted in Cincinnati, OH by colleagues from the U.S. EPA and Xavier University with a similar sampling design and methods. I predicted density of larval pond-breeding salamanders would have a significant effect on the density of aquatic invertebrates in wetland water columns.

CHAPTER II

GLOBAL CLIMATE CHANGE, NOT LAND-USE, DRIVES PREDICTED SUITABLE HABITAT DECLINES FOR MIDWESTERN UNITED STATES AMPHIBIANS

INTRODUCTION

Many believe we are currently undergoing a sixth mass extinction of global taxa, with losses of vertebrate species meeting or exceeding those of historic mass extinction events (Barnosky et al. 2011; Dirzo et al. 2014; Pievani 2014; McCallum 2015). The cause of these predicted and quantified extinctions are most prominently habitat change, global climate change, invasive species and over-collection – all of which are linked to human involvement (Pievani 2014). Two of the primary anthropogenic changes affecting terrestrial vertebrates are land-use and global climate change, each of which have been associated with declines in populations of mammals, birds, reptiles, and amphibians (Bryja et al. 2002; Chace and Walsh 2006; Fahrig and Rytwinski 2009; Delaney et al. 2010; Clipp and Anderson 2014). With a high percentage of land being modified within the past 30 years in the United States (Sleeter et al. 2013), land-use change has become a pervasive problem for conservation biology. Predictions of increased future land-use change in the United States (Radeloff et al. 2012) promotes the need for further study of the impact land-use changes have on biodiversity. In addition, global climate change is responsible for recent reductions of many vertebrate populations (McCarty 2001; Feehan et al. 2009; Lawler et al. 2009), and is likely to be a significant driver of extinctions in the future (Araujo et al. 2006). Studies examining the predicted synergistic effects of land-use and climate change can help elucidate the impact of change across ecosystems and assist with the formation of conservation plans to mitigate changes or losses.

Amphibians are declining at higher rates compared to other vertebrate classes on Earth (except fishes) (Stuart et al. 2004; McCallum 2007; Wake and Vredenburg 2008; Collins 2010; Wake 2012). Amphibian population declines have been linked to a variety of factors, such as habitat fragmentation, land-use changes, chemical pollution, climate change, and disease (Taylor et al. 2005; Fahrig and Rytwinski 2009; Todd et al. 2011; Pereira et al. 2013). Land-use characteristics and vegetative structure influence fine-scale microclimates, which are important for amphibians (Peterman and Semlitsch 2014), namely for maintaining physiological requirements, thus changes can drastically alter habitat suitability for amphibians. In addition, amphibians rely on land-use and habitat characteristics for proper breeding areas and refuge from predators (Trenham and Shaffer 2005; Scott et al. 2013; Osbourn et al. 2014). Consequently, anthropogenic conversion of natural habitat has resulted in declines among a number of amphibian populations (Naughton et al. 2000; Barrett and Guyer 2008; Pillsbury and Miller 2008; Price et al. 2011).

While land-use affects amphibian habitat suitability locally, climate is a critical factor that shapes the suitability of amphibian habitat at local, landscape and larger geographic regions. Amphibians are poikilothermic and thus rely on their external environment to maintain body functions for survival. In addition, the broader geographic distribution of species is also determined by larger climate regimes, as these broad regimes constitute the make-up of microclimates (Jimenez-Valverde et al. 2011). Global climate change threatens to significantly alter broad climatic regimes that directly shape the distributions of amphibians, therein forcing either their adaptation or migration. Broad shifts in distributions, however, could be problematic for many amphibian species because of their low dispersal abilities (Trenham and Shaffer 2005; Scott et al. 2013; Hillman et al. 2014) and relatively small home ranges (Findlay and Houlahan 1997) compared to other taxa. Therefore, predictions of how climate change and land-use changes may alter the suitability of habitat for amphibians are useful to assist in the creation of management or conservation efforts.

Forecasting changes in suitable habitat with species distribution modeling (SDM) serves as a useful tool to begin to understand how species may respond to anthropogenic change. Doing so for multiple species can uncover how biodiversity and ecosystem processes may change as well. For example, amphibians are important for nutrient cycling and storage within and between ecosystems (Regester et al. 2006; Semlitsch et al. 2014; Milanovich et al. 2015). A loss of functional diversity of amphibians could therein disrupt important ecological processes. Thus, modeling potential changes in amphibian biodiversity is important for understanding potential consequences for these processes. Ecological niche modeling has been employed to forecast the effects of climate change on amphibian habitat in recent studies (Milanovich et al. 2010; Barrett et al. 2014; Groff et al. 2014; Fong et al. 2015; Sutton et al. 2015) and these studies predict wide-ranging reductions in suitable habitat for nearly all amphibians under future climate change scenarios. Additionally, many of these studies find that predicted suitable habitat for species shifted toward areas with higher elevation to follow suitable habitat as predicted climate changes, which serves the same function as species shifting higher in latitude (Randin et al. 2013), but elevation offers this analogous change in climate over a shorter distance. For amphibians, adjacent climatic refuge may be essential because of their low vagility and inability for many species to migrate long distances in short periods of time. Therefore, regions with substantial amphibian diversity and relatively low relief (e.g., the Midwestern United States) may result in significant losses in suitable amphibian habitat. Yet, most amphibian SDM studies have focused on montane regions, potentially buffering their predicted effects (Milanovich et al. 2010; Sutton et al. 2015). In addition, land-use has seldom been included in amphibian SDMs, although it is widely recognized to be a limiting environmental variable for amphibian habitat.

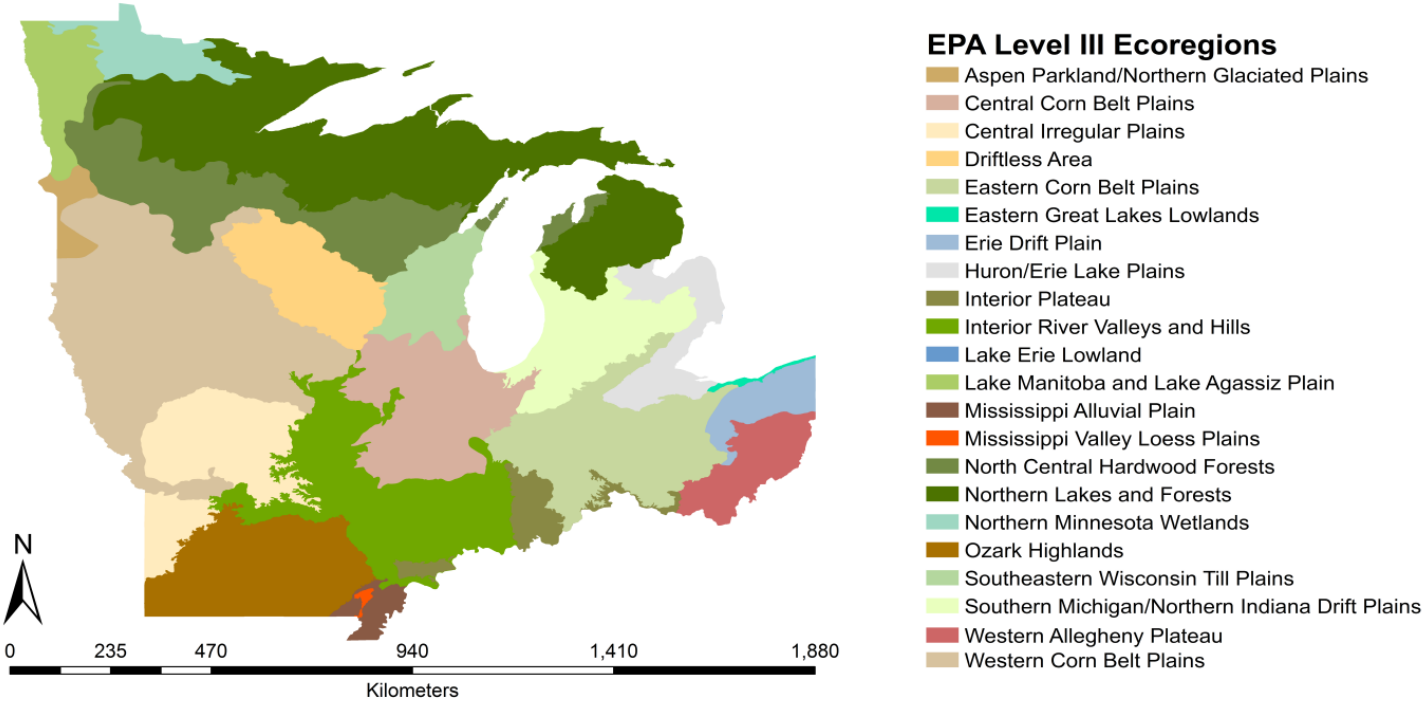
Our objectives were to utilize SDMs to predict the future effects of predicted global climate and predicted land-use change on the suitable habitat of amphibian species and resulting amphibian species richness in the Midwestern United States. We predict that Midwestern amphibians will show more predicted reduction in future suitable climatic habitat compared to other studies, and that predictions of suitable habitat reductions will increase through time and with the incorporation of predicted land-use change. Furthermore, we predict amphibian species richness predictions will respond to predicted declines in suitable habitat and also decrease via time.

MATERIALS AND METHODS

Study area and species

The aim of our study was to use ecological niche models to project species distributions of amphibians in the Midwestern United States (herein Midwest) based on several global climate change scenarios (herein climate-only models). The Midwest was defined by the boundaries of eight states: Minnesota, Iowa, Missouri, Illinois, Wisconsin, Michigan, Indiana, and Ohio. Although this state-based outline was somewhat subjective, it incorporated a high amount of amphibian diversity and represented an area with little relief, thus accomplishing our objectives to model amphibians of the Midwestern U.S. in an area largely void of montane habitat. The majority of our study region is dominated by similar habitats including floodplains, lowland forests, agriculture and prairies. However, it does contain some small portions of higher elevation habitats such as the Ozark Highlands, portions of the Interior Plateau, and the Western Allegheny Plateau (Fig. 1). We modeled the suitable climatic habitat of 33 amphibian (19 salamander, 14 anuran) species with any portion of their current known distribution within the study area (Appendix A;B). This represented 62% of the total number of amphibian species with some portion of their current known distribution within our study region. Other species were not included in models for lack of data (< 20 individual point localities). Four of the 33 species included represent species complexes. Complexes were comprised of species that were either two sub-species of the same complex, (*Plethodon glutinosus*/*Plethodon albagula* complex, *Eurycea bislineata*/*Eurycea cirrigera* complex and *Plethodon cinereus*/*Plethodon serratus* complex), or species that have overlapping ranges and are difficult to differentiate (*Hyla versicolor*/*Hyla chrysoscelis* complex). Species complexes were modeled as a single species.

Figure 1. The Midwest region (model region) depicted with EPA Level III Ecoregions.



Environmental data

We utilized four predicted future climate change scenarios from the IPCC 5th Assessment Report (AR5) under two global circulation models (GCM; CCSM4 [CCSM] and HadGEM2-ES [Hadley]) and two representative concentration pathway (RCP) greenhouse gas emissions projections, RCP 2.6 (Low) and RCP 8.5 (High), from each GCM – each across three decades: current (average of years 1950-2000), 2050 (average of years 2041-2060) and 2070 (average of years 2061-2080). Each RCP emissions scenario represents changed radiative forcing relative to pre-industrial atmospheric greenhouse gas levels (van Vuuren et al. 2011). The AR5 scenarios (RCPs 2.6, 4.5, 6.0, 8.5) range from anthropogenic greenhouse gas emissions reversal to continued anthropogenic greenhouse gas emissions through the year 2100. The RCP 2.6 scenario predicts anthropogenic greenhouse gas emissions peak before mid-century and decline thereafter, thus being the lowest predicted emissions scenario. The RCP 8.5 scenario is the highest predicted emissions scenario and predicts continued increased anthropogenic greenhouse gas emissions to the year 2100. Global circulation models were selected for our SDMs because of their previous versions' effectiveness in reproducing important Northern Hemisphere oscillations (Stoner et al. 2009), indicating their ability to accurately reproduce natural meteorological phenomenon. Two separate GCMs and RCP projections were used to account for potential bias from either predictive model on its own. Additionally, multi-GCM and RCP approaches are commonly used in climate-based SDMs (Milanovich et al. 2010; Matthews et al. 2011; Barbet-Massin et al. 2012; Barrett et al. 2014; Sutton et al. 2015) and the approach to create an ensemble of projections has received support (Araujo and New 2007). Climate data were downloaded from the WorldClim database (www.WorldClim.org) with 30 arc second resolution (~1 km^2). We used 11 out of 19 bioclimatic variables provided by WorldClim (Table 1). Bioclimatic variable layers used in models were selected based on previous use in a similar amphibian bioclimatic modeling study (Sutton et al. 2015) in which highly correlated variables were consolidated, which resulted in eleven bioclimatic variables used in models.

Occurrence data

Species occurrence data represent geographic locations from natural history museums of documented sightings and were accumulated from the Biodiversity Serving Our Nation (BISON) database (www.BISON.usgs.ornl.gov) and the HerpNET database (www.HerpNet.org). Coordinates of each datum point were discarded if less than four digits after the decimal to ensure accuracy within the resolution of our environmental data (1 km2). We chose 10,000 background samples at random within our study region to sample pseudo-absences for each species to build models. Supplementary to that, data were filtered in ArcMap™ version 10.2 to only include occurrence data within our study region and only within their respective current known distribution according to USGS National Amphibian Atlas county-based range maps (Lannoo 2005). We acknowledge limiting occurrence data within our study region and excluding data outside of this region limits our knowledge in some capacity. Excluding occurrence data beyond our study region results in eliminating data and species that could become a factor in future projections as species distributions potentially shift. In addition, by excluding external data we may lose the total variation of the ecological niche of any species, especially those with large portions of their distribution outside of our study area. Yet, our study area represents a large region with a high degree of variability in climate, and model projections show strong ability for models to predict continuity of suitable habitat with distribution shifts. Further, our results support the validity of our data encompassing enough variation in environmental values representing total variation across the distribution of a given species.

Maxent modeling

Projected current and future distributions of amphibians for climate-only models were performed using Maxent version 3.3.3k. Maxent is an ecological niche modeling program that uses presence-only points in concert with continuous environmental raster data to 'learn' the current ecological niche for each input species (Phillips et al. 2006). Predicted projections of future suitable habitat are made with Maxent by providing forecasted layers of the environmental data. Maxent then projects future predicted suitable habitat derived from environmental forecasts referencing 'learned' current niches. Since its introduction, Maxent has been used increasingly to model species distributions with presence-only data and there is a growing body of evidence on its superior accuracy to other presence-only modeling applications (Phillips et al. 2006; Merow et al. 2013).

Sampling bias is a well-known limitation of presence-only occurrence data because they are often a collection of datum from multiple sources likely with varying sampling efforts (Ruiz-Gutierrez and Zipkin 2011). Therefore it is difficult to distinguish areas with a high density of individuals between areas sampled with higher sampling effort. In addition, some areas are better represented in databases from heavier sampling frequency (e.g. an ecological research site) than others, creating pseudo-hotspots of occurrence. We accounted for this inherent bias by thinning data points within a 5 km radius of one another with the Spatial Rarify tool in the SDM Toolbox add-in (Brown 2014) for ArcMap. This distance is effective in eliminating bias within heavily sampled areas for amphibians (Barrett et al. 2014) improving model accuracy. In addition our study region incorporated many populated cities. Initial model runs showed population centers represented hotspots for amphibian occurrence in projections, likely the result of sampling bias from high incidental contact between humans and amphibians and not from truly suitable habitat. We accounted for this bias with a continuous raster of human population in Maxent's bias file. Population bias data was derived from 2006 U.S. census data (www.census.gov) based on population per street block. Census data was adjusted to represent sampling effort accurately. Grids with populations of zero to one were defined as a sampling effort of one. Then, each value of population density was given its actual value to accurately represent the population density in that grid. Maxent reads this bias file as a grid with a value of five being sampled five times more likely than a grid with a value of one. We avoided reclassifying our bias file into large classes to gain the most accurate and fine-scale effect. These data were up-scaled to align with the spatial scale of our environmental data.

Projecting future species suitable climatic habitat

For creation of climate-only SDMs we built an ensemble model design to create a gradient of predictions to reduce influence of single modeling variables. We used a replicate runs approach with ten replicate runs for each modeling scenario to obtain an average of model runs in Maxent. As described above, we created our SDMs for three decades (current, 2050 and 2070), two GCMs (CCSM4 and HadGEM2-ES), and two RCP emissions scenarios (RCP 2.6 and RCP 8.5). Additionally, we applied three statistical thresholds (derived from Maxent output) to the probability distribution maps output by Maxent to define areas of suitable habitat as presence/absence (1/0) binary maps: Liberal (Minimum Training Presence), Intermediate (Fixed 10 Cumulative), and

Strict (Maximum Test Sensitivity plus Specificity). A gradient of thresholds reduces the influence of a single threshold on predictions of suitable habitat (Araujo and New 2007; Nenzen and Araujo 2011). Our ensemble design resulted in 27 model scenarios per species.

Species distribution model performance was tested by the default Maxent area under the receiver operator characteristic curve (AUC). We used Bootstrap resampling method for sampling occurrence data for test data to test the accuracy of our models. We randomly selected ten percent of occurrence data for each species to test model performance. A regularization multiplier value of four was used in contrast to the default value of one. Regularization in Maxent is an option designed to account for model overfitting, a common problem in presence-only modeling. Overfitting occurs when Maxent predicts the functional niche to be smaller than the realized niche of any species. When SDMs were run with the default regularization multiplier value, current projections were over-fit for all thresholds. We chose to use a value of four because it corrected model overfitting and is a supported value to correct this issue (Radosavljevic and Anderson 2014).

Each binary map was clipped to a genus-based dispersal limitation to ensure realistic analyses for change in suitable habitat. Dispersal limitations were created by buffering current USGS county-based range maps of each species (Lannoo 2005) by a determined yearly dispersal distance multiplied by the number of years from 2015 to both 2050 (35) and 2070 (55). Our dispersal distances were created for a best-case scenario in which species could move without limitation from habitat resistance. We based our dispersal distances on a genus-specific ability for amphibians to traverse suitable habitat. This ranged from 20 kilometers per year (*Lithobates and Anaxyrus*), one kilometer per year (*Ambystoma*, *Hemidactylium*, *Notophthalmus*, *Hyla*, *Acris*, *Pseudacris, Eurycea*, *Gyrinophilus*, *Desmognathus*), and 100 meters per year (*Plethodon*) (Smith and Green 2005).

Quantifying predicted changes in species suitable climate habitat

Differences in suitable habitat from current to future projections were quantified by grid cell counts from the reclassified binary maps clipped by the dispersal limits. Current projections were also clipped by both the 2050 and 2070 dispersal distances so differences between current and future projections would be standardized. We report changes in suitable habitat as percent changes in relation to current projected habitat. Percent changes were quantified by subtracting the number of presence raster cells for each threshold for future projections from the number of presence raster cells for the corresponding threshold for the current projections and then dividing the result by the presence cells for the respective current projection.

