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hbgoldspiel@gmail.com

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FOREST LEGACY EFFECTS ON AMPHIBIANS POPULATIONS: INTEGRATING LAND AND LIFE HISTORIES IN CONSERVATION

by

Harrison B. Goldspiel

A thesis
submitted in partial fulfillment
of the requirements of the
Master of Science Degree
State University of New York
College of Environmental Science and Forestry
Syracuse, New York
May 2018

Approved by:
James P. Gibbs, Major Professor
Stephen Shaw, Chair, Examining Committee
Neil Ringler, Interim Department Chair
S. Scott Shannon, Dean, The Graduate School

ACKNOWLEDGMENTS

This research would not have been possible without the incredible support of many individuals and institutions. First and foremost, I would like to thank my academic advisor, James Gibbs, for providing me the opportunity to cultivate my curiosities and being a constant source of support and inspiration since I arrived at ESF. I am forever grateful for all his patience, guidance, and generosity. I would like to thank the members of my steering committee for enriching my research and graduate school experience through many helpful conversations and feedback: Greg McGee for his valuable perspectives on forest ecology and sampling methodologies, Jonathan Cohen for being the ultimate statistical guru and source of academic humor, and Brad Cosentino for sharing his expertise on land use legacies and contributing much needed external insight into my own study.

I am indebted to many dedicated technicians who collectively volunteered hundreds of hours of critical field support, lab assistance, and general companionship in the woods: Zac Babbit, Alex Roukis, Tim Bova, Allie Sholk, Cassie Schlosser, Caden Richardson, Noah Garwood, Olivia Iannone, and Joey Wagner. My time in graduate school was made more enjoyable and meaningful by the many strong friendships I developed in Syracuse. I‘d like to acknowledge members of the Gibbs lab and many other individuals, especially Julia Vanaman, Sam Dean, Sahila Kudalkar, Manoon “Ki” Pliosungnoen, Leah Nagel, Taylor Patterson, Vernon Coffey, Rea Manderino, and Hannah Griffin, for their camaraderie through many potluck dinners, game nights, squash matches, and wilderness expeditions. I would also like to thank Rabbi Yaakov Rapoport and Chanie Rapoport for their warm generosity in providing me with a vibrant Jewish community in central New York. Finally, I am grateful for my parents and sister for their unwavering support and enthusiasm in my choice to study nature and wildlife conservation. Thank you all for learning with me and sharing this journey.

This work was funded through grants awarded by the Chicago Herpetological Society and the ESF Graduate Student Association and Office of Instruction and Graduate Studies.

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ABSTRACT

H. B. Goldspiel. Forest Legacy Effects on Amphibian Populations: Integrating Land and Life Histories in Conservation. 102 pages, 6 tables, 8 figures, 7 appendices, 2018. APA style guide used.

Understanding how forests are shaped by historical disturbances is essential for developing effective conservation plans for forest-dwelling organisms threatened by habitat loss, such as amphibians. Salamander and frog populations and microhabitats were sampled using visual encounter surveys and forest habitat assessments in uplands varying in aquatic habitat resources (i.e., vernal pool densities) and disturbance history (i.e., secondary to residual forests) to assess agricultural land-use legacy effects on populations and terrestrial habitats of amphibians with different life histories. Pool-breeding, stream-breeding, and fully terrestrial salamanders were negatively associated with secondary forests, which featured shallower leaf litter, denser understory vegetation, and fewer cover objects than residual forests. Only wood frogs were unaffected by disturbance history, being solely influenced by available aquatic habitat. These results demonstrate the utility of historical ecology for amphibian population studies and suggest that secondary forests may not provide the same conservation value as residual forests for many amphibian species.

Key Words: agriculture, amphibians, binomial N-mixture model, central New York, climate extremes, habitat augmentation, land-use legacies, life histories, occupancy model, vernal pool

H. B. Goldspiel
Candidate for the degree of Master of Science, May 2018
Major Professor: James P. Gibbs, Ph.D.
Department of Environmental and Forest Biology
State University of New York College of Environmental Science and Forestry
Syracuse, New York
James P. Gibbs, Ph.D.

PROLOGUE

Land use history is fundamental to the ecology and conservation of forested ecosystems. The story of the expansively forested contemporary landscapes of the eastern United States is one of human interaction—from longstanding management practices of indigenous peoples to the rapid development and abandonment of farmlands by European settlers, and their subsequent transition to a myriad of new land uses. These processes have drawn much recent attention, as researchers and policymakers recognize the importance of land-use legacies to understanding modern forest ecosystems (Foster et al. 2003; Bürgi et al. 2017). Eastern forests have experienced dramatic transitions in the past century; after hundreds of years of forest destruction and the development of farmlands, agricultural fields have been largely abandoned and the region has experienced widespread forest regeneration (Whitney 1996). This period of forest regrowth has appeared to plateau and the region is again beginning to experience modest losses in forest cover due to various human activities (Drummond & Loveland 2010), to the potential detriment of the forest biota. Anthropogenic disturbances are responsible for modern global forest losses and agricultural activities remain a primary driver of contemporary forest change in many world regions (Hansen et al. 2013).

These recent forest declines and projected future losses highlight the need for comprehensive planning that considers the long-term impacts of historical land use activities such as agriculture on forest ecosystems and constituent organisms. A wide array of literature has emphasized the diverse and persistent impacts of agriculture on modern forest vegetation (Bellemare et al. 2002; Flinn & Vellend 2005; Thompson et al. 2013), ecosystem processes, and geochemical characteristics (Foster et al. 2003; Fraterrigo et al. 2005; Flinn & Marks 2007). Forest land-use legacies provide valuable opportunities to understand longitudinal effects of human disturbance on wildlife communities and to guide land management decisions to mitigate impacts of contemporary disturbances on forest-dwelling organisms of conservation concern. Within the forest-dependent biological community, amphibians are highly sensitive to land modifications and are thus a useful model for understanding the effects of land use legacies on forest ecosystems.

For over four decades, amphibian populations have steadily declined globally due to a combination of factors including habitat loss, climate change, invasive species, and pathogens (Stuart et al. 2004; Mendelson et al. 2006). Despite concerted international conservation efforts to confront stressors and preserve biodiversity, declines continue to worsen even in highly protected areas such as U.S. National Parks (Adams et al. 2013). As of 2017, 41% of all extant amphibians were listed as threatened by the International Union for Conservation of Nature (IUCN 2017). Habitat loss poses one of the greatest threats to amphibian biodiversity and population persistence (Collins & Storfer 2003; Gallant et al. 2007). Global population declines due to systemic factors such as climate change and pathogens are difficult to address directly, but declines stemming from habitat loss can potentially be mitigated by strategic management efforts on local and regional scales (Semlitsch 2002). Successful management programs must be tailored to their specific ecosystem and species assemblages in the context of life history requirements and current landscape conditions (Calhoun et al. 2014). However, much research is still needed to identify how past disturbances can influence management outcomes for populations of amphibians with different life histories.

Wetland-breeding species and landscape context

Most amphibians have complex life cycles, requiring both aquatic and terrestrial habitat to complete. Concurrently with historical changes to forested uplands, human disturbances have heavily influenced aquatic habitats across the same landscape. Many biphasic amphibians rely on freshwater wetlands for breeding, larval development, and refuge. Wetlands have been severely depleted over the past two centuries, with total wetland area in the conterminous 48 states decreasing by 53% between the 1780s and the 1980s (Johnston 1994). Much of these losses stemmed from the immense land and resource demands of agriculture (e.g., tile drainage); however public perception of wetlands as centers of disease was also a critical factor in historical wetland drainage (Whitney 1996). Changes to public education, drainage incentives, government policies, and conservation initiatives have contributed to gradual declines in wetland losses in the late 20th century and recent net gains in national wetland coverage (Mahaney & Klemens 2008; Dahl 2011). However, these gains are mostly limited to the preferential reestablishment of emergent freshwater ponds; forested wetlands, including forested vernal pools, remain vulnerable to losses (Windmiller & Calhoun 2008; Dahl 2011).

Lacking many of the regulatory protections that other larger (> 1 ha) and more permanent wetlands now receive, forested vernal pools are among the most threatened types of wetlands in post-glacial northeastern forests, where they are easily disturbed or destroyed by land modifications and extreme droughts caused by climate change (Baldwin & deMaynadier 2009; Calhoun et al. 2017). These small, isolated ephemeral wetlands constitute important breeding and larval habitat for several amphibian species in eastern forests, such as wood frogs (*Lithobates sylvaticus*) and mole salamanders (*Ambystoma* spp.) and function as necessary buffers to environmental stochasticity. Networks of vernal pools provide habitat connectivity for dispersal-limited species and are vital for maintaining robust metapopulations of pool-breeding organisms in forested landscapes (Gibbs 1993; Marsh & Trenham 2001; Petranka 2007). Vernal pools are largely omitted from federal and state wetland protections (Mahaney & Klemens

2008), despite growing evidence for their biological, biogeochemical, and hydrological connectivity to surrounding aquatic and terrestrial resources and their socioeconomic benefits (Cohen et al. 2016; Calhoun et al. 2017). With recent revisions to the implementation of the U.S. Clean Water Act that disregard wetland-related benefits in determining regulatory status (Boyle et al. 2017), vernal pools and other ephemeral aquatic habitats are likely to remain less protected than permanent wetlands.

Stream-breeding species and landscape context

Many biphasic amphibians are adapted to riparian breeding environments, such as forested streams, which have been heavily impacted from historical anthropogenic disturbances. For example, stream-dependent salamanders comprise roughly 40 percent of North American caudates, the majority of which are limited to forests in the eastern United States (Petranka 2010). Most of these species belong to a single family of lungless salamanders (Plethodontidae) that are widely distributed in eastern forests where they play important ecological roles, coupling riparian and terrestrial forest wood webs. These organisms can attain enormous densities where they occur (e.g., up to 2 individuals / m^2 in some southern Appalachian species, Petranka & Murray 2001) and are often the dominant vertebrate predators in temporary and ephemeral headwater streams (Davic & Welsh 2004). Forest clearance and agricultural land-use legacies are prevalent in these riparian systems and include long-term changes to chemical and physical stream processes (Maloney et al. 2008) as well as to biological communities (Harding et al. 1998; Maloney & Weller 2010). Very few studies have examined agricultural land-use legacy effects on stream salamanders, but some evidence from southern Appalachia has revealed negative population impacts that can persevere for at least 50 years after farm abandonment (Hicks & Pearson 2003; Surasinghe & Baldwin 2014). Like vernal pools, many small headwater streams and riparian zones are highly vulnerable to land modifications and climate change and receive inadequate protections under current legal and political frameworks (Acuña et al. 2017; González et al. 2017), threatening the population status of many stream-dependent salamander species.

Terrestrial-breeding species and landscape context

An extensive group of salamanders, mainly of the family Plethodontidae, in forests of the eastern United States are fully terrestrial. Terrestrial plethodontid salamanders have long been proposed as potentially useful indicators of forest biodiversity and ecosystem health, owing to their broad distribution throughout eastern forests and frequent high abundance where they occur, as well as their efficiency to sample, interactivity across forest food webs and trophic levels, and unique physiological restrictions and sensitivities (Welsh & Droege 2001). For these reasons, terrestrial salamanders and their habitat associations are relatively well-studied, and decades of research have tested these claims in the context of historical and contemporary forest changes (e.g., Pough et al. 1987; Petranka et al. 1993; DeMaynadier & Hunter, Jr. 1998; Harper & Guynn 1999; McKenny et al. 2006; Homyack & Haas 2009a; Hocking et al. 2013). Forest clearcutting and other intensive silvicultural practices can have devastating impacts on terrestrial salamander populations via sustained biological legacies in multiple forest strata, from the soil-litter interface to coarse woody debris quantities to understory and tree canopies (DeMaynadier & Hunter, Jr. 1998; Waldick et al. 1999). Furthermore, these impacts can extend beyond management areas, causing persistent legacy edge effects in undisturbed forests (Semlitsch et al. 2007; Hocking et al. 2013). Despite this wealth of evidence for land-use legacy effects on terrestrial salamanders, there is still considerable uncertainty regarding how long populations require for recovery and how species-specific responses vary with different intensities of disturbance (e.g., silviculture versus agriculture) and in different spatial regions (e.g., southern Appalachia versus the northeast).

Conservation strategies and knowledge gaps for forest-dwelling amphibians

Conservation and management strategies for forest-dwelling amphibians may include state and federal regulatory protections for threatened species and their biological habitat components (e.g., breeding pools, riparian zones, terrestrial buffers), public and private protected land designations (e.g. conservation easements), landowner engagement and incentives to stimulate management decisions on private lands (Baldwin & deMaynadier 2009; Smith et al. 2017), and habitat augmentation programs (e.g., structural complexity enhancements, vernal pool construction—McKenny et al. 2006; Otto et al. 2013; Calhoun et al. 2014). Identifying and implementing suitable conservation strategies requires the integration of species-specific life history processes with a comprehensive understanding of the past, present, and future landscape disturbances that limit them. These processes are often missing key ecological details, particularly for species with complex life cycles. For example, vernal pool creation is an increasingly common strategy for promoting growth of populations of pool-breeding forest-dwelling amphibians. These larval aquatic habitats should be complimented with equally suitable juvenile/adult terrestrial habitats; however, the relative roles of each habitat type in regulating population dynamics are largely unknown (Marsh and Trenham, 2001; Semlitsch and Skelly, 2008). These uncertainties are complicated further by landscape-setting factors and deterministic stressors such as climate change that can place additional limitations on population persistence. Conservation planners and managers must simultaneously consider how many pools are necessary to sustain robust populations and where in the landscape pool creation should be prioritized to guarantee long-term viability. Incorporating ancillary historical details directly into these difficult decision-making processes is essential for advancing amphibian conservation objectives.

Research objectives and hypotheses

I sought to address knowledge gaps concerning habitat requirements of forest-dwelling amphibians with respect to historical anthropogenic disturbance, focusing on the long-term effects of agriculture on frog and salamander populations in a northeastern forest. Compared to the effects of silviculture, the impacts of historical agriculture on contemporary forest-dwelling amphibians are poorly understood and demand greater attention than they have previously received. As agriculture constitutes a complete landscape transformation, both in structure and function, its legacies for contemporary forests persist longer than those of historical timber management. These legacies are further extended by historical reforestation practices on abandoned fields, which often included the establishment of conifer plantations that are typically less hospitable to amphibians such as plethodontid salamanders (Pough et al. 1987; Waldick et al. 1999). In two years with very different climate patterns, I surveyed amphibians and terrestrial habitat characteristics in upland sites varying in aquatic habitat availability (0–10 vernal pools) and disturbance history (post-agricultural secondary to primary forest gradient) to determine (1) the long-term effects of agriculture on amphibian terrestrial habitat characteristics in modern forests; (2) which landscape and habitat features are limiting for populations of species with different life histories (pool-breeding, stream-breeding, terrestrial-breeding); and (3) how landscape and habitat limitations on populations differ between years with different climate patterns (i.e., drought period versus wet period).

This thesis reflects the results of these two years of research at Heiberg Memorial Forest in Tully, New York, and contains two manuscripts written in format for eventual publication in academic journals. The first chapter, which focuses on pool-breeding amphibians, is titled "Integrating history into pool-breeding amphibian conservation: a case study of vernal pool creation and forest land use legacies," and is prepared for submission to the journal *Biological Conservation*. The second chapter, which focuses on plethodontid salamanders, is titled "Agricultural land use legacy effects on forest dwelling plethodontid salamanders," and is prepared for submission to the journal *Forest Ecology and Management.*

CHAPTER 1: INTEGRATING HISTORY INTO POOL-BREEDING AMPHIBIAN CONSERVATION: A CASE STUDY OF VERNAL POOL CREATION AND FOREST LAND USE LEGACIES

Abstract

Understanding how populations of organisms with complex life cycles, such as amphibians, are simultaneously affected by available larval versus adult habitat is critical for developing land management plans to conserve biodiversity. I examined for forest-dwelling amphibians the relative contributions of forest quality pertinent to adult life stages versus breeding pool enhancement pertinent to larval stages to the distribution of two pool-breeding and upland-dwelling species. Using area-constrained daytime visual encounter surveys in a mixed hardwood forest in central New York, USA over two consecutive years with strongly contrasting climate (extreme drought and extreme rainfall), I estimated occupancy of wood frogs (*Lithobates sylvaticus*) and spotted salamanders (*Ambystoma maculatum*) and characterized terrestrial microhabitats in 29 population neighborhoods (9.3 ha) varying in aquatic habitat availability (0 – 10 vernal pools) and disturbance history (residual versus post-agricultural secondary forest). Secondary forests featured shallower leaf litter, denser understory vegetation, and fewer natural cover objects than adjacent residual forest stands. Wood frog presence was solely affected by pool densities in both years whereas spotted salamander presence depended on both available wetland and upland conditions and with more positive associations with residual forests and pool densities during the drought year. These results suggest that pool construction can boost upland populations of amphibians, but climate and land-use disturbances may mediate conservation outcomes for long-lived habitat specialists.

Key words: *Ambystoma maculatum*, amphibians, complex life cycles, land-use history, occupancy, *Rana sylvatica*, spotted salamanders, wood frogs, vernal pools

Introduction

Most amphibians have biphasic life histories, requiring connected aquatic and terrestrial habitats to meet the demands of larval (aquatic) and adult (terrestrial) life stages. Such species, often with limited dispersal capabilities, are especially vulnerable to local and regional population declines; losses of either habitat type can increase susceptibility to stochastic environmental events (e.g., drought) and threaten broader metapopulation viability (Marsh & Trenham 2001). Accordingly, amphibians are among the most imperiled of vertebrate animals (Stuart et al. 2004b) with habitat loss and climate change as major contributing factors to global amphibian population declines (Collins & Storfer 2003; Cushman 2006). Maintaining intact landscapes that include core aquatic and terrestrial habitats is a critical element of amphibian population recovery plans (Semlitsch 2002), but practitioners should also consider the potential resiliency and functionality of both features to climate change to ensure conservation plans yield long-term population benefits.

In the United States, greater emphasis is typically placed on management of aquatic than terrestrial environments for the conservation of biphasic amphibians (Semlitsch & Jensen 2001). This bias in management approach is reflective of important concerns about wetland loss impacts on larval habitats. Historical legacies of forest clearance, agriculture, and wetland drainage have led to tremendous declines in wetland coverage in the conterminous 48 states, with 53% of total wetland area lost between the 1780s and the 1980s (Johnston 1994) and forested wetlands experiencing the greatest losses (Dahl 2011). Forested vernal pools are small ephemeral wetlands that provide critical habitat for multiple amphibian species and are highly vulnerable to losses from current and future land use practices (Baldwin & deMaynadier 2009) as well as climate change (Calhoun et al. 2017).

Despite abundant research highlighting the ecological value of vernal pools (Gibbs 1993; Semlitsch & Bodie 1998) and their biological, biogeochemical, and hydrological connectivity to surrounding landscapes (Cohen et al. 2016), these small aquatic habitats are largely not subject to federal and state wetland regulation under current legal frameworks (Mahaney & Klemens 2008; Calhoun et al. 2014). Vernal pool creation provides one means to augment larval habitats in areas where pools and other breeding sites have been destroyed. There is a growing consensus that vernal pool construction projects should reflect the physical and spatial characteristics of natural pools, but the areas targeted for conservation are often heavily degraded or lacking suitable "natural" conditions (Calhoun et al. 2014). In the absence of reference data, the number of pools needed to support robust amphibian populations is unclear. Wetland density is an important element of amphibian population structure (Semlitsch 2002) and connected networks of vernal pools serve to minimize upland dispersal distances and provide amphibians a needed buffer against stochastic events such as extreme drought (Semlitsch & Bodie 1998; Gibbs 2000; Petranka & Holbrook 2006; Karraker & Gibbs 2009). High levels of spatial connectivity of constructed pools are known to be beneficial for larval production of pool-breeding salamanders (Peterman et al. 2013), but how these spatial arrangements actually influence adults in forested uplands is unclear and confounded by the rich history of human disturbance found in most forests.

