

The Importance of Habitat Heterogeneity in Understanding the Effect of Forest
Management Practices on Salamanders.

Thesis

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Abstract

It is important to determine how forest management practices affect non-target species such as salamanders. Analyses commonly done at treatment or stand level suggest that salamander abundances decline after disturbance. However, salamanders have small home ranges on the scale of within-treatment habitat heterogeneity that is created by background conditions and silvicultural treatments. A finer scale within-treatment assessment of salamander responses is needed to determine how salamander species associate with the available range of habitats. Oak management regimes utilize prescribed fire, which affects forest stands unevenly due to differences in fire intensity. Salamander community data was collected from 2013-2014 in the unglaciated Appalachian plateau of Ohio three years after a series of treatments designed to mimic natural heterogeneous disturbance. The treatment consisted of thinning in 2000 followed by prescribed fires in 2001, 2005, 2010. Discriminant function analyses showed that sites did not group by treatment or replicate, and redundancy analysis showed that different salamander species associated with the range of microhabitats along a habitat gradient. Occupancy analyses were used to examine habitat relationships of the two most abundant species that represent two different life-history guilds. The common upland breeder, *Plethodon cinereus* (eastern red-backed salamander), associated with mesic habitats. In contrast, *Ambystoma opacum* (marbled salamander), a pool-breeding species, associated with increased oak composition in the overstory. Therefore, silvicultural management

designed to regenerate oaks creates habitat heterogeneity that supports salamander species diversity. One species or group is not sufficient as an indicator representing all salamanders as silviculture may differentially impact species with different habitat associations. This study showed that salamander biodiversity is maintained in oak forests managed with disturbance where heterogeneity provides habitat for a range of species.

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Fields of Study

Major Field: Environment and Natural Resources

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Chapter 1: Introduction

Worldwide declines in amphibian populations have led to increased concern about their ability to persist and fulfill their ecological roles in a rapidly changing environment (Stebbins and Cohen 1995). Though seldom seen, salamanders constitute a numerically and biologically large part of the forest fauna where they regulate invertebrate communities (Davic and Welsh 2004). Salamanders contribute to soil dynamics and carbon-nitrogen cycles by burrowing and moving nutrients through the soil column. They also serve to move nutrients from rich aquatic to nearby terrestrial habitats (Davic and Welsh 2004). Because of their ecological importance, salamanders are excellent indicators of ecological integrity for both forest and aquatic ecosystems (Welsh and Droege 2001, Micacchion 2002). Species diversity can be used to infer site quality, as species with narrow tolerances or habitat requirements are likely to inhabit primarily high quality sites. The abundance of dominant species provides a measure of the ecosystem function of the guild, and decline of abundant species has implications for the entire ecosystem (Davic and Welsh 2004).

A diverse salamander community inhabits the Appalachian region of Ohio, which has historically been dominated by oak forests (Hutchinson et al. 2008, Pfungsten et al. 2013). Oak ecosystems are important for many species, from birds and small mammals to white-tailed deer, *Odocoileus virginianus*, and black bears, *Ursus americanus* (McShea and Healy 2002, Dey et al. 2010). Acorns provide food for many of these species. Birds

are found to be more abundant and diverse in oak ecosystems, most likely as a result of increased arthropod prey, mast, and superior habitat structure (Rodewald and Abrams 2002). No relationship is known between amphibians and oak ecosystems. However, mesocosm studies suggest that amphibian larvae benefit from oak litter inputs in seasonal pools (Rubbo and Kiesecker 2004). Oak litter decays slowly, providing increased cover for forest floor denizens and their invertebrate prey (Fox et al. 2010). This may benefit salamanders through increased prey availability, higher and more stable moisture levels, or increased cover.

Loss of fire as a periodic disturbance has contributed to the “mesophication” of forests in eastern US hardwood stands, whereby shade intolerant fire-adapted species, such as oaks and hickories are replaced by shade tolerant species (Nowacki and Abrams 2008). Forest managers have begun to experiment with silvicultural treatments such as thinning and prescribed fire to create more biologically and economically productive forests. Prescribed fire has been effective in promoting oak regeneration in some but not all situations. The largest effects are seen if burns occur after a reduction in canopy or during the growing season (Brose et al. 2013). Oaks and hickories have higher potential recruitment after gap creation if the stand previously experienced multiple burns (Hutchinson et al. 2012). In the Appalachian region of Ohio, large competitive oak regeneration was shown to develop primarily on drier ridge-tops and south-facing slopes where prescribed fires burned more intensely, decreasing stand density and increasing canopy openness (Iverson et al. 2008). In mesic areas, fires are typically low intensity and have much less impact on stand structure. Thus fire may create greater habitat heterogeneity within the site.

The effect of low intensity disturbances and fire on salamanders is not well known, especially over long time-scales. Clear-cut harvesting has been shown to have mostly strong negative impacts on salamander populations with recovery projected after approximately 60 years (Petranka et al. 1993, Demaynadier and Hunter 1995). A meta-analysis by Tilghman et al. (2012) suggests that partial cuts result in a reduction in salamander population size, but the population soon begins a slow recovery process. Homyack and Haas (2009) found that treatments with the most canopy disturbance resulted in the largest reductions in salamanders. Corresponding population demography indicates that life-history mechanisms and habitat changes may reduce salamander populations. Microclimates with increased temperature can increase salamander metabolic rates and therefore energy requirements (Homyack et al. 2011). Changes in energetics may cause salamanders to reduce activity and remain in refugia or have lower reproductive output (Homyack et al. 2011). Forest management that incorporates prescribed fire intuitively seems detrimental to an animal with a moist permeable skin; however, the fossorial habitats of salamanders may mean that changes in habitat caused by burning have more substantial effects than the actual fire (Russell et al. 1999).

Little is known about the mechanisms by which salamander populations are reduced after disturbance. Stand-level trends can be understood by examining smaller scale trends that most likely drive changes in salamander abundances. A number of environmental conditions and microhabitat features are known to be important to a wide range of salamander species. Reduced canopy cover has been suggested as a factor in salamander declines in managed forests (Matthews et al. 2010, Tilghman et al. 2012, Peterman and Semlitsch 2013). Canopy cover reduces forest floor temperature, raises

humidity, and tempers fluctuations in both (Heatwole 1962, Chen et al. 1999). These physical conditions have been shown to be important to many species both in the lab and field (Heatwole 1962, Marangio and Anderson 1977, Wyman 1988, Demaynadier and Hunter 1995). Structural cover such as coarse woody debris, leaf litter, and rocks are important to salamanders because most species use refugia extensively (Demaynadier and Hunter 1995, Petranka 1998, Moseley et al. 2003, McKenny et al. 2006, Maerz et al. 2009). Cover objects help salamanders regulate temperature and humidity and provide a place to forage (Jaeger 1980, Homyack et al. 2011). Understory vegetation may be important for foraging (Jaeger 1978) and could provide similar environmental benefits as canopy cover (Homyack et al. 2011). Some species may be more sensitive to changes in particular habitat and environmental conditions than others. Therefore, silvicultural treatments that create within-treatment habitat changes are expected to affect salamander community composition.

Objectives—When evaluating management efforts to sustain oak forests, it is important that we consider how land use decisions affect non-target species. Variably-adapted salamander communities are an important part of the forest floor ecosystem. My objective was to determine if silvicultural treatments (thinning followed by prescribed fire) result in increased habitat heterogeneity and document habitat utilization by the broader salamander community. The most frequently captured species, *Ambystoma opacum* and *Plethodon cinereus*, occurred in the area with consistency and were identified a priori to elucidate how the two major life-history groups associate with available habitat. These results will allow us to better understand which aspects of habitat are most important to the maintenance of a diverse salamander community.

Methods— This study was conducted on experimental units designed and managed by the USDA Forest Service for the Ohio Hills site of the National Fire and Fire Surrogate Study (Albrecht and McCarthy 2006). The sites are in Vinton County, Ohio, part of the unglaciated Appalachian plateau. Control and treatment units at Vinton Furnace Experimental Forest and Zaleski State Forest are 20-25 ha each. The treatment sequence was a mid-story thinning during the winter of 2000-2001, followed by prescribed burns in April 2001, 2005, and 2010, prior to leaf-out (Chiang et al. 2008). Oaks make up a larger percentage of trees on sites with low integrated moisture index, a metric developed to capture inherent moisture regimes on these sites (Iverson et al. 1997). Salamanders were captured at each site from March through May of 2013 and 2014 using pitfall arrays. Habitat data was collected at each site to measure canopy openness, volume of coarse woody debris, sapling density, understory stem density, leaf litter depth, and percent of oaks in the overstory (Table A.1). These habitat metrics were derived from data that is commonly collected in studies of forest structure and composition and would be available to forest managers when considering or evaluating silvicultural treatments.

Analyses examined associations between salamander species and within-treatment habitat. A multivariate ordination was used to determine how all salamander species align with gradients of the habitat metrics. This was followed by a more focused examination of the two most abundant species that represent the two major life-history guilds. Predicted abundances of these two species were modeled using a set of N-mixture, occupancy models (Royle 2004). Occupancy models can better approximate habitat relationships by accounting for varying detection probability in unmarked

populations (MacKenzie et al. 2006), and are especially appropriate for salamanders, which exhibit low recapture rates (Bailey et al. 2004). Weather covariates were used to model detection, while habitat covariates, nested within replicate, were used to model predicted abundance. Small sample Akaike information criterion was used to select the model in the candidate set with the most support (MacKenzie et al. 2006).

Limitations— Only two replicates within the same region limit inference to other locations. Passive pitfall arrays, used to assess salamanders, are not biased by observer, availability of cover objects, type of cover objects, or observer expectations (Tilghman et al. 2012). However, bias toward individuals who are moving could obscure differences if larger home ranges were adopted in poor habitats. The power to detect differences in occupancy between sites with different habitat features may be limited by the small number of sites available for comparison. There were 16 within-treatment sites in 2013 and 20 sites in 2014.

Rationale and Significance— Knowledge of the upland habitat requirements and life history of *Ambystoma opacum* and most other pool breeding species is limited. This study contributes to basic understanding of habitat associations for this species. Biphasic species are rarely included in studies of silviculture impacts on salamanders (but see Semlitsch et al. 2009). Inclusion of *A. opacum* as a representative of pool-breeding species increases understanding of forest management on a broader diversity of species.

Maintenance of oak-hickory forest ecosystems is important for a number of wildlife species (McShea and Healy 2002). It is valuable to know how salamanders, as key components of the forest floor ecosystem, respond to changes in forest composition and structure that result from oak forest management activities. Since this study occurred

twelve years after the thin and three years after the most recent burn, the results will depict associations that were caused by changes in habitat rather than direct treatment effects (Demaynadier and Hunter 1995). Direct treatment effects and effects of increased energy requirements due to unfavorable microclimates will influence longer-term results primarily via demography (Homyack et al. 2011). Most studies that examine the effect of forest management practices on wildlife focus only on the scale of the treatment, but salamanders likely respond to finer-scale heterogeneity within treatments (Demaynadier and Hunter 1995). An understanding of how salamanders utilize habitats at an appropriate resolution allows us to make predictions about future environmental challenges. By looking at variability across the sites, we gain some understanding of how elements of the treatment affect persistence of salamander populations. This knowledge can assist in a more holistic evaluation of silvicultural practices designed to maintain oak ecosystems.

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Chapter 2: Characterizing salamander species composition in managed forests:
the role of within treatment habitat gradients.

Introduction

Salamanders are excellent indicators of ecological integrity for both forest and aquatic ecosystems because they are important ecologically (Welsh and Droege 2001, Micacchion 2002, Davic and Welsh 2004). Salamanders occupy a mid-trophic level, are long-lived, involved in nutrient cycling, sensitive to pH, moisture, and temperature, and share a microclimate niche with many other small hydrophilic forest organisms. Plethodontid salamanders often occur in high densities, reach peak abundances in mature forests, do not require aquatic environments, and have a low coefficient of variation in captures compared to other groups that might be used as indicators (Welsh and Droege 2001). Therefore, salamanders in general and plethodontids in particular are often adopted as indicators of the effect of forest management practices on non-target species (Demaynadier and Hunter 1995).