Quantifying predicted changes in species suitable climatic and land-use habitat

We utilized the United States Geological Survey (USGS) forecasted land cover scenarios based on storylines B1 and A2 (low emissions and high emissions, respectively) from the USGS EROS project (landcover-modeling.cr.usgs.gov) to examine the impact of current and predicted future land-use changes on predicted suitable habitat of amphibians. Current land-use data (Landsat imagery from 2011) were downloaded from the National Land Cover Database from the USGS Multi-Resolution Land

Characteristics Consortium website (www.mrlc.gov) and future projected land-use data were downloaded from the USGS Earth Resources Observation and Science Center dataset (landcover-modeling.cr.usgs.gov). Next, each land-use projected scenario map (current, 2050 B1, 2050 A2, 2070 B1, and 2070 A2) was reclassified from its initial classification down to six land cover classes: open water, developed, forest, agriculture, grassland, and wetlands. Each reclassified land-use projection scenario map was used to determine suitable land-use habitat for each genus modeled in climate-only SDMs by identifying suitable land-use categories for each genus. For example, salamanders in the genus *Plethodon* rely solely on cutaneous respiration and therefore typically inhabit areas with a high amount of canopy cover, so land-use cells other than forest were deemed unsuitable for this genus. Suitable land-use cells for each species representing genera level suitable land-use were thus removed from the reclassified land-use projection scenario maps to create maps showing only unsuitable habitat cells for each genus. Next, for each decade (current, 2050 and 2070) we clipped predicted suitable habitat projection maps from the climate-only SDM output with the reclassified land-use projection scenario maps representing unsuitable habitat for each genus to create a series of maps predicting the impact of both predicted global climate and land-use change (herein climate + land-use maps).

For climate + land-use maps we used years 2050 and 2070 for future land cover data because it represents the best replacement for an average of years provided by WorldClim for climate data. All land cover data were up-scaled from 30m^2 grids for current data and 250m^2 grids for future data to better match the spatial resolution of our climate data of 0.00083 degree grids (~1 km^2). Although USGS Multi-Resolution Land Characteristics Consortium data is based on a previous assessment of climate by the IPCC, the relative trends in climate change scenarios for the fourth and fifth assessments were similar, but differed in their predicted values (e.g. RCP 2.6 and B1 represent the same trend in emissions but with higher radiative forcing values in the fifth assessment scenarios). Land-use predictions based on the IPCC fourth assessment, therefore, are a conservative estimate compared to what may be projected according to the AR5 emissions – all have increased.

Quantifying predicted changes in species richness

We developed species richness maps to quantify the changes in habitat suitability across all species from current projections to future scenarios in both climate-only and climate + land-use predictions. Richness maps were created for each projected scenario by overlapping projections for each species within the same scenario. This assigned values to each grid cell with the number of species with a presence value in that cell. We present richness maps for our study averaged across decades (Current, 2050, and 2070). We also used EPA Level III Ecoregions to assess species richness changes within our study area to identify areas of important climatic and land-use refuge. Each Ecoregion received its respective weighted average of richness within its boundaries for each timeline. We did this to assign a richness value to each Ecoregion in order to identify ecoregions that sustained a high amount of species richness from current to future projections.

Statistical analyses

We used a two-way ANOVA to determine whether percent changes in predicted suitable habitat or ecoregion-level species richness (dependent variables) differed between climate-only and climate + land-use maps and decade (2050 or 2070). Ensemble model designs inherently have multiple factors potentially influencing the dependent variable. We attempted to gain a better understanding of how our modeling factors may influence suitable habitat changes by utilizing general linear models (GLMs) to analyze the influence of GCM, emissions scenario, threshold, and latitude on the percent changes in suitable habitat separately for each future decade. The interaction term between latitude and threshold for the GLM was significant; therefore, we utilized one-way ANOVA to examine whether percent change in suitable habitat differed across thresholds and used Bonferroni correction to determine statistical significance. We calculated the centroid of each species range (Lannoo, 2005) and used the latitude coordinate from those centroids as a continuous predictor variable in the GLM. This variable was important to include in the GLMs because there is potential species adapted to warmer climates (species with lower latitude centroids) may be affected differently than species adapted to cooler climates (species with higher latitude centroids). We corrected our percent changes for statistical analyses by adding a constant to each value to eliminate negative values. Each significant ANOVA was followed by a Tukey HSD multiple comparisons test. All statistical analyses were performed using STATISTICA 12.0 (Statsoft, Inc., Tulsa, OK) with an $\alpha = 0.05$.

RESULTS

Climate-only models predicted an average decline of suitable habitat for 24 of 33 species (73%) across all scenarios in 2050 and 25 of 33 species (76%) across all scenarios in 2070 (Appendix A). In our best-case modeling scenario (CCSM – RCP 2.6 for 2070), 19 of 33 species showed some predicted suitable habitat decline, seven species showed a >50% predicted decline and four species (*Ambystoma laterale*, *Hemidactylium scutatum*, *Lithobates pipiens*, and *Lithobates septentrionalis*) showed a predicted decline >75% of their current projected suitable habitat averaged across thresholds. The worst-case model scenario (Hadley – RCP 8.5 for 2070) predicted 27 of 33 species to lose suitable habitat in some capacity, in which 24 of those species were projected to lose >50% and 20 were projected to lose >75% of their current projected habitat, averaged across thresholds (Appendix A). Further in that same scenario, 17 species were projected to lose >90% of their current suitable habitat and eight species (*Ambystoma jeffersonianum*, *Ambystoma laterale*, *Eurycea bislineata*/*Eurycea cirrigera* complex, *Gyrinophilus porphyriticus*, *Hemidactylium scutatum*, *Lithobates septentrionalis*, *Plethodon dorsalis*, and *Plethodon electromorphus*) were projected to lose 100% of their predicted suitable habitat. All families experienced a species with predicted declines in suitable habitat in this model scenario. Alternatively, this scenario also predicted the highest increase in suitable habitat for any species with *Lithobates sphenocephalus* projected to gain an average of 410% of suitable habitat. Increases in suitable habitat were predicted for five species (*Ambystoma annulatum, Ambystoma tigrinum, Ambystoma texanum*, *Lithobates blairi*, and *Lithobates sphenocephalus*) in our worst case scenario. In addition, 18 species were projected to lose suitable habitat in every model scenario, and *Ambystoma laterale* were projected to lose 100% of predicted suitable habitat in every scenario (Appendix A). Alternatively, five species were projected to gain suitable habitat in every model scenario, while *Lithobates sphenocephalus* was projected to more than double its current predicted suitable habitat in every scenario, averaged across thresholds (Appendix A).

Suitable habitat changes were not significantly different between climate-only models and the climate + land-use predictions (Table 2; Fig. 2). For example, for climate + land-use 2050 projections 21 of 33 species were predicted to lose suitable habitat in some capacity while 10 of those species lost >50% of their current projected suitable habitat. Projections for 2070 predicted 23 of 33 species lost suitable habitat in some capacity and 15 of those species lost >50% of suitable habitat (Appendix B). Additionally, climate + land-use results predicted 17 species to lose suitable habitat across all scenarios while six species gained suitable habitat across all scenarios. Amphibian families varied in their effects from including the impact of land-use. Ambystomatidae, Hylidae, Plethodontidae, and Salamandridae decreased their average suitable habitat from climate-only to climate + land-use SDMs. Yet Bufonidae and Ranidae had a predicted increase in suitable habitat after land-use was included (Fig. 2).

Ecoregion-level species richness was significantly different across decades, with current species richness predicted to be significantly greater than both 2050 and 2070 (Table 3). Species richness dropped from an average of 10.8 species in current projections across the model region to an average of 7.8 and 7.7 species for 2050 and 2070 projections, respectively (Fig. 3). The highest richness value also dropped from 27 species in current projections in areas to 20 species in both 2050 and 2070 projections (Fig. 3). Many ecoregions also experienced declines in richness losing an average of six or more species, with all ecoregions losing richness from current to future projections (Fig. 3). However, the Ozark Highlands, Central Irregular Plains, and Western Corn Belt Plains conserved their richness compared to other ecoregions in both 2050 and 2070 projections (Fig. 3). The Western Allegheny Plateau, Erie Drift Plain, and Interior Plateau retain higher species richness compared to other ecoregions in future projections (Fig. 4).

With respect to the ensemble model factors and biotic characteristics that predicted the percent changes in suitable habitat, model factors such as GCM and emissions scenario were not significant in their influence on percent changes in predicted suitable habitat singly or in any interaction term (Table 4). As a result, for other analyses we did not separate GCM or emissions scenario, instead we report results as averages across GCMs and emissions scenarios, separated only by each future decade (2050 and 2070). Both 2050 and 2070 projections had significant influence from latitude, threshold, and the interaction between the two on percent changes in predicted suitable habitat (Table 4). Percent change in suitable habitat did not significantly vary across thresholds for 2050 (df = 2, MS = 3534, F = 0.616 $P = 0.540$) or 2070 (df = 2, MS = 5962, F = 0.767 $P = 0.464$). Latitude had a significant negative relationship on percent changes in predicted suitable habitat for all three thresholds (Fig. 5) indicating species with current distributions in the southern portion of the Midwest were predicted to have greater increase in suitable habitat while species with current distributions in the northern portion were predicted to have declines in suitable habitat. The strict threshold (Maximum Test Sensitivity plus Specificity) had the strongest negative relationship with latitude and percent change in predicted suitable habitat compared to the other thresholds in both timelines. Bioclimatic variables with greatest contribution to models varied across family (Table 1). However, BIO1 (Mean Annual Temperature) had the highest percentage of contribution to models for four of six families (Table 1).

Area under the curve values were on average >0.80 for 27 species while all others were >0.70, except for *Ambystoma tigrinum*, which had a lower AUC value at 0.63 on average. There is evidence that as a current distribution of a species increases (e.g., *A. tigrinum* had the largest current distribution of all species modeled), AUC values decrease. We attribute this to generalist species with multiple habitats and widespread distributions making it difficult for Maxent to predict their niche better than random. This is supported by our data as species with values under 0.80 were species with widespread distributions in the Midwest. We assign confidence to our model predictions because AUC values are within the accepted range for most species (Baldwin 2009) and are likely best-case values for species with widespread distributions.

Table 1. Mean (± SD) of bioclimatic variable percent contribution to models by family for each model decade. BIO1: Annual Mean Temp; BIO2: Mean Diurnal Range; BIO3: Isothermality; BIO7: Temperature Annual Range; BIO8: Mean Temperature of Wettest Quarter; BIO9: Mean Temperature of Driest Quarter; BIO15: Precipitation Seasonality; BIO16: Precipitation of Wettest Quarter; BIO17: Precipitation of Driest Quarter; BIO18: Precipitation of Warmest Quarter; BIO19: Precipitation of Coldest Quarter.

Decade	Family	BIO1	BIO2	BIO3	BIO7	BIO8	BIO9	BIO15	BIO16	BIO17	BIO18	BIO19
2050	Ambystomatidae	18 ± 20	4 ± 7	4 ± 5	8 ± 15	3 ± 4	17 ± 15	17 ± 2	2 ± 2	19 ± 19	3 ± 4	4 ± 3
	Bufonidae	22 ± 7	1 ± 0	3 ± 2	14 ± 4	9 ± 4	7 ± 4	8 ± 4	6 ± 6	23 ± 14	2 ± 0	6 ± 3
	Hylidae	22 ± 20	9 ± 12	6 ± 3	8 ± 6	7 ± 2	12 ± 8	10 ± 7	7 ± 5	6 ± 4	7 ± 3	5 ± 4
	Plethodontidae	6 ± 8	1 ± 2	7 ± 7	11 ± 12	2 ± 2	12 ± 13	14 ± 11	3 ± 4	32 ± 24	4 ± 3	7 ± 7
	Ranidae	42 ± 33	1 ± 1	4 ± 6	8 ± 8	4 ± 3	13 ± 14	10 ± 9	5 ± 4	6 ± 6	4 ± 5	3 ± 4
	Salamandridae	12 ± 0	2 ± 1	2 ± 0	10 ± 3	4 ± 1	4 ± 1	35 ± 2	1 ± 0	11 ± 0	4 ± 0	15 ± 2
2070	Ambystomatidae	17 ± 19	5 ± 8	4 ± 6	8 ± 15	4 ± 4	17 ± 15	18 ± 18	2 ± 2	18 ± 19	3 ± 3	4 ± 4

Bufonidae	23 ± 6	1 ± 0	2 ± 2	14 ± 3	8 ± 4	8 ± 4	10 ± 5	5 ± 3	23 ± 16	2 ± 1	4 ± 1
Hylidae	23 ± 20	8 ± 10	7 ± 5	8 ± 6	6 ± 2	13 ± 8	12 ± 9	8 ± 4	6 ± 4	6 ± 2	5 ± 4
Plethodontidae	6 ± 9	1 ± 2	7 ± 7	11 ± 11	2 ± 2	13 ± 15	16 ± 12	3 ± 3	30 ± 25	5 ± 3	7 ± 8
Ranidae	42 ± 33	1 ± 1	4 ± 7	9 ± 8	4 ± 3	13 ± 13	10 ± 9	4 ± 2	5 ± 6	4 ± 4	3 ± 4
Salamandridae	11 ± 1	2 ± 1	3 ± 1	10 ± 5	4 ± 0	3 ± 1	36 ± 2	1 ± 1	10 ± 2	4 ± 1	16 ± 5

Figure 2. Mean (± SE) percent change in predicted suitable habitat from current to (A) 2070 and (B) 2050 projections for Climate-Only and Climate + Land-use projections across each families. Dotted line at zero percent represents the cut-off for families that either gain (above line) or lose (below line) suitable habitat.

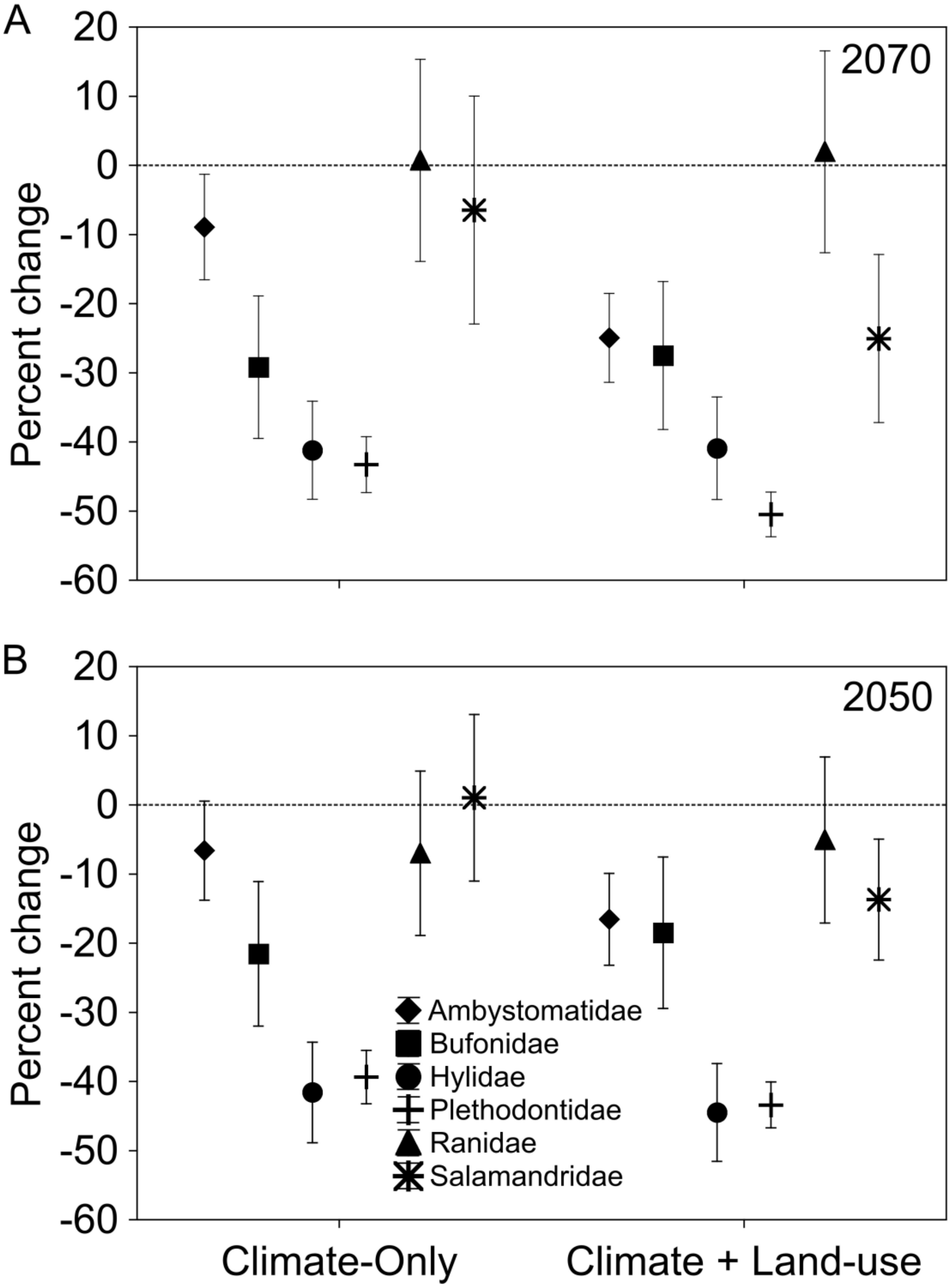


Table 2. Results from two-way ANOVA table investigating differences in percent suitable habitat change in Climate-only and Climate + land-use SDMs.

Effect	df	MS	F	*P*
SDM	1	28727	3.758	0.052
Decade	1	1660	0.217	0.641
SDM*Decade	1	781	0.102	0.749
Error	1580	7644	–	–

Table 3. Results from two-way ANOVA table investigating differences in species richness in Climate-only and Climate + land-use SDMs.

Effect	df	MS	F	*P*
Decade	2	117	5.033	0.008
SDM	1	5	0.231	0.632
Decade*SDM	2	4	0.181	0.834
Error	126	23	-	-

Figure 3. Mean (± SE) species richness change (weighted average of the number of species with suitable habitat) within EPA Level III Ecoregions across the Midwest from Current to (A) 2070 and (B) 2050 projections.