The vast majority of forests in the eastern United States are secondary forests, established in the early 1900s following three centuries of widespread forest removal and agricultural activities (Whitney 1996; Drummond & Loveland 2010). This history of intensive human disturbance creates additional complexity for pool-breeding amphibian conservation, as the presence of terrestrial land use legacies may place additional limitations on upland populations in many potential pool construction sites. Historical forest clearance and agriculture has long term effects on various structural habitat components associated with pool-breeding amphibians, including physical and chemical soil properties (Foster et al. 2003; Flinn & Marks 2007; Piché & Kelting 2015), the quantity and quality of organic substrates like coarse woody debris and leaf litter (Hughes & Fahey 1994; Hooker & Compton 2003), and the composition of understory and overstory plant communities (Bellemare et al. 2002; Flinn & Marks 2007). These structural changes to terrestrial habitats and associated microclimates (e.g., moisture, temperature) can have direct effects on amphibian populations, by creating stressful microclimate conditions, as well as indirect effects via impacts to other forest fauna (Bowen et al. 2007) that can restrict foraging opportunities and/or increase predation rates. Additionally, limited dispersal capabilities of forest-dwelling amphibians can further restrict species from successional sites due to prolonged recolonization times (Cosentino & Brubaker, in review). Amphibians generally display lower richness and abundance in secondary forests (Thompson & Donnelly 2018), likely due to a combination of these structural, biological, and dispersal mechanisms. However, despite these documented legacy effects of historical human disturbance on forest-dwelling amphibians, no research has addressed these effects on common pool-breeding species like wood frogs (*Lithobates sylvaticus*) and spotted salamanders (*Ambystoma maculatum*). These legacies require greater attention for understanding upland habitat preferences and designing successful management plans for species with complex life cycles.

Both aquatic (larval) and terrestrial (adult) habitats are essential for pool-breeding amphibians, yet the relative roles of each in regulating population dynamics are largely unknown (Marsh & Trenham 2001; Semlitsch & Skelly 2008). Aquatic larvae and terrestrial juveniles and adults have distinct behavioral and physiological adaptations, reflective of the unique opportunities and challenges presented by aquatic and terrestrial habitats. Many theoretical models have been developed to explain the life histories of species with complex life cycles. Most classic studies have focused on aquatic life history stages, stressing factors affecting larval performance and recruitment rates as the primary drivers of overall population dynamics (reviewed in Bruce 2005); however, recent research has highlighted the equal if not greater importance of terrestrial stage processes (Biek et al. 2002; Vonesh & De la Cruz 2002; Schmidt et al. 2005; Harper & Semlitsch 2007; Petranka 2007; Berven 2009).

There is a clear need for more integrated research on the aquatic and terrestrial drivers of amphibian populations to design effective conservation plans for complex organisms. The goal of the research was to examine how the relative availability and quality of larval and adult habitats limit distributions of pool-breeding amphibians in forested uplands of central New York. My objectives were to (1) quantify amphibian occupancy in forests varying in pool density and terrestrial habitat quality, (2) determine the relative contributions of larval habitat quantity and adult habitat quality to variation in habitat occupancy, (3) assess the relationships between historical land-use and terrestrial microhabitat features relevant to pool-breeding amphibians, and (4) evaluate the effectiveness of vernal pool creation on enhancing amphibian populations in forests with different histories of human disturbance. I expected occupancy to be positively influenced by pool availability and to increase with residual forest cover, where quality of terrestrial microhabitat features would be more suitable for adult life stage requirements. In addition to filling basic knowledge gaps on the dual requirements of species with complex life cycles, these results should provide further guidance to practitioners in selecting sites for conservation and optimizing pool construction projects to promote long-term population benefits.

Methods and Materials

Study Sites

This study was conducted in Heiberg Memorial Forest (HMF) (42°46'19" N, 76°5'6" W), a 1,600-ha Northeastern Mixed Forest (McNab et al. 2007) in Tully, New York. The northern portion of the site contains an array of 39 vernal pools constructed in 2010 (Figure 1.1). Pools were small (< 0.01 ha) and were placed in clusters of three quantities (one, three, and nine pools) assigned to the center of hexagonal land units (incircle radius: 164 m, area: 9.3 ha) selected to represent individual breeding “neighborhoods” of the targeted species – spotted salamanders and wood frogs (Rittenhouse and Semlitsch, 2007; Semlitsch, 1998; Semlitsch and Jensen, 2001). A small number of natural pools and preexisting constructed wetlands (constructed in the 1930s as water sources for fighting fires or incidentally created as borrow pits for extracting material for road construction) were also scattered across the study site. The land-use history of this site is representative of much of the northeastern United States, with a large percent of the native forest historically cleared for agriculture (mostly pasture and hayfields with scattered croplands) before abandonment in the early 1900s. Most of the property that was historically in agriculture has since regenerated to secondary mixed hardwood forest (*Acer, Fraxinus*) or been replaced with conifer plantations (*Picea, Pinus*) (Figure 1.1).

For simplicity, I define secondary forest as any stand, naturally regenerated or human-planted, that was previously cleared for agriculture, and residual forests as sites that have been continuously wooded throughout this historical period (Peterken 1981). Unlike old-growth forests, residual forests have experienced some degree of human disturbance (e.g., selective logging and grazing) while retaining a persistent canopy and relatively undisturbed soil organic layer. I obtained residual and secondary forest extents for the study region by georeferencing and manually delineating historical forest cover from six 1936 aerial photographs (USDA, 1936) in ArcMap 10.4.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA) and comparing those coverages with 2015 orthoimagery (NYS GIS Clearinghouse, 2015) and land cover data (NLCD 2011, Homer et al., 2015). These images, which were the oldest accessible aerial photographs for the site, were used to establish a baseline of historical conditions at the peak of forest clearance and contrasted with a historical image series from 1966 to approximate the range of secondary forest stand ages. Amphibian populations and terrestrial habitat characteristics were sampled in 30 hexagonal plots representing a range of aquatic habitat resources, stand age, and forest composition. Half of the plots contained constructed and/or natural vernal pools. For the remaining hexagons lacking pools, I selected a stratified random sample of hexagons containing forested uplands throughout HMF to include equal representation with respect to forest disturbance history (residual, secondary) and composition (deciduous, residual hemlock stands, secondary conifer plantations) such that hexagons with and without pools would encompass a similar gradient of forest disturbance history and modern composition.

Amphibian surveys

I conducted area-constrained daytime visual encounter surveys (VES) to sample amphibians in the summers of 2016 and 2017. Visual encounter surveys are an effective method for sampling the diversity and relative abundance of terrestrial amphibian assemblages in large areas (Dodd Jr. 2011). Each hexagon was searched during daylight for roughly three hours by walking in a standardized path and thoroughly inspecting under all large cover objects (≥ 10 cm in diameter), recording the total number of frogs and salamanders observed. I conducted 2–3 rounds of surveys each year to estimate site occupancy while accounting for imperfect detection, assuming closed populations. For each survey occasion, air temperature was measured with a digital thermometer and daily precipitation was documented by surveyors in situ and with supplementary data from the Cortland County Airport (42°35′33″N, 076°12′53″W). I recorded other factors potentially influencing detection rates, including time of day, survey duration, survey effort (relative number of objects sampled), and number of observers (one or two).

Terrestrial habitat sampling

Terrestrial habitat characteristics were sampled between August and September of 2016 by systematically establishing six, 100-m transects and 30 1-m^2 quadrats in each hexagon. Transects were oriented at equidistant 60° angles from the hexagon center with the start point randomly staggered 0-30 m from the center. I measured the diameter and intercept length of all coarse woody debris (≥ 10-cm diameter) that intersected the transects, noting the decay status of each object on a 1-5 scale (Class 1 = freshly fallen and containing intact branches; Class 5 = mostly incorporated into the soil (Sollins 1982a). These metrics were used to estimate volume, surface area, and decomposition of coarse woody debris in each hexagon (Marshall et al. 2003). Percent canopy cover (hemispheric photography), leaf litter depth (cm, ruler), and percent understory cover were measured in the quadrats, which I distributed evenly at 20-m intervals along transects. I took canopy photographs in the center of each quadrat with a smartphone and fisheye lens attachment, and manually calculated canopy cover from each hemispheric photograph in the program ImageJ (Rasband 2017). Leaf litter depth was estimated by averaging three ruler measurements from two corners and the center in each quadrat. Understory cover was recorded by visually estimating the proportion of vegetation under chest height (1.4 m) obstructing the ground within a gridded 1-m^2 quadrat.

Statistical analysis

I performed all analyses in R Version 3.3.2 (R Core Team 2017). Amphibian occurrence data was examined with single-species single-season occupancy models (Mackenzie et al. 2002) in the package “unmarked” (v0.12-2, Fiske and Chandler, 2011). I fit all hierarchical models with maximum likelihood estimation and compared candidate models using Akaike’s Information Criterion corrected for small sample sizes (AIC_c), which prioritizes model parsimony and penalizes for overfitting (Burnham & Anderson 2002). I used the package “AICcmodavg” (v2.1-1, Mazerolle, 2017) to generate model selection statistics. Models within two AIC_c units ($\Delta AIC_c < 2.00$) of the top ranked model and containing a similar model weight (ω_i) and deviance ($-2\log[\mathcal{L}]$) were considered to have equivalent support (Burnham & Anderson 2002). When models did not converge, I omitted those from the rankings and proceeded with selection from the remaining model list. I “stacked” the data across years and included a categorical year covariate (0 = 2016, 1 = 2017) in each detection (p) and occupancy (Ψ) model, thus enabling me to examine species responses over two distinct climate regimes (MacKenzie et al. 2017). An alternative approach would have been to fit dynamic multi-season occupancy models that explicitly model extinction and colonization rates; however this design can produce large parameter biases and uncertainty when number of visits, sites, and/or detection rates are low (McKann et al. 2013). Prior to constructing models, all continuous covariates were standardized to a mean of zero and a standard deviation of 1, and categorical variables were set as factors. I additionally selected only one from each pair of highly correlated variables ($r > 0.7$) in the same model to avoid collinearity among covariates.

Model selection was done in two parts: I first assessed a suite of 34 detection models for wood frogs (Appendix 1.1) and 32 for spotted salamanders (Appendix 1.2) from a combination of abiotic and biotic variables and their interactions (Table 1.1), using the occupancy model

$$\text{logit}(\Psi) = \beta_1 + \beta_2(\textit{pools}) + \beta_3(\textit{upland}) + \beta_4(\textit{pools} * \textit{upland}) + \beta_5(\textit{year})$$

and selected the detection model with the greatest support to compare 14 occupancy models that represented *a priori* hypotheses of larval and adult habitat requirements and potential mediating effects of climate on these life history components. This candidate set of models consisted of univariate larval (*pools*) and adult habitat (*upland*) models, additive (*pools + upland*) and interactive (*pools * upland*) habitat models, and either additive or interactive climate effects for each covariate (e.g., *pools + year* versus *pools * year*), as well as a detection model and null model. I assessed model fit of the most complex converging model for each species with a Pearson's χ^2 test of observed and bootstrapped data, using 1000 parametric bootstrapped samples (MacKenzie & Bailey 2004; Mazerolle 2017). From these tests I estimated overdispersion ($\hat{c}$) by dividing the observed χ^2 statistic by the mean simulated statistic. Models with a p-value > 0.05 and $\hat{c} \sim 1.0$ were considered to structurally adequate (Burnham & Anderson 2002). I used the top model for subsequent inference, or if there was model selection uncertainty I based inferences on model-averaged predictions.

Occupancy models contain several assumptions that I addressed with our sampling and analytical framework. Detection and occupancy probabilities were modeled with various temporal and spatial covariates to address potential sources of heterogeneity in detection and occupancy probabilities. Sites were designed at the approximate home range size for target species, with pools generally arranged close to plot centers to satisfy the closure assumption. Wood frogs and spotted salamanders typically display low movements within upland refugia during the summer when we conducted surveys (Madison 1997; Faccio 2003; Rittenhouse & Semlitsch 2007b). One plot was in proximity (< 150 m) to an open field containing a large breeding pond as well as an experimental array of 16 vernal pools and removed from the analysis to prevent confounding sources of upland amphibian activity. I also omitted all late summer observations of recently metamorphosed amphibians from the analysis, as these individuals constitute new entries to sites during the sampling period.

To enable inference about the potential mechanisms driving site occupancy patterns, I examined relationships between forest type (i.e., proportion residual forest) and upland habitat characteristics by creating simple linear regression models with microhabitat variables as dependent covariates. Assumptions of normality and homogeneity of variance were examined with residual plots and respectively confirmed with the Shapiro-Wilk (Royston 1982) and Breusch-Pagan (Breusch & Pagan 1979) tests. I additionally assessed descriptive scatter plots for nonlinear patterns of covariation. Canopy cover estimates were uniform across all sites ($\bar{x}$ = 0.92 ± 0.02); therefore, I did not model this variable.

Results

Amphibian occupancy relationships with landscape features

A total of 37 adult wood frogs and 32 adult spotted salamanders were detected at 22 out of 29 sites over the two seasons of study. Naïve occupancy (proportion of sites where a species was detected) differed between the study years: in 2016, naïve occupancy estimates were 0.17 (five sites) for wood frogs and 0.21 (six sites) for spotted salamanders whereas in 2017 naïve occupancy estimates were 0.45 (13 sites) for wood frogs and 0.41 (12 sites) for spotted salamanders.

The bootstrapped analyses showed no evidence of a lack of model fit for either species (wood frogs: $p = 0.585$; spotted salamanders: $p = 0.184$). One occupancy model for wood frogs (*pools* * *uplands* * *year*) produced parameter estimates with non-number (i.e., "NaN") error messages, and was dropped from the analysis. Of the remaining 13 candidate occupancy models for wood frogs, the top ranked model contained two terms — *pools* + *year* — with a model weight of 0.49 (Table 1.2). No other models were within two ΔAIC_c units. According to this model, probability of occupancy increased with increasing vernal pool density (Table 1.3) and did not differ between the two study years (Figure 1.3). Occupancy probability increased up to densities of 4 pools/ha (Figure 1.4). Two detection models had a ΔAIC_c less than 2, with the top-ranked model containing an indicator for whether it rained in the previous 24 hours to a survey and the second model containing an indicator for whether it rained during the survey. These models received nearly identical levels of support (Appendix 1.1); however, their deviances strongly differed (111.6 and 106.1, respectively), indicating that the second model was likely more appropriate. According to this model, detection of wood frogs decreased with increasing depth of the leaf litter (Table 1.3) yet this effect was reversed in the presence of rain as the interaction of rain and leaf litter depth was positive and greater than the main effect of litter depth (Table 1.3), and the predicted values support the strength of this interaction (Figure 1.3a,b). Overall, detection of wood frogs tended to be greater in 2017, when site conditions were wetter, although 95% confidence limits contained 0 (Table 1.3).

Three spotted salamander models — ψ(*uplands* + *pools* * *year*), ψ(*uplands* * *year* + *pools* * *year*), and ψ(*uplands* * *pools* * *year*) — were unable to converge and were subsequently dropped from the analysis. Of the remaining 11 models, one — ψ*(upland* * *pools* + *pools* * *year)* — was within ΔAIC_c of 2.00 with a model weight of 0.56 (Table 1.2). According to this model, probability of occupancy was influenced by the relative availability of vernal pools and residual forest cover (Table 1.3), but these patterns differed between years (Figure 1.5). In the drought year (2016), both aquatic and terrestrial habitats jointly limited occupancy given the interaction between pool density and residual forest (Table 1.3), with few salamanders observed in post-agricultural secondary forests with few to no pools (Figure 1.5). Salamanders exploited a greater diversity of habitats in the wet year (2017) and were less limited by pool concentrations under the moist conditions (Figure 1.5). There was greater detection model uncertainty for spotted salamanders. Six models had a ΔAIC_c less than 2.00 (Appendix 1.2). Models containing both litter depth and an indicator of rain seemed to perform better than the other detection models in this top list, according to model deviances. I did not detect a strong interaction between litter and rain ($\beta_{litter*rain1} = -1.35 \pm 2.17$) and opted to use the more parsimonious additive model (*litter + rain + year*) for modeling detection in the candidate occupancy model set. Both leaf litter and rain tended to inhibit detection of spotted salamanders (Figure 1.3c,d) although 95% confidence limits on the parameter estimates overlapped 0 (Table 1.3).

Terrestrial microhabitats relationships with forest disturbance history

Terrestrial microhabitat characteristics displayed several relationships with forest disturbance history. With increasing residual forest cover, leaf litter depth increased ($R^2 = 0.26$, $P = 0.004$) and understory vegetation density decreased ($R^2 = 0.28$, $P = 0.003$) (Figure 1.2). Leaf litter and understory vegetation both exhibited slight nonlinear relationships with residual forest cover, which was likely due to confounding variation in forest composition (i.e., deciduous versus coniferous) within the disturbance history gradient. I did not detect any direct general relationships between quantity or decay quality of coarse woody debris and residual forest extent, though residual forests tended to have more decayed debris ($P = 0.08$). There was a strong pattern in the variance of estimates across our land-use gradient, with secondary forests displaying greater heterogeneity in coarse woody debris quantities than residual forests (Figure 1.2c). Additionally, debris quantities declined with increasing secondary deciduous forest cover ($R^2 = 0.48$, $P < 0.0001$), suggesting there are important interactions between historical land-use and compositional trajectories of forest regeneration that may affect available microhabitat features in this system.

Discussion

Pool-breeding amphibians displayed species-specific occupancy patterns with aquatic and terrestrial habitat gradients. Whereas both the distribution of wood frogs and spotted salamanders were similarly affected by the availability of vernal pools, spotted salamanders were additionally influenced by landscape setting and climate, displaying an affinity for sites where the forest consisted of a minimum threshold of 25% residual forest cover and for pool densities that were lower the wet year. These results imply that historical agricultural and subsequent reforestation influence occurrence of pool-breeding salamander populations in contemporary forested landscapes and so should be considered in the development of conservation plans.

The relationships between forest history and amphibian occurrence are likely due to differences in life history traits and physiological limitations between the species studied. Spotted salamanders are a relatively larger, longer-lived species capable of breeding four or more times throughout their life span (Husting 1965). Wood frogs are relatively short-lived, with most individuals breeding only once or twice during their 3–4 year life span (Berven 1990, 2009). This reproductive constraint can be observed in their seasonal dispersal patterns. Both species are highly philopatric (Whitford & Vinegar 1966; Berven & Grudzien 1990); however, their movements in relation to breeding sites differ considerably. Although capable of dispersing farther into uplands than spotted salamanders in the spring and summer (Rittenhouse and Semlitsch, 2007b), wood frogs tend to overwinter closer to breeding sites (Regosin et al. 2005) indicating a stronger dependency on aquatic habitat availability and future breeding opportunities. Several studies have found contrasting relationships between breeding effort and habitat availability for wood frogs and spotted salamanders. Newcomb-Homan et al. (2004) observed species-specific occupancy trends in relation to surrounding forest cover in eastern Massachusetts, with wood frogs most sensitive to habitat loss closest (< 30 m) to breeding habitats and spotted salamanders more affected by forest loss at larger (i.e., > 1000 m) spatial scales. These results are consistent with those of Baldwin et al. (2006), who assessed amphibian populations in secondary forests that varied in pool assemblages and succession status following a catastrophic fire in the late 1940s. In their study, density and hydroperiod of pools were both important predictors of wood frog and spotted salamander breeding populations; however, spotted salamanders were additionally driven by forest age, displaying an affinity for pools surrounded by older forested uplands. Variation in life history traits is critical in determining species responses to habitat change; evidence from studies of other amphibian taxa suggests that anthropogenic disturbances may be more damaging to large, long-lived, habitat specialists (Surasinghe & Baldwin 2014), such as spotted salamanders.

Climate had an important mediating effect on where these species occurred and how likely they were to be found. The study region experienced consecutively extreme climate events, with 2016 the worst recorded drought on record (Sweet et al. 2017) and 2017 an abnormally wet spring and summer (NOAA 2017). Detection estimates were higher for wood frogs under the wetter conditions in 2017. While overall detection of spotted salamanders was similar in both years, occupancy was more variable. Spotted salamanders were less restricted by pool densities in 2017, with several individuals encountered in forests devoid of known vernal pools. This difference in occupancy between wet and dry years suggests adaptive migration to exploit alternative upland habitats in the wetter year. Spotted salamanders display strong avoidance to conspecifics in upland habitats (Regosin et al. 2003), which may have also displaced some individuals to marginal sites.