Forests dominated by oaks are important ecosystems for many species of wildlife (McShea and Healy 2002, Dey et al. 2010) and may also be important for salamanders (Rubbo and Kiesecker 2004). Oak ecosystems are becoming less dominant on the landscape as fire regimes have been altered and fire-adapted species, such as oaks and hickories are replaced by shade-tolerant species (Nowacki and Abrams 2008). Forest managers have begun to experiment with silvicultural treatments such as thinning and

prescribed fire to regenerate oak ecosystems (Hutchinson et al. 2012, Brose et al. 2013). In the Appalachian region of Ohio, oak regeneration was shown to be improved on drier ridges and southwest-facing slopes where prescribed burns were more intense and greater canopy openness was created (Iverson et al. 2008). Fires typically have less impact on mesic areas where fire intensity is lower. These differences in fire intensity across the landscape may create greater habitat heterogeneity within the site.

The effects of various silvicultural management practices on salamanders have been examined at the stand level but little has been done to identify within-treatment habitat changes that result in stand-level population changes (but see McKenny et al. 2006). Clear-cut harvesting has been shown to have strong negative impacts on salamander populations, but other treatments have had mixed effects (Demaynadier and Hunter 1995). A meta-analysis by Tilghman et al. (2012) suggests that partial cuts result in a reduction in salamander population size, which begins the slow process of recovery almost immediately. Without disturbance, forest ecosystems will continue to change and become more homogeneous. It is likely that any disturbance will have a negative effect on salamanders in the short-term. However, long-term changes in microhabitat characteristics could support a broader range of habitats allowing for the maintenance of salamander biodiversity.

Salamander species within the Appalachian region of Ohio employ a wide range of life history strategies (Table 2). For example, migratory species move to vernal pools to breed in synchrony, while those that breed in the uplands remain in small home ranges year-round. Upland breeding species, such as Plethodontids, lack the true larval stage that characterizes biphasic pool and stream breeding species like Ambistomatids (Petranka

1998). This mix of life history strategies undoubtedly leads to unique habitat associations across species. Environmental conditions and habitat structure are known to be important to a wide range of salamander species. Salamanders have been shown to tolerate fairly narrow ranges of temperature and humidity in both lab and field studies (Heatwole 1962, Marangio and Anderson 1977, Wyman 1988). Fluctuations in these conditions are mediated by structural habitat such as coarse woody debris, leaf litter, understory vegetation, and canopy cover (Jaeger 1978, Jaeger 1980, Chen et al. 1999, Homyack et al. 2011). Some species may be more sensitive to changes in particular habitats and environmental conditions than others. Therefore, silvicultural treatments that are expected to create within-treatment habitat changes may affect salamander community composition.

When evaluating management efforts to enhance oak communities, it is important that we consider how land use decisions may differentially influence diverse salamander communities. My objectives were to determine if silvicultural treatments (thinning followed by prescribed fire) result in increased habitat heterogeneity and how these habitats are utilized by salamanders. I address the following questions. 1) Is a wider range of habitat conditions available for salamander use in thin/burn units than control units? This was evaluated using a discriminant function analysis. I expected a greater range of habitats to be present in thin/burn than control areas. 2) How do patterns of salamander community and structure vary along gradients of microhabitat characteristics of vegetation and environmental determinants? This objective was explored using a redundancy analysis. 3) Do differences in when species are active over the spring season align with species' life history strategies? Seasonal trends were examined using chi-

squared analyses. I expected spring pool-breeding species to be more active early, while upland-breeders and fall-breeders would not be active until later in the season. Results inform forest management for species diversity and the effectiveness of salamanders as indicators.

Methods

Location—This study utilized experimental units designed and managed by the USDA Forest Service for the Ohio Hills site of the National Fire and Fire Surrogate Study (Chiang et al. 2008). The sites are in Vinton County, Ohio, part of the unglaciated Appalachian plateau. Control and thin/burn units at Vinton Furnace Experimental Forest and Zaleski State Forest are 20-25 ha each (Figure. 2.1). The thin/burn treatment sequence was a mid-story thinning (15-30 cm dbh) during the winter of 2000-2001. Subsequent burns occurred before trees had leafed out in April 2001, April 2005, and April 2010 (Albrecht and McCarthy 2006).

Study Design—Four sites were located in each of the four experimental units (Vinton Furnace control, Vinton Furnace thin/burn, Zaleski Control, Zaleski thin/burn) for a total of 16 upland sites in 2013. In 2014, sites were added to increase the base number of sites within the treatment areas to 20. The minimum distance between sites is 112 m.

Habitat Characterization— To quantify microhabitat availability for salamanders, habitat data were collected at the 20 upland sites from 22 May to 11 June 2013 and 24-26 May 2014. Transects were established from the center of each site 12 m in each of the four cardinal compass directions. Data from these transects and corresponding plots were summarized into the following six habitat metrics for each site (Table A.1). *Coarse*

woody debris (cwd) was total volume of decayed wood calculated from length and diameter at crossing for all transects. Only more degraded wood categorized as stage 3, 4, or 5 was included (MacKenzie 2010). *Stem density (stems)* included total number of woody stems < 1.4-m tall within 12, 1-m² plots located at meters 3, 6, and 9 on each transect. *Leaf litter depth* was mean depth of 24 samples (2 samples from each stem density plot) including litter, fermentation, and humus layers. Leaf litter depth has been found to be important to salamanders in other studies (Pough et al. 1987, Moseley et al. 2003, Matthews et al. 2010). There was more variation in leaf litter depth within sites than between; therefore, leaf litter depth was excluded from analysis (Figure A.1).

Percent oak (oak) was percent of trees > 10-cm dbh in genus *Quercus* located in a 10-m radius plot. Percent oak was related to the integrated moisture index developed for these sites by Iverson et al. (1997) and provides an important link to the silviculture objectives as well as capturing inherent moisture regimes. *Sapling density (saplings)* included all woody stems > 1.4-m and < 10-cm dbh within 2, 5-m radius sub-plots at each site.

Canopy openness (openness) was calculated using Gap Light Analyzer 2.0 (Frazer et al. 1999) from a hemispherical photo taken at 1.5m height at the center of the site on 25 or 26 May 2014. We assume that these metrics reflect important habitat differences that are relevant to the survival and reproduction of a wide variety of salamanders.

Salamander Data Collection— We used passive pitfall arrays to assess salamander community composition at each site. Pitfall arrays consist of three 5-m long drift fences arranged in a Y shape, with a 5-quart bucket buried in the center and at the end of each arm. Fences were constructed of 15-cm high aluminum flashing (Greenberg and Waldrop 2008). Bucket moisture was maintained with a 6 x 3.5 x 1.5 cm cellulose

sponge. Inverted plastic plates were held approximately 5 cm above each bucket by a treaded rod as a way to detect and prevent predator activity. Funnels in the top of each bucket were added on 29 March 2013 and the number of salamanders that escaped greatly decreased (Blyth unpublished data). Funnels were constructed from a clear-plastic pot liner with the bottom removed (Gardener's Blue Ribbon 8" Deep Liner, Woodstream Corp, Lititz PA). Pitfall arrays were monitored daily for salamanders when open. Arrays were open 59 nights in 2013 from 12 March 2013 to 21 May 2013 and 34 nights in 2014 from 20 March to 14 May. On 3 April 2014, eight arrays were not checked due to thunderstorms. Capture numbers from the following day were split between 3 April and 4 April for analysis of these arrays. Only the 50 nights after funnels were added are used in analyses in 2013.

Additional salamander arrays were located on the edge of both the control unit and the thin/burn unit at Vinton Furnace for both years. These four arrays were placed between vernal pools and the upland arrays. Six minnow traps were placed in the adjacent vernal pools to capture breeding salamanders. Vernal pools at both units were located in the floodplain of the Elk Fork. Pools at the thin/burn unit were part of an old oxbow with active beavers and included a population of adult *Notophthalmus viridescens*. Control unit pools dried completely by the end of the spring season excluding *N. viridescens*. Minnow traps were open and checked along with pitfall arrays to more fully capture pool breeding community and used only to assess timing of captures. Minnow traps were removed on 20 April 2013 and 13 April 2014, after the pools had dried or well after the breeding season. Animal handling methods were approved by the Ohio State

University Institutional Animal Care and Use Committee (IACUC Permit # 2011A00000082).

Analysis—Saplings and CWD were log transformed and stems were square root transformed to meet assumptions of normality. Discriminant function analysis (DFA) and MANOVA using Wilk's test was conducted on the five habitat variables for 20 sites across the study to determine if sites grouped by treatment or replicate. These results inform our ability to examine habitat associations with salamander community composition based on grouping strength of treatment and replicates. Principal component analysis (PCA) was conducted on the five standardized habitat variables to characterize within-treatment habitat gradients. PCA and the following redundancy analysis (RDA) were chosen because all habitat variables are quantitative and gradient lengths were unequal (Legendre and Legendre 1998). RDA on salamander count data constrained by habitat data was run to examine how each salamander species aligned with the habitat gradient. RDA is a multivariate ordination procedure that ordines each species in the salamander community (Y matrix) as function of the habitat variables (X matrix). The Y matrix was the number of each species captured at each site, and the X matrix was the quantification of each habitat variable at each site. *Plethodon cinereus* was the most common species overall. *Plethodon electromorphus* were found in small numbers instead of *P. cinereus* in the Vinton Furnace control; therefore, Vinton Furnace control was removed from RDA to remove the effect of no *P. cinereus* at this replicate. It is known that these species do not often co-occur locally, probably as a result of competition (Deitloff et al. 2008). Salamander counts were standardized with a hellinger transformation to reduce the influence of rare species and double zeros. This method

addresses the species abundance paradox that results from using the Euclidian distance based metric of RDA (Legendre and Gallagher 2001). RDA of the habitat variables and hellinger-transformed salamander count data for each array and species were run for each year separately and both combined. Pseudo-F tests, utilizing 1000 permutations, were run on the model as a whole as well as each axis to test model significance (Borcard et al. 2011). Spatial and temporal trends in salamander captures were examined graphically. The season was divided into four equal segments for seasonal chi-squared analyses of *P. cinereus*, *A. opacum*, all pool-breeding species, and all upland species to look at temporal activity trends between species with different life-history strategies. PCA, RDA, and DFA analyses were run in program R v 3.0.1 (R Core Team 2013) using packages *vegan* v 2.0-8 (Oksanen et al. 2013) and *MASS* (Venables and Ripley 2002). Maps were created in ArcMap v10.1 (ESRI 2012).

Results

Habitat characterization—Sites did not group by treatment ($w=0.641$, $F=1.57_{5,14}$, $p=0.23$) or replicate ($w=0.613$, $F=1.77_{5,14}$, $df=5$, $p=0.18$) in the DFA of habitat variables. There was overlap in the range of habitat found in control and thin/burn sites and between Zaleski and Vinton Furnace (Figure 2.2). Some thin/burn sites aligned with the control sites in the PCA (Figure 2.3). The primary axis ($\lambda_1=2.718$) and secondary axis ($\lambda=1.026$) explain 75% of variation observed in the data, with the principal axis containing 54% of variation (Table A.2). Stems, saplings, oaks, and openness dominated the principal axis (PC1 = 1.22 stems + 1.14 saplings + 1.14 oaks + 1.10 openness + 0.04 CWD). Control arrays occupy a smaller portion of the primary axis (1.165) than the

thin/burn sites (2.368) indicating that there is more habitat variation in the treatment than control. Since there is no clear grouping of sites by treatment or replicate in the DFA, sites were pooled for RDA. There were very few changes in the PCA when Vinton Furnace control sites were removed as was done in the RDA to remove the effect of no *P. cinereus* at those sites (Table A.2).

Salamander community composition—Eleven salamander species were captured across the study in 2013 and 10 in 2014 (Table 2.2). *P. cinereus* was the most numerous species followed by *A. opacum*. Several species were captured in very low numbers (Table 2.2). The RDA model for 2013 and 2014 combined explained 65% of variation in the data (Figure 2.4). The principal axis was dominated by openness, oaks, and saplings and represented 48% of variation (RDA1= -0.96 openness – 0.72 saplings – 0.69 oaks – 0.58 stems + 0.04 CWD). A pseudo-F test found that the model was marginally significant (d.f.=5, F=2.2, p=0.092, Table A.3). When separated by axis only the principal axis was significant ($F_{\lambda_1}=8.33$, $p_{\lambda_1}=0.016$). Therefore, emphasis was given to the principal axis when examining trends in the habitat gradient and species alignments. Salamander species do not group along the principal axis. *Plethodon cinereus* and *Ambystoma opacum* fall on opposite sides of the principal axis with the other species along the gradient in between. Results of the RDA on salamander data from 2013 and 2014 separately were similar to each other as well as to the combination presented above (Figure A.2).