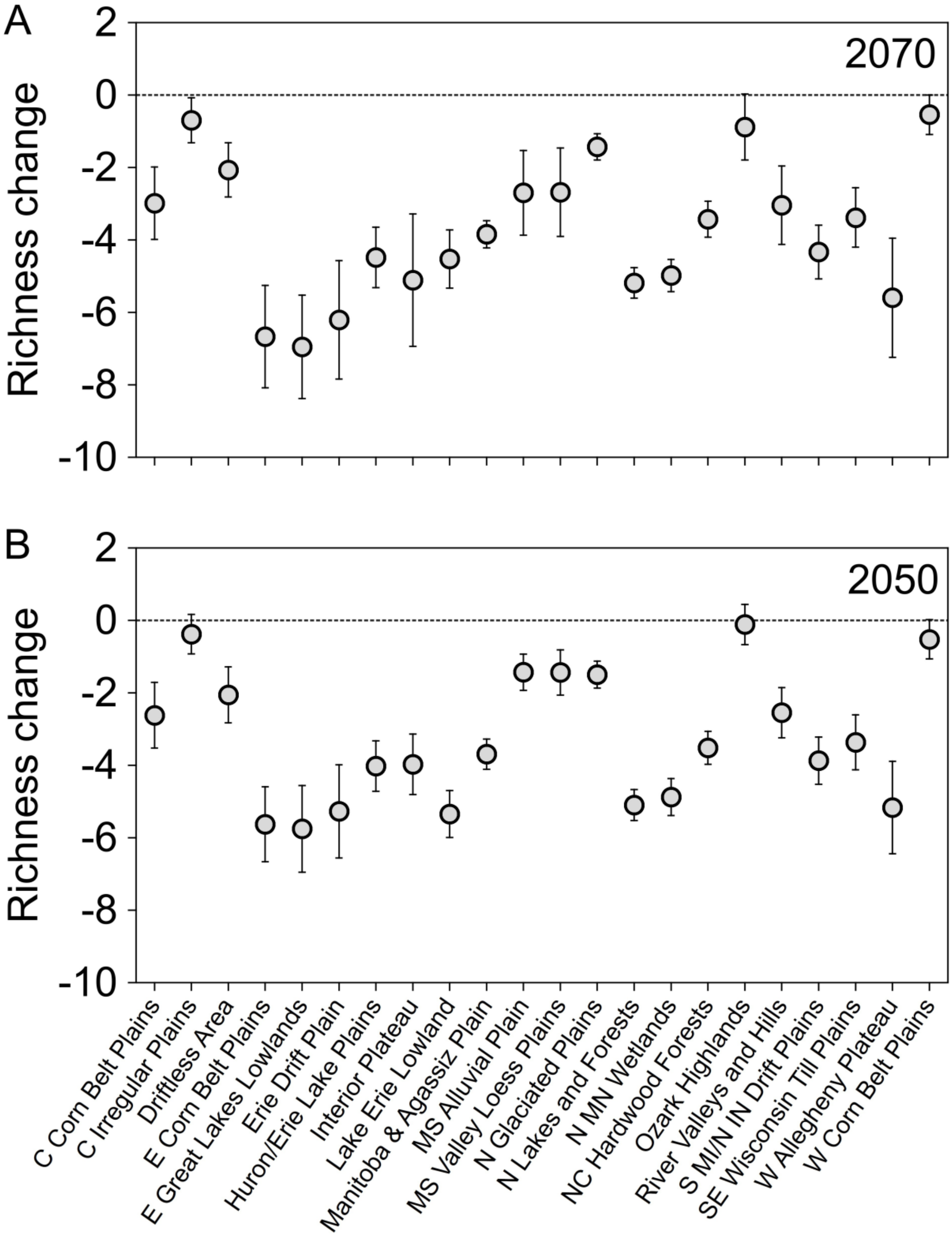


Figure 4. Species richness (weighted average of the number of species with suitable habitat) for EPA Level III Ecoregions in 2070 (A), 2050 (B), and Current (C). Species richness for entire Midwest region in 2070 (D), 2050 (E), and Current (F). Red and light coloration indicates higher species richness and blue or dark coloration indicates lower species richness.

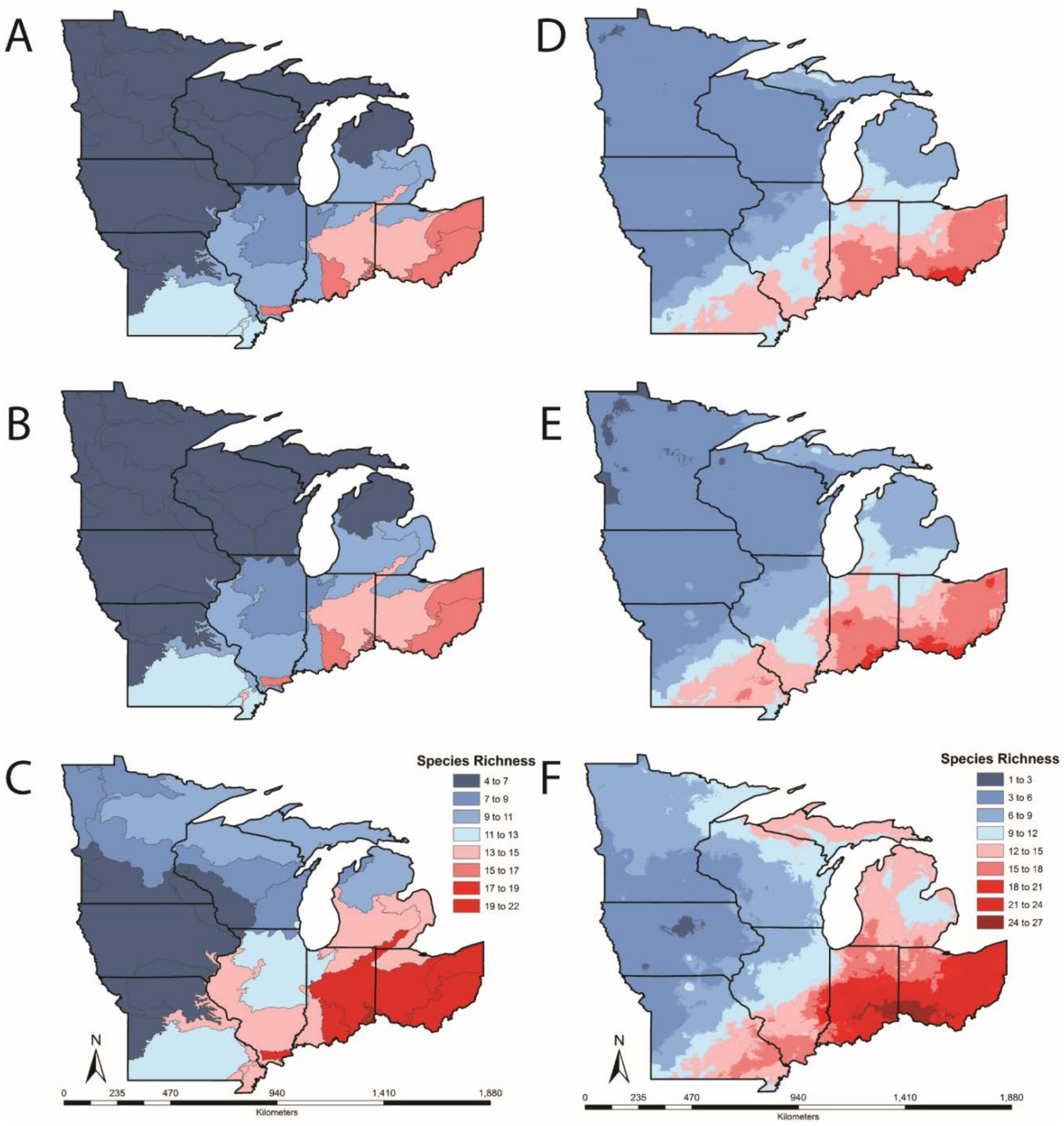
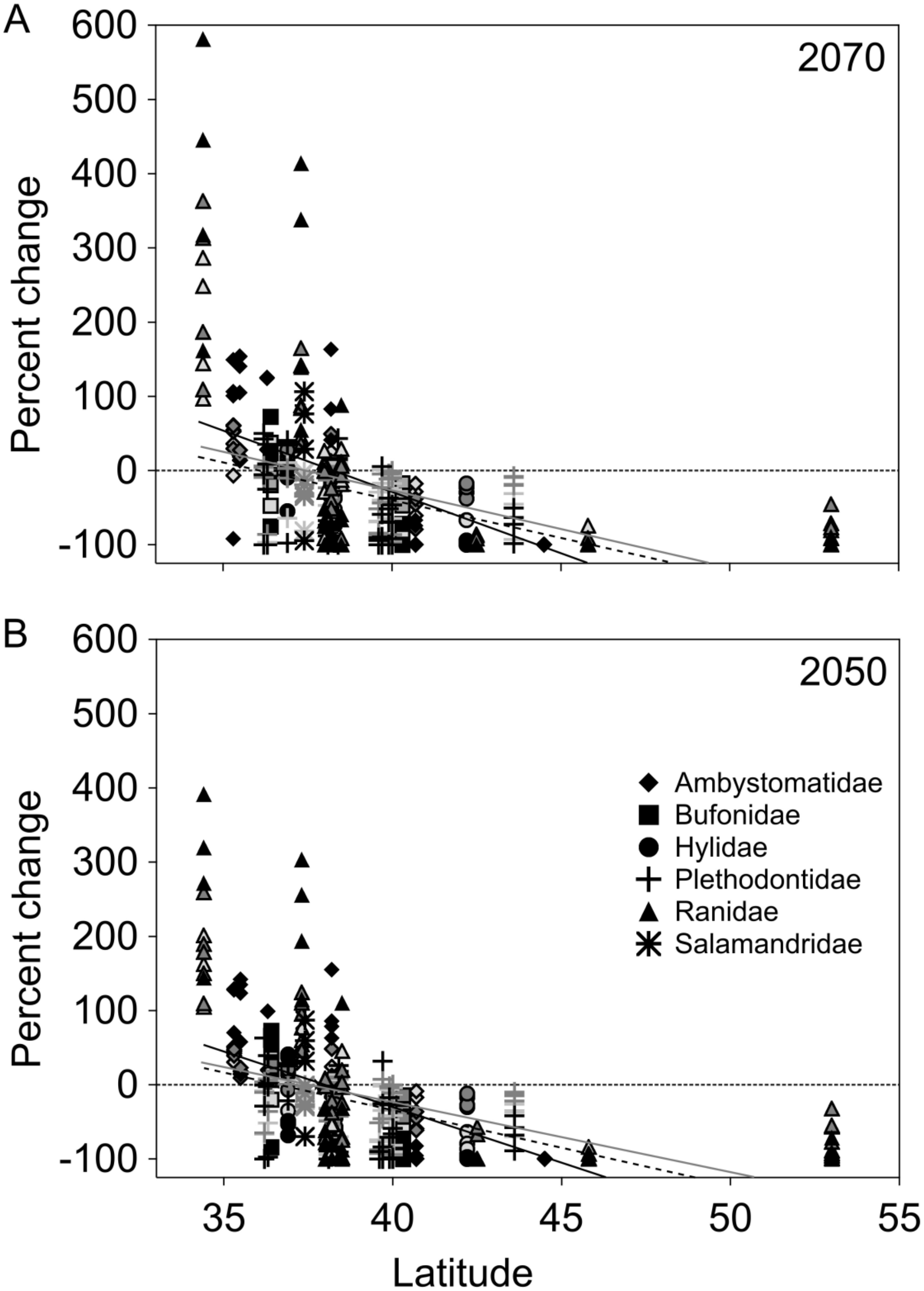


Table 4. Results from general linear model investigating the influence of model variables on percent suitable habitat change in 2050 and 2070 for Climate-only SDMs.

		2050			2070		
Effect	df	MS	F	*P*	MS	F	*P*
Threshold	2	15712	3.921	0.021	20849	3.664	0.027
Emission	1	1325	0.330	0.566	3273	0.575	0.449
GCM	1	2234	0.557	0.456	545	0.096	0.757
Latitude	1	662132	165.235	≤0.001	772962	135.841	≤0.001
Threshold*Emission	2	30	0.008	0.992	216	0.038	0.963
Threshold*GCM	2	66	0.017	0.984	263	0.046	0.955
Emission*GCM	1	8334	2.08	0.150	14625	2.570	0.110
Threshold*Latitude	2	15727	3.925	0.021	20046	3.523	0.031
Emission*Latitude	1	2035	0.508	0.476	4644	0.816	0.367
GCM*Latitude	1	3642	0.909	0.341	11	0.002	0.965
Threshold*Emission*GCM	2	524	0.131	0.878	88	0.016	0.985
Threshold*Emission*Latitude	2	19	0.005	0.995	163	0.029	0.972
Threshold*GCM*Latitude	2	30	0.008	0.993	202	0.036	0.965
Emission*GCM*Latitude	1	6312	1.575	0.210	11339	1.993	0.159
Error	374	4007	–	–	5690	–	–

Figure 5. Relationship between latitude and percent of suitable habitat change from current suitable habitat to (A) 2070 and (B) 2050 projections for each family examined categorized by model threshold. Linear regression equations for 2070 (A) are as follows: Strict threshold: $r^2 = 0.243$, $P < 0.001$, Percent change = 624.81 - 16.3998*Latitude; Intermediate threshold: $r^2 = 0.329$, $P < 0.001$, Percent change = 375.2678 - 10.3253*Latitude; Liberal threshold: $r^2 = 0.280$, $P < 0.001$, Percent change = 393.8155 - 10.4912*Latitude. Linear regression equations for 2050 (B) are as follows: Strict threshold: $r^2 = 0.275$, $P < 0.001$, Percent change = 568.2029 - 15.0076*Latitude; Intermediate threshold: $r^2 = 0.389$, $P < 0.001$, Percent change = 363.3885 - 9.9502*Latitude; Liberal threshold: $r^2 = 0.328$, $P < 0.001$, Percent change = 355.4857 - 9.4847*Latitude. Each point represents a threshold projection for each species, categorized by family: Intermediate threshold = light gray points, dashed black line; Liberal threshold = dark gray points, solid gray line; Strict threshold = black points, solid black line. Lines of fit represent significant effect of each threshold on percent changes.


A
2070
B
2050
Percent change
Percent change
600
500
400
300
200
100
0
-100
35
40
45
50
55
Latitude
◆ Ambystomatidae
■ Bufonidae
● Hylidae
+ Plethodontidae
▲ Ranidae
✳ Salamandridae

DISCUSSION

We predict a large proportion of Midwestern amphibians to lose significant portions of their current suitable habitat under future climate change scenarios. Over 70% of the species modeled in both 2050 and 2070 projections lost predicted suitable habitat in some capacity, with many species predicted to lose all suitable habitat. As a result, species richness also declined from current to both 2050 and 2070 projections (Figs. 2 and 3). Our results are consistent with other amphibian bioclimatic species distribution models that significant declines in suitable habitat for amphibians in the United States (Milanovich et al. 2010; Barrett et al. 2014; Sutton et al. 2015) and with studies over larger geographic areas that predicted expansions in suitable habitat for a few species (Araujo et al. 2006; Lawler et al. 2010). We also predicted large northerly shifts in suitable habitat for many species as the southern limit of their current distributions shifted northward from current to future projections also consistent with other studies. For example, Lawler et al., (2010) predicted a northerly shift in the suitable habitat of *Lithobates pipiens* across the western hemisphere, a shift our models also predicted, which resulted in significant losses of predicted suitable habitat for this species in the Midwest. Northward shifts of suitable habitat within the Midwest were visually noticeable in many future predictions and likely contributed to predicted extirpation of species with current distributions in the northern portions of our study area and high species turnover in many ecoregions. In addition, predicted land-use changes did not have significant influence over predicted suitable habitat. In fact, incorporating these changes had no measurable influence over model predictions; thus suggesting that predictions of global climate change are the primary drivers of amphibian distribution changes in the Midwest.

A majority of amphibian SDM studies limit their focus specifically to climate, similar to our climate-only SDMs. However, these results are limited because they project suitable habitat regardless if that area has suitable land-use characteristics. There exists a large body of evidence that supports land-use and its role in amphibian habitat suitability (Price et al. 2011; Scheffers and Paszkowski 2012; Peterman and Semlitsch 2013; Osbourn et al. 2014). Although we hypothesized including land-use change into SDMs would have an increased negative effect on suitable habitat, our results indicate that there was no significant difference in changes in suitable habitat from current to future projections between climate-only and climate + land-use (Table 2; Fig. 2). Although there are no significant differences, we do see variation in suitable habitat from climate-only and climate + land-use SDMs across families where we predict a decrease in suitable habitat when land-use is considered for some families (Ambystomatidae, Hylidae, Plethodontidae, and Salamandridae) and an increase in suitable habitat for others (Bufonidae and Ranidae; Fig. 2). This is likely an artifact of the general land-use tolerance of Bufonidae and Ranidae species as well as the relative land-use intolerance of species in the families predicted to decline. Thus, species with the ability to persist and survive in relatively intolerant habitat (e.g. agricultural or urban areas) may not be as negatively impacted by future degradation. Further, effects from climate change may overshadow the effects that land-use changes may have on suitable habitat. For example, we predict 100% current suitable habitat loss in many species for some scenarios in climate-only SDMs (Appendix A) which therefore provides no opportunity for land-use to affect predictions in suitable habitat. Therefore, for our study region, climate may be a more limiting factor in determining amphibian habitat than land-use. Additionally, more than 50% of the Midwest is currently used for agriculture while only 25% is forested. The threshold at which land-use changes affect amphibians may have already been surpassed, therein, showing little effect in our predictions. Land-use may have the greatest impact on dispersal abilities of amphibians in the future as traversing unfavorable habitat is a source of high mortality for amphibians (Lehtinen et al. 1999; Stevens et al. 2004; Goldberg and Waits 2010).

Changes in predicted suitable habitat were largely driven by the current climatic adaptation (e.g. latitude) of each species. Therefore, species with southerly current distributions tended to gain predicted suitable habitat within the Midwest and the opposite for northerly distributed species. Latitude was a significant driver, likely because of the shift in climate regimes in future decades (Feng et al. 2014), which therein shifted the distribution of amphibians in response. However, our data are limited in what we can predict about the effects of each species distribution outside of the Midwest, therefore we cannot confidently conclude the degree to which a species distribution changed outside of our study region. Therefore, predicted declines within our study area do not translate to overall declines in suitable habitat. Yet, the complete loss of species within our study region represents the high degree of species turnover within the Midwest, with some ecoregions losing on average six or more species (Fig. 3). In some instances, shifts were significant and occurred over several kilometers. For example, *L.*

sphenocephalus expanded the northern limit of its predicted distribution from northern Missouri to southern Minnesota, a shift of more than 400 km by 2070. Yet *L. septentrionalis* and *L. pipiens*, species within the same genus, lost their entire predicted suitable habitat in many scenarios, likely a result of their high-latitude current distributions. However, species richness both in the southern and northern portions of our study region were predicted to decline indicating some southern distributed species still lost suitable habitat (Appendix A). We conclude that other taxonomic or life history traits did not significantly affect distinctions of gains or losses in predicted suitable habitat as we observed this trend throughout all families. Recent evolutionary adaptation for specific climates may be more indicative of a species' ability to cope with future climate change, rather than any other biological or ecological traits (Urban et al. 2014).

We investigated the potential influence of our modeling factors on changes in predicted suitable habitat to identify important drivers of changes. Climate scenarios (e.g. GCM or RCP) did not significantly influence changes in predicted suitable habitat for amphibians likely because of their relatively close agreement in greenhouse gas emissions up to 2050 (van Vuuren et al. 2011) and the potentially low threshold of climate change at which amphibians are affected. However, the interaction of threshold and latitude was significantly influencing predicted suitable habitat changes. Our most conservative threshold had a stronger relationship with percent change in predicted suitable habitat and latitude than the other two thresholds (Fig. 5) and had high variability in its effects across species, even though percent change in suitable habitat did not significantly vary across thresholds alone. Others have noted caution in regard to using

Maxent’s threshold values because they are unrelated to any biological or ecological estimate, making their predictions somewhat arbitrary (Merow et al. 2013) and may also be affected by size of study area (Nenzen and Araujo 2011). This supports growing evidence towards the importance of using a multi-threshold approach, to reduce the influence of a single threshold. Further, we underscore the importance of threshold choice in model predictions, as our results indicate their significant influence on model predictions.