I detected several signatures of historical agriculture in terrestrial microhabitats that could influence populations of forest-dwelling amphibians. Secondary forests featured denser understory vegetation, shallower leaf litter, and more variable quantities of coarse woody debris than residual forests. These structural and functional differences are informative in the context of previous research on the long-term effects of agriculture on temperate forests. Forest-dwelling amphibian populations have been positively associated with understory vegetation cover (Pough et al. 1987; DeMaynadier & Hunter, Jr. 1998; Faccio 2003). Shrubs and herbaceous plants are important forest substrates that provide additional shade, moisture, and foraging habitat for many amphibian species. I estimated greater understory cover in secondary forests, however much of this vegetation consisted of dense patches of ferns and spruce seedlings in conifer plantations and thickets of invasive blackberries in some deciduous secondary stands. These uniform understory strata may not offer the same benefits for forest dwelling amphibians as the diverse herbaceous flora typically found in residual forests.

Coarse woody debris is a limiting upland habitat feature for most terrestrial salamanders, which heavily rely on cover objects for foraging and refuge. Quantity and especially quality (i.e., decay status) of coarse woody debris can determine habitat suitability in forests (Otto et al. 2013). The lack of a clear relationship between debris quantities and residual forest cover likely reflects forest management practices in residual stands and conifer plantations at HMF. Northern hardwood forests typically require at least 100 years for coarse woody debris to accumulate to pre-disturbance levels following canopy removal (McGee et al. 1999; Currie & Nadelhoffer 2002; Hooker & Compton 2003), but this successional relationship is confounded in managed forests, like HMF. The heteroscedastic coarse woody debris patterns at HMF may be a function of the range in secondary forest stand ages in this study (50–80 years) and limited amounts of management, the latter of which produces a steady influx of large woody objects to the forest floor in conifer plantations and prevents natural biomass accumulation patterns in established residual forests. Either source of heterogeneity could have potentially produced the greater observed variance of debris in secondary sites. However, spotted salamanders may have still been influenced by the availability of coarse woody debris, which was limited in secondary deciduous sites, and the quality of debris, which tended to be more decayed in residual forests. Furthermore, given their highly subterranean status, salamanders may have been affected by quantities of belowground coarse woody debris, including decaying roots and buried wood, which comprise the majority of dead woody biomass in managed forests (Debeljak 2006; Olajuyigbe et al. 2011) and can remain limited in post-agricultural successional sites (Marin-Spiotta et al. 2008). Leaf litter is another critical component of wood frog and spotted salamander terrestrial habitats, providing additional foraging opportunities and protection from stressful environmental conditions like drought. In radiotelemetry studies, both species have been found to seek out microhabitats that include well developed deciduous litter layers (Faccio, 2003; Rittenhouse and Semlitsch, 2007b). These results suggest that despite reduced litter availability, relatively mature secondary forests (≥ 50 years old) provide sufficient microhabitats for wood frogs during their terrestrial life stage.

Other structural and functional habitat components may additionally explain agricultural legacy effects on pool-breeding salamanders. A typical long-term consequence of agriculture in contemporary forests is the shift in plant species composition resulting in potential losses of species and genetic diversity (Bellemare et al. 2002; Foster et al. 2003; Vellend 2004; Flinn & Marks 2007; Rhemtulla et al. 2007). In central New York, conversions from sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*) dominated stands to those composed of red maple (*Acer rubrum*), white ash (*Fraxinus americana*), and white pine (*Pinus strobus*) are typical (Flinn & Marks 2007) and largely representative of current conditions at HMF. Whereas primary forests may appear structurally similar to secondary forests in some regards 50–80 years following agricultural abandonment, intensive land-use practices and drastic changes to plant communities can have broad effects on functional traits, including decomposition rates of coarse woody debris and litter (Compton & Boone 2000; Post & Kwon 2000), soil nutrient dynamics (Bellemare et al., 2002; Flinn and Vellend, 2005; Fraterrigo et al., 2005; Flinn and Marks, 2007), and resistance to exotic organisms, such as invasive plants and earthworms (Szlávecz & Csuzdi 2007; Kuhman et al. 2011). Examining dual effects of structural and functional characteristics of forests with different land-use histories on amphibians should provide a greater understanding of potential mechanisms that limit species responses.

Although not recorded in this study, subsurface environmental characteristics and community interactions may additionally explain spotted salamander preference for older forests. Another important physical legacy of cultivation is the spatial homogenization and physical compaction of soil organic layers that can persist for at least 60–100 years following forest regeneration, with slow recovery of subsoil root channels (Foster et al. 2003; Piché & Kelting

2015). As a fossorial species, spotted salamanders are highly dependent on underground niches, such as small mammal burrows, outside of the breeding season (Madison 1997; Regosin et al. 2003; Rothermel & Luhring 2005). These subterranean structures, and the assemblage of mammals that construct them, may be influenced by forest microtopography and associated with pit and mound features that are characteristic of primary forests (Faccio 2003; Flinn & Marks 2007). Spotted salamanders are particularly dependent on short-tailed shrew (*Blarina blevicauda*) burrows (Madison 1997), which may be more abundant in older forests (Ford et al., 1997). Small mammal burrows are an important component of core terrestrial habitat for many amphibian species (Semlitsch & Bodie 2003). Assessing these community interactions in forests with different land-use histories would provide necessary context for understanding these mechanisms and their relevance to pool-breeding amphibian conservation.

A primary benefit of occupancy modeling is the ability to account for imperfect detection in species occurrence estimates. Detection of both species was reduced in deep leaf litter environments, but this effect was reversed for wood frogs and intensified for spotted salamanders in the presence of precipitation. These effects can be explained by limitations of the survey method as well as the physiological constraints of amphibians. Due to time restrictions and the large plot sizes, we did not actively sample leaf litter profiles. Wood frogs are easily obscured in deep litter environments, and cover object surveys may have missed spotted salamanders exploiting these other substrates. Amphibians are reliant on cutaneous respiration and highly sensitive to changes in air moisture, as such they are typically more active in higher humidity conditions when desiccation risk is lower (Duellman & Trueb 1994). Accordingly, precipitation likely increased the proportions of surface active frogs and litter active salamanders, the latter of which would have been more difficult to detect. While occupancy is often utilized as a proxy for assessing population dynamics, caution should be exercised when attempting to translate occupancy to abundance (Efford & Dawson 2012; Bailey et al. 2014). This is particularly true for short-term studies of animal occurrence. Wood frog populations can fluctuate rapidly in response to extreme climate conditions and subsequent effects on pool hydroperiods (Berven 2009), such as those experienced over the course of this study. Spotted salamander populations are generally more stable; however, their relative longevity necessitates a longer study to better understand population trends, habitat associations, and the specific mechanisms driving these relationships.

Conclusions

A growing challenge for wildlife conservation is identifying and developing feasible management strategies for species facing numerous interrelated threats. This is particularly true for organisms with complex life cycles, which operate on multiple trophic and spatial dimensions. Intervention that does not consider threats in the context of life history processes and landscape setting may fail at supporting resilient populations in the long term. As I demonstrate, land-use legacies can play an important role in amphibian conservation efforts and better contextualize habitat augmentation practices for pool-breeding species with different life histories. Vernal pool construction can enhance populations in forests with limited breeding habitat, but stakeholders should consider pool density and site history with regards to focal populations to maximize conservation outcomes; focusing exclusively on secondary forests with limited leaf litter, denser and less diverse understory plants, and less decayed woody debris as candidate sites for pools may yield unfavorable outcomes for long-lived and highly fossorial organisms such as mole salamanders (*Ambystoma* spp.). Heterogenous designs that include a gradient of pool densities over large spatial scales are essential to support genetically diverse local and regional populations (Smith & Green 2005; Calhoun et al. 2014). I found that moderate densities (1 – 4 pools per 9.3 ha) can provide reasonable benefits for co-occurring amphibians with different life histories. Developing complex systems of pools with varying hydroperiods, rather than single isolated wetlands, are preferable for philopatric species with high dispersal capabilities; these designs provide needed buffers against environmental threats such as climate change and/or disease and promote long-term population persistence (Petranka & Holbrook 2006).

Finally, conservation plans that solely focus on current and future threats without carefully considering previous site conditions may ignore historical restraints on habitat suitability (Calhoun et al. 2003). Forest disturbance history might be more relevant for spotted salamanders when selecting sites for pool creation. Situating pools across a gradient of residual and secondary forests can help address historical wetland losses while also supporting the terrestrial habitat requirements of both pool-breeding species. Though this study only focused on the legacy effects of forest clearance and agriculture over the past two centuries, even older anthropogenic disturbances can contribute to forest conservation plans as well (Whitlock et al. 2018). Extending historical perspectives to include a comprehensive spatiotemporal range of land-use patterns can be informative to understanding ecological responses to current threats and developing adaptive management plans for species with complex life cycles.

Tables

Table 1.1. Summary of detection and occupancy model parameters assessed in this 2016–2017 study of aquatic and terrestrial habitat limitations of two vernal pool-breeding amphibians in forests with distinct land-use histories in central New York, USA.

Model	*Variable*	*Description*	*Unit*
Detection			
	date	survey date	Julian date (1 – 98)
	rain24	rain 24 hrs prior to a survey	0: no, 1: yes
	rain	rain during a survey	0: no, 1: yes
	temp	air temperature	°C
	obs	number of observers	0: 1, 1: 2
	litter	leaf litter depth	centimeters
	und[a]	understory cover	proportion
	effort[b]	relative # objects flipped	index (max: 1)
	year	survey year	0: 2016, 1: 2017
Occupancy			
	upland	residual forest cover	proportion
	pools	vernal pool density	number of pools (0–10)
	year	survey year	0: 2016, 1: 2017

[a] Parameter only included for *L. sylvaticus*

[b] Parameter only included for *A. maculatum*

Table 1.2. Model selection results for 2016–2017 wood frog and spotted salamander occupancy data in relation to larval versus adult habitat gradients in central New York. Only models with a $\Delta AIC_C \leq 2.0$ and the null model are shown. Model symbols: Ψ = occupancy, p = detection.

Model[a]	*K*	*ΔAIC_C*	*w_i*	*Deviance*
Wood frogs				
Ψ(pools + year) p(litter * rain + year)	8	0.00	0.49	106.20
Ψ(.) p(.)	2	9.12	0.01	130.04
Spotted salamanders				
Ψ(upland * pools + pools * year) p(litter + rain + year)	10	0.00	0.56	104.90
Ψ(.) p(.)	2	4.63	0.06	129.99

[a] Full list of model rankings for each species are available in Appendices 1.1–1.4.

Table 1.3. Parameter estimates for best supported wood frog and spotted salamander models relating occupancy to larval versus adult habitat gradients during divergent climate regimes from 2016–2017 in central New York.

Species	*Model parameter*	*Regression parameter*	*β*	*SE*	*Lower CI*	*Upper CI*
Wood frogs	*Occupancy*					
		Intercept	0.40	1.16	– 1.88	2.67
		pools	2.25	1.03	0.23	4.27
		year1	0.06	1.20	– 2.29	2.41
	Detection					
		Intercept	– 1.47	0.68	– 2.80	– 0.14
		litter	– 0.94	0.47	– 1.86	– 0.02
		rain1	1.20	1.07	– 0.90	3.30
		year1	1.44	0.78	– 0.09	2.97
		litter*rain1	2.62	1.12	0.42	4.82
Spotted salamanders	*Occupancy*					
		Intercept	2.61	2.06	– 1.43	6.65
		upland	3.25	1.78	– 0.24	6.74
		pools	8.12	3.63	1.01	15.23
		year1	– 2.97	2.33	– 7.54	1.60
		upland*pools	6.55	2.99	0.69	12.41
		pools*year1	– 9.67	4.28	– 18.06	– 1.28
	Detection					
		Intercept	– 0.60	0.52	– 1.62	0.42
		litter	– 1.40	0.79	– 2.94	0.15
		rain1	– 0.72	0.39	– 1.48	0.05
		year1	0.46	0.69	– 0.89	1.81

Figures

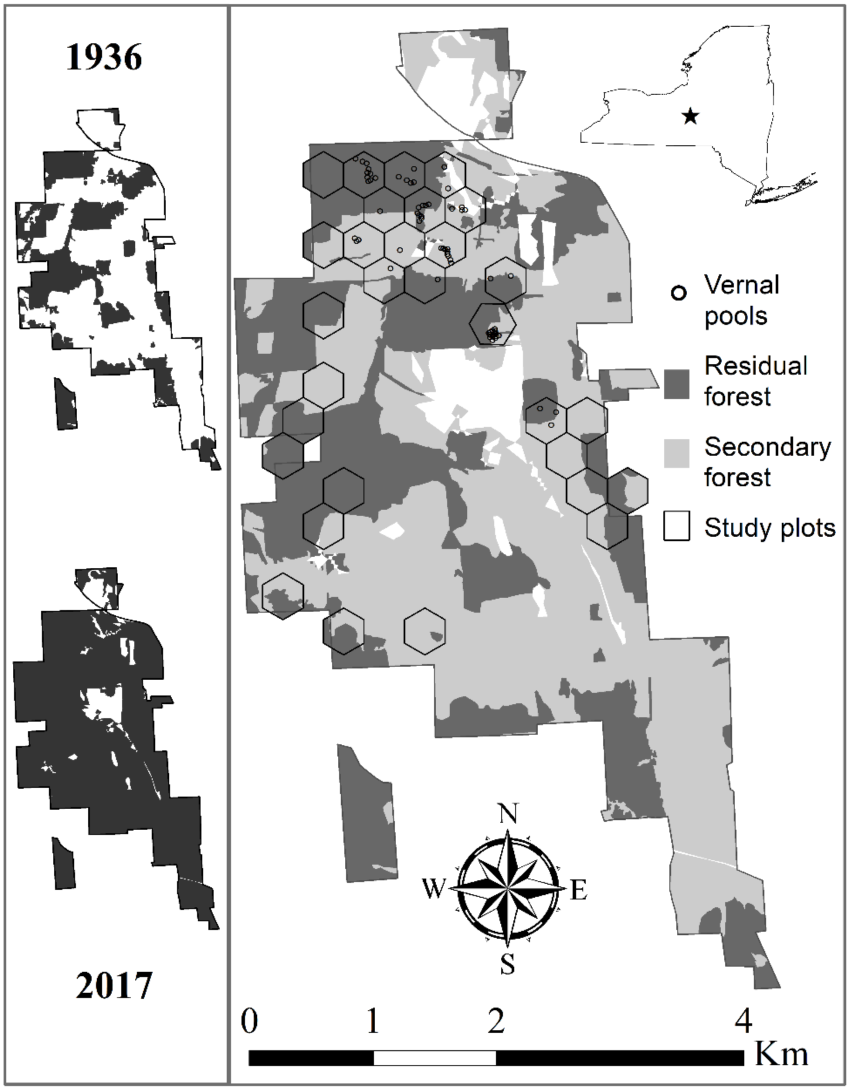

Figure 1.1. Region of study of aquatic and terrestrial habitat limitations of two vernal pool-breeding amphibians in forests with distinct land-use histories in central New York, USA during 2016 and 2017. Left panel: Overview of historical (1936) and current (2017) forest extent and vernal pools distributions at Heiberg Memorial Forest (HMF). Right panel: sampling plots and pool locations. Forest types were delineated from georeferenced historical aerial photographs and modern orthoimages. Secondary forests (light grey) were in agriculture prior to 1936 and residual forests (dark grey) have been continuously wooded throughout this historical period.

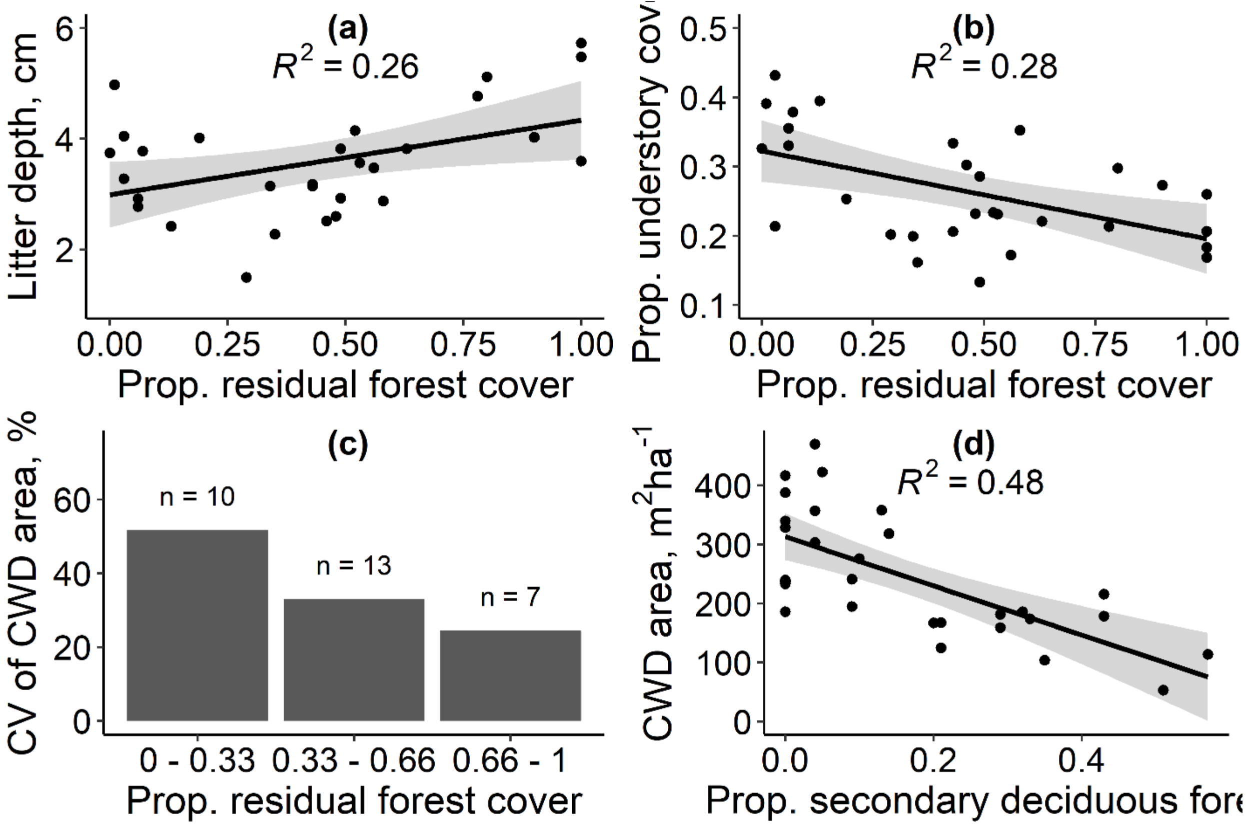

Figure 1.2. Upland habitat regression results from study on aquatic and terrestrial habitat limitations of pool-breeding amphibians in forests with distinct land-use histories in central New York between 2016–2017. Relationships between proportion cover by residual forest and (a) leaf litter depth, (b) understory vegetation, and (c) coefficient of variation (CV) of coarse woody debris (CWD) surface area. Plot (d) displays the relationship between proportion cover by secondary deciduous forest and CWD surface area.