Habitat was similar between the two controls (Figure 2.3), one inhabited by *P. cinereus* and one by *P. electromorphus*, which were captured less frequently. Vinton Furnace control was removed from the RDA to account for the effect of this

uninformative difference in species assemblage, which reduced the power of the analysis, but greatly strengthened the model. In analyses of 2014 only, three more sites could be included and resulted in more robust results; the first two axes were significant instead of only the first and the significance level increased to 0.001 from 0.09 for the global test (Table A.3).

Timing of captures—Salamanders were not captured at equal rates throughout the spring, with most individuals captured during the early and middle part of April ($\chi^2_{2013}=59.3$, $\chi^2_{2014}=129.8$ df=3, $p<0.001$). This was true of all species combined as well as *P. cinereus* ($\chi^2_{2013}=33.4$, $\chi^2_{2014}=100.5$, df=3, $p<0.001$) and *A. opacum* ($\chi^2_{2013}=48.7$, $\chi^2_{2014}=26.6$, df=3, $p<0.001$) for both 2013 and 2014. Peaks in captures were related to favorable weather events (Figure 2.5). In 2014, spring migratory species were captured most often during the earliest two weeks of the season, likely during their migration ($\chi^2_{2014}=14.2$, df=3, $p=0.002$). This pattern did not hold in 2013. Captures of migratory species also appear to be higher near breeding pools (Figure 2.6). Capture frequency varied between years. When comparing 20 arrays for dates that the funnels were in place, captures/night were lower in 2014 (0.62 captures/night) than 2013 (2.10) for *A. Opacum* ($t=1.9$, df=62.1, $p=0.057$). Captures were more frequent in 2014 (7.21 captures/night) than 2013 (3.26) for *P. cinereus* but only marginally significant ($t=-1.7$,df=51.8, $p=0.093$).

Discussion

Salamanders are key indicators of underlying environmental conditions (Welsh and Droege 2001, Micacchion 2002) and their diversity of habitat associations reflects species-specific sensitivity to microhabitat conditions. The within-treatment sites that we

studied represented a gradient of habitats that were not defined by treatment or replicate. Greater habitat variability in the treatment suggests that silvicultural management for oaks emulates a natural heterogeneous disturbance regime. The resulting range of habitats was utilized by a varied community of salamanders. The most common pool-breeding species, *A. opacum*, occupies a niche that includes an open canopy, high percentage of over-story oaks, and high stem and sapling densities. This diversity of associations has implications for management. A silvicultural treatment or disturbance may negatively affect some species while having a positive effect on others.

Silvicultural treatments were applied at site-specific scales aimed to achieve a mean response. However, in mixed-oak systems a vital objective is to increase light availability to enhance oak regeneration (Albrecht and McCarthy 2006), which often is achieved in a patch distribution across the site. Thin/burn treatments created a wider range of habitat variability than control units and this range included closed-canopy conditions similar to those in the control, likely as a result of differences in the intensity of fire (Iverson et al. 2008). Thus, closed-canopy habitats are available to salamanders in the thin/burn, although in reduced amounts. There were no detected differences in habitat between the two controls, one inhabited by *P. cinereus* and one by *P. electromorphus*. Although their ranges overlap extensively these salamander species do not often co-occur locally in Southern Ohio (Pfungsten et al. 2013). This supports work by Deitloff et al. (2008) who found competitive exclusion to be responsible for the lack of species overlap.

The positioning of salamander species across the habitat gradient indicates that different species use different habitats. Notably, the most frequently captured species fall on opposite sides of the habitat gradient in the RDA. *Plethodon cinereus* is a small

upland breeder while *A. opacum* is a large-bodied pool breeder. *Plethodon cinereus* aligns with a closed canopy, lower percent oak, and fewer stems in the understory. These characteristics are common in mesic areas where fires are less intense (Iverson et al. 2008). *Plethodon cinereus* are known to prefer moist, shaded areas where temperature and humidity are relatively stable (Heatwole 1962). Coarse woody debris was not a strong component of the habitat gradient. This is surprising as *P. cinereus* is commonly found inside logs (Heatwole 1962) and have been associated with coarse woody debris in other habitat studies (McKenny et al. 2006). *Ambystoma opacum* falls on the opposite side of the habitat gradient where it is found in sites with an open canopy, larger percentage of oaks, and higher numbers of stems and saplings. These tend to be the ridge-tops and south-facing slopes where fires were more intense and regeneration progresses rapidly due to an open canopy (Iverson et al. 2008). Iverson et al. (1997) found percent oak to be negatively related to an index of potential moisture availability.

Most captures occurred during early to mid April, the middle of the spring season. Salamanders are most active when it is warm and humidity is high. Warm temperatures promote activity as long as skin stays moist to allow for cutaneous respiration (Feder 1983). Therefore both early cool days and warm, dry days later in the season suppress movement, while rains increase moisture levels promoting salamander activity. As expected, salamander captures peaked after rains when temperatures were moderate (Figure 2.5). Captures of pool breeding species were expected to be highest early in the season when they were moving to breed; however, this relationship was only observed in 2014, probably because 2013 migration captures occurred before the addition of funnels

and were excluded from analysis. Capture numbers were very low overall (Table 2.2) and migration times were well sampled only in 2014.

The upland ecology of pool-breeding species, including *A. opacum*, is not well understood. Spring-breeding species were primarily encountered in low numbers and early in the season, presumably during migration. This limits the conclusions that can be made about these species upland associations. *Ambystoma opacum* breed in the fall; therefore, all spring captures should be associated with typical upland activities and habitat associations, not migration movement. Most ambystomatids, such as *A. maculatum* and *A. jeffersonianum* spend the bulk of the upland portion of their annual cycle in burrows where they rarely surface except to breed (Petranka 1998, Pfungsten et al. 2013). *Ambystoma laterale* is an exception and is known to be active above-ground (Petranka 1998). This might also be the case for *A. opacum*. *Ambystoma opacum* have not been found to be more tolerant of desiccation than other salamanders of similar size (Marangio and Anderson 1977). However, they have been previously reported in dry habitats (Bishop 1941, Parmelee 1993) and aligned with some of the drier habitats such as open canopy and oaks in our study. *Ambystoma opacum* were captured throughout the spring when *P. cinereus* was also most active. Either *A. opacum* is much more numerous on these sites than *A. maculatum* and *A. jeffersonianum*, or they exhibit different foraging and home range behaviors while in upland habitats.

Salamanders are sensitive to variation in ambient conditions and primarily surface to forage after rains when relative humidity is high and temperatures are moderate (Feder 1983, Petranka 1998). Passive pitfall arrays only capture surface-active individuals. The number of individuals moving to breed is known to vary considerably between years for

migratory pool-breeding species, but yearly variation in upland surface activity of salamanders is not well documented (Demaynadier and Hunter 1995). We observed differences in capture rates between years. Captures per night were lower in 2014 than 2013 for *A. Opacum*, but more frequent in 2014 than 2013 for *P. cinereus*. These differences are probably most attributable to differences in weather as captures increase dramatically after major rain events (Figure 2.5). *Ambystoma opacum* was one of the only species that showed a trend toward more captures in 2013. Life-history, behavior, or habitat differences may cause *A. opacum* to favor different conditions for activity. Although capture rate varied between years, there was little variation in the sites where a species was most prevalent.

Short-term treatment effects should not impact this study's results because of the long time between disturbance and sampling. Salamanders are negatively affected by management shortly after treatment with effect sizes declining over time (Tilghman et al. 2012). The mechanical thin occurred 13 years before data collection, allowing soils, vegetation, and salamander populations some time to recover from direct treatment effects. Prescribed fires occurred three, eight, and thirteen years before data collection. Fires should have little direct effect on salamanders, most of which are under cover objects or in below-ground refugia during daytime fires (Russell et al. 1999). Burns affect habitat, particularly in areas where they are intense, and salamanders likely respond to these habitat changes rather than directly to the treatment (Pilliod et al. 2003).

Management implications—Salamander species may be differentially affected by silviculture if management favors particular habitats. Plethodontids have been promoted as a useful measure of the effect of silviculture on an ecosystem (Welsh and Droege

2001) and our study supports this in closed canopy, mesic areas. However, this one group may not represent all salamanders since different species associate with different habitats. Intensive silviculture has been shown to have mostly negative effects on salamanders in the short-term (Demaynadier and Hunter 1995, Tilghman et al. 2012), but the long-term effects of low intensity management are not necessarily negative. In our system, “mesophication” is a recent shift in forest structure and composition. Management that returns some areas to oak dominance could benefit salamander species that are adapted to oak ecosystems. In this way management could change the relative abundance of species rather than affecting the entire group in a positive or negative way. Intermediate disturbances across the landscape create a patchwork of habitats that are each suitable for a different group species. Habitat diversity in a dynamic landscape will be able to support the widest range of species by providing habitats suitable for a diverse set of species.

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Table 2.1 Life history and habitat information for species encountered in Vinton County, Ohio in 2013 and 2014.

Species	Breeding Location	Peak breeding	Habitat preferences	citations
<i>Ambystoma jeffersonianum</i> Jefferson	Vernal pool	Feb-March	Upland deciduous forests. Reside in rodent burrows and other retreats.	Petranka, 1998; Pfungsten et al. 2013
<i>Ambystoma maculatum</i> Spotted	Vernal pool	March	Closed canopy hardwood and mixed-hardwood forests where they are underground 72%-91% of the time.	Pfungsten et al. 2013
<i>Ambystoma opacum</i> Marbled	Vernal pool	Sept-Nov	Mature deciduous, bottomland, and floodplain forests. Warmer, drier habitats than other Ambystomatids.	Bishop, 1941; Parmelee, 1993; Pfungsten et al. 2013
31 <i>Eurycea cirrigera</i> Southern Two-lined	Stream or seep	March-April	Margins of rocky streams and seeps and adjacent forests.	Weichert, 1945; Ashton and Ashton, 1978; Petranka, 1998
<i>Gyrinophilus porphyriticus</i> Spring	Stream or spring	Spring?	Small forested streams and springs that lack predatory fish.	Petranka, 1998
<i>Hemidactylium scutatum</i> Four-toed	Vernal pool	April	Forests surrounding breeding sites, possibly similar to Plethodontids. May be more active above-ground in the daytime.	Pfungsten et al. 2013; Petranka, 1998

Continued

Table 2.1 Continued

Species	Breeding Location	Peak breeding	Habitat preferences	citations
<i>Notophthalmus viridescens</i> Eastern Newt	Vernal pool	March-June	Aquatic adults inhabit permanent and semi-permanent ponds. Terrestrial efts spend 3-7 years in forest floor/leaf litter.	Petranka, 1998
<i>Plethodon cinereus</i> Eastern Red-backed	Upland	Spring-early summer	Forests with moderate temp, high humidity, and plentiful cover objects. Below-ground retreats during unfavorable conditions.	Heatwole, 1962; Petranka, 1998
<i>Plethodon electromorphus</i> Northern Ravine	Upland	May-early summer	Wooded slopes where they prefer rocks for cover.	Duellman, 1954, Pfriend et al. 2013
32 <i>Plethodon glutinosus</i> Northern Slimy	Upland	Spring-early summer	Moist upland slopes and ravines where they inhabit cracks, crevices and logs.	Pfriend et al. 2013; Petranka, 1998

Table 2.2 Number of each salamander species captured in pitfall arrays at each replicate and treatment. Range of captures at individual sites in brackets. Majority of individuals caught in pools were in the pools near the treatment; number caught near the control in parenthesis. Data from Vinton County Ohio in spring of 2013 and 2014 combined. Treatment was a mid-story thin in 2000 followed by prescribed burns in 2001, 2005, and 2010.

Species	Vinton Furnace Control	Vinton Furnace treatment	Zaleski control	Zaleski treatment	Vinton Furnace pools
<i>Ambystoma jeffersonianum</i>	5 [0:2]	1 [0:1]	3 [0:2]	0	19 (1)
<i>Ambystoma maculatum</i>	6 [0:4]	8 [0:4]	1	1	17 (1)
<i>Ambystoma opacum</i>	35 [0:13]	50 [1:14]	23 [0:12]	23 [0:14]	1
33 <i>Eurycea cirrigera</i>	6 [0:2]	0	2 [0:1]	1	0
<i>Eurycea longicauda</i>	0	1	0	0	0
<i>Gyrinophilus porphyriticus</i>	0	0	0	3 [0:3]	0
<i>Hemidactylum scutatum</i>	4	9 [0:4]	1	0	0
<i>Notophthalmus viridescens</i>	2	4 [0:3]	4 [0:2]	5 [0:4]	60
<i>Plethodon cinereus</i>	0	81 [2:34]	262[21:147]	110[14:44]	0
<i>Plethodon electromorphus</i>	39 [0:21]	0	0	0	0
<i>Plethodon glutinosus</i>	10 [0:7]	3 [0:2]	5 [0:2]	2 [0:1]	0



Figure 2.1 Location of study sites in Vinton County, Ohio. Treatment (T) was a mid-story thinning (15-30 cm dbh) during the winter of 2000-2001 followed by prescribed fires that occurred before trees had leafed out in April 2001, April 2005, and April 2010. Control (C) plots are adjacent at Zaleski State Forest and within 1.5 km at Vinton Furnace State Experimental forest. Plots are 20-25 ha each.