Ecological niche models are limited in their capacity to predict the realized niche of any given species as there are a variety of both biotic and abiotic variables that influence suitable amphibian habitat (e.g. competition, predation, chemical pollution, disease, etc.). The inherent variability and multifaceted nature of these variables make them difficult to include in predictive models, especially doing so across our large study region (Holt 2009; Kissling et al. 2012). Although we did not build a complete ecological niche for Midwest amphibians, the relationships we modeled between climate and land-use are important to understand how climate and land-use influence habitat for amphibians, two major drivers of amphibian habitat suitability. With these baseline relationships, we can then include more complex relationships in the future. Occurrence-only SDMs are also limited given that occurrence data originate from multiple sources with varying sampling efforts and techniques. Such variation has the potential to create biases between data from one source to another (Ruiz-Gutierrez and Zipkin 2011) leading to skewed representation of environmental variables in heavily sampled locations. We addressed this bias with two techniques agreed as effective solutions (Barrett et al. 2014;

Fourcade et al. 2014), yet it is difficult to identify if these techniques correct this issue fully. We acknowledge that our model is limited in its ability to predict the realized ecological niche of species, therefore, we are limited in how we interpret our results. Our SDMs should not be seen as specific forecasts; however, the relationships between amphibians, climate and land-use are useful interpretations of our models. For example, *Ambystoma opacum* is predicted to expand its distribution in future climate projections in 2050. The actual percent expansion may not be an accurate representation of what will happen in the future; yet noting the areas to which this species is predicted to shift is meaningful. From these data we can gauge which species are most at-risk within the Midwest and identify areas in which conservation efforts may be most fruitful.

The ecological niche used to predict suitable habitat for SDMs is derived from climate variables for several known habitat localities. However, it is not known if the climate at the collection of localities represents the total variation in which a species can tolerate. Understanding the climatic variation in which a species can tolerate is important because climate change will not consistently shift from year to year, but will likely have inter- and intra-annual variation significantly impacting the ability for species to survive (Early and Sax 2011). In addition, it is possible that species will adapt to novel climates over time, increasing their physiological tolerances. However, plasticity of most species is unknown. Yet, using a mechanistic and correlative approach, we could test the physiological limits of species and transfer that knowledge to the predicted spatial distribution of climate. Mechanistic models have been used to accurately project amphibian distributions (Kearney et al. 2008) and will provide a more comprehensive prediction of the climatic niche of a given species (Kearney et al. 2010). However, we lack the data on the physiological limits of most species; therefore, there is a need for more mechanistic investigations on climatological tolerances at the species level. Such investigations will help build more robust models and better-inform climate-based predictions of habitat changes.

CHAPTER III

FACTORS THAT INFLUENCE POND-BREEDING SALAMANDER DENSITY AND PREDATION IN MIDWESTERN UNITED STATES EPHEMERAL WETLANDS

Introduction

Wetlands are important sites for harboring biodiversity, assisting in dispersal of animals, and improving several hydrologic factors (e.g., Gibbs, 1993; Semlitsch and Bodie 1998; Mitsch and Gosselink 2000). However, more than half of the wetlands in the United States have been converted for agriculture or urbanization (Mitsch and Gosselink 2000). Therefore, increasing our understanding of biological functions within wetlands is critical to perform more effective conservation actions. Factors that influence biota inhabiting wetlands are variable. For example, several reviews have highlighted the importance of hydrology, location, and anthropogenic influence on the community composition of biota in wetlands (Webb et al. 2012, Batzer 2013). Understanding what factors influence density of biota in wetlands is essential to formulate ideal conservation plans for restoration of existing or construction of new wetlands.

Amphibians utilize wetlands for a variety of purposes, and comprise a primary component of wetland ecosystems. Within wetlands, amphibians can occur in great abundance, density and are a large constituent of wetland biodiversity (Gibbons et al. 2006). Amphibian density in wetlands is dictated by several factors. In the Midwestern

United States, the degree of adjacent urbanization and increased habitat heterogeneity has negative and positive effects on amphibian abundance and richness, respectively (Knutson et al. 1999). Other studies in the Midwestern United States have shown the importance of water permanency, number of adjacent wetlands (positive influence; Kolozsvary and Swihart 1999), the presence of predatory fish (negative influence), and shallow water (positive influence; Porej and Hetherington 2005) on amphibian dynamics. Predatory pond-breeding salamanders (genus *Ambystoma*), such as *Ambystoma jeffersonianum, Ambystoma laterale and Ambystoma tigrinum*, are abundant in many fishless Midwestern United States ephemeral wetlands (Lannoo 2005) where densities can reach between 0.1 – 39.4 individuals/m^2 (Petranka 1989; Ousterhout et al. 2015). Ambystomatids inhabit upland forest as adults and emerge to breed and oviposit eggs in adjacent wetlands. Once hatched, larvae are predatory, and these salamanders can consume large amounts of invertebrates daily and where present serve as top predators of ephemeral wetland ecosystems (Whiles et al. 2004, DuRant and Hopkins 2008, Chaparro-Herrera et al. 2011). For example, larval Ambystoma consumed over 24,000 individual prey items across wetlands in central Kentucky (Smith and Petranka 1987). Therefore, larval ambystomatids could potentially have significant influence over invertebrate or amphibian communities in wetlands via predation, but some evidence suggest their role is limited (Zimmer et al. 2000). Many abiotic factors associated with wetland characteristics have been shown to significantly impact the breeding quality and quantity of ambystomatid salamanders in wetlands (Pechmann et al. 2001, Gorman et al. 2009, Walls et al. 2013), however research focused on their interaction with the natural biotic communities in these systems is sparsely studied. Conversely, little information exists on the effects of predatory salamanders on natural biotic communities in wetlands or how natural biotic communities may support predatory salamanders and therefore their overall populations. This lack of knowledge is particularly alarming, given my results from Chapter 2, which suggests suitable habitat for some species within the family Ambystomatidae may be non-existent in the Midwestern U.S. by the year 2050.

Aquatic invertebrates comprise a major biotic component of ephemeral wetland ecosystems (Boix et al. 2001) where diversity and abundance are similar to or exceeds permanent systems (Whiles and Goldowitz 2005). Aquatic invertebrates are also an important link between primary producers and secondary consumers (Batzer and Wissinger 1996). For example, secondary production of aquatic invertebrates has been found to be important prey resource for fish in aquatic systems (Anderson et al. 2012). Additionally, aquatic invertebrates accelerate leaf litter breakdown in aquatic systems (Cook and Hoellein 2016; Wright and Covich 2005) and facilitate nutrient cycling (Schaller 2013). Since ambystomatid salamanders feed primarily on aquatic invertebrates (e.g. Whiles et al. 2004), understanding factors that drive aquatic invertebrate abundance and density is primary to understanding potential impacts on ambystomatids. Invertebrates that colonize ephemeral wetlands show a similar varied response to several environmental and biological variables as ambystomatid salamanders. For example, Batzer (2013) summarized wetland invertebrate responses to environmental variables and concluded that anthropogenic change, predation, plants, and hydrology were common factors that influenced their composition and density. Little is known about whether macroinvertebrate communities can be dictated by predation by ambystomatids alone, or if site-or landscape-level factors work in combination with predation pressure.

The purpose of this study was to determine if adjacent urbanization or site-level (abiotic and biotic) variables, such as water quality, could influence density of ambystomatid salamanders and their invertebrate prey base within ephemeral wetlands. We also examined whether predation by larval pond-breeding salamanders could influence macroinvertebrate community density or structure. To do this, we examined what factors influence the density of biota in a series of wetlands with varying adjacent urbanization and densities of predatory larval salamanders at two locations in the Midwestern United States; Illinois and Ohio.

Methods

Study species

We examined the larvae of three species of ambystomatids across two sampling locations in the Midwestern United States; *Ambystoma tigrinum tigrinum* (Eastern Tiger Salamander) and *Ambystoma laterale* (Blue-spotted Salamander) in Illinois and *Ambystoma jeffersonianum* (Jefferson's Salamander) in Ohio. *Ambystoma tigrinum* are the largest of the three species and are of the largest within the genus *Ambystoma*, typically growing to nearly 20 cm as adults. Likely because of their large size, *A. tigrinum* breed in a variety of water bodies from permanent to ephemeral (Lannoo 2005). Additionally, *A. tigrinum* occur throughout the Eastern United States from Florida to Minnesota and from the Mississippi River east to the Atlantic Coast (Lannoo 2005).

Both *A. laterale* and *A. jeffersonianum* have similar life histories and ecology and are known to hybridize where sympatric. These species are smaller than *A. tigrinum* and reach from 14-18 cm as adults. Collectively *A. laterale* and *A. jeffersonianum* are distributed from Canada south to Kentucky and Virginia and east to Maine, with *A. laterale* representing the northern half and *A. jeffersonianum* representing the southern half of that distribution with an area of hybridization in the middle (Lannoo 2005).

Illinois sampling design

We sampled five wetlands in Lake County, Illinois, USA for larval salamanders and water column invertebrates. Wetlands were surrounded by a matrix of forest, agriculture and urbanization (Table 5). All wetlands were fishless; however, each wetland contained one to several species of non-predatory amphibians including *Lithobates catesbeiana, Lithobates clamitans* and *Pseudacris triseriata* one or both species of predatory larval salamanders, *A. tigrinum* or *A. laterale*. Monthly we measured hydrology by determining the wetted width from a wetland center point toward each cardinal direction and used three parallel transects to measure depth every five meters, dissolved oxygen (DO; mg/L) using a Hach HQd/IntelliCAL sonde, and size (length X width) of each wetland.. We quantified the adjacent land-use within 300 meters to each wetland by calculating the percentages of each land-use type after collapsing the USGS 2006 NLCD (30 m pixels; Fry et al. 2011) land-cover categories to forest (classes 41–43), agricultural (81–82), and urban (classes 21–24). This distance represents the core terrestrial habitat of amphibians (Semlitsch and Bodie 2003).

Larval amphibian sampling.–We quantitatively sampled amphibians bi-weekly from 13 May to 3 September 2015. Each sampling period consisted of three consecutive nights of trapping using 15 to 25 Promar minnow traps (46 x 25 cm) with trapping density dictated by wetland area in addition, to "pipe sampling" (Werner et al. 2007). The pipe sampler consisted of a 52 X 27 cm galvanized steel trash can with the bottom removed and perimeter smoothed to not harm taxa. The can sampled a 0.2 m^2 area of the sediments and associated water column. Each sample was taken by quietly approaching the sampling site and quickly pushing the can into the substratum of the wetland. Nets (23 X 15 cm) were employed to remove all animals within the can and water column where circular sweeps within the can were taken until 10 consecutive empty sweeps were taken (see Mullins et al. 2004). We took five pipe samples per wetland; however, if the wetland area was reduced due to drying, and samples could not be taken at least 2 m apart, the number of samples was reduced accordingly. Relative density of larval salamanders and non-predatory amphibians (i.e., anuran larvae) was quantified by assuming one minnow trap (Ousterhout et al. 2015) and/or five pipe samples sampled approximately 1 m^2 of wetland. For diet analysis, once per month we collected five to 10 larval *A. tigrinum* (50 total) and *A. laterale* (47 total) across all wetlands. Specimens were sacrificed using an Orajel® solution (Cecala et al. 2007) immediately after capture, then within 5 minutes of sacrifice fixed using 10% neutral buffer formalin for 24 hours, and stored in 70% EtOH. Later the samples were measured (snout-vent length [SVL], anterior portion of the snout to the posterior portion of the vent; 0.1 mm), weighed (wet mass, 0.01 g), and dissected to remove the stomach and intestinal tract. Stomach and intestinal tracts were preserved in 70% EtOH and then contents were analyzed to the lowest possible taxon using (Merritt et al. 2008) and (Thorp and Covich 2001).

Invertebrate sampling.–Water column invertebrates were sampled with 80 µm plankton cone nets. Plankton nets were attached to a 1.5 m wooden handle and swept in front of the sampler. An equal number of plankton net sweeps were taken within a 1 m^2 area to sample water column invertebrates at three replicate locations within each wetland once per month. Invertebrate samples were directly preserved in 70% EtOH. Each replicate sample was subsampled to process samples more efficiently. All organisms were identified to family and genus when possible using (Merritt et al. 2008) and (Thorp and Covich 2001).

Ohio sampling design

We sampled 6 wetlands located across Hamilton, Butler, and Cleremont Counties, Ohio, USA from 29 March to 24 July 2012. This region contains a number of ephemeral and permanent wetlands, and is surrounded by a matrix of urbanization, agriculture, and forested land. All wetlands were fishless; however, each wetland contained one to several species of non-predatory amphibians including *Anaxyrus americanus, Acris crepitans, Hyla chrysoscelis, Lithobates catesbeiana, Lithobates clamitans, Notopthalmus viridescens, and Pseudacris crucifer*. All wetlands contained predatory larval salamanders, *Ambystoma jeffersonianum*. Measurements of dissolved oxygen (DO; mg/L) were collected during each visit near the center of each wetland using a YSI6600 Data Sonde multi-parameter field probe. Additionally, the initial size (length X width) of each wetland was measured. We quantified the adjacent land use within 300 meters to each wetland as detailed above.

Larval amphibian sampling.–Amphibians were quantitatively sampled using the "pipe sampling" technique (Werner et al. 2007); see above. Five to10 pipe samples were taken per wetland, depending upon size; wetlands ≤ 300 m^2 were sampled with five can samples and 10 samples were taken for wetlands ≥ 300m^2. Samples were randomly located at least 2 m from adjacent samples. If the wetland area was reduced due to drying, and samples could not be taken at least 2 m apart, the number of samples was reduced accordingly. Density (number of individuals per m^2) was calculated as the number of individuals captured within five pipe samples (0.2 m^2 each). For diet analysis, we collected a series of larval *A. jeffersonianum* from five wetlands (n = 20 to 30; 325 total). Within 30 min of collection all salamanders were euthanized by immersion in a 0.1% solution of neutral pH-buffered MS-222 (ethyl m-amino-benzoate methanesulfonate; Gentz 2007). Samples were then processed as above and stomach contents were analyzed to the lowest possible taxon.

Invertebrate sampling.–Water column invertebrates were sampled using a dipper consisting of a white plastic container (11 cm diameter; 350 ml volume). The number of samples collected was standardized based on site size and habitat diversity, for example, 15 (for wetlands ≤ 300 m^2) or 30 dips (wetlands ≥ 300 m^2) were taken at each wetland. Each sample was rinsed through a sieve with a pore size of 63 µm and preserved in 70% ethanol (EtOH). These semi-quantitative dip samples included sieved material (mainly small macroinvertebrates and vegetation if present).

Statistical Analyses

We used general linear models (GLMs) to determine which factors (independent variables) were contributing to the variation in densities of each species of predatory salamander and total water column invertebrates (dependent variables) for each study location (Illinois and Ohio). We included factors that have significant effects on wetland biota supported by previous research such as DO (Spieles and Mitsch 2000, Sacerdote and King 2009) and percent urbanization surrounding wetlands (Shilla and Shilla 2011, Alix et al. 2014). In addition we included other factors we hypothesized would impact densities of wetland biota such as month sampled, non-predatory amphibian density, and predatory salamander density by species. We used non-metric multi-dimensional scaling (nMDS) ordinations to identify if diet items of *Ambystoma* were unique to the water column invertebrate communities within wetlands using bray-curtis dissimilarities. Next, we used ANOSIM post hoc tests to test for significant differences between diet items and water column invertebrates. These analyses were aimed to help identify potential relationships between *Ambystoma* diet items and the prey available to them in the water column. We further investigated differences in salamander diets and available water column invertebrates with Ivlev’s Selectivity index to determine predation biases of salamanders on certain taxa and functional groups. This index uses relative abundances of diets and water column invertebrates where high values indicate taxa low in relative abundance in the water column yet high in diets meaning selection for those taxa and taxa with high relative abundance in the water column yet low in diets meaning avoidance of those taxa. All percentage data (including relative abundances) were square root transformed. All analyses were performed in STATISTICA 12.0 (Statsoft, Inc., Tulsa, OK) with the exception of nMDS and ANOSIM which were performed in PRIMER 6.

Results

Illinois wetlands

Urbanization within 300 meters of wetlands in Illinois ranged from 0 to 47.6 percent and three of the five wetlands had no adjacent urbanization (Table 5). Dissolved oxygen averaged 2.51 mg/L (±1.748) across all wetlands in Illinois (Table 5). Wetland size and hydroperiod were comparable in May and varied in their drying rates throughout the sampling period (Table 5).

In total, we captured 1,072 *Ambystoma tigrinum* and 814 *Ambystoma laterale*. Densities averaged 0.5 (±0.7) per m^2 for *A. tigrinum* and 0.3 (±0.5) per m^2 for *A. laterale* across all wetlands and sample months with highest densities in the month of June (Table 5). Non-predatory amphibian density ranged from 0 to 1.5 per m^2. We captured a total of 28,009 individual water column invertebrates representing 42 taxa across all Illinois wetlands from May to September. Invertebrate communities were dominated by Cladocera (*Daphnia*), Copepoda (Nauplii) and Diptera (*Chaoborus*) (Fig. 1; Appendix A).

A total of 4,829 individual invertebrates were consumed by *Ambystoma* larvae represented by 30 taxa in Illinois wetlands (Fig. 1; Appendix A). Diet of both Illinois species of *Ambystoma* consisted mostly of Cladocera, Copepoda, Ostracoda, Chironomidae, Amphipoda and smaller proportions of other macroinvertebrates (Figure 7). *Ambystoma tigrinum* and *A. laterale* consumed different relative proportions of taxa.

For example *A. laterale* diets consisted of 41.4% Cladocera, 27% Copepoda and 19% Ostracoda, and *A. tigrinum* consumed 74% Cladocera with the next highest taxon group being Ostracoda with only 5% of diets (Figure 7). Per capita consumption was on average 24.78 invertebrates/day by *A. laterale* and 104.29 invertebrates/day by *A. tigrinum* (average number of individual taxa found in each stomach). Ambystomatid densities within wetlands varied by month and wetland ranging from 0 to 5.3 per m^2 for *A. laterale*, 0 to 2.88 per m^2 for *A. tigrinum* (Table 5).

Ohio wetlands

The gradient of adjacent urbanization in Ohio wetlands resulted in one wetland (FB) having ≥ 60% urbanized land use within 300 m and the remaining wetlands having between 0 to 20% adjacent urbanization (Table 5). Water quality variables varied across sites and months, for example, DO ranged from 1.6 to 14 mg/L. Wetland size also varied across each month, where some wetlands dried completely. Larval salamander density averaged 6.7 (±21.2) per m^2 across all wetlands with highest densities in March. Non-predatory amphibian density averaged 25.1 (±55.45) per m^2 across all wetlands. In total, 21,776 invertebrates representing 48 taxa were quantified across all wetlands in Ohio (Fig. 1; Appendix B). Water column invertebrates were dominated by Cladocera followed by Gastropoda, Copepoda, and Diptera larvae (Chaoboridae, Culcidae and Chironomidae; Fig. 1; Appendix B).

Diets of *A. jeffersonianum* were also dominated by Cladocera (83%) and Chironomidae (10%) with much smaller proportions of other taxa such as Copepoda and Ostracoda (Figure 7; Appendix B). A total of 15,882 invertebrates representing 25 taxa were consumed by *A. jeffersonianum* throughout our sampling period and per capita consumption was on average 47.32 invertebrates per day.