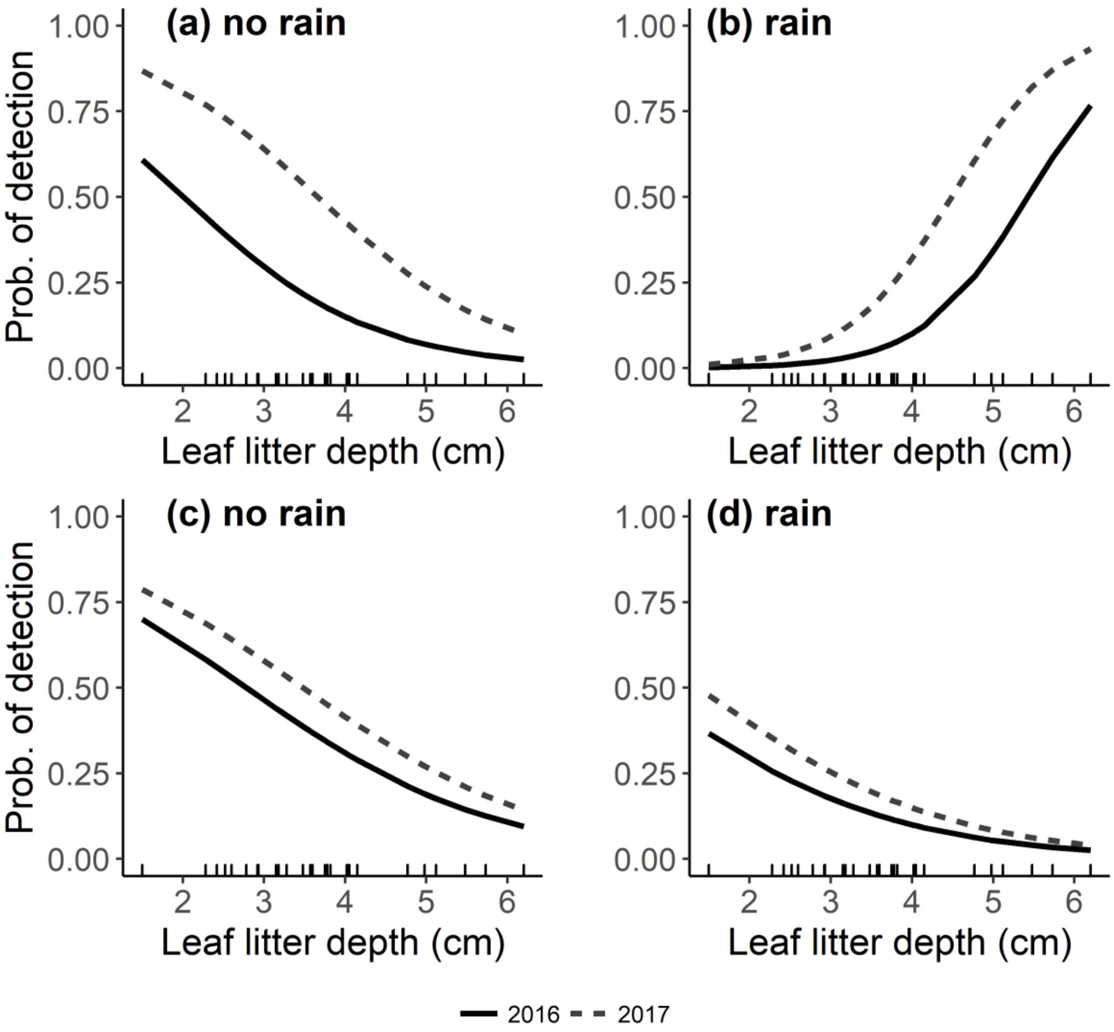

Figure 1.3. Predicted effects of leaf litter depth on detection of wood frogs during surveys with rain (a) and without rain (b) and spotted salamanders with rain (c) and without rain (d) from 2016–2017 in central New York. Model estimates are plotted for both study years (solid lines = 2016, dashed lines = 2017). The distribution of leaf litter depth values from all sites is shown as a rug plot at the bottom of each figure.

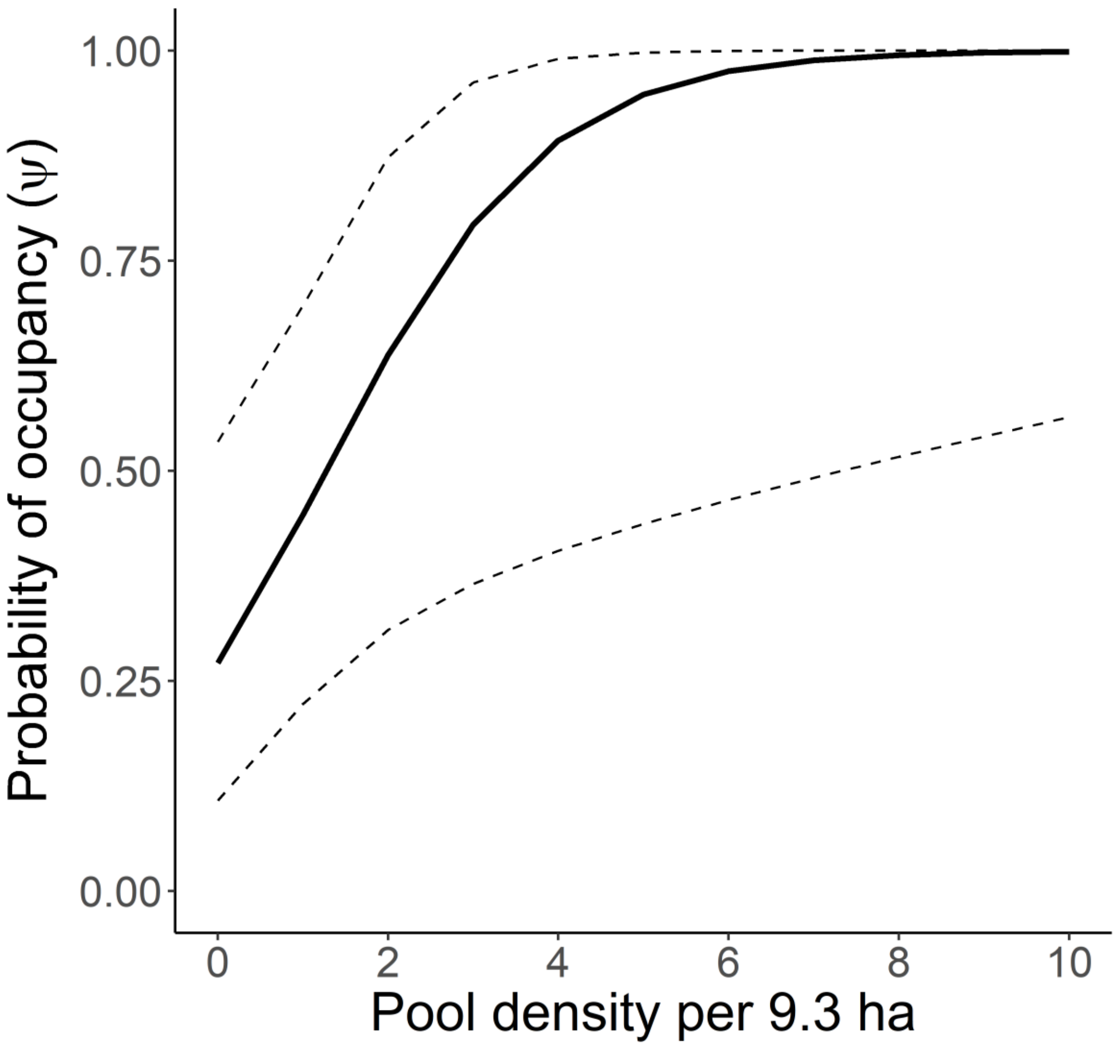

Figure 1.4. Predicted occupancy estimates for wood frogs versus pool density from 2016–2017 in central New York, based on the top supported model. 95% prediction intervals are shown. Predictions were identical between study years, but with less confidence in 2016 (not shown).

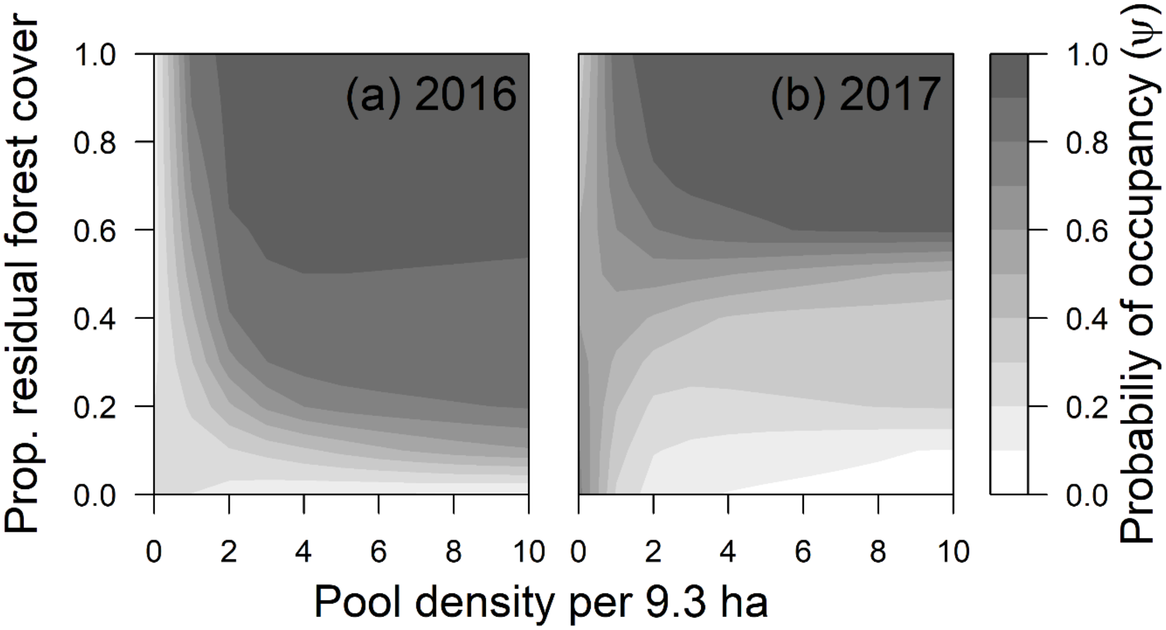

Figure 1.5. Relationship between spotted salamander occurrence and breeding pool availability in the context of forest disturbance history in (a) a dry year (2016) and (b) a wet year (2017) in central New York. Figure depicts model-averaged predictions of spotted salamander occupancy from the full suite of candidate occupancy models.

CHAPTER 2: AGRICULTURAL LAND-USE LEGACY EFFECTS ON FOREST-DWELLING PLETHODONTID SALAMANDERS

Abstract

Developing effective conservation strategies for plethodontid salamanders—a group of terrestrial salamanders displaying tremendous amounts of biomass and nutrient cycling in many forests—requires a comprehensive understanding of the long-term effects of landscape modifications to species and their associated habitats; however, most research has only focused on the impacts of timber management and very few studies have explored the longitudinal effects of more intensive land-use practices such as agriculture. To address these knowledge gaps, I investigated the legacy effects of agriculture on plethodontid salamanders and terrestrial microhabitats over two years in central New York. Using forest habitat assessments and daytime visual encounter surveys, I described terrestrial microhabitat relationships with disturbance history and estimated abundance patterns of two plethodontid species—red-backed salamanders (*Plethodon cinereus*) and dusky salamanders (*Desmognathus* sp.)—from upland plots (N = 30) along a post-agricultural secondary to residual forest gradient. Secondary forests contained shallower leaf litter, denser understory vegetation, and fewer natural cover objects than neighboring residual forests. These habitat components were all strongly implicated in salamander abundance patterns, with both species limited by the availability of natural cover objects, red-backed salamanders negatively associated with dense understory vegetation, and dusky salamanders positively associated with leaf litter depth and negatively associated with increasing distance to streams. These results suggest that agriculture imparts persistent legacies on modern forested landscapes and that terrestrial and stream-dependent woodland salamanders are sensitive to these effects for at least 50–80 years after farm abandonment.

Key words:, agriculture, land-use history, microhabitat, *N*-mixture model, terrestrial salamanders

Introduction

Forest ecosystems are governed by disturbance and successional cycles across multiple spatial and temporal scales (Perry et al. 2008). These dynamic processes are fundamental to the establishment and persistence of different biological communities associated with specific successional habitats and environmental conditions. Anthropogenic activities, such as clearcutting and agriculture, are important drivers of global forest change (Hansen et al. 2013). These intensive land-use practices can impart numerous long-lasting legacies on ecosystem structure, composition, and function (Foster et al. 2003) and affect forest responses to disturbance regimes modified by climate change (Dale et al. 2001). Understanding how legacies of historical agriculture impact forest-dependent species can provide valuable insight for conservation and management plans of contemporary forests and guide protections for organisms with specific habitat requirements.

The northeastern United States offers rich opportunities for studying land-use legacies in forest ecosystems. Over the past century, northeastern forests have undergone a swift transformation. After hundreds of years of extensive forest clearing and agricultural activity, farmlands have largely been abandoned and the region has experienced widespread regeneration (Whitney 1996). The prospect of future forest losses in this region (Drummond & Loveland 2010) underscores the need to fill knowledge gaps on agricultural legacy effects on forest organisms of conservation concern. There is a wide gap of knowledge on forest land use legacy effects on wildlife in temperate forests, and this is particularly true for forest-dwelling amphibians like terrestrial salamanders (Bowen et al. 2007; Thompson & Donnelly 2018).

Terrestrial salamanders (family: Plethodontidae) have long been advocated as indicators of forest biodiversity and ecosystem integrity in North America, owing to their extreme sensitivity to habitat modifications, interactivity across multiple forest trophic levels, and high population densities (Welsh & Droege 2001; Davic & Welsh 2004). These lungless salamanders are completely reliant on cutaneous respiration in terrestrial environments and are therefore highly sensitive to fine-scale habitat disturbances that increase desiccation risk (Feder 1983). Plethodontid salamanders may play significant roles in eastern forests, as both top predators in soil-litter food webs and important prey for a variety of reptiles, birds, and small mammals (Wyman 1998; Davic & Welsh 2004). Species such as red-backed salamanders (*Plethodon cinereus*) often display extremely high densities where they occur and comprise a significant proportion of animal biomass in forests (Burton and Likens, 1975a; Jaeger, 1980), highlighting their ecological importance and utility for quantifying the long-term effects of disturbances on forest ecosystems.

Most studies of land-use legacy effects on plethodontid salamanders have focused on historical impacts of silviculture and alternative forest management practices (e.g., DeMaynadier and Hunter, Jr., 1998; Dupuis et al., 1995; Ford et al., 2002; Harper and Guynn, 1999; Semlitsch et al., 2007). Salamander populations typically experience sharp declines immediately following clearcutting (Ash 1997; Hocking et al. 2013), as the loss of the forest canopy, vegetation, and ground-level substrates temporarily reduces foraging opportunities (Harper & Guynn 1999) and increases desiccation risk (Petranka et al. 1993). The expected population recovery time following timber extraction in southern Appalachia ranges from 20–70 years (Petranka et al.

1993; Ash 1997), or longer where abandoned logging roads can have persistent negative effects on salamander communities (Semlitsch et al. 2007). Fewer studies have explicitly examined the long term effects of agriculture and subsequent reforestation processes on plethodontid salamanders, which may be equal to or greater than those resulting from silviculture (Pough et al. 1987; Hicks & Pearson 2003; Surasinghe & Baldwin 2014). More research is needed to fully parse these effects in different forested regions with distinct salamander communities, particularly in the northeastern United States (Thompson & Donnelly 2018).

To address these knowledge gaps, I assessed populations of plethodontid salamanders and terrestrial microhabitat characteristics along a secondary to residual forest gradient in central New York. The goal of this research was to identify potential long-term effects of agriculture on terrestrial salamander microhabitats in modern northeastern forests. The objectives were to (1) estimate patterns of salamander abundance in relation to microhabitat components along a historical disturbance gradient, and (2) compare population responses of red-backed salamanders and dusky salamanders (*Desmognathus* spp.), two plethodontid species with distinct life histories (fully terrestrial versus semiaquatic), to agricultural legacies. I expected abundances of both species to be reduced in secondary forests, where persistent modifications of leaf litter, coarse woody debris, understory vegetation, and canopy cover would limit adult populations. From this approach, I sought to expand on the literature of agricultural legacy effects in eastern forests, quantify these effects on established indicators of ecosystem integrity, and elaborate on the species-specific habitat requirements of forest-dwelling salamanders and their sensitivity to landscape change.

Methods and Materials

Study Sites

I conducted fieldwork at Heiberg Memorial Forest (HMF), a 1,600-ha property located 33 km south of Syracuse, NY (42°46'19" N, 76°5'6" W) and owned by the State University of New York College of Environmental Science and Forestry. The site is part of the northern glaciated Alleghany Plateau in the Northeastern Mixed Forest Province, a region characterized by moderately long winters, summer peaking precipitation, and a mixture of broadleaf deciduous and boreal coniferous vegetation (McNab et al. 2007). The forest is currently composed largely of sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*), with scattered plantations of Norway spruce (*Picea abies*) and red pine (*Pinus resinosa*) and smaller amounts of poplar, cherry, and oak. The property was originally purchased under the New York State Reforestation Law of 1929 and the Hewitt Amendment of 1931, by which the state acquired abandoned farmlands and designated them for reforestation (R. Nyland, *personal communication*). Roughly half of the original forest was cleared for agriculture (mostly pasture and hayfields with scattered croplands) during the 18th and 19th centuries prior to abandonment and reforestation in the early 20th century (Figure 2.1). The site currently consists of patches of residual and secondary forests, including naturally restored stands, conifer plantations, and actively managed sugar bushes. I define *secondary forest* as any stand (naturally regenerated or human planted) that was previously cleared for agriculture and *residual forest* as stands that have been continuously wooded throughout this historical period (Peterken 1981). The site's residual forest stands were largely maintained by farmers as personal woodlots and selectively cut for fuelwood, timber, and supplementary sources of income, without being cleared (R. Nyland, *personal communication*).

This investigation was performed as part of ongoing study of created wetlands and pool-breeding amphibians at HMF such that sampling plots reflected home range sizes of wood frogs (*Lithobates sylvaticus*) and spotted salamanders (*Ambystoma maculatum*) and was distributed in part according to configurations of natural and constructed wetlands throughout the site. Salamanders and terrestrial habitat characteristics were surveyed in 30 large (9.3 ha) hexagonal plots that encompassed complete gradients of forest type (secondary to residual) and composition (coniferous to deciduous). Primary and secondary forest extents for HMF were obtained by manually delineating forest cover from six georeferenced historical aerial photographs (circa 1936) and comparing those coverages with contemporary orthoimages (circa 2015) (NYS GIS Clearinghouse, 2015) and land cover data (NLCD 2011, Homer et al., 2015) in ArcMap 10.4.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA, 2016). Half of the plots contained vernal pools and were established prior to the start of this study, with nine plots clustered on a single experimental array of constructed wetlands that was split evenly between adjacent residual and secondary forest stands. The remaining plots were stratified randomly selected from a grid of hexagons to include a representative sample of disturbance extent (i.e., proportion secondary forest cover) and forest composition (i.e., proportion deciduous versus coniferous cover).

Salamander surveys

I inventoried salamanders on sampling sites May-August 2016 and 2017 using area-constrained visual encounter surveys. Visual encounter surveys is an effective method for sampling terrestrial amphibian populations in large areas (Dodd 2011). Each plot was searched between 0800-1500 for approximately three person-hours by walking in a standardized path and thoroughly examining under all moveable “cover objects” (≥ 10 cm in diameter) that might provide refuge for amphibians, including rocks, logs, and bark, recording the total number of salamanders observed. To maximize survey efficiency in our large plots, I did not sift through leaf litter for additional observations. Two to three rounds of surveys were conducted in each plot each year to estimate abundance while accounting for imperfect detection, assuming closed populations within single seasons. Precipitation was documented *in situ* by surveyors and with supplementary data from the Cortland County Airport (42°35′33″N, 076°12′53″W) to determine time-since-rain (TSR) in days for each survey. Air temperature was measured with a digital thermometer at the start of each survey. I additionally recorded other visit details relevant to detection, including time of survey, survey effort (number of cover objects flipped relative to the site maximum), and number of surveyors (one to two persons).

Terrestrial habitat sampling

Forest microhabitat characteristics were sampled between August and September of 2016, with some additional vegetation sampling in 2017. Habitat variables were measured at the plot level to quantify differences between forest types and model salamander responses to these components. I interpreted the maximum number of cover objects flipped at each site as the density of available cover objects, including all moveable logs, bark, and rocks. I used a combination of line intersect and small quadrat sampling to estimate several ground and vegetation substrates predicted to be associated with forest salamanders. Six 100-m long transects and 30 1-m^2 quadrats were stratified randomly established in each plot to collect data on coarse woody debris (CWD) volume, surface area, and decay status, canopy cover, leaf litter depth, and understory vegetation cover. Transects were arranged at equidistant 60° angles along the plot circumradii with the start points randomly staggered 0-30 m from the hexagon center. We measured the diameter and intersection length of all downed CWD (≥ 10 cm in diameter) crossing the transects to calculate total estimated volume (m^3 ha^{-1}) and surface area (m^2 ha^{-1}) of CWD for each plot (Marshall et al. 2003). Decay class was recorded for each intersecting CWD object (Class 1 = freshly fallen, containing intact branches; Class 5 = mostly incorporated into the soil) (Sollins 1982b), which we used to calculate quantities of less decayed (decay class 1 – 2) and more decayed (decay class 3 – 5) CWD. All other habitat components were measured in the quadrats, which were arranged at 20 m intervals along transects. I sampled canopy cover by taking single hemispheric photographs (iPhone 5s camera, 2-cm diameter fisheye lens attachment) from the center of each quadrat and manually calculating percent coverage for each image in the program ImageJ (Rasband 2017). Leaf litter depth was averaged from three ruler measurements taken in two random corners and the center each quadrat. Understory cover was recorded by visually estimating the proportion of woody and herbaceous vegetation under chest height (1.4 m) obstructing the ground within the gridded quadrat.