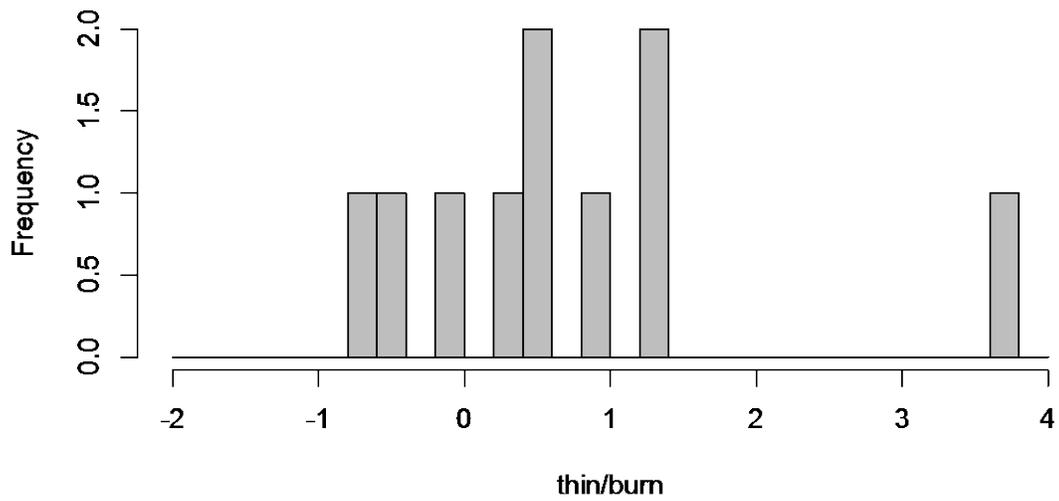
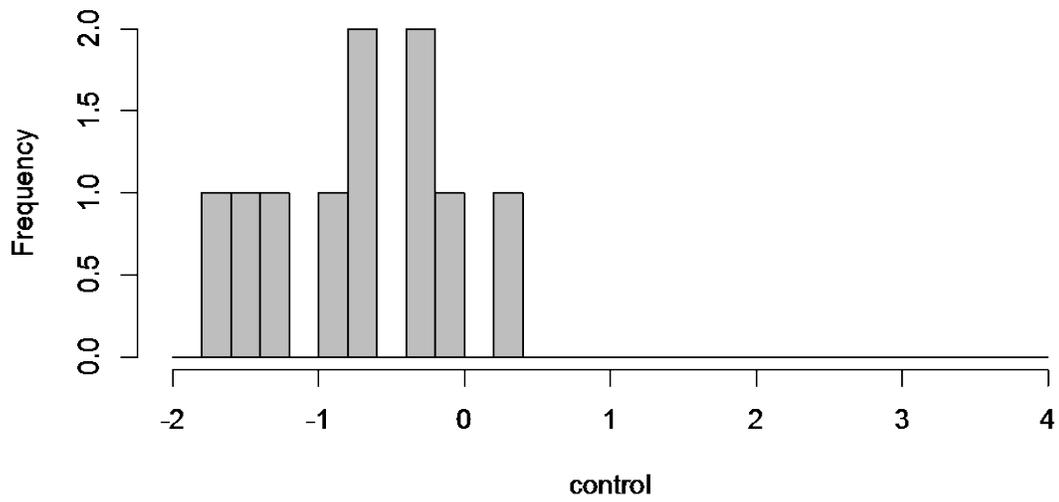


Figure 2.2 Histogram of sites by their Discriminant Function Analysis loadings. Loadings from the Discriminant Function Analysis: $\text{treatment} = 0.91 \text{ openness} + 0.61 \text{ stems} + 0.61 \text{ oaks} + 0.47 \text{ saplings} + 0.21 \text{ CWD}$.

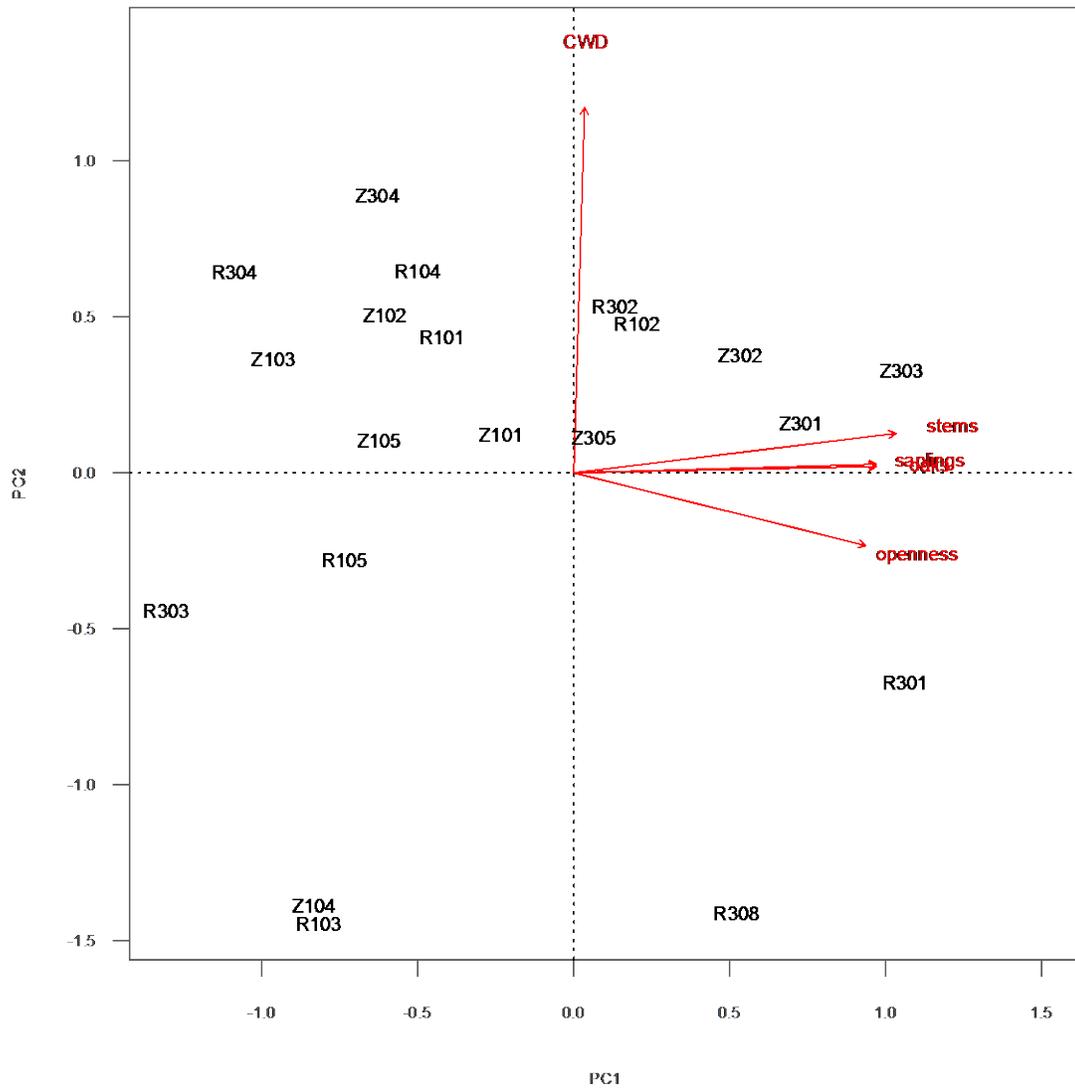


Figure 2.3 Principal component biplot of five habitat variables across 20 sites. Sites plotted in black; control sites numbered in the 100s, treatment in the 300s. The primary axis ($\lambda_1=2.718$) and secondary axis ($\lambda=1.026$) explain 75% of variation observed in the data, with the principal axis explaining 54% of variation. Habitat variables include number of saplings (saplings), percent canopy open (openness), number of understory woody stems (stems), percent of trees > 10 cm dbh in genus *Quercus* (oaks), and volume of more decayed coarse woody debris (CWD).

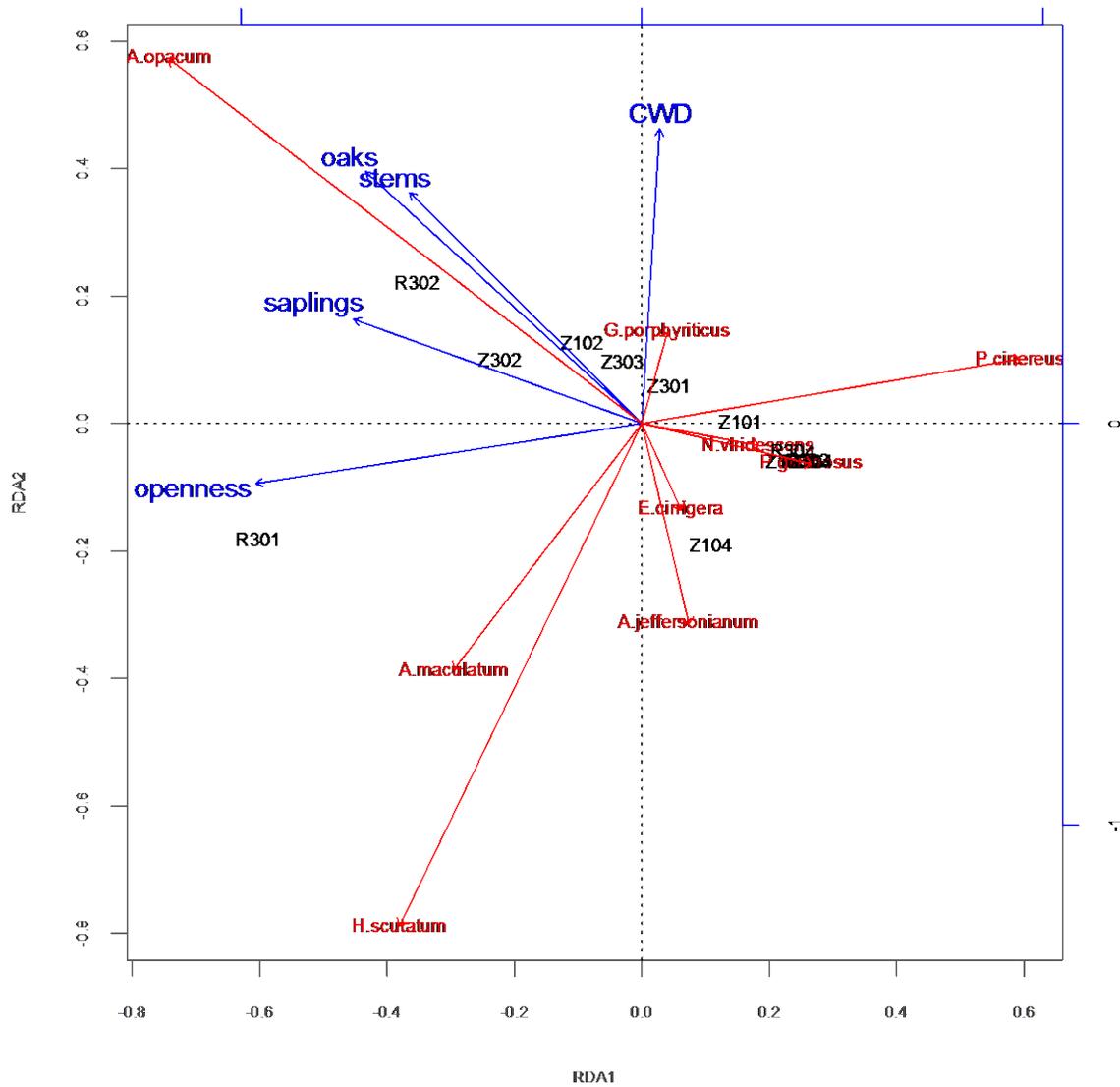


Figure 2.4 Triplot of redundancy analysis for both 2013 and 2014 combined. Salamander species in red, constrained by habitat variables, in blue. Sites plotted in black. The model explained 65% of variation, and the principal axis represented 49% of this variation ($\lambda_1=0.069$, $\lambda_2=0.012$).