*Factors influencing biotic variable*s

Density of *Ambystoma* species at both Illinois and Ohio were best explained by the variation by percent urbanization within 300 meters of wetlands (Table 6). In addition, *A. laterale* (Illinois) density was influenced by DO (Table 6). Density of water column invertebrates was best explained by the variation in non-predatory amphibian density in Illinois and Ohio (Table 7). Additionally, DO was an important factor influencing water column invertebrate density in Illinois wetlands (Table 7). Predatory amphibian density had no measurable effect on invertebrate density at either Illinois or Ohio (Table 7).

Non-metric multi-dimensional scaling (nMDS) ordination showed a distinct grouping of diet items from water column taxa (Figure 8) in which diet items and water column invertebrate relative abundances were significantly different for Illinois ($P <$ 0.001, Global R = 0.626) and Ohio ($P = 0.022$, Global R = 0.159). Selectivity of *Ambystoma* for water column invertebrates varied by species and geographic location; however, there were a few similarities (Figure 9). All species had positive selectivity for Cladocera, Chironomidae (Diptera), and a negative selectivity for copepods. Therefore, there were high relative abundances of copepods in the water column but low relative abundances in salamander diets and relatively low abundances of Cladocera and Chironimidae (more so Chironomidae) in the water column but represented in much higher relative abundances in diets. The strongest selective values represented *A. laterale* selecting for chironomids, and many invertebrate taxa were strongly selected against by *A. jeffersonianum.* Copepoda were strongly selected against by all species, especially by *A. tigrinum* (Figure 9). In addition, all species had preferences for collector-filterers, collector-gatherers, detritivores and avoidance of predator functional groups (Figure 9).

Table 5. Description of wetlands studied showing study location, average wetland size (m2), number of days each wetland held water within study period (No. days with water; DWW), average (±SD) DO, percent urbanization within 300 meters of each wetland (%Urb) and average (±SD) density of larval salamanders.

						Salamander density (±SD)		
Wetland	Location	Size (m^2)	DWW	DO (±SD)	%Urb	*A. jeffersonianum*	*A. tigrinum*	*A. laterale*
Ethel's West	Illinois	376.74	59	1.63 (±0.05)	0	–	–	2.625 (±1.590)
Ethel's East	Illinois	942.82	97	1.62 (±0.39)	0	–	0.422 (±0.476)	0.354 (±0.526)
Ethel's Center	Illinois	1538.38	114	4.26 (±2.33)	0	–	0.085 (±0.150)	0.041 (±0.057)
Grainger	Illinois	803.62	85	1.47 (±0.46)	17	–	0.030 (±0.039)	0.224 (±0.247)
Rollins Savanna	Illinois	741.96	171	2.25 (±1.55)	43	–	1.288 (±0.901)	0.022 (±0.062)
Farbach Werner	Ohio	21.32	27	4.22 (±2.67)	64	0.750 (±0.957)	–	–
Woodland Mound	Ohio	457.14	118*	4.70 (±4.18)	14	29.000 (±46.882)	–	–
Spring Pond	Ohio	1509.59	118*	2.89 (±3.07)	11	1.667 (±3.561)	–	–
Oak Glen	Ohio	199.61	118*	7.33 (±3.61)	6	3.667 (±8.200)	–	–
Glenwood Gardens	Ohio	3749.14	56	10.88 (±6.42)	2	0.571 (±1.133)	–	–
Shawnee Forest	Ohio	34.37	118*	3.83 (±3.22)	0	30.625 (±33.221)	–	–

Values with an (*) indicate wetlands with water the entire sampling period.

Figure 6. Number of individuals for the four most abundant taxa found in water columns in (A) Illinois and (B) Ohio wetlands separated by month.

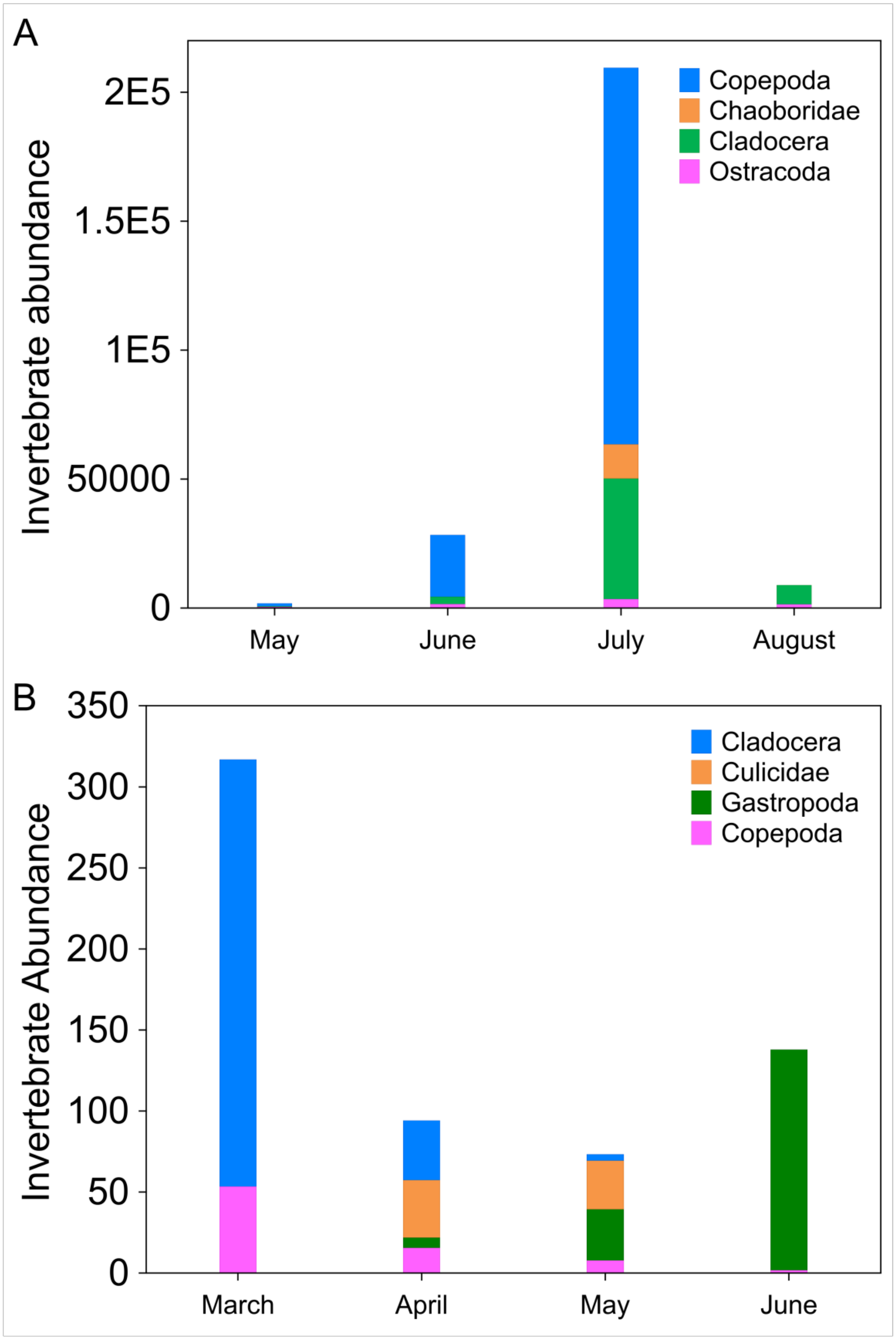


Figure 7. Percentage of taxa in (A) water columns and (B) diets of *Ambystoma*. Water column taxa are categorized by location and diet items by *Ambystoma* species.

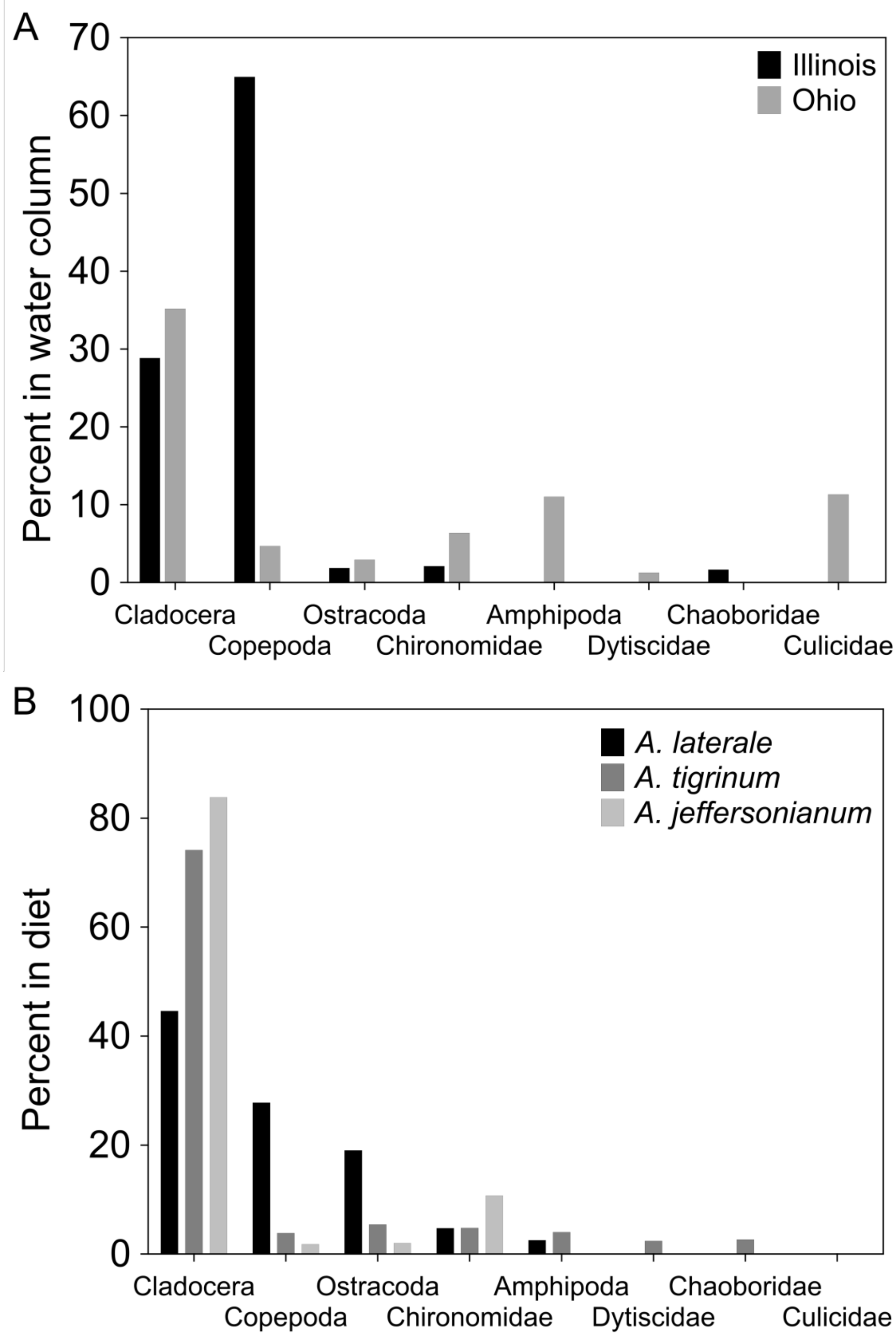


Table 6. General linear model results for abiotic factors (independent variables) affecting *Ambystoma* larvae densities (dependent variable) in Illinois wetlands (*A. tigrinum* and *A. laterale*) and Ohio wetlands (*A. jeffersonianum*).

	A. tigrinum				*A. laterale*				*A. jeffersonianum*			
Effect	df	MS	F	*P*	df	MS	F	*P*	df	MS	F	*P*
DO	1	0.704	1.972	0.164	1	9.073	8.747	0.005	1	153.64	0.59	0.444
%Urb	1	16.803	47.054	<0.001	1	14.180	13.670	<0.001	1	2085.244	8.113	0.007
Month	4	0.876	2.454	0.052	1	0.894	0.861	0.358	3	252.094	0.981	0.429
Error	84	0.357	–	–	53	1.037	–	–	73	420.922	–	–

Table 7. General linear model results for factors (independent variables) affecting water column invertebrate density (dependent variable) in Illinois wetlands and Ohio wetlands.

	Illinois				Ohio			
Effect	df	MS	F	*P*	df	MS	F	*P*
DO	1	4.447E+11	14.868	<0.001	1	1.369E+08	0.719	0.403
%Urb	1	9.188E+08	0.031	0.861	1	2.199E+06	0.011	0.915
A. laterale density	1	2.592E+10	0.867	0.352	–	–	–	–
A. tigrinum density	1	9.180E+10	3.069	0.080	–	–	–	–
A. jeffersonianum density	–	–	–	–	1	3.090E+07	0.162	0.690
Non-predatory density	1	1.878E+11	6.281	0.012	1	2.638E+09	13.84	<0.001
Month	4	5.651E+10	1.889	0.109	3	7.066E+07	0.370	0.774
Error	2090	2.991E+10	–	–	30	1.905E+08	–	–

Figure 8. Non-metric multi-dimensional scaling (nMDS) ordinations of *Ambystoma* diet items (e.g. gut-content; GC) and water column (WC) taxa for (A) Illinois and (B) Ohio. Each point represents a sampling month at an individual wetland. Ovals indicate grouping of water columns (WC; gray ovals) or diet items (GC; black ovals).

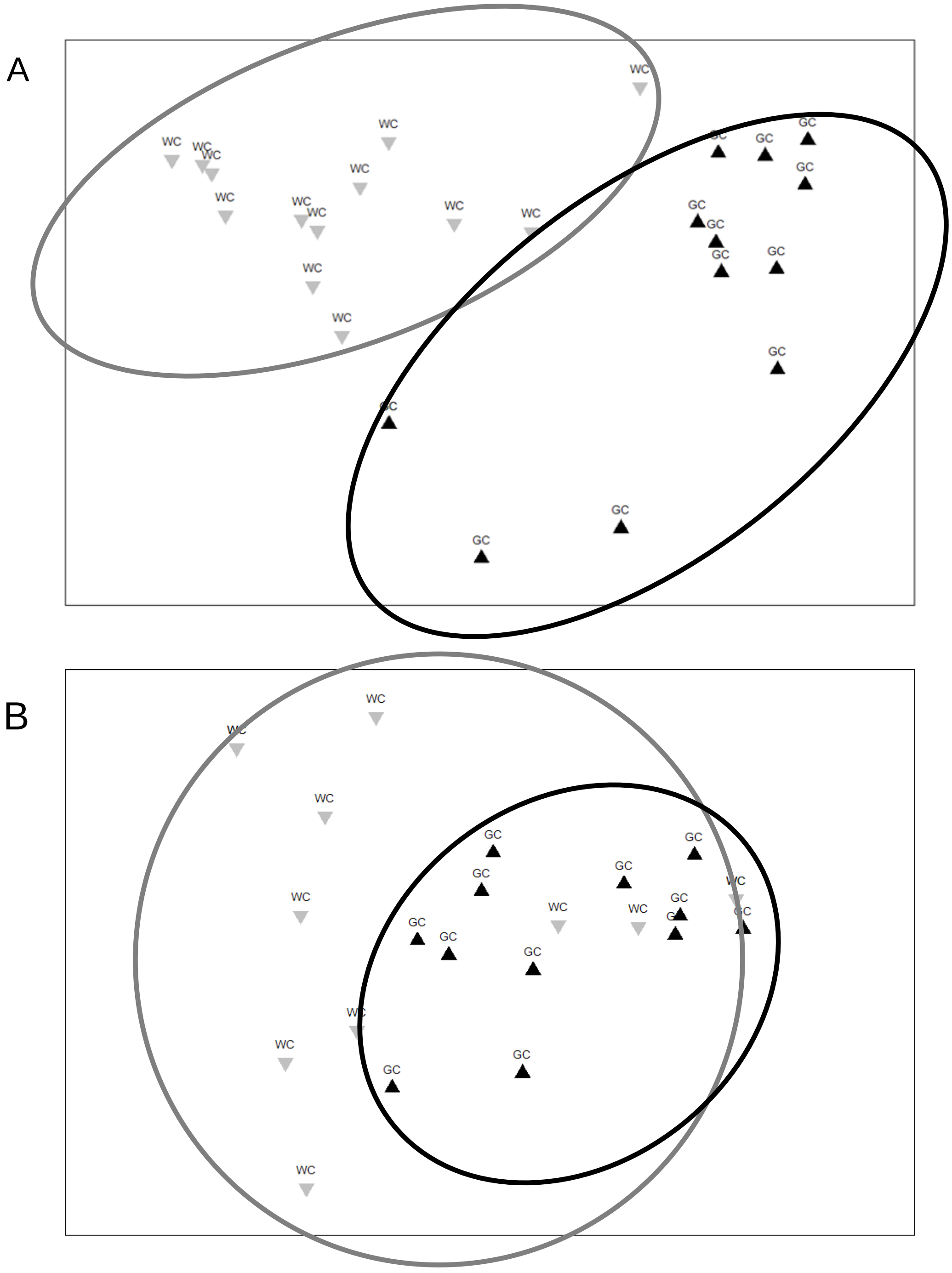
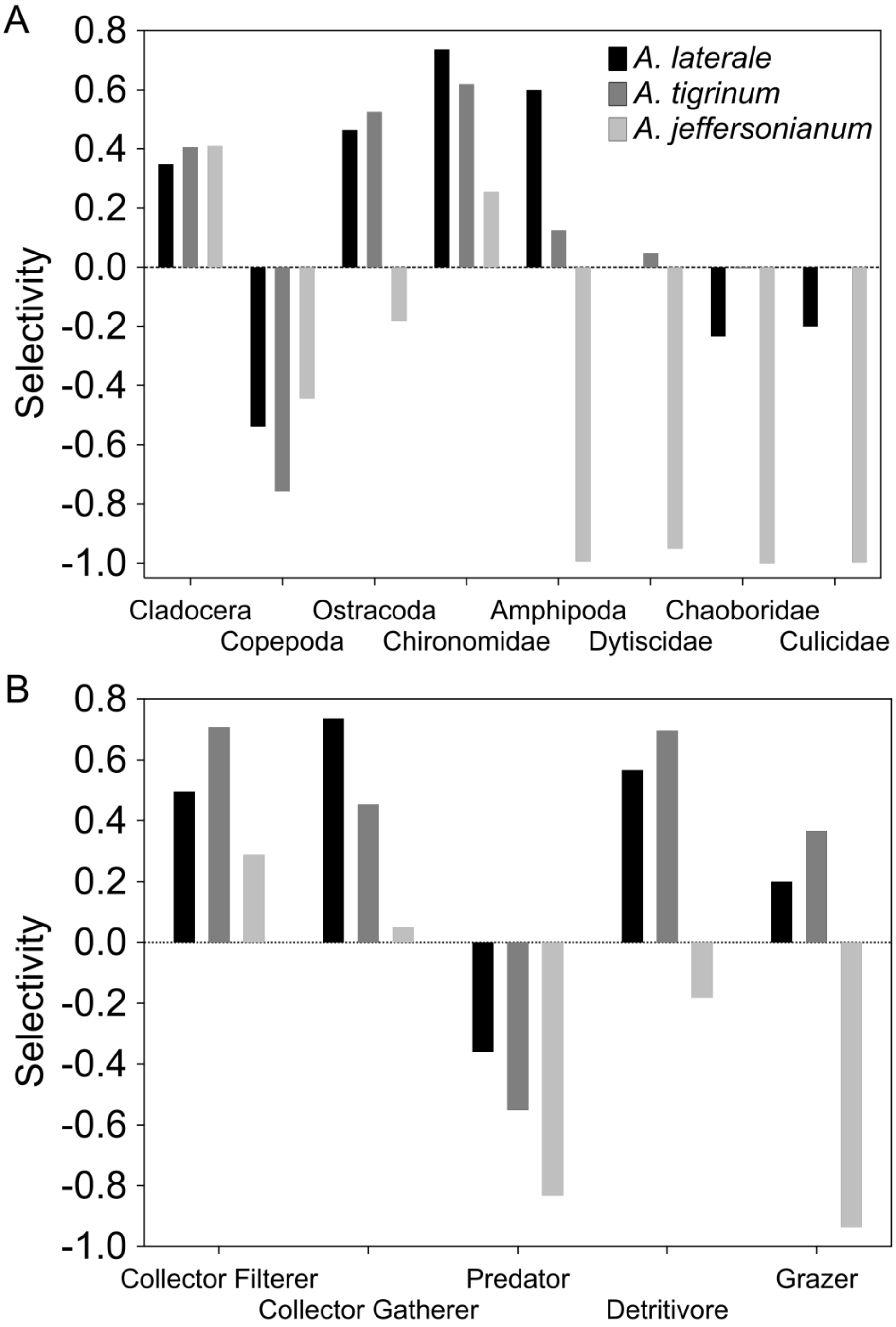


Figure 9. Ivlev's Selectivity Index scores for (A) water column taxa and (B) functional groups observed. Positive numbers indicate salamanders selecting for invertebrate taxa/functional groups while negative numbers represent selection against invertebrate taxa/functional groups.