Statistical analysis

All analyses were performed in R Version 3.3.2 (R Core Team 2017). A description of habitat analyses relating forest disturbance history (i.e., secondary versus residual forest) to terrestrial microhabitat characteristics can be found in Chapter 1 (Methods).

Salamander abundances were estimated with binomial *N*-mixture models (Royle 2004) in the package “unmarked” (v0.12-2, Fiske & Chandler 2011). I used the *pcount* function to fit all hierarchical models with maximum likelihood estimation and compared candidate models using the corrected Akaike’s Information Criterion (AIC_c), which adds an additional penalty for overfitting with a small sample size (Burnham & Anderson 2002). Model rankings were generated with the *aictab* function from the “AICcmodavg” package (v2.1-1, Mazerolle 2017). Models within two AIC_c units ($\Delta AIC_c < 2.00$) of the top ranked model and containing a similar model weight (ω_i) and deviance ($-2\log[\mathcal{L}]$) were considered to have similar support. I combined the data across years by "stacking" the site count data and included a categorical covariate for year (0 = 2016, 1 = 2017) in each detection (p) and abundance (λ) model, allowing me to examine species responses to habitat gradients over two years (Kéry & Royle 2016). All continuous covariates were standardized on a z-scale to zero mean and single unit of standard deviation to promote model convergence, with categorical variables set as factors prior to model development. Individual covariates were not included in the same model when they displayed high correlation ($r > 0.7$).

Model selection was done sequentially to first identify important detection covariates and then examine a candidate list of *a priori* habitat abundance models. I examined a total of 39 detection models from a suite of abiotic and biotic variables (Table 2.1), using a global abundance model for each species, and selected the detection model with the greatest support for comparing habitat abundance models. Amphibian surveys spanned consecutively extreme climate periods: 2016 was the driest year on record for New York (Sweet et al. 2017) and 2017 was an abnormally wet year; therefore, before constructing the final candidate model list, I compared univariate abundance models containing either additive or interactive year effects to identify any important climate mediated habitat relationships to include in the final model set. Abundance models consisted of univariate and bivariate groupings of litter, cover object, and vegetation components, including additive and interactive effects to account for multiple sources of terrestrial salamander population regulation. For stream salamanders, terrestrial habitat covariates were paired with an aquatic habitat covariate (i.e., distance to streams) to account for biphasic habitat requirements. I assessed goodness-of-fit of the global model for each species with a bootstrapped Chi-square statistic, using 1000 replicates (Mazerolle 2017), and estimated overdispersion (ĉ) by dividing the observed Chi-square statistic by the mean of simulated values. Models with a p-value > 0.05 and ĉ ~ 1.0 were considered to be structurally adequate (Burnham & Anderson 2002); goodness-of-fit statistics and residual diagnostic plots were compared between Poisson and negative binomial models in instances when the Poisson distribution was inadequate. Zero-inflated Poisson models were not considered because of the low frequency of zero counts for both species. I selected the best fitting distribution for model comparison and inference, correcting for overdispersion by using quasi-likelihood values ($QAIC_c$) and adjusting parameter uncertainty (SEs and CIs) by the level of ĉ (Burnham & Anderson 2002).

Binomial *N*-mixture models have been widely used since their development as they can provide abundance estimates from count data of unmarked organisms by simultaneously modeling two processes: the state process (i.e., abundance or λ, typically a Poisson distribution) and the observation process (i.e., detection or p, a binomial distribution). The model has several important assumptions to avoid biased parameter estimates: (1) sites should be closed (i.e., no births, deaths, or movements in or out of sites) between visits within the same season; (2) species must be identified correctly (i.e., no false-positive errors); (3) individuals must be detected independently from each other; (4) detection should be homogenous or modeled with appropriate covariates; and (5) *N*-mixture models make specific parametric assumptions, which I tested using the goodness-of-fit procedure described earlier to specify the most appropriate error distribution. Plethodontid salamanders exhibit vertical migrations between surface and underground refugia during summer months; however these movements should not constitute closure violations because they are generally temporary and random and only modify the interpretation of abundance to have a superpopulation meaning (Kéry & Royle 2016). To ensure that there were no false positives I grouped counts of dusky salamanders (*Desmognathus fuscus* and

Desmognathus ochrophaeus) by genus, as these species are often difficult to distinguish. Woodland plethodontid salamanders typically display high territoriality (Bruce et al. 2000) under discrete cover objects; therefore, detection is largely independent among individuals.

Counts of dusky salamanders were significantly different between survey rounds ($p < 0.0001$, Pearson's chi-square), with the highest counts recorded toward later survey dates; however, this trend was not explained by survey effort or site-specific precipitation events. Due to concerns of possible closure violations because of migration and/or recruitment of dusky salamanders from streams, I decided to use negative binomial generalized linear models (GLMs) with the *glm.nb* function in the MASS package (v7.3-47, Venables and Ribley, 2002) to examine relative abundance in relation to terrestrial habitat characteristics and stream availability (Barker et al. 2017). Streams were delineated from a 3 m digital elevation model in ArcMap and average distance to streams was calculated for each plot. Categorical survey and year variables, as well as a stream distance covariate, were included in each model and paired with terrestrial habitat components according to different additive combinations. I included a quadratic effect of leaf litter to account for possible sources of imperfect detection under natural cover objects in plots with deeper litter.

Results

Terrestrial microhabitat relationships with forest disturbance history

Several terrestrial salamander microhabitat characteristics displayed significant relationships with forest disturbance history, with shallower leaf litter ($R^2 = 0.26$, $p = 0.004$), denser understory vegetation cover ($R^2 = 0.28$, $p = 0.003$, and more variable quantities of coarse woody debris in secondary forests (Table 2.2, Figure 1.2). Detailed habitat regression model results can be found in Chapter 1 (Results).

Salamander abundance relationships with microhabitat features

A total of 2,344 red-backed salamanders and 806 dusky salamanders were observed over the course of the study. Red-backed salamanders were detected on all study plots and dusky salamanders in 27 out of 30 plots. The bootstrapped analyses showed evidence of poor model fit for red-backed salamanders under a Poisson distribution ($p < 0.001$) with moderate overdispersion ($\hat{c} = 2.60$). A negative binomial global model was less overdispersed ($\hat{c} = 1.58$) and favored by $\mathrm{AIC_c}$ (Poisson $\Delta\mathrm{AIC_c} = 25.90$), so I used this distribution in the final candidate set of models and calculated quasi-likelihood statistics ($\mathrm{QAIC_c}$) for model selection, adjusting the uncertainty of parameter estimates for additional overdispersion.

Cover object density and understory cover additively best explained red-backed salamander abundance, with one model showing strong support ($w_\mathrm{i} = 0.71$):

$$\log(\lambda) = \beta_1 + \beta_2(\mathit{objects}) + \beta_3(\mathit{und}) + \beta_5(\mathit{year})$$

and no other models having $\Delta\mathrm{QAIC_c} < 2$. (Appendix 2.2). Abundance was greater with more available cover objects and less understory vegetation, and similar between years (Table 2.3, Figure 2.1). These abundance estimates had greater precision in 2017, corresponding to the additional count data from a third survey round. One detection model had clear support in explaining detections of red-backed salamanders ($w_i = 1.00$):

$$\mathrm{logit}(p) = \beta_1 + \beta_2(\mathit{effort}) + \beta_3(\mathit{effort}^2) + \beta_4(\mathit{date}) + \beta_5(\mathit{year})$$

According to this model, detection was greater with increasing survey effort and gradually declined later into the summer (Figure 2.2). Detection was also greater in 2017, when site conditions were wetter (Table 2.3, Figure 2.2).

A Chi-squared goodness-of-fit test indicated sufficient fit ($p = 0.23$) for the global model for dusky salamanders. One model received relatively strong support ($w_i = 0.60$) according to $\mathrm{AIC_c}$. Dusky salamander counts were strongly driven by leaf litter depth cover object density and stream availability with higher observed counts in sites with deeper leaf litter, more abundant cover objects, and less distance to streams (Table 2.3, Figure 2.3). The positive effect of leaf litter tended to plateau with deeper litter levels (> 5 cm), where detection under natural cover objects may have been more restricted. Counts were greater in successive surveys, but not different between years.

Discussion

Historical agriculture exerted multiple legacy effects on contemporary upland forest conditions in central New York. Despite 50–80 years of forest regeneration, key components of salamander habitats such as leaf litter, cover object availability, and understory vegetation remain strongly dependent on site disturbance history. Salamander abundances varied along these habitat gradients, implying that historical agriculture and subsequent regeneration can have long-lasting effects on amphibian populations via their associated microhabitat conditions. These legacy effects were apparent for both plethodontid salamanders, evidently with slightly different habitat mechanisms for each.

The observed negative association between red-backed salamanders and understory vegetation in this study may be more a function of changes to plant composition than cover.

Much of the dense vegetation in secondary sites consisted of homogenous patches of ferns and spruce seedlings in conifer plantations and thickets of invasive blackberries in many deciduous stands. Post-agricultural forests are more susceptible to invasions of shade-tolerant vegetation (Kuhman et al. 2011). These uniform and weedy understory strata may not offer the same foraging and microclimate benefits for forest dwelling amphibians as diverse herbaceous flora, which are more associated with residual forests (Bellemare et al. 2002). Dense understory vegetation may also result in drier soil conditions due to greater evapotranspiration or be a symptom of other factors more directly affecting salamander populations, such as non-native earthworms and their detrimental effect on leaf litter and litter-dependent organisms (Maerz et al. 2009). There is a general lack of knowledge regarding plant community interactions with plethodontid salamanders (but see Maerz et al., 2009); studies that investigate these fine-scale ecological relationships would be useful for understanding forest legacy effects on amphibians and their relevance to contemporary landscape change.

My results are consistent with other studies documenting agricultural legacy effects on plethodontid salamanders via changes to vegetation and ground cover characteristics, and the first to measure these impacts while accounting for imperfect detection. Hicks and Pearson (2003) recorded lower abundances of plethodontid salamanders in post-agricultural forests in southern Appalachia, which featured a greater proportion of herbaceous vegetation. Cosentino and Burbaker (*in review*) found a similar negative association between red-backed salamanders and herbaceous vegetation in post-agricultural forests in central New York. Understory vegetation is typically positively associated with terrestrial salamanders (Pough et al., 1987; Dupuis et al. 1995), providing necessary shade, moisture, and foraging habitat for species such as red-backed salamanders (Jaeger 1978, 1980).

Abundance of both species in this study were strongly associated with the density of available cover objects, which was 73% lower in secondary than primary forests. The relationship between forest disturbance history, cover object density, and salamander abundance has been noted in other regional studies on forest legacy effects on amphibians (Cosentino and Burbaker, *in review*). This relationship did not hold up for CWD quantities, which displayed complex associations with forest composition and disturbance history. CWD gradually accumulates following agricultural abandonment and can require up to a century to be restored to reference levels (Currie & Nadelhoffer 2002; Hooker & Compton 2003). The observed heterogeneity in CWD among our secondary sites may reflect differences in management, where conifer plantations receive supplementary fuels from occasional logging and deciduous secondary stands represent a more natural trajectory of slow detrital recovery following agriculture. Regardless of these trends with historical and modern land-use, neither salamander species displayed strong abundance associations with CWD variability in the landscape. Density of cover objects may be more limiting than size of cover objects for plethodontid salamanders (McKenny et al. 2006), which are highly aggressive and territorial in forested uplands (Maerz & Madison 2000). Adult red-backed salamanders and dusky salamanders exhibit high degrees of inter- and intraspecific competition, actively defending individual cover objects and associated underground retreats (Smith & Pough 1994). Secondary forests that lack sufficient densities of cover objects may be inadequate for supporting robust populations of these species, particularly where they co-occur.

Leaf litter showed a strong relationship with land-use history, with litter 1.5 times deeper in primary than secondary forests. Forest floor biomass accumulation can be slow in regenerating forests (Compton & Boone 2000), requiring at least 50 years to return to pre-disturbance levels

(Hughes & Fahey 1994) and may be further limited by faster litter decomposition rates due to altered plant species assemblages (Kuhman et al. 2011) or greater abundances of earthworms (Hooker & Compton 2003; Szlávecz & Csuzdi 2007). Deep piles of leaf litter are associated with pit and mound topographic structures, which are greatly reduced in forests following agriculture (Flinn & Marks 2007). Moist leaf litter is a critical resource for plethodontid salamanders, functioning as both a protective buffer against dehydration and an important location for foraging and reproduction (Bruce et al. 2000; Maerz et al. 2009). Curiously, variation in leaf litter only explained the abundance patterns of dusky salamanders in our sites, with salamander counts increasing with plot litter depth until an average depth of 5 cm, whereafter there was a slight decline in counts that may reflect the detection limitations of natural cover object surveys. While ample evidence suggests that red-backed salamanders are strongly dependent on deep deciduous litter (Jaeger 1980; DeMaynadier & Hunter, Jr. 1998; Maerz et al. 2009), the range of litter depths in our study region (2–6 cm) may have been adequate to satisfy their physiological requirements and provide sufficient foraging opportunities. Dusky salamanders have complex life cycles and are dually impacted by the availability of aquatic and terrestrial resources (Crawford & Semlitsch 2008). Their biphasic life history and stream-dependence may create greater moisture demands than fully terrestrial species, especially in the context of extreme drought when there is a higher risk of desiccation in semi-permanent streams and seepage habitats. Variation in life history characteristics likely plays an important role in mediating the effects of historical agriculture on amphibians (Chapter 1) and deserves greater attention.

Salamander abundances appeared to be similar between the two study years despite striming differences in climate conditions. In contrast, detection probabilites for red-backed salamanders were significantly lower in 2016, when the study region experienced one of its strongest recorded droughts (Sweet et al. 2017). Terrestrial salamander activity and microhabitat use patterns is strongly associated with moisture conditions, with individuals displaying vertical (subsurface burrows to cover objects) and horizontal (cover objects to leaf litter) movements with increasing precipitation and moisture (Jaeger 1980; O'Donnell et al. 2014). Because no sampling occurred prior to the drought 2016, it is unclear how population levels may have differed from pre-drought conditions. Limited and extended periods of drought can have harmful effects on salamander population size (Currinder et al., 2014), demography (Price et al. 2012), and physiology (Bendik & Gluesenkamp 2013; Caruso et al. 2014). Climate change and land cover changes are prominent factors driving amphibian declines (Milanovich et al. 2010; Hof et al. 2011), and land-use legacies may play an important role in mediating the effects of climate extremes on plethodontid salamanders.

Other potential mechanisms that may provide additional explanations for these legacy effects include diet, quality of stream habitats, availability of subsurface retreats, and colonization restrictions. The primary prey of plethodontid salamanders are small invertebrates (Burton 1976). Agriculture can have lasting negative effects on stream and terrestrial invertebrates after abandonment (Harding et al. 1998; Callaham Jr. et al. 2006), and potentially drive demographic patterns (births, deaths, emigration, imigration) of salamanders dependent on these communities. More research is needed to understand agricultural legacy effects on forest detrital food webs. Forested streams are heavily influenced by watershed-scale disturbances, such as intensive agriculture. These land conversions have longitudinal impacts on erosion, sedimentation, and streamflow processes (Jackson et al. 2005; Ambers et al. 2006) that could place additional stress on stream salamander populations and further limit their distribution in uplands. Plethodontid salamanders spend a considerable portion of their life cycle underground in subterranean retreats. These subsurface structures, and the assemblage of invertebrates and small mammals that construct them, may be influenced by disturbance history and its effects on forest soils and microtopography (Mitchell et al. 1997). Salamanders may also be limited by more internal population processes, such as colonization rates. Red-backed and dusky salamanders have small home ranges typically less than 30 m in radius (Barthalmus & Bellis 1972; Kleeberger & Werner 1982). Such dispersal-limited organisms may require many generations to colonize novel habitats following agricultural abandonment, particularly when connectivity to residual primary forests is limited (Cosentino et al., 2014; Cosentino and Burbaker, *in review*). Collectively, these habitat gradients, ecological interactions, and demographic processes could play important roles in determining salamander responses to historical land-use.

Long-term effects of human disturbance on salamanders is likely more nuanced than the abundance relationships captured in this study, which has some limitations. Amphibian habitat suitability is mediated by demographic processes and varies between larvae, juveniles, and adults (Welsh et al. 2008; Homyack & Haas 2009b). While abundance provides a valuable measure of population status, additional data on demography and body condition would provide more insight into population health beyond population size (Welsh et al. 2008). The predicted abundances in this study are significantly lower than those estimated by Burton and Likens (1975a) and others for plethodontid salamanders in eastern forests. Whereas natural cover object searches are efficient for sampling large areas, this method does not capture subterranean individuals or those at the litter-soil interface which require more intensive and destructive sampling techniques to observe. Salamanders are highly cryptic and perform frequent vertical migrations that are difficult to detect in observational studies of unmarked populations. More precise parameter estimates can be obtained by explicitly modeling temporary emigration (O'Donnell et al. 2015), which is strongly driven by variable weather conditions and climate extremes like those experienced during this study. Though they provide a flexible alternative for modeling abundance data in the case of a closure violation, count models may produce biased results when a single variable produces variation in both state and observation processes. Finally, the effects of historical land-use on plethodontids is highly context dependent and is known to vary regionally and taxonomically; therefore, caution should be exercised when making inferences about forest legacy effects across species and physiographic provinces (Ford et al., 2002). Due to site limitations, this study did not explicitly compare the effects of different types of agriculture; contrasting the effects of historical grazing and more intensive cultivation practices would better contextualize these legacies and provide useful information for land managers.

Conclusion

Land-use history plays an important role in shaping contemporary ecological processes and biological communities (Bürgi et al. 2017). Historical ecology provides a useful framework for reconciling past disturbances with current landscape changes and informing conservation and management objectives for forests and forest-dependent organisms, such as plethodontid salamanders. Measuring longitudinal effects of anthropogenic disturbances on plethodontid salamanders can address important questions about ecological (e.g., habitat suitability) and evolutionary (e.g., adaptation — Cosentino and Droney, 2016) processes, while also providing valuable references for understanding population recovery times and overall forest health. A large amount of research has measured salamander responses to historical timber practices, estimating population recovery times ranging from 20–70 years (Petranka et al. 1993; Ash 1997) that can vary by species (Ford et al., 2002; Tilghman et al., 2012) and disturbance intensity (Grialou et al. 2000; Karraker & Welsh 2006; Tilghman et al. 2012). This study contributes to a growing body of evidence that suggests that populations of terrestrial and stream-dependent plethodontid salamanders can be negatively impacted by historical agriculture for at least 50–80 years due to sustained modifications to microhabitat quality following forest regeneration. These effects may be mediated by the regeneration histories of secondary forests (i.e., naturally restored stands versus plantations), as plethodontids tend to perform poorly in the conifer plantations that comprise many post-agricultural eastern forests (Pough et al. 1987; Waldick et al. 1999). Comparing the effects of different types of former agriculture (e.g., pasture, croplands) and reforestation pathways on amphibian communities could better define these legacy effects and their implications for forest health.

Land-use demands are driving many regional and global forest changes (Drummond & Loveland 2010; Hansen et al. 2013), with the latter shifts largely a consequence of the increasing agricultural demands of growing urban populations in the tropics (Defries et al. 2010). Simultaneously, habitat loss is a major contributing factor to global amphibian population declines (Collins & Storfer 2003) and identifying landscape factors that influence populations of different species and is essential for developing successful amphibian conservation strategies (Cushman 2006). Site history should be carefully considered when making conservation and management decisions for forest ecosystems. Prioritizing protections for primary forests and ensuring the continued restoration of suitable successional sites would likely benefit many sensitive organisms, such as forest-dwelling plethodontid salamanders.

Tables

Table 2.1. Summary of detection and abundance covariates assessed in this 2016–2017 study of agricultural legacy effects on plethodontid salamanders in central New York. For model, p = detection and λ = abundance.