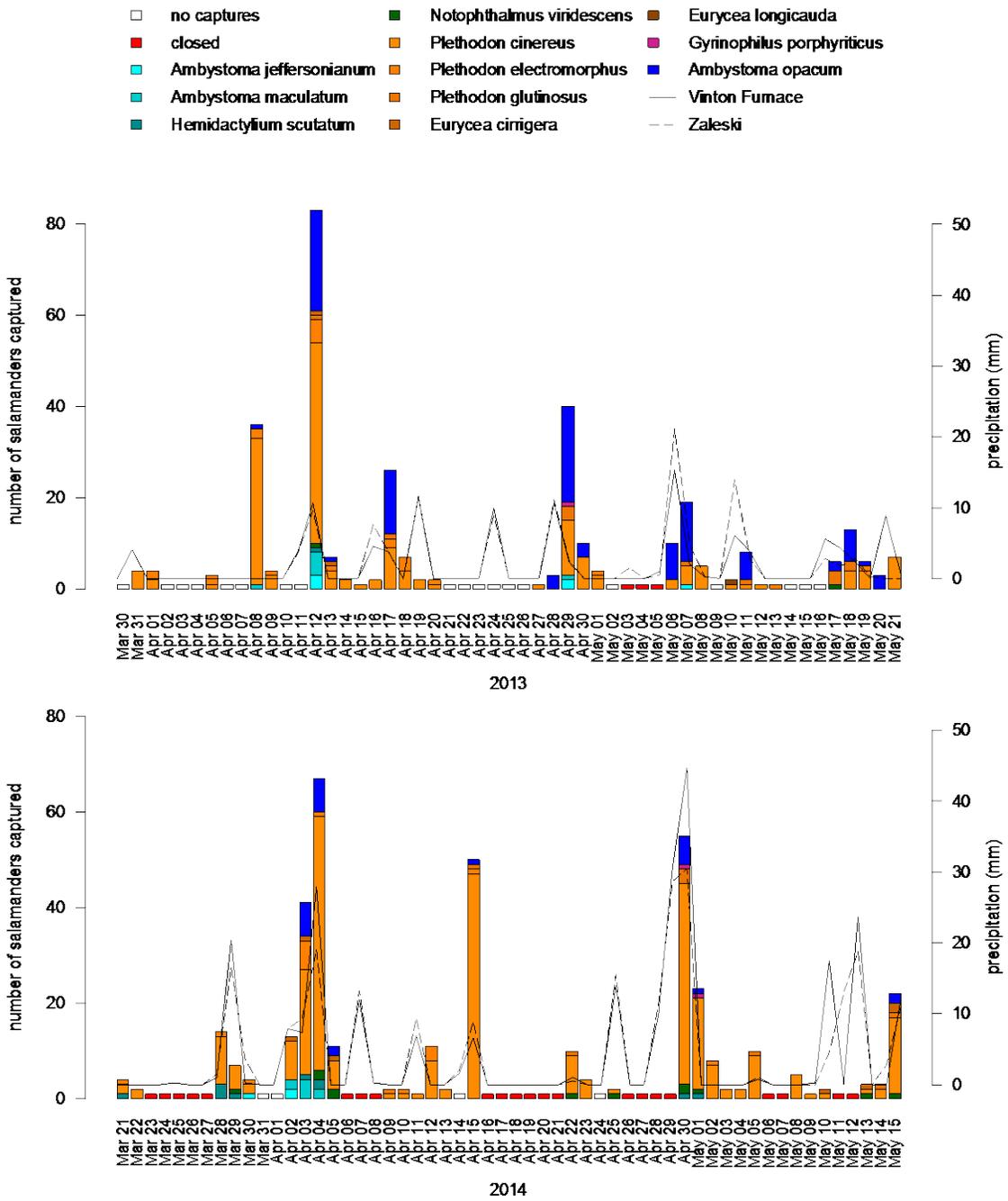
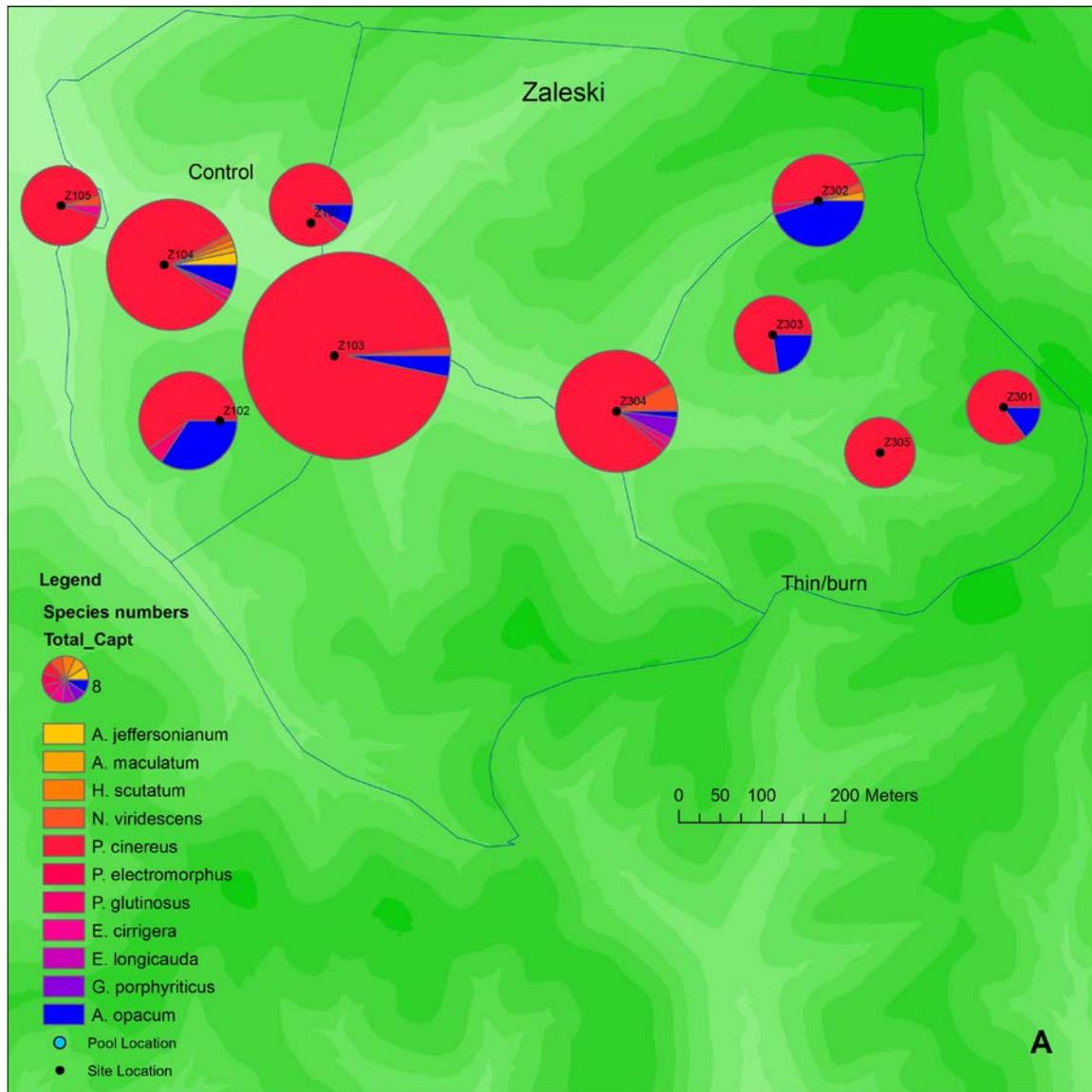


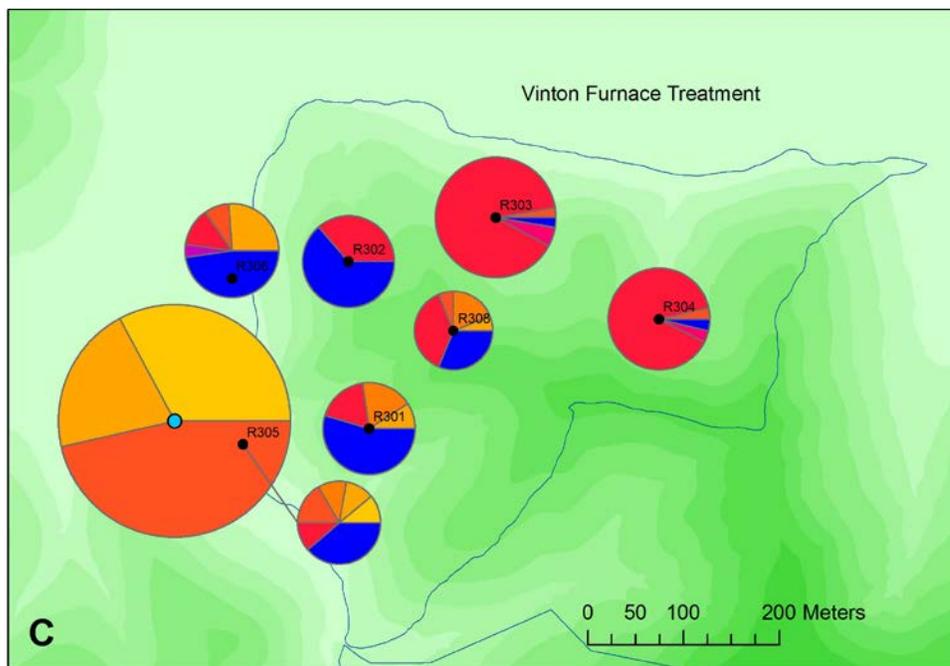
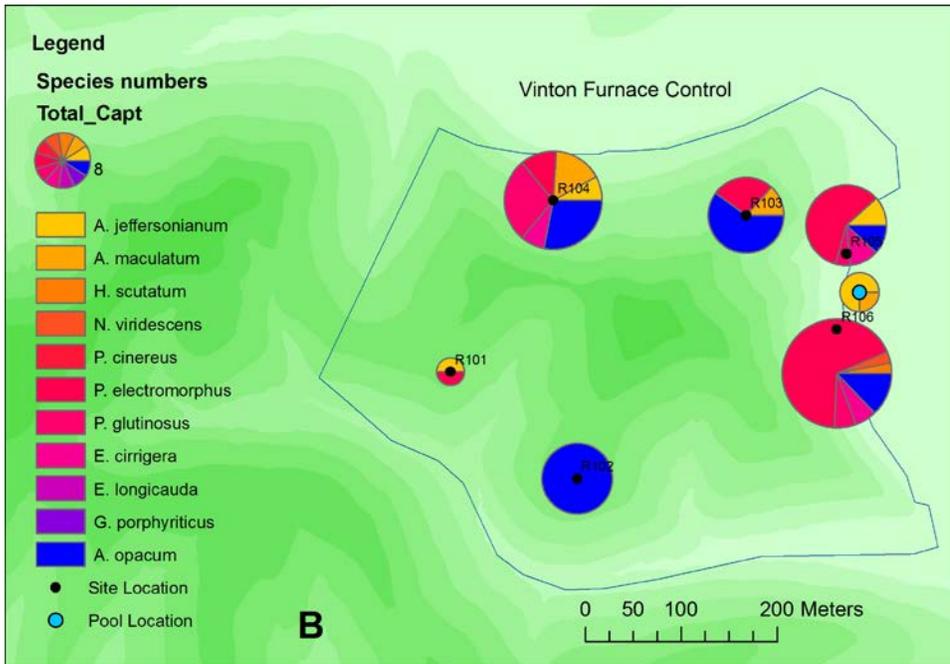
Figure 2.5 Number of individuals captured in pitfall arrays each night across the study in 2013 and 2014. Daily precipitation at Vinton Furnace State Experimental Forest and Zaleski State Forest replicates plotted above the bars in black. Spring pool breeders in cyan, non-breeding/pool breeding newts in green, upland breeders in orange, and fall pool breeder in blue. *A. jeffersonianum* and/or *A. maculatum* were captured in nearby vernal pools in 2013 on Mar 12 (43), Apr 6 (1), and Apr 12 (2), and in 2014 on Mar 22 (25), Mar 30 (1), Apr 3 (5), and Apr 4 (2).