Discussion

Factors that influence larval salamander densities

We found both landscape-level and site-level factors have measurable influence on ambystomatid salamander density at two locations in the Midwestern United States. Larval ambystomatid densities were influenced by percent urbanization within 300 meters of wetlands in both Illinois and Ohio, and DO in Illinois wetlands. Previous studies support these findings and have suggested a 300 meter buffer around breeding wetlands as core habitat for the terrestrial population of pond-breeding salamanders (Semlitsch and Bodie 2003) and the importance of forest within this boundary (Osbourn et al. 2014). Urbanization within adjacent terrestrial habitat of wetlands has also been found to be negatively associated with ambystomatid breeding (Skidds et al. 2007), conversely, other studies note the success of some ambystomatid species breeding in wetlands within disturbed habitats (Scheffers et al. 2013, Scheffers and Paszkowski 2013, Holzer 2014). Site-level factors have also driven ambystomatid densities. For example, Scheffers et al. (2013) suggested suitable wetlands may be as important as surrounding terrestrial habitat for ambystomatid salamanders and Peterman et al. (2014) found multiple wetland metrics related to larval densities of ambystomatids; including canopy cover, pond slope and hydroperiod. Previous research has provided evidence for DO affecting ambystomatid hatching success (Sacerdote and King 2009) which may therein affect the densities of larvae and eventually recruitment. Dissolved oxygen significantly impacted *A. laterale* densities in Illinois wetlands and may be lasting effects from hatching success.

Factors that influence invertebrate density

Ambystomatid consumption rates of invertebrates in mesocosm settings suggest their impact could be significant in wetland ecosystems (Benoy 2008, Urban 2013), and may cause a trophic cascade (Holomuzki et al. 1994). However, our results suggest site-level factors primarily influence aquatic invertebrate densities in Illinois and Ohio rather than effects directly from consumption (Table 7). This finding is congruent with other research which has suggested site-level variables such as DO as an important factor in shaping aquatic invertebrate communities (Spieles and Mitsch 2000, Jones et al. 2016); although DO was only a significant factor in Illinois wetlands in our study. Similarly, there is evidence to suggest other site level water chemistry variables influence aquatic invertebrate communities such as total phosphorous, pH, conductivity and turbidity among others (Chen et al. 2011, Dulic et al. 2014, Epele and Miserendino 2015) but we did not measure these variables as our systems were not known to be excessively polluted or eutrophic, which is typically linked to deviations in acceptable levels of those variables for aquatic invertebrates (Morrice et al. 2008, Epele and Miserendino 2015). Other studies also suggest landscape-level factors influence invertebrate communities in wetlands, specifically surrounding land-use (Dodson et al. 2005, Plenzler and Michaels 2015). The intensity of land-use in the surrounding landscape likely dictates the degree to which wetland biota are influenced or the degree to which abiotic factors are altered, indirectly impacting wetland biota. Further, time since disturbance may also impact wetland aquatic invertebrate communities (Dodson and Lillie 2001) though we found no such relationship between surrounding urbanization and aquatic invertebrate densities

(Table 7) which may indicate relatively stable conditions of the surrounding land-use adjacent to the wetlands we investigated.

Our data suggest non-predatory amphibian densities as an important factor predicting aquatic invertebrate densities in both Illinois and Ohio wetlands. Mokany (2007) found non-predatory amphibian assemblages may have impacts on wetland ecosystems that facilitate colonization or proliferation of invertebrate taxa, such as course particulate organic matter (CPOM) breakdown or enhanced nutrient input by excrement. Alternatively, predatory salamander densities within wetlands had no measurable influence on invertebrate communities or densities (Table 7), suggesting densities or consumption rates of salamanders were not high enough to significantly reduce aquatic invertebrate densities via direct predation. Similarly, Holomuzki et al. (1994) found no significant effects by larval ambystomatids on aquatic invertebrate densities in natural wetlands. Thus, salamander populations may not be effective in direct top-down pressure on food webs, or perhaps are only so at higher densities.

Factors that influence salamander predation

We provide evidence that *Ambystoma* larvae have distinctly different proportions of aquatic invertebrates in diets than the available water column invertebrates (Figure 8). This suggests *Ambystoma* species we studied have a predation bias. Diet of all three salamander species were dominated by Cladocera and Copepoda taxa, which is consistent with other studies examining the diet items of *Ambystoma* species in wetlands (Holomuzki et al. 1994, Whiles et al. 2004, Bardwell et al. 2007). For example, Whiles et al. (2004) found *Ambystoma cingulatum* diets were dominated by Cladocera in South

Carolina and Florida wetlands. This is interesting given the large ontogenetic size differences in ambystomatid larvae, for example *A. tigrinum* larvae grew to a maximum of 80 mm SVL while *A. laterale* and *A. jeffersonianum* grew to a maximum of 29 and 37 mm SVL respectively. Wetland water columns contained a distinctly higher proportion of copepods followed by cladocerans and much smaller proportions from other taxa (Figure 7). Our results suggest that *Ambystoma* species select Cladocera and Chironomidae in wetlands and avoid Copepoda, this being consistent for three species and across two geographic locations (Illinois and Ohio; Figure 9). Selection for Cladocera and against Copepoda has been shown in other planktivores such as fish (Fink et al. 2012) as well as other *Ambystoma* species (Ghioca-Robrecht and Smith 2008). This may be a function of Copepoda evasiveness compared to other more slow moving prey items like Cladocera (Amundsen et al. 2009, Peterka and Matena 2009). Interestingly, Chironomidae had a relatively low percentage of diet items but had some of the highest selectivity values. Regester et al. (2008) investigated the contribution of production from *Ambystoma* diet item taxa and found Chironomidae to be a significant contributor to larval production. This notion is also supported by research on secondary production of Chironomidae in other freshwater systems and their support of fish populations (Anderson et al. 2012). Chironomidae may also be important to *Ambystoma* species across a wide variety of habitats and geographic locations as they are one of the most ubiquitous taxonomic groups of aquatic insects (Merritt et al. 2008) and other studies investigating *Ambystoma* species diets have documented Chironomidae as a prey item (Holomuzki et al. 1994, Benoy et al. 2002, Whiles et al. 2004). In addition, larval salamanders avoided only predators while selecting for all other functional groups, potentially enhancing predation on *Ambystoma* prey items as well as other organisms not within *Ambystoma* diets; potentially having an over-arching effect. This may partly explain the observations by Holomuzki et al. (1994) which observed *Ambystoma* larvae had no effect on invertebrate densities directly but found a significant impact on primary production; a similar effect which observed when additional predators are introduced into aquatic systems (e.g. Herbst et al. 2009). Therefore, avoidance of predators as prey items for *Ambystoma* could have significant effects for whole-ecosystem processes while not significantly impacting densities of any particular taxa, thus selection for or against functional groups in further research may provide interesting avenues for investigation.

Local factors affected aquatic invertebrate densities while landscape-level factors influenced larval salamander densities. Although we show these factors have significant effects on densities of wetland biota, further research investigating the relationships these variables have on densities of aquatic taxa are needed. For example, more research on the effects of non-predatory amphibian density on aquatic invertebrates should be investigated as we consistently found a relationship between these two taxa. We also provide evidence that *Ambystoma* species consistently select for and avoid certain prey items and functional groups while not significantly affecting aquatic invertebrate densities. Further investigation of altered ratios in wetland functional groups may unveil indirect effects of *Ambystoma* predation. Namely, experimental manipulation of predator densities on factors such as primary production and CPOM breakdown may give insight into the full ecological significance of larval predatory salamanders in isolated wetlands.

APPENDIX A

PERCENT CHANGES IN SUITABLE HABITAT FOR AMPHIBIAN SPECIES IN THE MIDWESTERN UNITED STATES

Table A1. Percent changes from current to the ensemble of projections for each species in 2050 and 2070 for climate-only models (Chapter II).

Species	2050				2070			
	CCSM 2.6	CCSM 8.5	Hadley 2.6	Hadley 8.5	CCSM 2.6	CCSM 8.5	Hadley 2.6	Hadley 8.5
Ambystoma annulatum	39.63	39.64	39.66	39.30	50.69	51.00	51.05	51.05
Anaxyrus americanus	-49.90	-64.20	-48.48	-75.25	-42.15	-73.02	-68.78	-78.85
Ambystoma barbouri	-63.91	-9.19	-55.14	-88.00	-47.06	-8.44	-80.68	-95.94
Acris crepitans	-29.98	-10.13	26.77	2.84	12.31	6.74	14.70	-16.86
Anaxyrus fowleri	36.24	11.00	48.31	-29.98	9.90	26.79	39.86	-47.26
Ambystoma jeffersonianum	-52.55	-42.55	-73.62	-99.99	-49.59	-41.05	-80.06	-100.00
Ambystoma laterale	-100.00	-100.00	-100.00	-100.00	-100.00	-100.00	-100.00	-100.00
Ambystoma maculatum	-27.55	-12.81	-13.64	-41.92	-12.21	-21.10	-21.24	-93.61
Ambystoma opacum	46.46	74.17	75.29	72.20	64.76	88.18	70.82	-23.20
Ambystoma tigrinum	23.46	33.23	56.98	30.44	32.82	9.23	59.76	19.15
Ambystoma texanum	28.32	53.58	57.27	59.72	45.67	66.58	61.99	66.32
Desmognathus fuscus	-23.33	-27.14	-57.64	-99.99	-17.80	-31.92	-32.92	-99.85
*Eurycea bislineata/Eurycea cirrigera**	-11.78	-8.25	-44.96	-99.94	-28.88	-15.25	-54.68	-100.00
Eurycea longicauda	13.63	13.90	14.04	-67.50	9.26	19.59	13.81	-99.41
Eurycea lucifuga	10.79	11.96	11.88	-4.93	15.97	18.09	17.20	-57.27
Gyrinophilus porphyriticus	-55.90	-87.29	-89.53	-100.00	-56.88	-83.52	-84.19	-100.00
*Hyla versicolor/Hyla chrysoscelis**	-35.78	-51.17	-47.38	-80.91	-40.45	-49.34	-57.06	-93.15
Hemidactylium scutatum	-98.98	-99.76	-96.25	-91.71	-80.77	-98.83	-96.78	-100.00
Lithobates blairi	66.18	114.32	142.04	168.15	41.22	187.92	89.48	222.14
Lithobates catesbeianus	-21.24	-8.24	-20.61	-67.70	-11.93	-11.48	-34.67	-64.15
Lithobates clamitans	-52.56	-54.20	-51.13	-75.23	-45.81	-63.32	-57.33	-79.04

Lithobates palustris	58.32	-10.44	-60.77	-90.96	42.93	-28.02	-24.44	-97.14
Lithobates pipiens	-100.00	-100.00	-89.00	-85.75	-95.87	-95.39	-99.99	-97.30
Lithobates septentrionalis	-92.08	-99.99	-99.79	-100.00	-88.40	-100.00	-99.78	-100.00
Lithobates sphenocephalus	119.42	223.85	200.11	283.83	122.53	335.70	216.12	410.20
Lithobates sylvaticus	-53.27	-78.87	-90.72	-97.20	-68.63	-93.42	-88.71	-99.84
Notophthalmus viridescens	6.28	17.26	19.59	-38.98	28.46	-4.68	20.38	-70.00
Pseudacris crucifer	-28.95	-53.06	-57.28	-81.40	-37.69	-56.86	-46.21	-86.26
Plethodon dorsalis	-15.63	22.93	1.17	-77.08	-7.76	16.98	18.65	-100.00
Plethodon electromorphus	13.24	-16.61	-54.57	-100.00	0.67	-32.86	-57.60	-100.00
*Plethodon cinereus/Plethodon serratus**	-26.47	-41.39	-34.74	-57.73	-30.17	-44.33	-41.75	-69.79
*Plethodon albagula/Plethodon glutinosis**	0.86	18.23	1.32	-61.45	8.39	17.97	-2.86	-94.15
Pseudacris triseriata	-63.55	-64.73	-73.51	-65.92	-64.18	-77.14	-72.10	-70.79

Table A2. Percent changes from current to the ensemble of projections for each species in 2050 and 2070 for climate + land-use models (Chapter II).

Species	2050				2070			
	CCSM 2.6	CCSM 8.5	Hadley 2.6	Hadley 8.5	CCSM 2.6	CCSM 8.5	Hadley 2.6	Hadley 8.5
Ambystoma annulatum	27.77	27.79	27.79	27.79	36.75	36.84	36.84	36.84
Anaxyrus americanus	-46.38	-48.71	-48.71	-63.28	-39.14	-60.82	-50.19	-54.35
Ambystoma barbouri	-72.96	-21.40	-21.40	-81.47	-70.79	-26.30	-93.84	-95.09
Acris crepitans	-36.35	25.20	25.20	58.42	-13.35	38.30	15.99	-21.25
Anaxyrus fowleri	52.30	24.80	24.80	-48.95	20.55	33.61	45.75	40.45
Ambystoma jeffersonianum	-74.05	-54.99	-54.99	-99.50	-77.74	-74.44	-78.45	-99.89
Ambystoma laterale	-100.00	-100.00	-100.00	-100.00	-100.00	-100.00	-100.00	-100.00

Ambystoma maculatum	-28.54	-17.43	-17.43	-37.73	-25.71	-21.35	-42.50	-85.62
Ambystoma opacum	62.44	87.12	87.12	59.03	38.79	108.04	73.75	31.70
Ambystoma tigrinum	146.54	139.09	139.09	130.70	111.72	72.22	72.69	237.63
Ambystoma texanum	36.92	129.87	129.87	79.24	53.67	152.87	122.35	156.08
Desmognathus fuscus	-23.00	-25.75	-25.75	-99.34	-22.23	-21.94	-59.06	-97.87
*Eurycea bislineata/Eurycea cirrigera**	-25.75	-15.74	-15.74	-95.05	-32.99	-15.03	-60.63	-97.79
Eurycea longicauda	30.83	35.61	35.61	-78.09	-8.44	30.70	0.78	-97.55
Eurycea lucifuga	38.08	31.78	31.78	2.46	30.22	51.31	42.20	-12.49
Gyrinophilus porphyriticus	-68.10	-67.92	-67.92	-100.00	-41.46	-72.88	-86.12	-100.00
*Hyla versicolor/Hyla chrysoscelis**	-20.98	-23.55	-23.55	-59.29	-45.15	-52.09	-50.73	-75.59
Hemidactylium scutatum	-81.26	-93.03	-93.03	-90.51	-77.07	-95.71	-82.86	-100.00
Lithobates blairi	74.31	120.58	120.58	205.60	42.10	177.25	121.75	249.48
Lithobates catesbeianus	-0.29	7.43	7.43	-50.47	-13.59	-4.92	-34.64	-44.02
Lithobates clamitans	-48.04	-47.91	-47.91	-64.50	-43.00	-58.96	-53.47	-70.47
Lithobates palustris	85.07	15.82	15.82	-86.70	89.05	-17.78	-33.78	-92.09
Lithobates pipiens	-80.14	-78.34	-78.34	-97.82	-74.22	-98.79	-94.55	-96.56
Lithobates septentrionalis	-92.95	-99.98	-99.98	-100.00	-90.25	-100.00	-99.92	-100.00
Lithobates sphenocephalus	92.90	187.96	187.96	249.64	80.83	268.66	149.05	403.41
Lithobates sylvaticus	-79.51	-80.99	-80.99	-95.73	-75.66	-95.22	-80.12	-99.45
Notophthalmus viridescens	-8.67	18.74	18.74	-32.13	15.98	-2.56	-24.42	46.33
Pseudacris crucifer	-17.14	-36.07	-36.07	-74.11	-32.87	-57.17	-52.06	-68.06
Plethodon dorsalis	-25.56	20.88	20.88	-81.51	-22.83	37.02	10.88	-99.74
Plethodon electromorphus	9.48	-24.08	-24.08	-99.74	-4.76	-30.55	-51.08	-100.00
*Plethodon cinereus/Plethodon serratus**	-39.30	-39.13	-39.13	-68.51	-38.71	-38.94	-39.19	-71.32
*Plethodon albagula/Plethodon glutinosis**	14.97	14.13	14.13	-26.74	20.98	26.65	0.15	-62.93
Pseudacris triseriata	-74.74	-53.78	-53.78	-49.88	-68.84	-69.17	-36.58	-68.38

APPENDIX B

ABUNDANCE OF QUANTIFIED TAXA IN WETLAND WATER COLUMNS AND IN AMBYSTOMATID SALAMANDER STOMACHS

Table B1**.** Table listing all taxa found in Illinois wetlands and their counts within water columns (WC) and diets of *Ambystoma* (D) for each month (Chapter III).