Variable	Description	Unit	Model
Survey components			
date	survey date	Julian date (1 – 98)	p
effort	relative no. cover objects sampled	index (min: 0, max: 1)	p
obs	number of observers	0: 1, 1: 2	p
rain24	rain 24 hrs prior to survey	0: no, 1: yes	p
rain	rain during survey	0: no, 1: yes	p
temp	air temperature during survey	°C	p
TSR	time-since-rain	days	p
year	survey year	0: 2016, 1: 2017	p, λ
Habitat components			
cwdvol	total volume of CWD	m^3 ha^{-1}	λ
cwdarea	total surface area of CWD	m^2 ha^{-1}	λ
decayhigh	more-decayed CWD area	m^2 ha^{-1}	λ
decaylow	less-decayed CWD area	m^2 ha^{-1}	λ
litter	leaf litter depth	centimeters	p, λ
objects	density of available cover objects	integer	λ
streams[a]	mean distance to streams	meters	λ
und	understory cover	proportion	λ

[a] Stream proximity was only included in dusky salamander models.

Table 2.2. Mean (SE) habitat variables and salamander counts in relation to forest type (secondary to residual forest gradient) from data collected during 2016–2017 in central New York.

Variable	Forest type (percent residual forest cover)		
	Young (< 33%) (*N* = 10)	Mixed (33 - 67%) (*N* = 13)	Mature (> 67 %) (*N* = 7)
		Mean (SE)	
Leaf litter depth (cm)	3.35 (0.31)	3.19 (0.15)	4.99 (0.35)
CWD area (m^2 ha^{-1})	265.60 (25.10)	245.85 (19.03)	306.81 (13.75)
CWD area (DC 1–2)	129.51 (14.59)	106.27 (12.86)	118.23 (11.43)
CWD area (DC 3–5)	136.09 (15.12)	139.58 (12.02)	188.57 (9.44)
Object density (ha^{-1})	25.13 (2.61)	34.55 (1.71)	34.28 (1.90)
Understory cover (prop.)	0.33 (0.03)	0.24 (0.02)	0.23 (0.02)
Canopy cover (prop.)	0.92 (0.01)	0.92 (0.01)	0.94 (0.01)
Stream distance (m)	167.01 (29.60)	103.70 (18.46)	162.73 (25.19)
		Mean count (SE)	
Plethodon cinereus count	10.3 (1.8)	19.4 (1.5)	16.6 (2.4)
Desmognathus spp. count	1.4 (0.5)	5.5 (1.9)	6.5 (2.0)

Table 2.3. Parameter estimates and 95% confidence intervals for top-ranked ($\Delta QAIC_c$ or $\Delta AIC_c \leq 2.0$) plethodontid salamander models relating abundance to forest microhabitat components from 2016–2017 in central New York.

Species	Model parameter	Regression parameter	β estimate	SE[b]	Lower CI[a]	Upper CI[a]
Red-backed salamanders	*Detection*					
		Intercept	– 1.70	0.24	– 2.18	– 1.22
		effort	0.19	0.05	0.10	0.28
		effort^2	– 0.06	0.04	– 0.14	0.02
		date	– 0.13	0.03	– 0.19	– 0.07
		year1	0.66	0.27	0.13	1.19
	Abundance					
		Intercept	4.42	0.20	4.01	4.83
		und	– 0.15	0.05	– 0.25	– 0.05
		objects	0.37	0.07	0.24	0.50
		year1	– 0.37	0.24	– 0.85	0.11
Dusky salamanders	*Relative abundance*					
		Intercept	0.43	0.22	0.00	0.86
		survey2	0.55	0.23	0.10	1.00
		survey3	0.83	0.30	0.24	1.42
		year1	0.46	0.26	– 0.05	0.97
		TSR	– 0.18	0.11	– 0.40	0.04
		litter	0.39	0.13	0.14	0.64
		litter^2	– 0.16	0.08	0.00	0.32
		objects	0.56	0.12	0.32	0.80
		streams	– 0.77	0.12	– 1.01	– 0.53

[a] SEs and 95% CIs were adjusted for overdispersion in *Plethodon cinereus* with $\hat{c} = 1.58$.

Figures

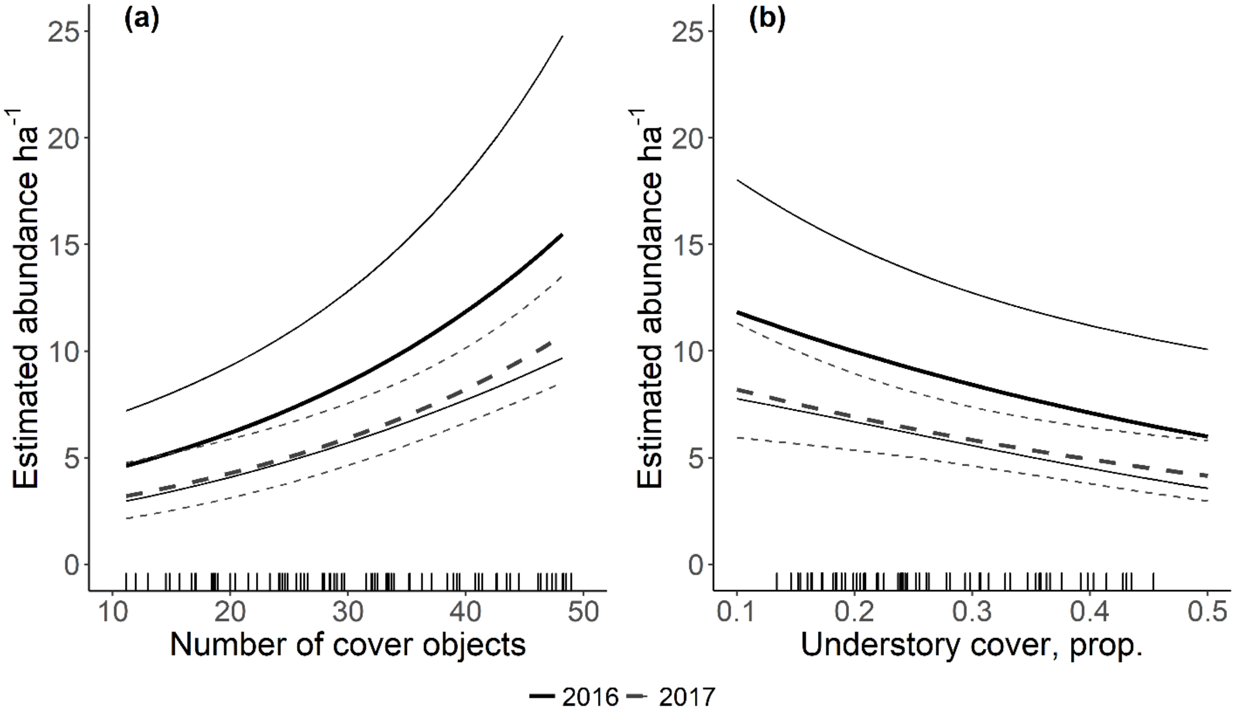

Figure 2.1. Relationship between eastern red-backed salamander abundance and number of cover objects (a) and understory vegetation cover (b) over two years (solid lines = 2016, dashed lines = 2017) in central New York. Predicted parameter estimates and error (95% prediction intervals) are presented. The distribution of cover object and understory cover values from all sites is shown as a rug plot at the bottom of each figure. The average values of complementary habitat variables were used to make the individual covariate predictions.

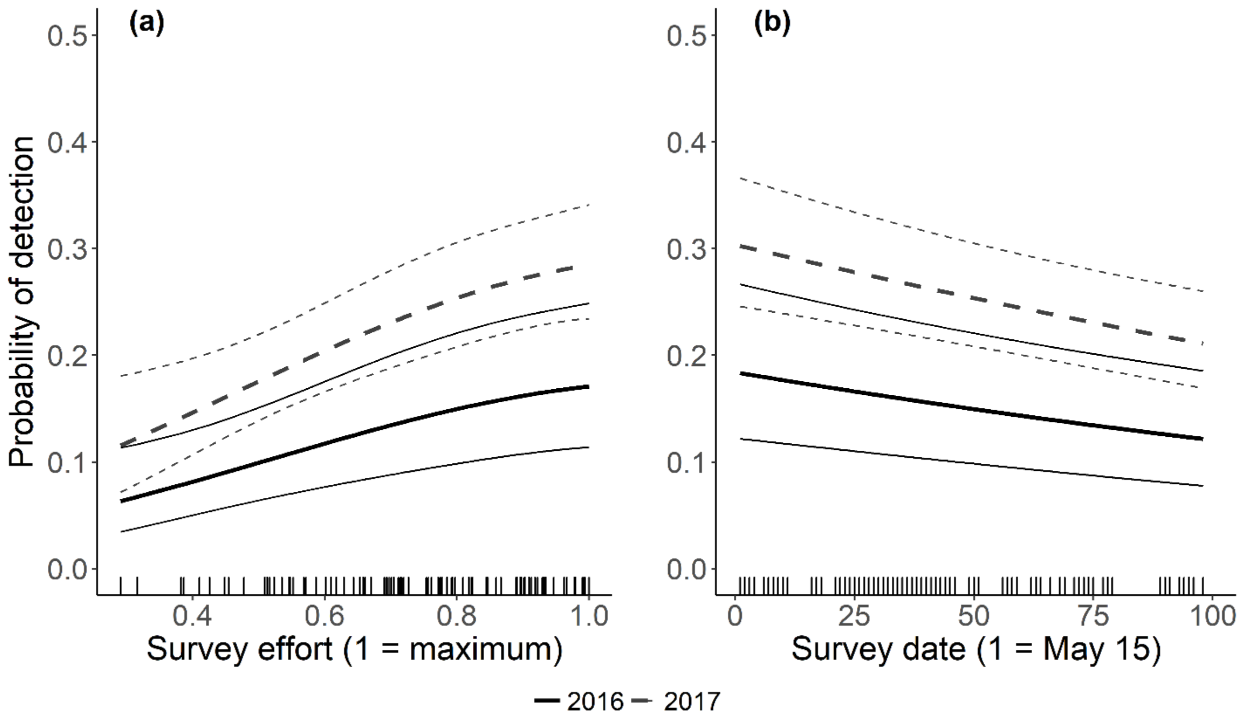

Figure 2.2. Relationship between survey effort (a), Julian date (b), and detection of red-backed salamanders over two years (solid lines = 2016, dashed lines = 2017) in central New York. Predicted parameter estimates and error (95% prediction intervals) are presented. The distribution of survey effort and Julian date values from all sites is shown as a rug plot at the bottom of each figure. The average values of complementary survey variables were used to make the individual covariate predictions.

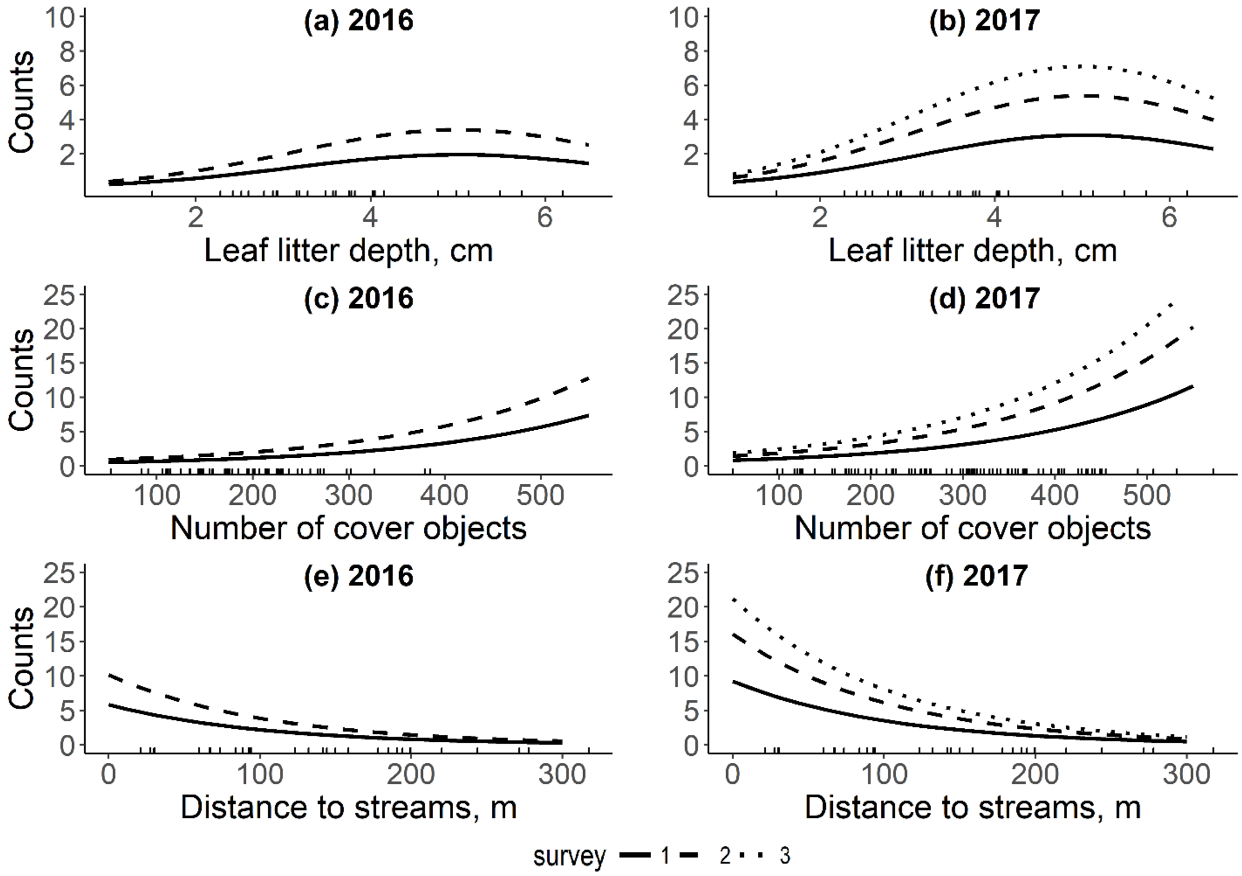

Figure 2. 3. Relationships between dusky salamander counts and leaf litter depth (a, b), cover object density (c, d), and distance to streams (e, f) in forest plots in central New York from 2016–2017. Predicted parameter estimates are shown for each survey (solid lines = May–June dashed lines = June–July, dotted lines = July–August) and year (2016 = a, c, e; 2017 = b, d, f). The distribution of habitat values from all sites is shown as a rug plot at the bottom of each figure. The average values of each remaining habitat variable were used to make the individual covariate predictions.

EPILOGUE

The interplay between natural environmental disturbances and human activity have driven substantial change over the last century in eastern forests of the United States. Human activities are directly modifying forest ecosystems with intensive land-use practices and indirectly via altered environmental disturbance regimes (e.g., invasive species, climate change). These anthropogenic stressors present synergistic challenges for amphibians, populations of which are in global decline, and for which conservation is a priority for many stakeholders. This research sought to better understand how historical human activities drive modern forest conditions and what that means for current amphibian populations and conservation strategies.

I found evidence for multiple land-use legacies in amphibian microhabitats 50–80 years after agricultural abandonment and stand recovery. Compared to residual forests, post-agricultural secondary forests contained less leaf litter, fewer natural cover objects, more variable coarse woody debris quantities, and denser understory vegetation. These findings were consistent with many previous studies in eastern forests, but displayed some inconsistencies with others, which may reflect regional heterogeneity in forest recovery and the confounding effects of conifer plantations, which comprise many secondary forest stands, and management practices, which disrupt natural succession patterns. Explicitly comparing these legacies in these two types of “secondary forests” — passively regenerated stands and actively planted conifer stands — would bring greater clarity to these issues and strengthen the applications for amphibian conservation.

Occupancy rates and abundance estimates of amphibians displayed distinct relationships with aquatic and terrestrial macrohabitat and microhabitat components, likely reflecting differences in species longevity and other life history traits. As expected, both pool-breeding species were driven by vernal pool densities in forested uplands, but these patterns were more complex for spotted salamanders than wood frogs. Whereas wood frog occupancy was solely influenced by available breeding habitat, spotted salamander occupancy was additionally driven by forest disturbance history and climate conditions. Spotted salamanders appeared to display an aversion to secondary forests, and this occupancy pattern was stronger during the abnormally wet season of 2017. These findings confirm that vernal pool construction is effective as a conservation strategy for maintaining adult populations of pool-breeding species in sites with few natural breeding sites. However, site history should be carefully reviewed prior to restoration as pool additions to secondary forests may not yield the same benefits for species with different life histories. Wood frog occupancy was greatest in sites with four or more pools, regardless of landscape setting or climate, whereas spotted salamander occupancy only peaked in sites where some of the surrounding forest was mature and relatively undisturbed, and that shoulder was different depending on climate conditions (> 25% primary forest cover in the dry year of 2016, > 60% residual forest cover in the wet year of 2017, with some marginal secondary sites additionally displaying high levels of occupancy).

According to these results, managers should expect to yield stable wood frog populations after constructing a moderate density of pools (i.e., four or more per 9.3 ha) in primary or maturing secondary forests. Producing the same benefits is more complicated for spotted salamanders; Sites with a minimum threshold of relatively undisturbed forest may need to be prioritized for habitat restoration for this species and other large-bodied, long-lived *Ambystoma* salamanders. These suggestions obviously assume that the quality of the pools themselves is sufficient for breeding, which is a difficult assumption as there can be tremendous variation in reproduction and recruitment among similarly sized pools. While this research did not attempt to determine those suitable pool-level criteria, many others have addressed those questions and continue to do so.

Climatic variation produced unexpected amphibian occupancy patterns with habitat covariates, with wood frog and spotted salamander dependence on pool densities seemingly unaffected by precipitation extremes and spotted salamanders more constrained to predominantly mature primary forests during wet periods. Because this study was limited to two years of observations, the first of which taking place in the middle of an extreme drought, these data only capture a snapshot of amphibian occurrence dynamics which could fluctuate more over the course of a longer sampling period. The complementary effects of “droughts” and “floods” on amphibians may produce time-lagged colonization and extinction events that require longer to observe in upland juvenile and adult populations than in pools themselves.

Both plethodontids were generally limited in predominantly secondary forests and displayed strong abundance patterns with corresponding microhabitat land-use legacies. If we assume plethodontid salamanders are accurate indicators of forest health, as suggested by others, these results would indicate that secondary forests have not yet fully “recovered” the valuable processes and functionalities that residual forests provide for a diverse community of organisms. However, recent skepticism of the utility of amphibians as effective indicator organisms may challenge these conclusions, as some evidence shows greater tolerance of environmental contamination than previously thought in many species (Kerby et al. 2010).

Some similarities were observed between the population patterns of plethodontid species in this study, with both red-backed and dusky salamander abundances positively influenced by cover object densities which were greater in primary forests. The different observed species associations with leaf litter and understory vegetation could reflect the differences in life histories discussed earlier (Chapter 2) but may also be a consequence of the sampling design and different analytical methods used. Plots were designed at the scale of pool-breeding species' home ranges. Though I was able to collect ample abundance data on plethodontid salamanders, these organisms operate at much smaller spatial scales than wood frogs and spotted salamanders (thus the choice to estimate microhabitat relationships and not larger landscape effects on abundance). Red-backed and dusky salamanders were clearly limited in sites with little available residual forest cover (Table 2.2), but the mechanisms behind these limitations are likely more complex than the simple habitat relationships estimated here and may require even more fine-scale data (e.g., soil chemistry and physical characteristics, litter-soil moisture profiles, prey availability, and small mammal and earthworm burrow densities) to understand. Likewise, daytime natural cover object surveys are a convenient method for sampling amphibians over large spatial areas, but this choice of sampling method misses (a) the available litter-soil population and (b) nocturnal activity patterns that could be more effectively measured with trapping techniques, litter searches, and/or nighttime surveys.

Detection played an interesting role in these analyses, particularly for pool-breeding species which were greatly affected by leaf litter gradients. This effect of habitat on amphibian detection raises questions about survey methodologies for these organisms, especially if the desired objective is a greater understanding of how habitat influences state processes. Sampling natural cover objects (e.g., logs) without investigating leaf litter can lead to biased interpretations of occupancy and abundance if only a small percentage of the available population is under the natural cover objects. This single-stratum method also fails to distinguish between vertical migrations (i.e., between burrows and leaf litter) and horizontal migrations (i.e., between cover objects and leaf litter), both of which frequently occur among salamanders in response to climate variability. Estimating these movements is important, not only to account for imperfect detection, but also to move beyond a static understanding of species-habitat relationships.

Beyond their ecological utility, conservation concern, and positive public valuation, amphibians function as useful model organisms for understanding long-term effects of human disturbance on forest ecosystems. Their diverse suite of life histories and activity patterns over space and time provide a useful window into land-use legacies in forested landscapes. The conservation challenges facing amphibians are complex and cannot be resolved in a vacuum. An awareness and integration of these land-use legacies in conservation and management plans is essential for guaranteeing long-term population persistence and biodiversity benefits for amphibians and other forest-dwelling organisms.