Continued

Figure 2.6 Topographic maps depicting the mix of species captured at each site for Zaleski control and treatment (a), Vinton Furnace control (b), Vinton Furnace treatment (c). Size of the pie represents total number of captures. Captures from minnow traps in nearby pools at Vinton Furnace are depicted around a blue dot. Actual site location marked in black; some graphics are shifted to avoid overlap. Data from 2013 and 2014 combined. Zaleski 105, Zaleski 305, and Vinton Furnace 308 were only open in 2014. Each shade of green represents 11.2 m of elevation.

Figure 2.6 continued



Chapter 3: Habitat heterogeneity in a managed oak ecosystem supports two salamander species with different life-histories.

Introduction

Forests dominated by oaks are important ecosystems for many birds and mammals including *Meleagris gallpavo*, *Odocoileus virginianus*, *Peromyscus leucopus*, and *Sciurus spp.* (McShea and Healy 2002, Dey et al. 2010). Loss of fire has resulted in the “mesophication” of forests in eastern US hardwood stands, whereby shade-intolerant fire-adapted species, such as oaks and hickories are being replaced by shade-tolerant species (Nowacki and Abrams 2008). In the Appalachian region of Ohio, oaks and hickories primarily occur on moisture-limited ridges and southwest-facing slopes where they can compete against shade-tolerant species such as *Acer rubrum* and *Acer saccharum* (Iverson et al. 1997). Treatments including prescribed fire have increased heterogeneity across sites due to varied fire intensity, and these sites are regenerating oaks in dry and intermediate sites with open canopy (Iverson et al. 1997).

Salamanders are key predators in the forest floor ecosystem and contribute to carbon-nitrogen cycles by moving nutrients through the soil column and between aquatic and terrestrial environments (Davic and Welsh 2004). Salamanders are often used as an indicator of ecosystem function because of their middle trophic level and links to biotic and abiotic processes (Welsh and Droege 2001, Micacchion 2002). Studies of the relationship between oak ecosystems and salamanders are lacking. However, mesocosm

studies suggest that amphibian larvae benefit from oak litter inputs in seasonal pools (Rubbo and Kiesecker 2004). Oak litter decays slowly providing increased cover for forest floor denizens and their invertebrate prey (Fox et al. 2010). This may benefit salamanders through increased prey availability, higher and more stable moisture levels, or increased cover. *Ambystoma opacum* and *Plethodon cinereus* represent the two major salamander species groups in the Appalachian region of Ohio. *A. opacum* is a large, biphasic pool breeder that inhabits the uplands most of the year (Pfungsten et al. 2013). *P. cinereus* is a lungless upland breeder that is abundant across a wide range and is typical of plethodontids (Petranka 1998). Both species are active and non-migratory in spring when ambient humidity and moderate temperatures allow them to emerge from retreats.

Like other biphasic species, *A. opacum* require high quality upland habitats connected to high quality breeding pools to sustain viable populations (Stebbins and Cohen 1995). *A. opacum* differs from other pool-breeding species in that breeding and egg-laying occur in autumn instead of spring. Females create nests in dry vernal pools, leaving when the water rises and larvae hatch. Larvae have a competitive advantage over spring-breeding amphibians in the pool (Pfungsten et al. 2013). Their breeding and larval habitat requirements are well known, but preferred upland habitat and upland life-history have only been inferred from anecdotes and knowledge of other members of the genus. *A. opacum* are often found under moist cover objects (Parmelee 1993) and can enlarge existing crevices and holes to form underground retreats (Semlitsch 1983). Although several authors suggest that they are more tolerant of warmer, drier habitats than other members of the genus (Bishop 1941, Smith 1961, Parmelee 1993), other authors counter

that they exhibit no known physiological adaptation to desiccation and are similar in their tolerances to other large-bodied salamanders (Marangio and Anderson 1977).

Plethodon cinereus is abundant, well studied, and often used as an indicator of the effects of silvicultural treatments on salamanders (Demaynadier and Hunter 1995, Petranka 1998, Welsh and Droege 2001). *P. cinereus* inhabits small home ranges (3.0-4.9 m², with a mean activity radius of 12.9-24.3 m²) in moist environments with moderate temperatures that allow for cutaneous respiration (Kleeberger and Werner 1982, Feder 1983). They are found in mesic habitats and emerge only when surface conditions are favorable to forage in the leaf litter and on understory vegetation (Jaeger 1978). Structural cover, such as coarse woody debris, help regulate temperature and humidity and provide a protected place to forage (Heatwole 1962, Jaeger 1980). *P. cinereus* is found more often under a closed canopy (Tilghman et al. 2012) and under cover objects that are shaded than those in the sun (Strojny and Hunter 2010). Although other factors likely contribute, canopy cover reduces forest floor temperature, raises humidity, and tempers fluctuations in both (Heatwole 1962). Habitat requirements of all salamanders are often assumed to be similar to *P. cinereus* or other Plethodontids; however, growing evidence suggests that this may not be the case (Semlitsch et al. 2009).

As an ecological indicator of forest floor processes, salamanders can be used to evaluate silvicultural treatments. Variation in prescribed fire intensity and inherent differences in microclimate and soils affect within-treatment habitat conditions at the scale where salamanders are likely to respond due to small home range size. Salamanders are more likely to colonize favorable habitats where they will surface more often due to favorable conditions and increase population size via higher reproductive output. I

examined how differences in within-treatment microhabitat affect relative salamander abundances of two species with very different life-history requirements. I compared habitat associations of *P. cinereus* and *A. opacum*, commonly captured representatives of their life-history guilds, by studying them simultaneously across the same habitat gradient. A multi-model framework based on a constrained set of working hypotheses was used to identify habitat features associated with each species (Table 3.1). Knowledge of habitat associations of both upland and migratory salamander species inform management for biological diversity.

Methods

Location—This study was conducted on experimental units designed and managed by the USDA Forest Service for the Ohio Hills site of the National Fire and Fire Surrogate Study (Albrecht and McCarthy 2006). The sites are in Vinton County, Ohio, part of the unglaciated Appalachian plateau. Control and thin/burn units at Vinton Furnace Experimental Forest and Zaleski State Forest were 20-25 ha each (Figure 3.1). Thin/burn treatment was a mid-story thinning (15-30 cm dbh) during the winter of 2000-2001. Subsequent burns occurred before trees had leafed out in April 2001, April 2005, and April 2010 and varied in intensity across the stand (Iverson et al. 2008).

Salamander Data Collection— We used passive pitfall arrays to establish occupancy of *A. opacum* and *P. cinereus*. Four pitfall array sites were located in each of the four experimental units (Vinton Furnace control, Vinton Furnace thin/burn, Zaleski control, Zaleski thin/burn) for a total of 16 sites in 2013. Four additional sites were added in 2014 to increase the total number of sites to 20. The minimum distance between sites

was 112 m. Pitfall arrays consisted of three 5-m long drift fences arranged in a Y shape, with a 5-quart bucket buried in the center and at the end of each arm. Fences were constructed from 15-cm high aluminum flashing (Greenberg and Waldrop 2008). Bucket moisture was maintained with a 6 x 3.5 x 1.5 cm cellulose sponge. Inverted plastic plates were held approximately 5 cm above each bucket by a treaded rod as a way to detect and prevent predator activity. Funnels in the top of each bucket greatly reduced the number of salamanders that escaped (Blyth unpublished data). Funnels were constructed from a clear-plastic pot liner with the bottom removed (Gardener's Blue Ribbon 8" Deep Liner, Woodstream Corp, Lititz PA). Pitfall arrays were monitored daily for salamanders when open. Arrays were open 50 nights in 2013 from 30 March 2013 to 21 May 2013 and 34 nights in 2014 from 21 March to 15 May. On 3 April 2014, eight arrays were not checked due to thunderstorms. For these arrays, capture numbers from the following day were split between 3 April and 4 April for analysis. Animal handling methods were approved by the Ohio State University Institutional Animal Care and Use Committee (IACUC Permit # 2011A00000082).

Habitat Characterization—Habitat data was collected at each of the 20 sites from 22 May - 11 June 2013 and 24 - 26 May 2014. Transects were established from the center of each salamander array 12 m in each of the four cardinal directions. Data from these transects and corresponding plots were summarized into the following six habitat metrics for each site (Table A.1). *Coarse woody debris (cwd)* was total volume of decayed wood, calculated from length and diameter at transect crossing of all four transects (MacKenzie 2010). *Stem density (stems)* included total number of woody stems < 1.4-m tall within 12, 1-m² plots located at meters 3, 6, and 9 on each transect. *Leaf litter depth* was mean depth

of 24 samples (2 samples from each stem density plot) including litter, fermentation, and humus layers. Leaf litter has been found to be important to salamanders in other studies (Pough et al. 1987, Moseley et al. 2003, Matthews et al. 2010). There was more variation in leaf litter depth within sites than between; therefore, leaf litter depth was excluded from analysis (Figure A.1). *Percent oak (oak)* was percent of trees > 10-cm dbh in genus *Quercus* located in a 10-m radius plot. Percent oak was related to the integrated moisture index developed for these sites by Iverson et al. (1997) and provides an important link to the silviculture objectives as well as capturing inherent moisture regimes. *Sapling density (saplings)* included all woody stems > 1.4-m tall and < 10-cm dbh within 2, 5-m radius sub-plots at each site. *Canopy openness (openness)* was calculated using Gap Light Analyzer 2.0 (Frazer et al. 1999) from a hemispherical photo taken approximately 1.5m high at the center of the site on 25 or 26 May 2014.

Analysis— Occupancy models can better approximate habitat relationships by accounting for varying detection probabilities in unmarked populations (Mackenzie et al 2006). These models estimate site occupancy (λ) while accounting for variable probability of detection (p). Occupancy models have been adopted as an alternative to mark-recapture studies for salamanders, because mark and recapture rates are low do to vertical movements through the soil column (Taub 1961, Mazerolle et al. 2007). N-mixture occupancy models were used to estimate the relative importance and direction of relationships between salamander occupancy and three habitat covariates. N-mixture models allow count data to be incorporated into the occupancy framework (Royle 2004). Assumptions of population closure were met by limiting sampling to a three-month period in the spring when *A. opacum* are upland residents. We also assumed that there

was no unmodeled heterogeneity in detection probabilities, that differences in site occupancy were modeled by covariates, and that detection at each site was independent. Low or highly variable detection probabilities can also bias occupancy estimates (MacKenzie et al. 2006). Each species and year was modeled separately, resulting in four model sets. Dates and sites included varied between data sets (Table 3.2).

Detection covariates were selected to describe the weather conditions when salamander activity, and therefore detection, was more likely. Salamanders are known to be sensitive to humidity and temperature; therefore, mean daily relative humidity (humidity), mean daily air temperature (temp), mean daily air temperature squared, (temp^2) and total daily precipitation (precip) were selected. Mean humidity and temperature were averaged across the day traps where checked (t) and t-1. Total precipitation on the previous two days was summed ((t-1) + (t-2)). Two days of data accounted for time it may take for animals in underground burrows to respond by surfacing, and to account for weather data that begins at midnight being offset from trap checks that occur from 8:00 to 16:00. Three habitat covariates were selected to maximize biological habitat information gained. This reduced the number of models considered and increased degrees of freedom, which were limited by the low number of sites. Openness, percent oaks, and volume of coarse woody debris were selected. Correlation between the metrics was less than 0.2 and non-significant, with the exception of oaks and openness that were correlated ($r=0.50$, $t=2.42$, $df=18$, $p=0.03$). Replicate (rep) was also considered as an occupancy covariate to account for site level dependency between Zaleski and Vinton Furnace State Forests locations.

All possible combinations of the detection covariates were modeled in program R (R Core Team 2013) using package unmarked (Fiske and Chandler 2011). Temp² was only included if temp was also in the model. An information theoretical approach using Akaike's Information Criterion corrected for small sample size (AICc) was used for model selection (MacKenzie et al. 2006). The model with the most support was then used for the detection component of subsequent modeling where all possible combinations of the four occupancy covariates were considered. Model averaging, including all possible covariates, was conducted using package MuMIn (Bartoń 2014) for model sets with more than 2 plausible models ($\Delta\text{AICc} < 2$). Confidence intervals that do not overlap zero and relative model weight were presented as characterizing overall model fits to assess the strength of modeled covariates. Adequate methods for assessing model fit have not been developed for these models (MacKenzie et al. 2006). The same habitat data was used for both years, but salamander and weather data was unique to year. Therefore between-year comparisons were used to support the model. Interpretation was limited to direction of relationships, and predicted abundance estimates were considered to be relative.