		Grainger May	Rollins May	Ethel's East May	Ethel's West May	Ethel's Center May	Grainger June	Rollins June	Ethel's East June	Ethel's West June	Ethel's Center June	Rollins July	Rollins August	Ethel's East August
Daphnia	WC	104.0	10.3	46.3	31.0	187.0	21.0	26.7	20.3	6.0	18.7	52.3	23.7	18.3
	D	15.2	24.5	4.2	1.5	2.0	12.2	25.0	6.0	1.2	0.5	242.4	72.8	167.8
Cyclopoid	WC	29.7	6.7	100.3	132.0	225.3	76.0	130.3	35.7	9.0	36.0	26.0	2.3	20.0
	D	1.2	0.3	0.2	1.9	0.4	1.4	0.7	2.5	4.9	4.5	0.2	0.6	11.2
Nauplii	WC	64.7	124.7	115.3	184.0	232.7	362.7	549.3	189.3	20.0	658.7	57.0	7.3	30.3
	D	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Chaoborus	WC	0.0	0.0	0.0	0.0	4.0	2.3	6.7	1.3	0.0	2.0	5.0	9.0	6.7
	D	0.0	0.0	0.0	0.0	0.0	0.5	0.9	0.1	0.0	0.0	6.0	3.0	40.2
Diaptomus	WC	47.3	104.7	34.0	0.0	38.3	0.0	57.7	4.3	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lycneus	WC	17.7	4.7	0.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	2.2	0.6	0.0	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0
Ostracoda	WC	5.7	2.7	52.7	29.0	3.7	1.3	1.0	7.7	1.0	0.7	0.0	0.3	6.0
	D	0.4	2.2	0.4	8.0	1.2	1.5	0.2	0.6	1.2	1.0	2.2	1.6	28.8
Harpactoid	WC	0.0	2.3	16.3	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleuroxis	WC	0.7	0.0	16.0	1.0	3.3	2.0	5.7	20.3	2.0	3.7	1.7	3.0	26.0
	D	1.2	0.0	0.0	0.7	0.3	7.3	0.0	20.0	0.2	48.5	0.0	0.0	52.6
Physella	WC	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	WC	0.7	0.3	1.0	4.0	1.7	0.3	0.7	0.0	0.0	0.0	0.3	0.0	5.3
	D	0.4	0.0	0.0	0.1	0.2	0.3	0.4	0.3	0.9	0.0	3.0	9.4	10.8
Scapholoberis	WC	0.3	0.0	0.0	13.0	0.0	0.7	0.3	3.7	0.0	0.7	0.0	19.7	12.7
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Braconidae	WC	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cybister	WC	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gammaridae	WC	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.3	0.2	2.4	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0
Odontomyia	WC	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lestes	WC	0.0	0.0	0.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
	D	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.2
Corixidae	WC	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.6	0.2	0.0
Gastropoda	WC	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Notonectidae	WC	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Anopholes	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Culicoides	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Collembola	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	0.3	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syrphidae	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Psychodidae	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ranatra	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dytistcidae	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.2
Baetidae	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aranae	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Formicidae	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Ladona	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Acilius	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Coleoptera	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.4
Asellus	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.2	0.0	0.1	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Unknown	WC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	D	0.0	0.3	0.4	0.0	0.3	0.2	0.0	0.0	0.0	0.0	0.2	0.2	0.0

Table B2. Table listing all taxa found in Ohio wetlands and their counts within water columns (WC) and diets of *Ambystoma* (D) for each month (Chapter III).

		SH	OG	GW	SP	WM	SH	WM	SH	OG	WM	SH	WM
		April	April	April	April	April	June	June	March	March	March	May	May
Cladocera	WC	0	7	10	0	3	637	0	1	429	192	0	7
	D	48.67	69.10	1.5	19.76	1.36	314.07	3.7	3.06	1.27	7.39	0.63	2.43
Chironomidae	WC	45	68	26	11	195	37	84	32	39	80	134	49
	D	6.35	1.34	0.8	2.38	4.8	21.035	3.36	1.8	1.41	0.32	7.93	7.76
Copepoda	WC	43	3	25	8	11	16	0	10	27	20	153	5
	D	0.90	3	0.1	1.28	0.6	0.17	0.06	0.06	3.34	0.21	0	0.46
Gastropoda	WC	0	1	103	18	31	0	168	0	0	1	0	91
	D	0	0.06	0.37	0.28	0.86	0	1	0	0	0	0	0.5
Ostracoda	WC	8	4	0	21	17	0	12	28	22	9	0	12
	D	0.25	0.86	2.3	0.66	1.53	0.03	1.4	1.8	0.06	0.32	1.5	1.93
Amphipoda	WC	0	0	0	788	0	0	0	0	0	0	0	0
	D	0	0	0	0.23	0	0	0	0	0	0	0	0
Bivalvia	WC	0	0	0	0	0	0	0	0	0	0	0	0
	D	0	0	0	0.04	0	0	0	0	0	0	0	0
Pleidae	WC	0	0	10	0	0	1	0	0	7	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Haliplidae	WC	0	0	0	0	0	0	0	0	5	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Notonectidae	WC	5	17	0	1	4	0	1	0	1	11	0	4
	D	0	0.17	0	0	0	0	0	0	0	0	0	0
Terrestrial	WC	9	13	21	2	4	4	3	1	5	2	5	8
	D	0	0	0	0	0.06	0	0	0	0	0	0	0.03
Mesoveliidae	WC	0	0	7	5	7	0	3	0	11	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Culicidae	WC	168	0	0	95	26	62	1	4	37	13	80	59
	D	0.06	0	0	0	0	0	0	0	0	0	0	0.03
Collembola	WC	0	56	0	160	39	0	89	0	2	109	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Libellulidae	WC	1	0	3	0	0	0	1	0	1	0	0	2
	D	0	0.03	0	0	0	0	0	0	0	0	0	0.06
Coenagrionidae	WC	0	2	0	1	7	0	0	0	2	8	0	4
	D	0	0	0	0	0.03	0	0.06	0	0	0	0	0.03
Aeshnidae	WC	0	0	1	0	0	11	0	0	0	0	0	0
	D	0	0.03	0	0	0	0	0	0	0	0	0	0

Dytiscidae	WC	0	6	1	6	1	0	2	5	6	2	3	1
	D	0	0.13	0	0	0.03	0	0	0	0	0	0	0
Curculionidae	WC	0	0	0	0	2	0	0	0	0	3	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Aranae	WC	0	0	0	1	0	0	0	1	0	1	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Stratiomyiidae	WC	0	0	10	0	0	0	1	0	0	1	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Asellidae	WC	0	0	0	47	0	0	0	0	0	1	0	0
	D	0	0	0	0	0	0	0	0	0	0	0.06	0
Mesoveliidae	WC	0	1	0	1	0	0	0	0	0	2	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Oligocheata	WC	0	0	0	2	0	0	0	19	0	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Scirtidae	WC	1	0	0	42	0	0	0	3	0	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Diptera pupae	WC	0	2	0	0	0	0	0	1	0	0	0	0
	D	0.45	1.24	0	0	0.03	0.21	0.13	0.67	0.06	0	0.1	0.13
Schiomyziidae	WC	0	0	1	5	1	0	0	1	0	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophildae	WC	0	24	1	0	1	1	6	0	0	0	0	9
	D	0	0.03	0	0	0	0	0.06	0	0	0	0	0
Ceratapogonidae	WC	0	0	0	0	0	0	0	0	0	0	0	0
	D	0.03	0.20	0	0	0	0	0.03	0.03	0	0	0	0
Hebridae	WC	2	4	0	0	0	4	0	0	0	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Gerridae	WC	20	20	0	6	8	6	0	0	0	0	1	1
	D	0	0.03	0	0	0	0	0	0	0	0	0	0
Diptera Casings	WC	9	0	0	0	0	0	0	0	0	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Ephyridae	WC	0	0	0	0	2	0	0	0	0	0	0	1
	D	0	0	0	0	0	0	0	0	0	0	0	0
Corixidae	WC	0	0	0	0	0	0	0	0	0	0	0	0
	D	0	0	0	0	0.03	0	0	0	0	0	0	0
Corydalidae	WC	0	0	0	0	0	0	11	0	0	0	1	13
	D	0	0	0	0	0	0	0	0	0	0	0.03	0
Lepidoptera	WC	0	0	0	0	0	0	0	0	0	0	0	0
	D	0	0	0	0	0.03	0	0.03	0	0	0	0	0
Chaoboridae	WC	0	0	0	0	0	2	0	0	0	0	0	0
	D	0.03	0.41	0	0	0.26	0.10	0.0	0	0.10	0	0	0.03
Aphididae	WC	0	0	0	0	0	0	1	0	0	0	0	0

	D	0	0	0	0	0	0	0	0	0	0	0	0
Baetidae	WC	0	0	1	0	0	0	0	0	0	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Tabanidae	WC	0	0	1	0	0	0	0	0	0	0	0	0
	D	0	0	0	0	0	0	0	0	0	0	0	0
Ambystoma	WC	0	0	0	0	0	0	0	0	0	0	0	0
	D	0.06	0	0	0	0.06	0	0	0	0	0.03	0	0
Unkown	WC	0	0	0	0	0	0	0	0	0	0	0	0
	D	0	0.03	0	0	0.03	0	0	0.03	0	0	0.03	0

LITERATURE CITED

Alix, D. M., C. J. Anderson, J. B. Grand, and C. Guyer. 2014. Evaluating the effects of land use on headwater wetland amphibian assemblages in coastal Alabama. Wetlands 34:917-926.

Amundsen, P. A., A. Siwertsson, R. Primicerio, and T. Bohn. 2009. Long-term responses of zooplankton to invasion by a planktivorous fish in a subarctic watercourse. Freshwater Biology 54:24-34.

Anderson, T. J., R. S. Stelzer, H. G. Drecktrah, and S. L. Eggert. 2012. Secondary production of Chironomidae in a large eutrophic lake: Implications for lake sturgeon production. Freshwater Science 31:365-378.

Araujo, M. B. and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology & Evolution 22:42-47.

Araujo, M. B., W. Thuiller, and R. G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33:1712-1728.

Baldwin, R. A. 2009. Use of Maximum Entropy Modeling in Wildlife Research. Entropy 11:854-866.

Barbet-Massin, M., W. Thuiller, and F. Jiguet. 2012. The fate of European breeding birds under climate, land-use and dispersal scenarios. Global Change Biology 18:881-890.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471:51-57.

Bardwell, J. H., C. M. Ritzi, and J. A. Parkhurst. 2007. Dietary selection among different size classes of larval Ambystoma jeffersonianum (Jefferson Salamanders). Northeastern Naturalist 14:293-299.

Barrett, K. and C. Guyer. 2008. Differential responses of amphibians and reptiles in riparian and stream habitats to land use disturbances in western Georgia, USA. Biological Conservation 141:2290-2300.Barrett, K., N. P. Nibbelink, and J. C. Maerz. 2014. Identifying priority species and conservation opportunities under future climate scenarios: amphibians in a biodiversity hotspot. Journal of Fish and Wildlife Management 5:282-297.

Batzer, D. P. 2013. The seemingly intractable ecological responses of invertebrates in North American wetlands: A review. Wetlands (Wilmington, N.C.) 33:1-15.

Batzer, D. P. and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. Annual Review of Entomology 41:75-100.

Benoy, G. A. 2008. Tiger salamanders in prairie potholes: A “Fish in amphibian’s garments?”. Wetlands (Wilmington, N.C.) 28:464-472.

Benoy, G. A., T. D. Nudds, and E. Dunlop. 2002. Patterns of habitat and invertebrate diet overlap between tiger salamanders and ducks in prairie potholes. Hydrobiologia 481:47-59.

Blaustein, A. R., B. A. Han, R. A. Relyea, P. T. J. Johnson, J. C. Buck, S. S. Gervasi, and L. B. Kats. 2011. The complexity of amphibian population declines: understanding the role of cofactors in driving amphibian losses. Year in Ecology and Conservation Biology 1223:108-119.

Blaustein, L., J. Friedman, and T. Fahima. 1996. Larval Salamandra drive temporary pool community dynamics: Evidence from an artificial pool experiment. Oikos 76:392-402.

Bocsi, T., J. M. Allen, J. Bellemare, J. Kartesz, M. Nishino, and B. A. Bradley. 2016. Plants' native distributions do not reflect climatic tolerance. Diversity and Distributions 22:615-624.

Boix, D., J. Sala, and R. Moreno-Amich. 2001. The faunal composition of espolla pond (NE Iberian peninsula): The neglected biodiversity of temporary waters. Wetlands 21:577-592.

Bosch, J., L. M. Carrascal, L. Duran, S. Walker, and M. C. Fisher. 2007. Climate change and outbreaks of amphibian chytridiomycosis in a montane area of Central Spain; is there a link? Proceedings of the Royal Society B-Biological Sciences 274:253-260.

Brown, J. L. 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods in Ecology and Evolution 5:694-700.

Bryja, J., M. Heroldova, and J. Zejda. 2002. Effects of deforestation on structure and diversity of small mammal communities in the Moravskoslezske Beskydy Mts (Czech Republic). Acta Theriologica 47:295-306.

Capps, K. A., K. A. Berven, and S. D. Tiegs. 2015. Modelling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. Freshwater Biology 60:500-511.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science advances 1:e1400253.

Cecala, K. K., S. J. Price, and M. E. Dorcas. 2007. A comparison of the effectiveness of recommended doses of MS-222 (tricaine methanesulfonate) and Oragel® (benzocaine) for amphibian anesthesia. Herpetological Review 38:63-66.

Chace, J. F. and J. J. Walsh. 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74:46-69.

Chaparro-Herrera, D. D., S. Nandini, S. S. S. Sarma, and L. Zambrano. 2011. Feeding behaviour of larval Ambystoma mexicanum. Amphibia-Reptilia 32:509-517.

Chen, P. Y., P. F. Lee, C. J. Ko, C. H. Ko, T. C. Chou, and C. J. Teng. 2011. Associations between water quality parameters and planktonic communities in three constructed wetlands, Taipei. Wetlands 31:1241-1248.

Clipp, H. L. and J. T. Anderson. 2014. Environmental and anthropogenic factors influencing salamanders in riparian forests: A review. Forests 5:2679-2702.

Collins, J. P. 2010. Amphibian decline and extinction: what we know and what we need to learn. Diseases of Aquatic Organisms 92:93-99.

Collins, J. P. and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions 9:89-98.

Cook, A. R., and T. J. Hoellein. 2016. Environmental drivers of leaf breakdown in an urban watershed. Freshwater Science 35:311-323.

Davic, R. D. and H. H. Welsh. 2004. On the ecological roles of salamanders. Annual Review of Ecology Evolution and Systematics 35:405-434.

Delaney, K. S., S. P. D. Riley, and R. N. Fisher. 2010. A rapid, strong, and convergent genetic response to urban habitat fragmentation in four divergent and widespread vertebrates. PloS one 5.

Denton, R. D., and S. C. Richter. 2013. Amphibian communities in natural and constructed ridge top wetlands with implications for wetland construction. Journal of Wildlife Management 77:886-896.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401-406.

Dodson, S. I. and R. A. Lillie. 2001. Zooplankton communities of restored depressional wetlands in Wisconsin, USA. Wetlands 21:292-300.

Dodson, S. I., R. A. Lillie, and S. Will-Wolf. 2005. Land use, water chemistry, aquatic vegetation, and zooplankton community structure of shallow lakes. Ecological Applications 15:1191-1198.

Dulic, Z., Z. Markovic, M. Zivic, M. Ciric, M. Stankovic, G. Subakov-Simic, and I. Zivic. 2014. The response of phytoplankton, zooplankton and macrozoobenthos communities to change in the water supply from surface to groundwater in aquaculture ponds. Annales De Limnologie-International Journal of Limnology 50:131-141.

DuRant, S. E. and W. A. Hopkins. 2008. Amphibian predation on larval mosquitoes. Canadian Journal of Zoology 86:1159-1164.

Early, R. and D. F. Sax. 2011. Analysis of climate paths reveals potential limitations on species range shifts. Ecology Letters 14:1125-1133.

Epele, L. B. and M. L. Miserendino. 2015. Environmental quality and aquatic invertebrate metrics relationships at Patagonian wetlands subjected to livestock grazing pressures. Plos One 10.

Fahrig, L. and T. Rytwinski. 2009. Effects of roads on animal abundance: An empirical review and synthesis. Ecology and Society 14.

Feder, M. E. and W. W. Burggren, editors. 1992. Environmental Physiology of the Amphibians. University of Chicago Press.

Feehan, J., M. Harley, and J. van Minnen. 2009. Climate change in Europe. 1. Impact on terrestrial ecosystems and biodiversity. A review (Reprinted). Agronomy for Sustainable Development 29:409-421.

Feng, S., Q. Hu, W. Huang, C. H. Ho, R. P. Li, and Z. H. Tang. 2014. Projected climate regime shift under future global warming from multi-model, multi-scenario CMIP5 simulations. Global and Planetary Change 112:41-52.

Findlay, C. S. and J. Houlahan. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. Conservation Biology 11:1000-1009.

Fink, P., A. Kottsieper, M. Heynen, and J. Borcherding. 2012. Selective zooplanktivory of an invasive Ponto-Caspian mysid and possible consequences for the zooplankton community structure of invaded habitats. Aquatic Sciences 74:191-202.

Fitzpatrick, L. C. 1973. Energy allocation in the Allegheny Mountain salamander, Desmognathus ochrophaeus. Ecological Monographs 43:43-58.

Flory, A. R., S. Kumar, T. J. Stohlgren, and P. M. Cryan. 2012. Environmental conditions associated with bat white-nose syndrome mortality in the north-eastern United States. Journal of Applied Ecology 49:680-689.

Fong G, A., N. Vina Davila, and G. M. Lopez-Iborra. 2015. Amphibian hotspots and conservation priorities in eastern Cuba identified by species distribution modeling. Biotropica 47:119-127.

Fourcade, Y., J. O. Engler, D. Roedder, and J. Secondi. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PloS one 9:e97122.

Ghioca-Robrecht, D. M. and L. M. Smith. 2008. Feeding ecology of polymorphic larval barred tiger salamanders in playas of the Southern Great Plains. Canadian Journal of Zoology-Revue Canadienne De Zoologie 86:554-563.

Gibbons, J. W., C. T. Winne, D. E. Scott, J. D. Willson, X. Glaudas, K. M. Andrews, B. D. Todd, L. A. Fedewa, L. Wilkinson, R. N. Tsaliagos, S. J. Harper, J. L. Greene, T. D. Tuberville, B. S. Metts, M. E. Dorcast, J. P. Nestor, C. A. Young, T. Akre, R. N. Reed, K. A. Buhlmann, J. Norman, D. A. Croshaw, C. Hagen, and B. B. Rothermel. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: Implications for wetland conservation. Conservation Biology 20:1457-1465.

Gibbs, J. P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands 13:25-31.

Goldberg, C. S. and L. P. Waits. 2010. Comparative landscape genetics of two pond-breeding amphibian species in a highly modified agricultural landscape. Molecular Ecology 19:3650-3663.

Gong, D. Y. and C. H. Ho. 2003. Detection of large-scale climate signals in spring vegetation index (normalized difference vegetation index) over the Northern Hemisphere. Journal of Geophysical Research-Atmospheres 108.

Gorman, T. A., C. A. Haas, and D. C. Bishop. 2009. Factors related to occupancy of breeding wetlands by flatwoods salamander larvae. Wetlands 29:323-329.

Groff, L.A., S.B. Marks, and M.P. Hayes. 2014. Using ecological nich models to direct rate amphibian surveys: A case study using the Oregon Spotted Frog (*Rana pretiosa*). Herpetological Conservation and Biology 9:354–368.

Hautier, Y., D. Tilman, F. Isbell, E. W. Seabloom, E. T. Borer, and P. B. Reich. 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348:336-340.

Herbst, D. B., E. L. Silldorff, and S. D. Cooper. 2009. The influence of introduced trout on the benthic communities of paired headwater streams in the Sierra Nevada of California. Freshwater Biology 54:1324-1342.