LITERATURE CITED

Acuña V, Hunter M, Ruhí A. 2017. Managing temporary streams and rivers as unique rather than second-class ecosystems. Biological Conservation **211**:12–19.

Adams MJ et al. 2013. Trends in amphibian occupancy in the United States. PLoS ONE **8**:6–10.

Ambers RKR, Druckenbrod DL, Ambers CP. 2006. Geomorphic response to historical agriculture at Monument Hill in the Blue Ridge Foothills of Central Virginia. Catena **65**:49–60.

Ash AN. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge mountains. Conservation Biology **11**:983–989.

Bailey LL, Mackenzie DI, Nichols JD. 2014. Advances and applications of occupancy models. Methods in Ecology and Evolution **5**:1269–1279.

Baldwin RF, Calhoun a. JK, deMaynadier PG. 2006. The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes. Canadian Journal of Zoology **84**:1604–1615.

Baldwin RF, deMaynadier PG. 2009. Assessing threats to pool-breeding amphibian habitat in an urbanizing landscape. Biological Conservation **142**:1628–1638. Elsevier Ltd.

Barker RJ, Schofield MR, Link WA, Sauer JR. 2017. On the reliability of N-mixture models for count data. Biometrics.

Barthalmus GT, Bellis ED. 1972. Home range, homing and the homing mechanism of the salamander, Desmognathus fuscus. Copeia:632–642.

Bellemare J, Motkzkin G, Foster DR. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. Journal of Biogeography **29**:1401–1420.

Bendik N, Gluesenkamp A. 2013. Body length shrinkage in an endangered amphibian is associated with drought. Journal of Zoology **290**:35–41.

Berven KA. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog. Ecology **71**:1599–1608.

Berven KA. 2009. Density dependence in the terrestrial stage of wood frogs: Evidence from a 21-year population study. Copeia **2009**:328–338.

Berven KA, Grudzien TA. 1990. Dispersal in the wood frog (Rana sylvatica): Implications for genetic population structure. Evolution **44**:2047–2056.

Biek R, Funk WC, Maxell BA, Mills LS. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conservation Biology **16**:728–734.

Bowen ME, McAlpine CA, House APN, Smith GC. 2007. Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna. Biological Conservation **140**:273–296.

Boyle KJ, Kotchen MJ, Smith VK. 2017. Deciphering dueling analyses of clean water regulations. Science **358**:49–50.

Breusch T, Pagan A. 1979. A simple test for heteroscedasticity and random coefficient variation. Econometrica **47**:1287–1294.

Bruce RC. 2005. Theory of complex life cycles: Application in plethodontid salamanders.

Herpetological Monographs **19**:180–207.

Bruce RC, Jaeger RG, Lynne D Houck, editors. 2000. The biology of plethodontid salamanders.

Bürgi M, Östlund L, Mladenoff DJ. 2017. Legacy effects of human land use: ecosystems as time-lagged systems. Ecosystems **20**:94–103.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: A practical information-theoretic approach (2nd ed). Ecological Modelling. Springer-Verlag, New York, NY.

Burton TM. 1976. An analysis of the feeding ecology of the salamanders (Amphibia, Urodela) of the Hubbard Brook Experimental Forest. Journal of Herpetology **10**:187–204.

Burton TM, Likens GE. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia **1975**:541–546.

Calhoun AJK, Arrigoni J, Brooks RP, Hunter ML, Richter SC. 2014. Creating successful vernal pools: A literature review and advice for practitioners. Wetlands **34**:1027–1038.

Calhoun AJK, Mushet DM, Bell KP, Boix D, Fitzsimons JA, Isselin-Nondedeu F. 2017. Temporary wetlands: challenges and solutions to conserving a “disappearing” ecosystem. Biological Conservation **211**:3–11. Elsevier Ltd.

Calhoun AJK, Walls TE, Stockwell SS, Mccollough M. 2003. Evaluating vernal pools as a basis for conservation strategies : a Maine Case Study **23**:70–81.

Callaham Jr. M, Richter Jr. D, Coleman D, Hofmockel M. 2006. Long-term land-use effects on soil invertebrate communities in Southern Piedmont soils, USA. European Journal of Soil Biology **42**:S150–S156.

Caruso NM, Sears MW, Adams DC, Lips KR. 2014. Widespread rapid reductions in body size of adult salamanders in response to climate change. Global Change Biology **20**:1751–1759.

Cohen MJ et al. 2016. Do geographically isolated wetlands influence landscape functions? Proceedings of the National Academy of Sciences **113**:201512650.

Collins JP, Storfer A. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distribution **9**:89–98.

Compton JE, Boone RD. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology **81**:2314–2330.

Cosentino BJ, Droney DC. 2016. Movement behaviour of woodland salamanders is repeatable and varies with forest age in a fragmented landscape. Animal Behaviour **121**:137–146. Elsevier Ltd.

Cosentino BJ, Schooley RL, Bestelmeyer BT, Kelly JF, Coffman JM. 2014. Constraints and time lags for recovery of a keystone species (Dipodomys spectabilis) after landscape restoration. Landscape Ecology **29**:665–675.

Crawford JA, Semlitsch RD. 2008. Abiotic factors influencing abundance and microhabitat use of stream salamanders in southern Appalachian forests. Forest Ecology and Management **255**:1841–1847.

Currie WS, Nadelhoffer KJ. 2002. The imprint of land-use history: Patterns of carbon and nitrogen in downed woody debris at the Harvard Forest. Ecosystems **5**:446–460.

Currinder B, Cecala KK, Northington RM, Dorcas ME. 2014. Response of stream salamanders to experimental drought in the southern Appalachian Mountains, USA. Journal of

Freshwater Ecology **29**:579–587. Taylor & Francis.

Cushman SA. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation **128**:231–240.

Dahl TE. 2011. Status and trends of wetlands in the conterminous United States 2004 to 2009. U.S. Department of the Interior; Fish and Wildlife Service, Washington, D.C.

Dale VH et al. 2001. Climate change and forest disturbances. BioScience **51**:723–734.

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

Debeljak M. 2006. Coarse woody debris in virgin and managed forest. Ecological Indicators **6**:733–742.

Defries RS, Rudel T, Uriarte M, Hansen M. 2010. Deforestation driven by urban population growth and agricultural trade in the twenty-first century. Nature Geoscience **3**:178–181.

DeMaynadier PG, Hunter, Jr. ML. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology **12**:340–352.

Dodd Jr. CK. 2011. Amphibian ecology and conservation. Oxford University Press, New York, NY.

Drummond M a., Loveland TR. 2010. Land-use pressure and a transition to forest-cover loss in the eastern United States. BioScience **60**:286–298.

Duellman WE, Trueb L. 1994. Biology of amphibians. Johns Hopkins University Press, Baltimore, Maryland.

Dupuis LA, Smith JNM, Bunnell F, Bunnellt F. 1995. Relationship of terrestrial-breeding amphibian abundance to tree-stand age. Conservation Biology **9**:645–653.

Efford MG, Dawson DK. 2012. Occupancy in continuous habitat. Ecosphere **3**:1–15.

Faccio SD. 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. Journal of Herpetology **37**:479–489.

Feder ME. 1983. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica **39**:291–310.

Fiske IJ, Chandler RB. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software **43**:1–23.

Flinn KM, Marks PL. 2007. Agricultural legacies in forest environments: tree communities, soil properties, and light availability. Ecological Applications **17**:452–463.

Flinn KM, Vellend M. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment **3**:243–250.

Ford W, Chapman B, Menzel M, Odom R. 2002a. Stand age and habitat influences on salamanders in Appalachian cove hardwood forests. Forest Ecology and Management **155**:131–141.

Ford WM, Menzel MA, Odom RH. 2002b. Elevation, aspect, and cove size effects on southern Appalachian salamanders. Southeastern Naturalist **1**:315–324.

Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A. 2003. The importance of land-use legacies to ecology and conservation. BioScience **53**:77–88.

Fraterrigo JM, Turner MG, Pearson SM, Dixon PM. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. Ecological Monographs **75**:215–230.

Gallant AL, Klaver RW, Casper GS, Lannoo MJ. 2007. Global rates of habitat loss and implications for amphibian conservation. Copeia **2007**:967–979.

Gibbs JP. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands **13**:25–31.

Gibbs JP. 2000. Wetland loss and biodiversity conservation. Conservation Biology **14**:314–317.

González E, Felipe-Lucia MR, Bourgeois B, Boz B, Nilsson C, Palmer G, Sher AA. 2017. Integrative conservation of riparian zones. Biological Conservation **211**:20–29. Elsevier Ltd.

Grialou JA, West SD, Wilkins RN, The S, Management W, Jan N. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. The Journal of wildlife management **64**:105–113.

Hansen MC et al. 2013. High-resolution global maps of 21st-century forest cover change. Science **342**:850–853.

Harding JS, Benfield EF, Bolstad P V., Helfman GS, Jones EBD. 1998. Stream biodiversity: The ghost of land use past. Proceedings of the National Academy of Sciences **95**:14843–14847.

Harper CA, Guynn DC. 1999. Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains. Forest Ecology and Management **114**:245–252.

Harper EB, Semlitsch RD. 2007. Density dependence in the terrestrial life history stage of two anurans. Oecologia **153**:879–889.

Hicks NG, Pearson SM. 2003. Salamander diversity and abundance in forests with alternative land use histories in the Southern Blue Ridge Mountains. Forest Ecology and Management **177**:117–130.

Hocking DJ, Babbitt KJ, Yamasaki M. 2013. Comparison of silvicultural and natural disturbance effects on terrestrial salamanders in northern hardwood forests. Biological Conservation **167**:194–202. Elsevier Ltd.

Hof C, Araújo MB, Jetz W, Rahbek C. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature **480**:516–519.

Homer C, Dewitz J, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold N, Wickham J, Megown K. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States - representing a decade of land cover change information. Photogrammetric Engineering & Remote Sensing **81**:345–354.

Homyack JA, Haas CA. 2009a. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biological Conservation **142**:110–121.

Homyack JA, Haas CA. 2009b. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biological Conservation **142**:110–121.

Hooker TD, Compton JE. 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. Ecological Applications **13**:299–313.

Hughes JW, Fahey TJ. 1994. Litterfall dynamics and ecosystem recovery during forest development. Forest Ecology and Management **63**:181–198.

Husting EL. 1965. Survival and breeding structure in a population of Ambystoma maculatum. Copeia **1965**:352–362.

IUCN. 2017. The IUCN red list of threatened species: Version 2017-3.

Jackson CR, Martin JK, Leigh DS, West LT. 2005. A southeastern Piedmont watershed sediment budget: evidence for a multi-millennial agricultural legacy. Journal of Soil and Water Conservation **60**:298–310.

Jaeger RG. 1978. Plant climbing by salamanders: periodic availability of plant-dwelling prey. Copeia **1978**:686–691.

Jaeger RG. 1980. Microhabitats of a terrestrial forest salamander. Copeia **1980**:265–268.

Johnston CA. 1994. Cumulative impacts to wetlands. Wetlands **14**:49–55.

Karraker NE, Gibbs JP. 2009. Amphibian production in forested landscapes in relation to wetland hydroperiod: A case study of vernal pools and beaver ponds. Biological Conservation **142**:2293–2302.

Karraker NE, Welsh HH. 2006. Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians in Northwestern California. Biological Conservation **131**:132–140.

Kéry M, Royle JA. 2016. Modeling abundance with counts of unmarked individuals in closed populations. Pages 219–312 Applied hierarchical modeling in ecology. Acadmic Press, Waltham, Massachusetts, USA.

Kleeberger SR, Werner JK. 1982. Home range and homing behavior of Plethodon cinereus in northern Michigan. Copeia **1982**:409–415.

Kuhman TR, Pearson SM, Turner MG. 2011. Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. Canadian Journal of Forest Research **41**:920–929.

MacKenzie DI, Bailey LL. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics **9**:300–318.

Mackenzie DI, Nichols JD, Lachman GB, Droege S, Andrew J, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248–2255.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE. 2017. Occupancy estimation and modeling, second edition: Inferring patterns and dynamics of species occurrence. Academic Press, Cambridge, MA.

Madison DM. 1997. The emigration of padio-implanted spotted salamanders, Ambystoma maculatum. Journal of Herpetology **31**:542–551.

Maerz JC, Madison D. 2000. Environmental variation and territorial behavior in a terrestrial salamander. Pages 395–406 in R. C. Bruce, R. G. Jaeger, and L. D. Houck, editors. The biology of plethodontid salamanders. Springer, Boston, MA.

Maerz JC, Nuzzo VA, Blossey B. 2009. Declines in woodland salamander abundance associated with non-native earthworm and plant invasions. Conservation Biology **23**:975–981.

Mahaney WS, Klemens MW. 2008. Vernal pool conservation policy: the federal, state, and local context. Pages 193–212 in A. J. K. Calhoun and P. G. deMaynadier, editors. Science and conservation of vernal pools in northeastern North America. CRC Press, Boca Raton, FL.

Maloney KO, Feminella JW, Mitchell RM, Miller SA, Mulholland PJ, Houser JN. 2008. Landuse legacies and small streams: identifying relationships between historical land use and contemporary stream conditions. Journal of the North American Benthological Society **27**:280–294.

Marin-Spiotta E, Cusack DF, Ostertag R, Silver WL. 2008. Trends in above and belowground carbon with forest regrowth after agricultural abandonment in the neotropics. Pages 22–72 in R. W. Myster, editor. Post-agricultural succession in the neotropics. Springer-Verlag New York, New York, NY.

Marsh DM, Trenham PC. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology **15**:40–49.

Marshall PL, Davis G, Taylor SW. 2003. Using line intersect sampling for coarse woody debris: practitioners wuestions addressed. Forest Research Extension Note:1–10.

Mazerolle MJ. 2017. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).

McGee GG, Leopold DJ, Nyland RD. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. Ecological Applications **9**:1316–1329.

McKann PC, Gray BR, Thogmartin WE. 2013. Small sample bias in dynamic occupancy models. The Journal of Wildlife Management **77**:172–180.

McKenny HC, Keeton WS, Donovan TM. 2006. Effects of structural complexity enhancement on eastern red-backed salamander (Plethodon cinereus) populations in northern hardwood forests. Forest Ecology and Management **230**:186–196.

McNab WH, Cleland DT, Freeouf JA, J.E. Keys J, Nowacki GJ, Carpenter CA. 2007. Ecological subregions: Sections of the conterminous United States. Page Gen. Tech. Report WO-76B.

Mendelson III J et al. 2006. Confronting amphibian declines and extinctions. Science **313**:48.

Milanovich JR, Peterman WE, Nibbelink NP, Maerz JC. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. PLoS ONE **5**.

Mitchell JC, Pagels JF, Buhlmann KA, Mitchell JC, Rinehart SC, Pagels JF, Buhlmann KA. 1997. Factors influencing amphibian and small mammal assemblages in central Appalachian forests. Forest Ecology and Management **95**:65–76.

Newcomb Homan R, Windmiller BS, Reed JM. 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. Ecological Applications **14**:1547–1553.

NOAA. 2017. NOAA national centers for environmental information, climate at a glance: statewide mapping, precipitation. Available from https://www.ncdc.noaa.gov/temp-and-precip/climatological-rankings.

O’Donnell KM, Thompson FR, Semlitsch RD. 2014. Predicting variation in microhabitat utilization of Terrestrial Salamanders. Herpetologica **70**:259–265.

O’Donnell KM, Thompson FR, Semlitsch RD. 2015. Partitioning detectability components in populations subject to within-season temporary emigration using binomial mixture models. PLoS ONE **10**:1–18.

Olajuyigbe SO, Tobin B, Gardiner P, Nieuwenhuis M. 2011. Stocks and decay dynamics of above- and belowground coarse woody debris in managed sitka spruce forests in ireland.

Forest Ecology and Management **262**:1109–1118.

Otto CR V, Kroll AJ, McKenny HC. 2013. Amphibian response to downed wood retention in managed forests: A prospectus for future biomass harvest in North America. Forest Ecology and Management **304**:275–285. Elsevier B.V.

Perry DA, Oren R, Hart SC. 2008. Forest Ecosystems, 2nd edition. Johns Hopkins University Press, Baltimore, Maryland.

Peterken GF. 1981. Woodland Conservation and Management. Chapman and Hall, London, UK.

Peterman W, Anderson T, Drake DL, Ousterhout BH, Semlitsch RD. 2013. Maximizing pond biodiversity across the landscape: A case study of larval ambystomatid salamanders. Animal Conservation.

Petranka JW. 2007. Evolution of complex life cycles of amphibians: Bridging the gap between metapopulation dynamics and life history evolution. Evolutionary Ecology **21**:751–764.

Petranka JW. 2010. Salamanders of the United States and Canada. Smithsonian Books, Washington, D.C.

Petranka JW, Eldridge ME, Haley KE. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology **7**:363–370.

Petranka JW, Holbrook CT. 2006. Wetland restoration for amphibians: Should local sites be designed to support metapopulations or patchy populations? Restoration Ecology **14**:404–411.

Petranka JW, Murray SS. 2001. Effectiveness of Removal Sampling for Determining Salamander Density and Biomass: A Case Study in an Appalachian Streamside Community.

Journal of Herpetology **35**:36–44.

Piché N, Kelting DL. 2015. Recovery of soil productivity with forest succession on abandoned agricultural land. Restoration Ecology **23**:645–654.

Post WM, Kwon K. 2000. Soil carbon sequestration and land-use change: processes and potential. Global Change Biology **6**:317–327.

Pough HF, Smith EM, Rhodes DH, Collazo A. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management **20**:1–9.

Price SJ, Browne RA, Dorcas ME. 2012. Resistance and Resilience of A Stream Salamander To Supraseasonal Drought. Herpetologica **68**:312–323.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasband W. 2017. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA://imagej.nih.gov/ij/.

Regosin J V., Windmiller BS, Reed JM. 2003. Influence of abundance of small-mammal burrows and conspecifics of the density and distribution of spotted salamanders (Ambystoma maculatum) in terrestrial habitats. Canadian Journal of Zoology **81**:596.

Regosin J V, Windmiller BS, Homan RN, Reed JM. 2005. Variation in terrestrial habitat use by four pool-breeding amphibian species. Journal of Wildlife Management **69**:1481–1493.

Rhemtulla JM, Mladenoff DJ, Clayton MK. 2007. Regional land-cover conversion in the U.S. upper Midwest: magnitude of change and limited recovery (1850 – 1935 – 1993). Landscape Ecology:57–75.

Rittenhouse T, Semlitsch R. 2007a. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands **27**:153–161.

Rittenhouse T, Semlitsch RD. 2007b. Postbreeding Habitat Use of Wood Frogs in a Missouri Oak-hickory Forest. Journal of Herpetology **41**:645–653.

Rothermel BB, Luhring TM. 2005. Burrow Availability and Desiccation Risk of Mole Salamanders (Ambystoma talpoideum) in Harvested versus Unharvested Forest Stands. Journal of Herpetology **39**:619–626.

Royle JA. 2004. N-Mixture Models for Estimating Population Size from Spatially Peplicated Counts. Biometrics **60**:108–115.

Royston JP. 1982. An Extension of Shapiro and Wilk 's W Test for Normality to Large Samples. Applied Statistics **31**:115–124.

Schmidt BR, Feldmann R, Schaub M. 2005. Demographic processes underlying population growth and decline in Salamandra salamandra. Conservation Biology **19**:1149–1156.

Semlitsch R. 2002. Critical Elements for Biologically Based Recovery Plans of Aquatic Breeding Amphibians. Conservation Biology **16**:619–629.

Semlitsch RD. 1998. Biological Delineation of Terrestrial Buffer Zones for Pond-Breeding Salamanders. Conservation Biology **12**:1113–1119.

Semlitsch RD, Bodie JR. 1998. Are small, isolated wetlands exendable. Conservation Biology **12**:1129–1133.

Semlitsch RD, Bodie JR. 2003. Biological Criteria for Buffer Zones around Wetlands and Riparian Habitats for Amphibians and Reptiles. Conservation Biology **17**:1219–1228.

Semlitsch RD, Jensen JB. 2001. Core habitat, not buffer zone. National Wetlands **23**:4–6.

Semlitsch RD, Ryan TJ, Hamed K, Chatfield M, Drehman B, Pekarek N, Spath M, Watland A. 2007. Salamander abundance along road edges and within abandoned logging roads in Appalachian Forests. Conservation Biology **21**:159–167.