Results

Ambystoma opacum— The ability to detect *A. opacum* was positively related to humidity and increased at intermediate temperatures in both 2013 and 2014 (Figure 3.2). The top detection-only model for both 2013 and 2014 was $p(\text{humidity} + \text{temp} + \text{temp}^2) \cdot \lambda()$. A more complex model including precipitation was also plausible in 2013, but the simpler model was selected because the confidence interval for precipitation overlapped zero ($\text{precip}_{\text{estimate}} = -0.04 [-0.09, >0.00]$). Occurrence of *A. opacum* was

positively related to the percent of oak overstory trees (> 10 cm dbh) in both 2013 and 2014 (Figure 3.3). The top overall model was $p(\text{humidity}+\text{temp}+\text{temp}^2)\cdot\lambda(\text{oak})$ for both 2013 and 2014. In 2014 there were three other plausible models with ΔAICc less than 2 (Table 3.3). Model averaging of the top four models resulted in an average model with parameter values close to $p(\text{humidity}+\text{temp}+\text{temp}^2)\cdot\lambda(\text{oak})$, and only those parameters also in that model had confidence intervals that did not overlap zero (Table 3.4, $\text{oak}_{\text{estimate}} = 0.03$, [0.01, 0.04], $\text{replicate}_{\text{estimate}} = -0.26$, [-1.67, 0.16], $\text{openness}_{\text{estimate}} = 0.01$, [0.00, 0.06], $\text{CWD}_{\text{estimate}} = -0.01$, [-0.16, 0.03]).

Plethodon cinereus—The ability to detect *P. cinereus* was positively related to humidity and increased at intermediate temperatures in 2014 (Figure 3.4). The top detection model for 2014 was $p(\text{humidity} + \text{temp} + \text{temp}^2)\cdot\lambda()$. This detection component was used in all models with an occupancy component. The top overall model was $(\text{humidity}+\text{temp}+\text{temp}^2)\cdot\lambda(\text{oak}+\text{rep})$ (Table 3.3). Occurrence of *P. cinereus* was negatively related to the percent of overstory trees that were oak (Figure 3.5, Table 3.4). Predicted abundance was 48% less at Vinton Furnace than Zaleski, requiring a replicate parameter in the model. This could be the result of higher abundances at Zaleski or lack of control site at Vinton Furnace.

In 2013, the top detection model was $p(\text{temp} + \text{temp}^2)\cdot\lambda()$ for *P. cinereus*. *Plethodon cinereus* was negatively associated with canopy openness and coarse woody debris in the top overall model (Table 3.4, $\text{openness}_{\text{estimate}} = -0.10$ [-0.15, -0.06], $\text{CWD}_{\text{estimate}} = -0.03$ [-0.05, -0.01]). Detection was predicted to be low for this model (mean = 0.014 [0.00, 0.03]) and could potentially bias occupancy results. The 2013 data set contains only 12 sites, probably not enough sites to produce meaningful models.

Discussion

While salamanders are often characterized as preferentially inhabiting mesic environments, this study found that *A. opacum* was associated with oak-dominated sites that are generally more xeric. Oak ecosystem benefits, such as an oak-litter based food web, may outweigh the costs of living in a drier habitat. Percent of oaks in the overstory was the strongest predictor of both *A. opacum* (positive) and *P. cinereus* (negative) abundance. Percent oak is most easily interpreted as a measure of habitat type. These relationships suggest that *A. opacum* associated with oak habitats while *P. cinereus* associated with mesic habitats; Keyser et al. (2004). also establishes the latter association. Percent oak was negatively related to the Integrated Moisture Index developed by Iverson et al (1997) to measure potential moisture availability in our system. By extension, *A. opacum* associates with drier habitats while *P. cinereus* is more likely to occur in more moist habitats. These results emphasize that not all salamander species associate with the same habitats. Management may affect two resident salamander species differently by changing habitat and conditions within the stand. Therefore, all salamanders should not be represented by a subset of Plethodontids as *A. opacum* and other pool-breeders have different habitat requirements.

Species associations in this study reflect longer-term habitat differences rather than direct disturbance effects due to the extended time interval between treatments (thinning followed by series of multiple low intensity burns) and salamander sampling. Three mechanisms have been proposed to explain salamander population reductions after disturbance: mortality, evacuation from the site, and retreat to subterranean refugia in a

reduced activity state (Demaynadier and Hunter 1995). Demographic effects of reduced reproductive output could also cause changes in abundance over a longer time-period (Homyack et al. 2011). Sampling occurred three years after the last burn and twelve years after mechanical thinning. Direct mortality and evacuations from the thin/burn units would have occurred well before the start of the study. Since the thin/burns were patchy, salamanders may have immigrated to better locations nearby after the burn. Salamanders in poor habitats may have lower reproductive output and spend more time in retreats, reinforcing trends of lower abundance in poor habitats. This allows us to relate results to habitat differences instead of direct disturbance effects.

Oak ecosystems may benefit *A. opacum* by providing higher quality leaf litter and prey items. Salamanders are a keystone predator in the forest floor food web (Walton 2013). Changes in the abundance of salamanders can impact the rate of decomposition (Wyman 1998). Leaf litter depth varied more within sites than between; therefore, it was not included in analysis. Leaf litter composition was not measured, but should reflect overstory tree composition. Oak leaf litter inputs may benefit salamanders through the food web and provide cover that reduces detrimental fluctuations in temperature and humidity (Heatwole 1962). As an integral part of the forest floor community, salamanders are likely sensitive to changes in tree species composition.

Humidity and moisture levels are critical to salamander survival. Lower moisture at sites where oaks are abundant might explain the negative association between oaks and *P. cinereus*, but does not explain the positive relationship between oaks and *A. opacum*. Parmelee (1993) found *A. opacum* in retreats that were drier than *Ambystoma texanum* and *Ambystoma tadpoideum* and warmer than *Ambystoma maculatum*. Bishop (1941)

observed *A. opacum* on coarse or sandy, dry soils, and Smith (1961) suggested that they may be less tolerant of cold temperatures than other members of the genus. Tolerance of drier sites makes *A. opacum* better adapted to use oak ecosystems. Perhaps a behavioral adaptation can account for the difference between these observations and physiology. For instance, the benefits of an oak-dominated ecosystem and food web might outweigh the cost of frequent visits to retreats to rehydrate after foraging in drier surface conditions.

Few captures are expected when the weather is not favorable for surface movement. As ectotherms, salamanders depend on external conditions to regulate temperature and maintain moist, permeable skin for cutaneous respiration (Feder 1983). They are usually found in moist environments where they emerge from retreats only when high ambient humidity and moderate temperatures allow surface activity. The detection component of the model accounted for differences in the likelihood that salamanders are available for capture. Captures occur when individuals are moving on the surface. Both species were caught in greater numbers when average relative humidity was high and temperature was moderate, as expected based on established relationships between salamanders and environmental conditions (Demaynadier and Hunter 1995). The thermal optimum for *P. cinereus*, 16.0 - 21.0°C (Homyack et al. 2011), falls in the middle of the range of air temperatures observed during the study (1.2 - 25.5°C). Including these climate variables increases detection probability and strengthens occupancy estimates in the model.

Pitfall arrays have many advantages for sampling salamanders, but are biased toward individuals moving on the surface. In our analyses we assumed that salamanders are moving similar distances with similar frequency in all habitats, because more or less

movement could result in biased capture rates. The most problematic bias would occur if individuals in a poor habitat utilized a larger home range to satisfy their requirements. Salamanders have very low energetic requirements and are known to remain in retreats until favorable conditions are present (Feder 1983). This would suggest that salamanders in poor habitats are less likely to be active, and therefore captured, than those in better habitats. A meta-analysis by Tilghman et al. (2012) found that passive sampling methods resulted in a smaller canopy disturbance effect on salamander abundance than active sampling methods, and are therefore more conservative. Passive sampling avoids habitat, observer, and observer expectation biases. I hypothesize that the advantages of passive sampling outweigh the possibility of a movement bias.

Management implications—This study found that two salamander species with different life-history strategies associate with different habitats within the same forest stands. Variation in prescribed fire intensity across the landscape increased habitat heterogeneity in the thin/burn units thereby providing habitat for both salamander species. Prescribed burns resulted in open oak forests, with greater regeneration of oak on dry ridges and south facing slopes (Iverson et al. 2008); this habitat was favored by *A. opacum*. *P. cinereus* associated with closed-canopy mesic sites that were present in both untreated controls and mesic areas within thin/burn units. Mesic areas may also provide refugia from burns, a source population for recolonization, and connectivity between habitats with different management (Ford et al. 2002). Semlitsch et al. (2009) also found life-history and species differences when examining the effect of timber harvest on pool-breeding amphibians. Habitat type is important for many species of wildlife and is likely also important for salamanders. In our study system, *A. opacum* utilizes oak habitats

while *P. cinereus* utilizes mesic habitats. Conservation of salamander biodiversity is possible in managed oak forests where heterogeneity provides habitat for a range of species.

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Table 3.1 Expected directions of relationships for detection and occupancy covariates based on known weather and habitat relationships of *Ambystoma opacum* and *Plethodon cinereus*.

	Covariate	Prediction	
		A. opacum	P. cinereus
Detection	Temperature	=	=
	Temperature ²	-	-
	Precipitation	+	+
	Humidity	+	+
Occupancy	Canopy Openness	=	-
	Percent Oak	-	-
	Coarse Woody Debris	+	+

Table 3.2. Number of sites and visits used in occupancy models for each of the four data sets. Number of sites included vary because sites were added in 2014 and Vinton Furnace control was excluded from *P. cinereus* data sets.

Data set	Number of sites	Start date	End date	Nights open (visits)
2013 <i>P. cinereus</i>	12	30 March	21 May	50
2013 <i>A. opacum</i>	16	30 March	21 May	50
2014 <i>P. cinereus</i>	15	21 March	15 May	34
2014 <i>A. opacum</i>	20	21 March	15 May	34

Table 3.3. Number of parameters, AICc, Δ AICc, and AICc weight for N-mixture models with AICc weight > 0.05 and the null model. Model sets for 2013 *A. opacum*, 2014 *A. opacum*, and 2014 *P. cinereus*.

Model	nPars	AICc	AICc	wt
<i>2013 A. opacum</i>				
p(humidity+temp+temp ²)•λ(oak)	6	447.41	0.00	0.54
p(humidity+temp+temp ²)•λ()	5	449.13	1.72	0.29
p(humidity+temp+temp ²)•λ(cwd)	6	451.93	4.52	0.06
<i>2014 A. opacum</i>				
p(humidity+temp+temp ²)•λ(oak)	6	139.33	0.00	0.33
p(humidity+temp+temp ²)•λ(oak+openness)	7	140.29	0.96	0.21
p(humidity+temp+temp ²)•λ(oak+rep)	7	140.53	1.20	0.18
p(humidity+temp+temp ²)•λ(oak+cwd)	7	140.72	1.39	0.17
p(humidity+temp+temp ²)•λ(rep+openness+cwd)	8	143.08	3.75	0.05
p(humidity+temp+temp ²)•λ()	5	153.20	13.87	0.00
<i>2014 P. cinereus</i>				
p(humidity+temp+temp ²)•λ(oak+rep)	7	1061.36	0.00	0.72
p(humidity+temp+temp ²)•λ(oak)	6	1064.84	3.47	0.13
p(humidity+temp+temp ²)•λ(openness)	6	1066.01	4.64	0.07
p(humidity+temp+temp ²)•λ()	5	1084.17	22.81	0.00

Table 3.4. Parameter estimates and upper and lower bounds of the 95% confidence intervals for the top models in each of the four data sets.