Hillman, S. S., R. C. Drewes, M. S. Hedrick, and T. V. Hancock. 2014. Physiological vagility and its relationship to dispersal and neutral genetic heterogeneity in vertebrates. Journal of Experimental Biology 217:3356-3364.

Hocking, D. J., G. M. Connette, C. A. Conner, B. R. Scheffers, S. E. Pittman, W. E. Peterman, and R. D. Semlitsch. 2013. Effects of experimental forest management on a terrestrial, woodland salamander in Missouri. Forest ecology and management 287:32-39.

Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences of the United States of America 106:19659-19665.

Holomuzki, J. R. and J. P. Collins. 1987. Trophic dynamics of a top predator, Ambystoma tigrinum nebulosum (Caudata: Ambystomatidae), in a lentic community. Copeia:949-957.

Holomuzki, J. R., J. P. Collins, and P. E. Brunkow. 1994. Trophic control of fishless ponds by tiger salamander larvae. Oikos 71:55-64.

Holzer, K. A. 2014. Amphibian use of constructed and remnant wetlands in an urban landscape. Urban Ecosystems 17:955-968.

Homyack, J. A. and C. A. Haas. 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biological Conservation 142:110-121.

Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. P. Peters. 2011. Lessons Learned While Integrating Habitat, Dispersal, Disturbance, and Life-History Traits into Species Habitat Models Under Climate Change. Ecosystems 14:1005-1020.

James, T. Y., L. F. Toledo, D. Rodder, D. D. Leite, A. M. Belasen, C. M. Betancourt-Roman, T. S. Jenkinson, C. Soto-Azat, C. Lambertini, A. V. Longo, J. Ruggeri, J. P. Collins, P. A. Burrowes, K. R. Lips, K. R. Zamudio, and J. E. Longcore. 2015. Disentangling host, pathogen, and environmental determinants of a recently emerged wildlife disease: lessons from the first 15years of amphibian chytridiomycosis research. Ecology and Evolution 5:4079-4097.

Jimenez-Valverde, A., N. Barve, A. Lira-Noriega, S. P. Maher, Y. Nakazawa, M. Papes, J. Soberon, J. Sukumaran, and A. T. Peterson. 2011. Dominant climate influences on North American bird distributions. Global Ecology and Biogeography 20:114-118.

Jones, C. C., S. A. Acker, and C. B. Halpern. 2010. Combining local- and large-scale models to predict the distributions of invasive plant species. Ecological Applications 20:311-326.

Jones, S., R. Perissinotto, N. K. Carrasco, and A. Vosloo. 2016. Impact of a flood event on the zooplankton of an estuarine lake. Marine Biology Research 12:158-167.

Kearney, M., B. L. Phillips, C. R. Tracy, K. A. Christian, G. Betts, and W. P. Porter. 2008. Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. Ecography 31:423-434.

Kearney, M. R., B. A. Wintle, and W. P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters 3:203-213.

Keitzer, S. C. and R. R. Goforth. 2013. Salamander diversity alters stream macroinvertebrate community structure. Freshwater Biology 58:2114-2125.

Kissling, W. D., C. F. Dormann, J. Groeneveld, T. Hickler, I. Kuhn, G. J. McInerny, J. M. Montoya, C. Romermann, K. Schiffers, F. M. Schurr, A. Singer, J. C. Svenning, N. E. Zimmermann, and R. B. O'Hara. 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. Journal of Biogeography 39:2163-2178.

Knutson, M. G., J. R. Sauer, D. A. Olsen, M. J. Mossman, L. M. Hemesath, and M. J. Lannoo. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, U.S.A. Conservation Biology 13:1437-1446.

Kolozsvary, M. B. and R. K. Swihart. 1999. Habitat fragmentation and the distribution of amphibians: Patch and landscape correlates in farmland. Canadian Journal of Zoology 77:1288-1299.

Koprivnikar, J., D. J. Marcogliese, J. R. Rohr, S. A. Orlofske, T. R. Raffel, and P. T. J. Johnson. 2012. Macroparasite Infections of Amphibians: What Can They Tell Us? EcoHealth 9:342-360.

Lannoo, M. 2005. Amphibian declines: The conservation status of United States species. University of California Press, Berkeley, California, USA.

Lawler, J. J., S. L. Shafer, B. A. Bancroft, and A. R. Blaustein. 2010. Projected climate impacts for the amphibians of the Western Hemisphere. Conservation Biology 24:38-50.

Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. P. Maurer, A. R. Blaustein, and P. J. Bartlein. 2009. Projected climate-induced faunal change in the Western Hemisphere. Ecology 90:588-597.

Lehtinen, R. M., S. M. Galatowitsch, and J. R. Tester. 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19:1-12.

Marsh, D. M. and N. G. Beckman. 2004. Effects of forest roads on the abundance and activity of terrestrial salamanders. Ecological Applications 14:1882-1891.

Matthews, S. N., L. R. Iverson, A. M. Prasad, and M. P. Peters. 2011. Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. Ecography 34:933-945.

McCallum, M. L. 2007. Amphibian decline or extinction? Current declines dwarf background extinction rate. Journal of Herpetology 41:483-491.

McCallum, M. L. 2015. Vertebrate biodiversity losses point to a sixth mass extinction. Biodiversity and Conservation 24:2497-2519.

McCarty, J. P. 2001. Ecological consequences of recent climate change. Conservation Biology 15:320-331.

Merow, C., M. J. Smith, and J. A. Silander. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36:1058-1069.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America. Fourth edition. Kendall Hunt Publishing Company.

Milanovich, J., W. E. Peterman, N. P. Nibbelink, and J. C. Maerz. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. PloS one 5:e12189.

Milanovich, J. R., J. C. Maerz, and A. D. Rosemond. 2015. Stoichiometry and estimates of nutrient standing stocks of larval salamanders in Appalachian headwater streams. Freshwater Biology 60:1340-1353.

Milanovich, J. R. and W. E. Peterman. 2016. Revisiting Burton and Likens (1975): Nutrient Standing Stock and Biomass of a Terrestrial Salamander in the Midwestern United States. Copeia 104:165-171.

Mitsch, W. J. and J. G. Gosselink. 2000. The values of wetlands: Landscapes and institutional perspectives. Ecological Economics 35:25-33.

Morrice, J. A., N. P. Danz, R. R. Regal, J. R. Kelly, G. J. Niemi, E. D. Reavie, T. Hollenhorst, R. P. Axler, A. S. Trebitz, A. M. Cotter, and G. S. Peterson. 2008. Human influences on water quality in Great Lakes coastal wetlands. Environmental Management 41:347-357.

Naughton, G. P., C. B. Henderson, K. R. Foresman, and R. L. McGraw. 2000. Long-toed salamanders in harvested and intact Douglas-fir forests of western Montana. Ecological Applications 10:1681-1689.

Nenzen, H. K. and M. B. Araujo. 2011. Choice of threshold alters projections of species range shifts under climate change. Ecological Modelling 222:3346-3354.

Osbourn, M. S., G. M. Connette, and R. D. Semlitsch. 2014. Effects of fine-scale forest habitat quality on movement and settling decisions in juvenile pond-breeding salamanders. Ecological Applications 24:1719-1729.

Ousterhout, B. H., T. L. Anderson, D. L. Drake, W. E. Peterman, and R. D. Semlitsch. 2015. Habitat traits and species interactions differentially affect abundance and body size in pond-breeding amphibians. Journal of Animal Ecology 84:914-924.

Parra-Olea, G., E. Martínez-Meyer, and G. P.-P. d. León. 2005. Forecasting Climate Change Effects on Salamander Distribution in the Highlands of Central Mexico. Biotropica 37:202-208.

Pechmann, J. H. K., R. A. Estes, D. E. Scott, and J. W. Gibbons. 2001. Amphibian colonization and use of ponds created for trial mitigation of wetland loss. Wetlands 21:93-111.

Pereira, P. L. L., A. M. C. Torres, D. F. M. Soares, M. Hijosa-Valsero, and E. Becares. 2013. Chytridiomycosis: a global threat to amphibians. Revue Scientifique Et Technique-Office International Des Epizooties 32:857-867.

Peterka, J. and J. Matena. 2009. Differences in feeding selectivity and efficiency between young-of-the-year European perch (Perca fluviatilis) and roach (Rutilus rutilus) - field observations and laboratory experiments on the importance of prey movement apparency vs. evasiveness. Biologia 64:786-794.

Peterman, W. E. and R. D. Semlitsch. 2013. Fine-scale habitat associations of a terrestrial salamander: The role of environmental gradients and implications for population dynamics. PloS one 8.

Peterman, W.E. and R. D. Semlitsch. 2014. Spatial variation in water loss predicts terrestrial salamander distribution and population dynamics. Oecologia 176:357-369.

Peterman, W. E., T. L. Anderson, D. L. Drake, B. H. Ousterhout, and R. D. Semlitsch. 2014. Maximizing pond biodiversity across the landscape: A case study of larval Ambystomatid salamanders. Animal Conservation 17:275-285.

Petranka, J. W. 1989. Density-Dependent Growth and Survival of Larval Ambystoma: Evidence from Whole-Pond Manipulations. Ecology 70:1752-1767.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231-259.

Pievani, T. 2014. The sixth mass extinction: Anthropocene and the human impact on biodiversity. Rendiconti Lincei-Scienze Fisiche E Naturali 25:85-93.

Pillsbury, F. C. and J. R. Miller. 2008. Habitat and landscape characteristics underlying anuran Plenzler, M. A. and H. J. Michaels. 2015. Terrestrial habitat quality impacts macroinvertebrate diversity in temporary wetlands. Wetlands 35:1093-1103.

Porej, D. and T. E. Hetherington. 2005. Designing wetlands for amphibians: The importance of predatory fish and shallow littoral zones in structuring of amphibian communities. Wetlands Ecology and Management 13:445-455.community structure along an urban-rural gradient. Ecological Applications 18:1107-1118.

Price, S. J., K. K. Cecala, R. A. Browne, and M. E. Dorcas. 2011. Effects of urbanization on occupancy of stream salamanders. Conservation Biology 25:547-555.

Qian, H. 2010. Environment-richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. Ecological Research 25:629-637.

Radeloff, V. C., E. Nelson, A. J. Plantinga, D. J. Lewis, D. Helmers, J. J. Lawler, J. C. Withey, F. Beaudry, S. Martinuzzi, V. Butsic, E. Lonsdorf, D. White, and S. Polasky. 2012. Economic-based projections of future land use in the conterminous United States under alternative policy scenarios. Ecological Applications 22:1036-1049.

Radosavljevic, A. and R. P. Anderson. 2014. Making better MAXENT models of species distributions: complexity, overfitting and evaluation. Journal of Biogeography 41:629-643.

Randin, C. F., J. Paulsen, Y. Vitasse, C. Kollas, T. Wohlgemuth, N. E. Zimmermann, and C. Koerner. 2013. Do the elevational limits of deciduous tree species match their thermal latitudinal limits? Global Ecology and Biogeography 22:913-923.

Regester, K. J., K. R. Lips, and M. R. Whiles. 2006. Energy flow and subsidies associated with the complex life cycle of Ambystomatid Salamanders in ponds and adjacent forest in southern Illinois. Oecologia 147:303-314.

Regester, K. J., M. R. Whiles, and K. R. Lips. 2008. Variation in the trophic basis of production and energy flow associated with emergence of larval salamander assemblages from forest ponds. Freshwater Biology 53:1754-1767.

Richgels, K. L. D., R. E. Russell, M. J. Adams, C. L. White, and E. H. C. Grant. 2016. Spatial variation in risk and consequence of Batrachochytrium salamandrivorans introduction in the USA. Royal Society Open Science 3.

Roloff, G. J., T. E. Grazia, K. F. Millenbah, and A. J. Kroll. 2011. Factors Associated with Amphibian Detection and Occupancy in Southern Michigan Forests. Journal of Herpetology 45:15-22.

Ruiz-Gutierrez, V. and E. F. Zipkin. 2011. Detection biases yield misleading patterns of species persistence and colonization in fragmented landscapes. Ecosphere 2.

Sacerdote, A. B. and R. B. King. 2009. Dissolved oxygen requirements for hatching success of two Ambystomatid salamanders in restored ephemeral ponds. Wetlands 29:1202-1213.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Biodiversity - Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Schaller, J. 2013. Invertebrate grazers are a crucial factor for grass litter mass loss and nutrient mobilization during aquatic decomposition. Fundamental and Applied Limnology 183:287-295.

Scheffers, B. R., B. L. S. Furman, and J. P. Evans. 2013. Salamanders continue to breed in ephemeral ponds following the removal of surrounding terrestrial habitat. Herpetological Conservation and Biology 8:715-723.

Scheffers, B. R. and C. A. Paszkowski. 2013. Amphibian use of urban stormwater wetlands: The role of natural habitat features. Landscape and Urban Planning 113:139-149.

Scheffers, B. R. and C. A. Paszkowski. 2012. The effects of urbanization on North American amphibian species: Identifying new directions for urban conservation. Urban Ecosystems 15:133-147.

Schriever, T. A., M. W. Cadotte, and D. D. Williams. 2014. How hydroperiod and species richness affect the balance of resource flows across aquatic-terrestrial habitats. Aquatic Sciences 76:131-143.

Scott, D. E., M. J. Komoroski, D. A. Croshaw, and P. M. Dixon. 2013. Terrestrial distribution of pond-breeding salamanders around an isolated wetland. Ecology 94:2537-2546.

Semlitsch, R. D. 1998. Biological Delineation of Terrestrial Buffer Zones for Pond-Breeding Salamanders. Conservation Biology 12:1113-1119.

Semlitsch, R. D. and J. R. Bodie. 1998. Are small isolated wetlands expendable? Conservation Biology 12:1129-1133.

Semlitsch, R. D. and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation biology 17:1219-1228.

Semlitsch, R. D., K. M. O'Donnell, and F. R. Thompson. 2014. Abundance, biomass production, nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest ecosystems. Canadian Journal of Zoology 92:997-1004.

Shilla, D. J. and D. A. Shilla. 2011. The effects of catchment land use on water quality and macroinvertebrate assemblages in Otara Creek, New Zealand. Chemistry and Ecology 27:445-460.

Skidds, D. E., F. C. Golet, P. W. C. Paton, and J. C. Mitchell. 2007. Habitat correlates of reproductive effort in wood frogs and spotted salamanders in an urbanizing watershed. Journal of Herpetology 41:439-450.

Sleeter, B. M., T. L. Sohl, T. R. Loveland, R. F. Auch, W. Acevedo, M. A. Drummond, K. L. Sayler, and S. V. Stehman. 2013. Land-cover change in the conterminous United States from 1973 to 2000. Global Environmental Change-Human and Policy Dimensions 23:733-748.

Smith, C. and J. Petranka. 1987. Prey size-distributions and size-specific foraging success of Ambystoma larvae. Oecologia 71:239-244.

Smith, M. A. and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography (Copenhagen) 28:110-128.

Spieles, D. J. and W. J. Mitsch. 2000. Macroinvertebrate community structure in high- and low-nutrient constructed wetlands. Wetlands 20:716-729.

Steen, D. A., L. L. Smith, G. J. Miller, and S. C. Sterrett. 2006. Post-breeding terrestrial movements of Ambystoma tigrinum (Eastern Tiger Salamanders). Southeastern Naturalist 5:285-288.

Stevens, V. M., E. Polus, R. A. Wesselingh, N. Schtickzelle, and M. Baguette. 2004. Quantifying functional connectivity: Experimental evidence for patch-specific resistance in the Natterjack toad (*Bufo calamita*). Landscape Ecology 19:829-842.

Stoner, A. M. K., K. Hayhoe, and D. J. Wuebbles. 2009. Assessing general circulation model simulations of atmospheric teleconnection patterns. Journal of Climate 22:4348-4372.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783-1786.

Sutton, W. B., K. Barrett, A. T. Moody, C. S. Loftin, P. G. deMaynadier, and P. Nanjappa. 2015. Predicted Changes in Climatic Niche and Climate Refugia of Conservation Priority Salamander Species in the Northeastern United States. Forests 6:1-26.

Taylor, B., D. Skelly, L. K. Demarchis, M. D. Slade, D. Galusha, and P. M. Rabinowitz. 2005. Proximity to pollution sources and risk of amphibian limb malformation. Environmental Health Perspectives 113:1497-1501.

Todd, B. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. Proceedings: Biological Sciences 278:2191-2197.

Thorp, J. H. and A. P. Covich, editors. 2001. Ecology and classification of North American freshwater invertebrates. Second edition. Academic Press.

Trenham, P. C. and H. B. Shaffer. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15:1158-1168.

Urban, M. C. 2013. Evolution mediates the effects of apex predation on aquatic food webs. Proceedings of the Royal Society B-Biological Sciences 280.

Urban, M. C. 2015. Accelerating extinction risk from climate change. Science 348:571-573.

Urban, M. C., J. L. Richardson, and N. A. Freidenfelds. 2014. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. Evolutionary Applications 7:88-103.

van Vuuren, D. P., J. Edmonds, M. Kainuma, K. Riahi, A. Thomson, K. Hibbard, G. C. Hurtt, T. Kram, V. Krey, J. F. Lamarque, T. Masui, M. Meinshausen, N. Nakicenovic, S. J. Smith, and S. K. Rose. 2011. The representative concentration pathways: An overview. Climatic Change 109:5-31.

Wake, D. B. 2012. Facing extinction in real time. Science 335:1052-1053.

Wake, D. B. and V. T. Vredenburg. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences of the United States of America 105:11466-11473.

Wallace, J. B. and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41:115-139.

Walls, S. C., W. J. Barichivich, M. E. Brown, D. E. Scott, and B. R. Hossack. 2013. Influence of drought on salamander occupancy of isolated wetlands on the southeastern coastal plain of the United States. Wetlands 33:345-354.

Webb, J. A., E. M. Wallis, and M. J. Stewardson. 2012. A systematic review of published evidence linking wetland plants to water regime components. Aquatic Botany 103:1-14.

Welsh, H. H. and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: A case study from California's redwoods. Ecological Applications 8:1118-1132.

Werner, E., D. Skelly, R. Relyea and K. Yurewicz. 2007. Amphibian species richness across environmental gradients. Oikos, 116:1697-1712.

Whiles, M. R., and B. S. Goldowitz. 2005. Macroinvertebrate communities in Central Platte River wetlands: Patterns across a hydrologic gradient. Wetlands 25:462-472.

Whiles, M. R., J. B. Jensen, J. G. Palis, and W. G. Dyer. 2004. Diets of larval flatwoods salamanders, Ambystoma cingulatum, from Florida and South Carolina. Journal of Herpetology 38:208-214.

Worner, S. P. and M. Gevrey. 2006. Modelling global insect pest species assemblages to determine risk of invasion. Journal of Applied Ecology 43:858-867.

Wright, M. S., and A. P. Covich. 2005. The effect of macroinvertebrate exclusion on leaf breakdown rates in a tropical headwater stream. Biotropica 37:403-408.

Zhou, Q. F., J. B. Zhang, J. J. Fu, J. B. Shi, and G. B. Jiang. 2008. Biomonitoring: An appealing tool for assessment of metal pollution in the aquatic ecosystem. Analytica Chimica Acta 606:135-150.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2000. Factors influencing invertebrate communities in prairie wetlands: A multivariate approach. Canadian Journal of Fisheries and Aquatic Sciences 57:76-85.

VITA

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