Semlitsch RD, Skelly DK. 2008. Ecology and conservation of pool-breeding amphibians. Pages 127–148 in A. J. K. Calhoun and P. G. deMaynadier, editors. Science and conservation of vernal pools in northeastern North America. CRC Press, Boca Raton, FL.

Skelly DK, Halverson MA, Freidenburg LK, Urban MC. 2005. Canopy closure and amphibian diversity in forested wetlands. Wetlands Ecology and Management **13**:261–268.

Smith EM, Pough F. 1994. Intergeneric aggression among salamanders. Journal of Herpetology **28**:41–45.

Smith MA, Green DM. 2005. Dispersal and the metapopulation in amphibian and paradigm ecology are all amphibian conservation: populations metapopulations ? Ecography **28**:110–128.

Smith R, Meredith H, Sutherland W. 2017. Amphibian Conservation. Pages 9–67 in W. Sutherland, L. Dicks, N. Ockendon, and R. Smith, editors. What Works in Conservation 2017. Open Book Publishers, Cambridge, UK.

Sollins P. 1982a. Input and decay of course woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research **12**:18–28.

Sollins P. 1982b. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research **53**:1689–1699.

Stuart SN, Chanson JS, Cox N a, Young BE, Rodrigues ASL, Fischman DL, Waller RW. 2004a. Status and trends of amphibian declines and extinctions worldwide. Science (New York, N.Y.) **306**:1783–1786.

Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues AS, Fischman DL, Waller RW. 2004b. Status and Trends of Amphibian Declines and Extinctions Worldwide. Science **306**:1783–1786.

Surasinghe T, Baldwin RF. 2014. Ghost of land-use past in the context of current land cover: evidence from salamander communities in streams of Blue Ridge and Piedmont ecoregions. Canadian Journal of Zoology **92**:527–536.

Sweet SK, Wolfe DW, DeGaetano A, Benner R. 2017. Anatomy of the 2016 drought in the Northeastern United States: Implications for agriculture and water resources in humid climates. Agricultural and Forest Meteorology **247**:571–581. Elsevier.

Szlávecz K, Csuzdi C. 2007. Land use change affects earthworm communities in Eastern Maryland, USA. European Journal of Soil Biology **43**:S79–S85.

Thompson JR, Carpenter DN, Cogbill C V., Foster DR. 2013. Four Centuries of Change in Northeastern United States Forests. PLoS ONE **8**:1–15.

Thompson ME, Donnelly MA. 2018. Effects of Secondary Forest Succession on Amphibians and Reptiles: A Review and Meta-analysis. Copeia **106**:10–19.

Tilghman JM, Ramee SW, Marsh DM. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biological Conservation **152**:1–9. Elsevier Ltd.

Vellend M. 2004. Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. Ecology **85**:3043–3055.

Venables WN, Ribley BD. 2002. Modern Applied Statistics with SFourth Edi. Springer, New York, NY.

Vonesh JR, De la Cruz O. 2002. Complex life cycles and density dependence: Assessing the contribution of egg mortality to amphibian declines. Oecologia **133**:325–333.

Waldick RC, Freedman B, Wassersug RJ. 1999. The consequences for amphibians of the conversion of natural, mixed-species forests to conifer plantations in southern New Brunswick. Canadian Field-Naturalist **113**:408–418.

Welsh H, Droege S. 2001. A case for Using Plethodontid Salamanders for Using Ecosystem Integrity Monitoring Biodiversity and Ecosystem Integrity of North American Forests. Conservation Biology **15**:558–569.

Welsh HH, Pope KL, Wheeler CA. 2008. Using multiple metrics to assess the effects of forest succession on population status: A comparative study of two terrestrial salamanders in the US Pacific Northwest. Biological Conservation **141**:1149–1160.

Whitford WG, Vinegar A. 1966. Homing, Survivorship, and Overwintering of Larvae in Spotted Salamanders, Ambystoma maculatum. Copeia:515–519.

Whitlock C, Colombaroli D, Conedera M, Tinner W. 2018. Land-use history as a guide for forest conservation and management. Conservation Biology **32**:84–97.

Whitney GG. 1996. From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America 1500 the the Present. Page Cambridge University

Press. Cambridge University Press, Cambridge.

Windmiller B, Calhoun AJK. 2008. Conserving vernal pool wildlife in urbanizing landscapes. Pages 233–252 in A. J. K. Calhoun and P. G. DeMaynadier, editors. Science and conservation of vernal pools in northeastern North America. CRC Press, Boca Raton, FL.

Wyman RL. 1998. Experimental assessment of salamanders as predators of detrital food webs: Effects on invertebrates, decomposition and the carbon cycle. Biodiversity and Conservation **7**:641–650.

APPENDICES

Appendix 1.1. Full detection model AIC$_c$ rankings for wood frogs.

Model	*K*	*AIC$_c$*	*ΔAIC$_c$*	*w_i*	*Cum. wt.*	*Deviance*
rain24 + year	8	130.53	0.00	0.25	0.25	111.59
litter * rain + year	10	130.79	0.26	0.22	0.47	106.11
litter + rain24 + year	9	132.91	2.38	0.08	0.54	111.16
und + rain24 + year	9	133.10	2.57	0.07	0.61	111.35
obs + rain24 + year	9	133.30	2.77	0.06	0.67	111.55
null	2	134.26	3.73	0.04	0.71	130.04
temp + year	8	134.87	4.34	0.03	0.74	115.93
litter * rain24 + year	10	134.94	4.41	0.03	0.77	110.26
rain + year	8	135.07	4.54	0.03	0.79	116.13
und * rain24 + year	10	135.37	4.84	0.02	0.81	110.69
year	4	135.59	5.06	0.02	0.83	126.84
temp + temp^2 + year	9	135.64	5.11	0.02	0.85	113.89
litter + year	8	136.19	5.66	0.01	0.87	117.25
date + year	8	136.37	5.84	0.01	0.88	117.43
und + year	8	136.42	5.89	0.01	0.89	117.48
litter + temp + year	9	136.67	6.14	0.01	0.91	114.92
litter + rain + year	9	136.84	6.31	0.01	0.92	115.09
obs + year	8	136.92	6.39	0.01	0.93	117.99
und + temp + year	9	136.99	6.46	0.01	0.94	115.24
date + date^2 + year	9	137.16	6.63	0.01	0.95	115.41
litter + litter^2 + year	9	137.56	7.03	0.01	0.95	115.81
obs + temp + year	9	137.67	7.14	0.01	0.96	115.92
und + rain + year	9	137.71	7.18	0.01	0.97	115.96
obs + rain + year	9	137.88	7.35	0.01	0.97	116.13
litter + und + year	9	138.69	8.16	0.00	0.98	116.94
litter + obs + year	9	138.93	8.40	0.00	0.98	117.18
litter * temp + year	10	138.98	8.45	0.00	0.98	114.30
obs + date + year	9	139.18	8.65	0.00	0.99	117.43
und + obs + year	9	139.23	8.70	0.00	0.99	117.48
und + und^2 + year	9	139.23	8.70	0.00	0.99	117.48
und * rain + year	10	139.55	9.02	0.00	1.00	114.87
und * temp + year	10	139.72	9.19	0.00	1.00	115.04
und * obs + year	10	142.10	11.57	0.00	1.00	117.42
global	13	147.04	16.51	0.00	1.00	112.76

Appendix 1.2. Full detection model AICc rankings for spotted salamanders.

Model	*K*	AIC_c	ΔAIC_c	w_i	*Cum. wt.*	*Deviance*
litter + year	8	131.66	0.00	0.11	0.11	112.72
litter + rain + year	9	131.71	0.06	0.11	0.23	109.96
rain + year	8	132.17	0.51	0.09	0.31	113.23
litter * rain + year	10	132.71	1.05	0.07	0.38	108.03
date + year	8	132.90	1.24	0.06	0.44	113.96
litter + date + year	9	133.15	1.49	0.05	0.50	111.40
date + date^2 + year	9	133.66	2.00	0.04	0.54	111.91
effort + year	8	133.73	2.07	0.04	0.58	114.79
temp + year	8	134.10	2.45	0.03	0.61	115.17
rain24 + year	8	134.11	2.45	0.03	0.65	115.17
obs + year	8	134.14	2.48	0.03	0.68	115.20
null	2	134.21	2.55	0.03	0.71	129.99
litter +effort + year	9	134.21	2.55	0.03	0.75	112.46
litter + rain24 + year	9	134.39	2.73	0.03	0.77	112.64
litter + litter^2 + year	9	134.42	2.77	0.03	0.80	112.67
litter + temp + year	9	134.47	2.81	0.03	0.83	112.72
effort + rain	9	134.56	2.90	0.03	0.86	112.81
obs + rain + year	9	134.82	3.17	0.02	0.88	113.07
obs + date + year	9	135.65	3.99	0.02	0.90	113.90
litter * date + year	10	135.98	4.32	0.01	0.91	111.30
effort + obs + year	9	136.36	4.70	0.01	0.92	114.61
effort + rain24 + year	9	136.53	4.87	0.01	0.93	114.78
temp + temp^2 + year	9	136.89	5.24	0.01	0.94	115.14
obs + temp + year	9	136.90	5.24	0.01	0.95	115.15
obs + rain24 + year	9	136.90	5.24	0.01	0.96	115.15
litter * effort + year	10	136.93	5.27	0.01	0.96	112.25
year	4	137.11	5.45	0.01	0.97	128.36
litter * temp + year	10	137.19	5.53	0.01	0.98	112.51
litter * rain24 + year	10	137.21	5.55	0.01	0.99	112.53
effort * rain + year	10	137.24	5.58	0.01	0.99	112.56
effort * rain24 + year	10	137.55	5.89	0.01	1.00	112.87
global	13	143.33	11.67	0.00	1.00	109.05
litter + year	8	131.66	0.00	0.11	0.11	112.72
litter + rain + year	9	131.71	0.06	0.11	0.23	109.96
rain + year	8	132.17	0.51	0.09	0.31	113.23
litter * rain + year	10	132.71	1.05	0.07	0.38	108.03
date + year	8	132.90	1.24	0.06	0.44	113.96
litter + date + year	9	133.15	1.49	0.05	0.50	111.40
date + date^2 + year	9	133.66	2.00	0.04	0.54	111.91
effort + year	8	133.73	2.07	0.04	0.58	114.79

Appendix 1.3. Full occupancy model AIC_c rankings for wood frogs.

Model	*K*	*AIC_c*	*ΔAIC_c*	*w_i*	*Cum. wt.*	*Deviance*
pools + year	8	125.134	0.000	0.494	0.494	106.200
pools * year	9	127.280	2.146	0.169	0.663	105.530
upland + pools + year	9	127.886	2.751	0.125	0.788	106.140
upland * year + pools * year	11	129.150	4.016	0.066	0.854	101.410
upland + pools * year	10	130.084	4.949	0.042	0.895	105.400
upland * year + pools	10	130.320	5.185	0.037	0.932	105.640
upland * pools + year	10	130.790	5.656	0.029	0.962	106.110
detection	7	132.794	7.660	0.011	0.972	116.550
upland * pools + pools * year	11	133.070	7.936	0.009	0.982	105.330
upland * pools + upland * year	11	133.322	8.188	0.008	0.990	105.580
null	2	134.257	9.123	0.005	0.995	130.040
upland + year	8	134.911	9.777	0.004	0.999	115.970
upland * year	9	137.172	12.038	0.001	1.000	115.420

Appendix 1.4. Full occupancy model AIC$_c$ rankings for spotted salamanders.

Model	*K*	*AIC$_c$*	*ΔAIC$_c$*	*w_i*	*Cum. wt.*	*Deviance*
upland * pools + pools * year	10	129.579	0.000	0.560	0.560	104.900
upland * pools + year	9	131.714	2.135	0.193	0.752	109.960
null	2	134.211	4.632	0.055	0.808	129.990
upland * pools + upland * year	10	134.262	4.683	0.054	0.861	109.580
upland + year	7	134.420	4.841	0.050	0.911	118.180
detection	6	135.749	6.170	0.026	0.937	122.100
pools * year	8	136.402	6.823	0.018	0.955	117.460
upland + pools + year	8	136.562	6.982	0.017	0.972	117.620
upland * year	8	136.732	7.153	0.016	0.988	117.790
pools + year	7	138.303	8.724	0.007	0.995	122.060
upland * year + pools	9	139.084	9.505	0.005	1.000	117.330

Appendix 2.1. Full detection model AIC$_c$ rankings for red-backed salamanders.

Model	*K*	*AIC$_c$*	*ΔAIC$_c$*	*w_i*	*Cum. wt.*	*Deviance*
effort + date + year	12	1021.66	0.00	1.00	1.00	991.03
effort + obs + year	12	1042.29	20.63	0.00	1.00	1011.66
effort * rain + year	14	1046.37	24.71	0.00	1.00	1009.04
effort + year	11	1048.81	27.15	0.00	1.00	1021.31
effort + rain + year	12	1049.46	27.80	0.00	1.00	1018.82
litter * effort + year	14	1049.51	27.85	0.00	1.00	1012.18
litter + effort + year	11	1049.93	28.27	0.00	1.00	1022.43
effort + TSR + year	12	1051.10	29.44	0.00	1.00	1020.47
effort + rain24 + year	12	1051.93	30.26	0.00	1.00	1021.29
litter + effort + TSR + year	12	1052.17	30.51	0.00	1.00	1021.53
effort * TSR + year	14	1056.91	35.24	0.00	1.00	1019.57
effort * rain24 + year	14	1058.29	36.62	0.00	1.00	1020.95
date + date^2 + year	11	1076.19	54.53	0.00	1.00	1048.69
date + year	10	1086.17	64.51	0.00	1.00	1061.68
obs + date + year	11	1088.97	67.31	0.00	1.00	1061.47
temp + year	10	1117.98	96.32	0.00	1.00	1093.49
litter * temp + year	12	1119.76	98.10	0.00	1.00	1089.12
litter + temp + year	11	1120.23	98.57	0.00	1.00	1092.73
temp + temp^2 + year	11	1120.31	98.65	0.00	1.00	1092.81
temp + rain + year	11	1120.42	98.75	0.00	1.00	1092.92
obs + temp + year	11	1120.98	99.31	0.00	1.00	1093.48
litter * rain24 + year	12	1130.01	108.35	0.00	1.00	1099.38
TSR + year	10	1131.63	109.97	0.00	1.00	1107.14
TSR + TSR^2 + year	11	1132.26	110.60	0.00	1.00	1104.76
litter + TSR + year	11	1134.12	112.46	0.00	1.00	1106.62
rain + year	10	1134.30	112.64	0.00	1.00	1109.81
obs + TSR + year	11	1134.64	112.98	0.00	1.00	1107.14
rain24 + year	10	1134.89	113.22	0.00	1.00	1110.40
litter + year	10	1135.90	114.23	0.00	1.00	1111.41
obs + year	10	1136.17	114.51	0.00	1.00	1111.69
litter + litter^2 + year	11	1136.85	115.19	0.00	1.00	1109.35
litter + rain + year	11	1136.86	115.20	0.00	1.00	1109.36
litter * TSR + year	12	1136.91	115.24	0.00	1.00	1106.27
obs + rain + year	11	1137.13	115.47	0.00	1.00	1109.63
litter + rain24 + year	11	1137.29	115.63	0.00	1.00	1109.79
obs + rain24 + year	11	1137.82	116.16	0.00	1.00	1110.32
litter * rain + year	12	1139.73	118.07	0.00	1.00	1109.10
year	4	1351.01	329.35	0.00	1.00	1342.29
null	2	1438.02	416.35	0.00	1.00	1433.81

Appendix 2.2. Full abundance model AIC_c rankings for red-backed salamanders.

Model	*K*	AIC_C	ΔAIC_C	w_i	*Cum. wt.*	*Deviance*
und + objects + year	11	636.94	0	0.66	0.66	609.44
und * objects + year	12	639.11	2.17	0.22	0.89	608.47
objects + year	10	641.11	4.17	0.08	0.97	616.62
litter + objects + year	11	643.69	6.75	0.02	0.99	616.19
global	14	646.10	9.16	0.01	1.00	608.77
litter + lowdecay + highdecay + objects + year	13	648.53	11.59	0.00	1.00	614.62
und + year	10	657.07	20.12	0.00	1.00	632.58
und + highdecay + year	11	659.31	22.37	0.00	1.00	631.81
und + cwdarea + year	11	659.88	22.94	0.00	1.00	632.38
und + litter + year	11	659.96	23.02	0.00	1.00	632.46
und + und^2 + year	11	660.07	23.13	0.00	1.00	632.57
detection + year	8	660.38	23.44	0.00	1.00	641.56
und * cwdarea + year	12	660.41	23.47	0.00	1.00	629.77
und * litter + year	12	662.15	25.21	0.00	1.00	631.51
und * highdecay + year	12	662.28	25.34	0.00	1.00	631.64
litter + year	10	665.70	28.76	0.00	1.00	641.21
cwdvol + year	10	665.88	28.93	0.00	1.00	641.39
cwdarea + year	10	666.01	29.06	0.00	1.00	641.52
highdecay + year	10	666.03	29.09	0.00	1.00	641.54
litter + highdecay + year	11	668.60	31.65	0.00	1.00	641.10
litter + cwdvol + year	11	668.69	31.75	0.00	1.00	641.19
litter + cwdarea + year	11	668.71	31.77	0.00	1.00	641.21
lowdecay + highdecay + year	11	668.88	31.94	0.00	1.00	641.38
litter + lowdecay + highdecay + year	12	671.65	34.71	0.00	1.00	641.01
null	4	738.63	101.68	0.00	1.00	729.90

Appendix 2.3. Full abundance model AIC_c rankings for dusky salamanders.

Model[a]	*K*	*AIC_C*	*ΔAIC_C*	*w_i*	*Cum. wt.*	*Deviance*
litter + objects	10	681.70	0.00	0.60	0.60	660.11
litter + cwdarea + objects	11	683.77	2.07	0.21	0.81	659.86
global	13	684.89	3.19	0.12	0.93	656.21
objects	8	687.03	5.33	0.04	0.97	670.01
und + objects	9	687.75	6.05	0.03	1.00	668.46
und + litter	10	694.78	13.08	0.00	1.00	673.20
litter + cwdvol	10	696.21	14.52	0.00	1.00	674.63
litter + $litter^2$	9	696.83	15.13	0.00	1.00	677.54
litter + cwdarea	10	698.80	17.10	0.00	1.00	677.21
litter + lowdecay + highdecay	11	699.18	17.48	0.00	1.00	675.27
litter + highdecay	9	699.82	18.12	0.00	1.00	680.54
cwdvol	8	702.21	20.51	0.00	1.00	685.18
highdecay	8	704.52	22.82	0.00	1.00	687.50
streams	7	705.14	23.44	0.00	1.00	690.35
und	8	705.22	23.53	0.00	1.00	688.20
und + highdecay	9	705.61	23.92	0.00	1.00	686.33
lowdecay + highdecay	9	706.34	24.64	0.00	1.00	687.05
cwdarea	8	706.77	25.07	0.00	1.00	689.75
und + und^2	9	706.93	25.23	0.00	1.00	687.64
und + cwdarea	9	707.27	25.57	0.00	1.00	687.98
survey + year + TSR	6	733.29	51.60	0.00	1.00	720.71
null	2	753.88	72.18	0.00	1.00	749.80

[a] all models (except for the null) contain a time-since-rain (TSR) variable and categorical variables for survey occasion and sampling year.

VITA

Name: Harrison Balopole Goldspiel

Date and Place of Birth: February 24, 1991, Mineola, New York, USA

Education:

	Name and Location	Dates	Degree
High School:	Benjamin N. Cardozo H.S., Bayside, NY	2005-2009	Diploma
College:	Brandeis University Waltham, MA	2009-2013	B.A.
Graduate School:	State University of New York College of Environmental Science and Forestry Syracuse, NY	2016-2018	M.S.

Employment:

Employer	Dates	Title
SUNY-ESF Syracuse, NY	Jan. 2016 – May 2018	Teaching/Research Assistant
Sierra Streams Institute Nevada City, CA	October 2014 – October 2015	AmeriCorps River Scientist
Archbold Biological Station Venus, FL	March 2014 – Sept. 2014	Herpetology Research Intern
Brandeis University Waltham, MA	Jan 2013 – May 2013	Research Intern
NYLCV New York, NY	May 2010 – Aug 2010	Environmental Politics Intern