Model	Parameter	Estimate	Lower	Upper
2013 <i>A. opacum</i>	$p(\text{humidity}+\text{temp}+\text{temp}^2)\cdot\lambda(\text{oak})$			
	oak	0.01	>0.00	0.02
	humidity	0.06	0.04	0.08
	temp	2.81	1.85	3.77
	temp ²	-0.09	-0.12	-0.06
2014 <i>A. opacum</i>	$p(\text{humidity}+\text{temp}+\text{temp}^2)\cdot\lambda(\text{oak})$			
	oak	0.03	0.02	0.05
	humidity	0.13	0.08	0.18
	temp	0.76	-0.04	1.55
	temp ²	-0.03	-0.06	<0.00
2014 <i>A. opacum</i>	average model of top four plausible models			
	oak	0.03	0.01	0.04
	replicate	-0.16	-1.67	0.16
	openness	0.01	>0.00	0.07
	CWD	-0.01	-0.16	0.03
	humidity	0.14	0.08	0.20
	temp	0.88	-0.11	1.87
	temp ²	-0.04	-0.07	<0.00
2013 <i>P. cinereus</i>	$p(\text{temp}+\text{temp}^2)\cdot\lambda(\text{openness}+\text{CWD})$			
	openness	-0.10	-0.15	-0.06
	CWD	-0.03	-0.05	-0.01
	temp	1.25	0.80	1.71
	temp ²	-0.04	-0.05	-0.02
2014 <i>P. cinereus</i>	$p(\text{humidity}+\text{temp}+\text{temp}^2)\cdot\lambda(\text{oak}+\text{rep})$			
	oak	-0.02	-0.02	-0.01
	replicate	0.74	0.26	1.22
	humidity	0.07	0.06	0.08
	temp	0.78	0.57	1.00
	temp ²	-0.03	-0.04	-0.02



Figure 3.1. Location of thin/burn (T) and control (C) plots in Vinton County, Ohio. Sites are within Zaleski State Forest and Vinton Furnace Experimental Forest. Inset map highlights the location of Vinton County within Ohio

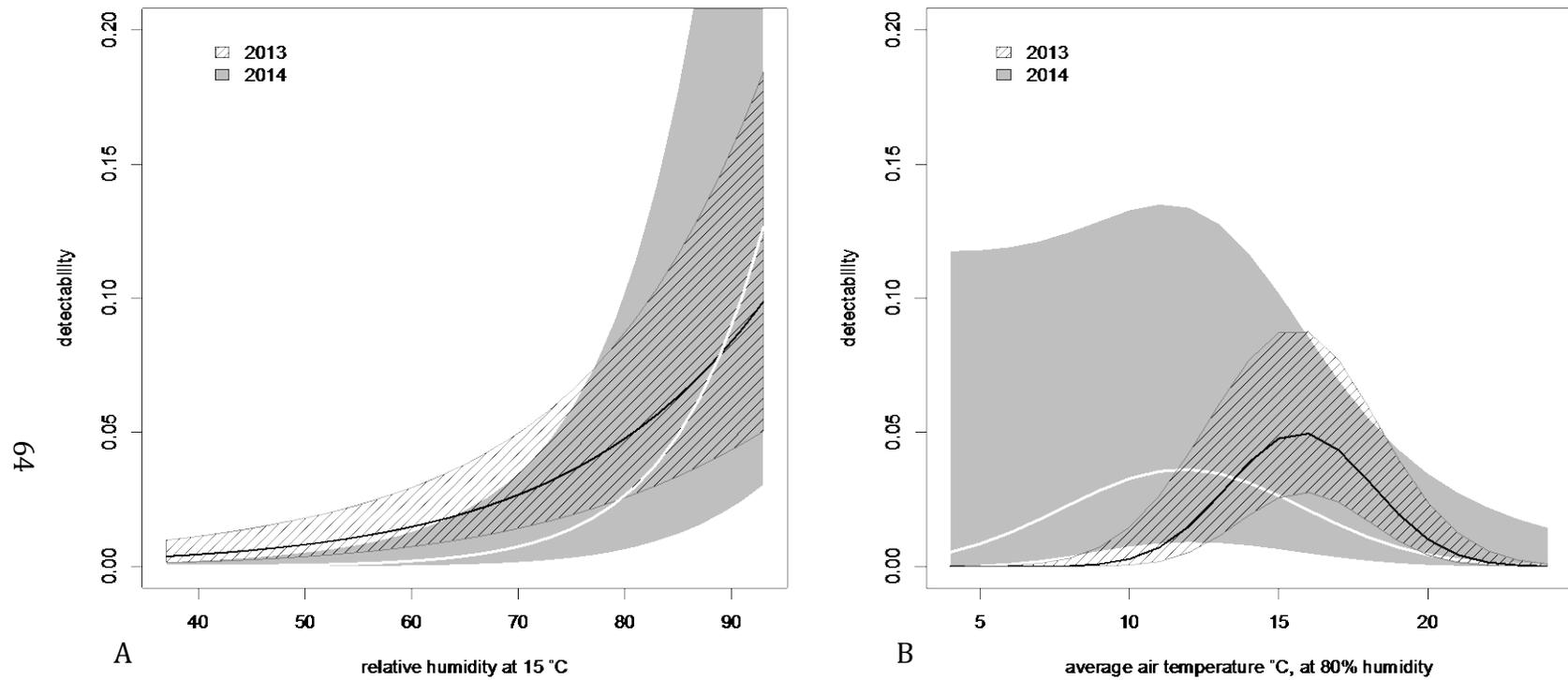


Figure 3.2. Detectability of *Ambystoma opacum* plotted against average relative humidity of the day of capture and the previous day (a), and mean temperature of the day of capture and the previous day (b). Model is $p(\text{humidity} + \text{temp} + \text{temp}^2) \cdot \lambda(\text{oak})$ for both 2013 and 2014. 95% intervals are also plotted.

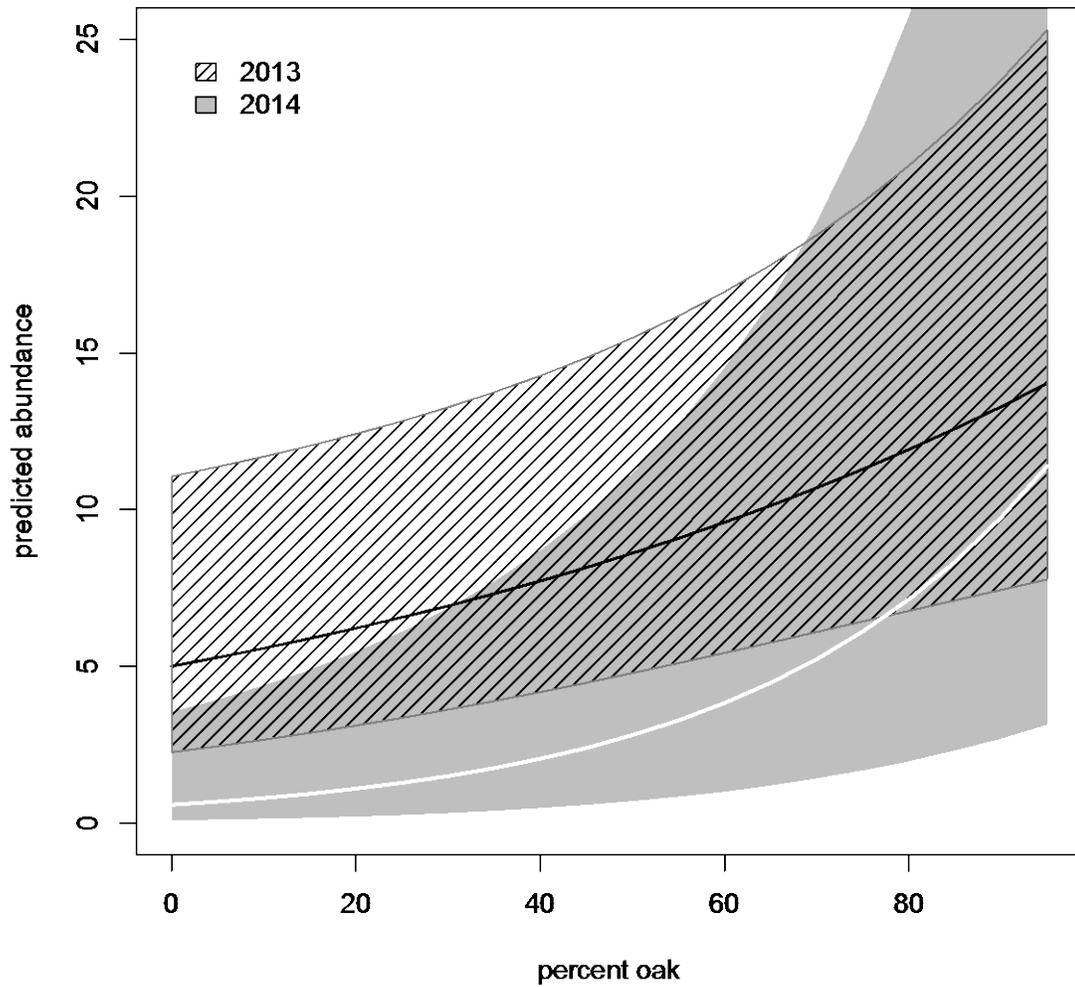


Figure 3.3. Predicted abundance of *Ambystoma opacum* plotted against percent of overstory trees (> 10 cm dbh) that are genus *Quercus* (b). Model is $p(\text{humidity}+\text{temp}+\text{temp}^2)\cdot\lambda(\text{oak})$ for both 2013 and 2014. 95% intervals are also plotted.

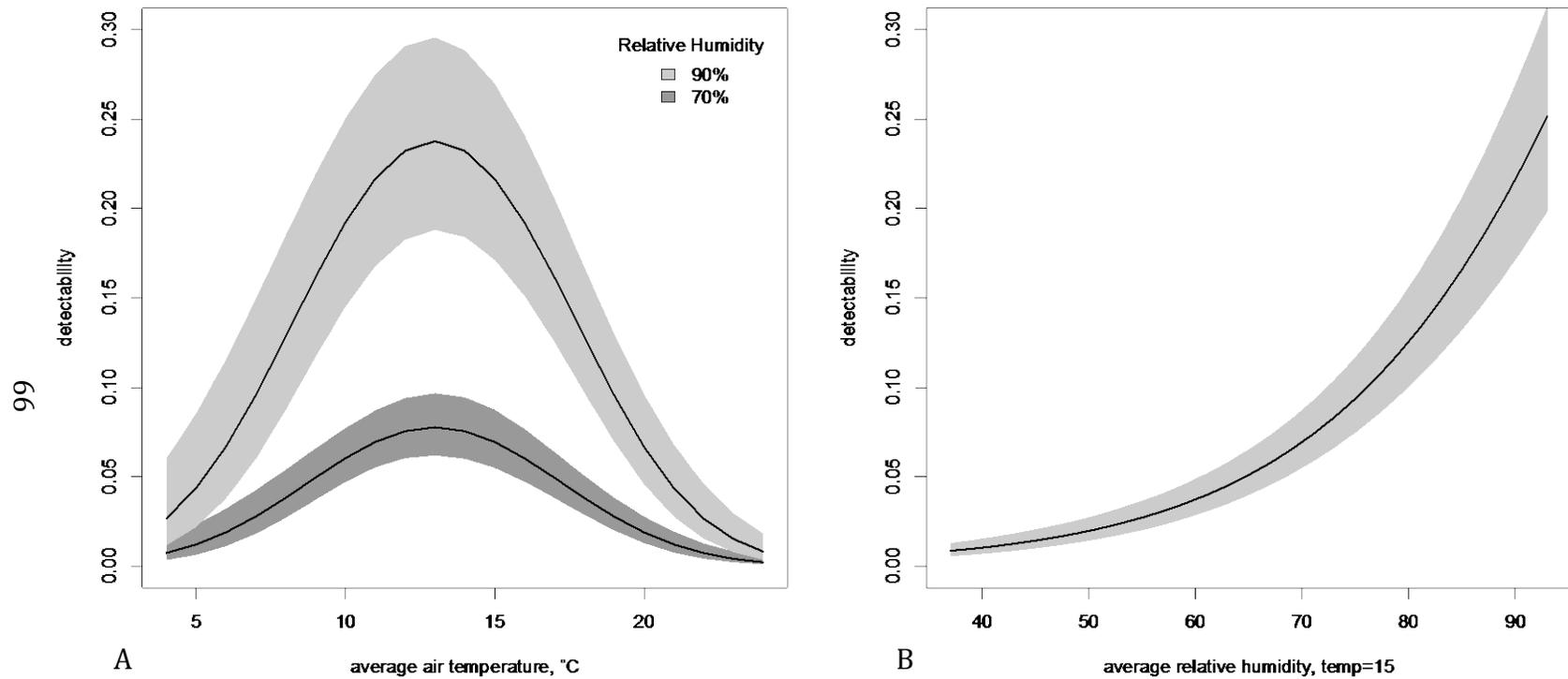


Figure 3.4. Detectability of *Plethodon cinereus* across the range of temperature (a) and humidity (b) observed in 2014 at Vinton Furnace State Experimental Forest and Zaleski State Forest. Humidity and temperature were averaged across the day of capture and the previous day. Model is $p(\text{humidity} + \text{temp} + \text{temp}^2) \cdot \lambda(\text{oak} + \text{rep})$.

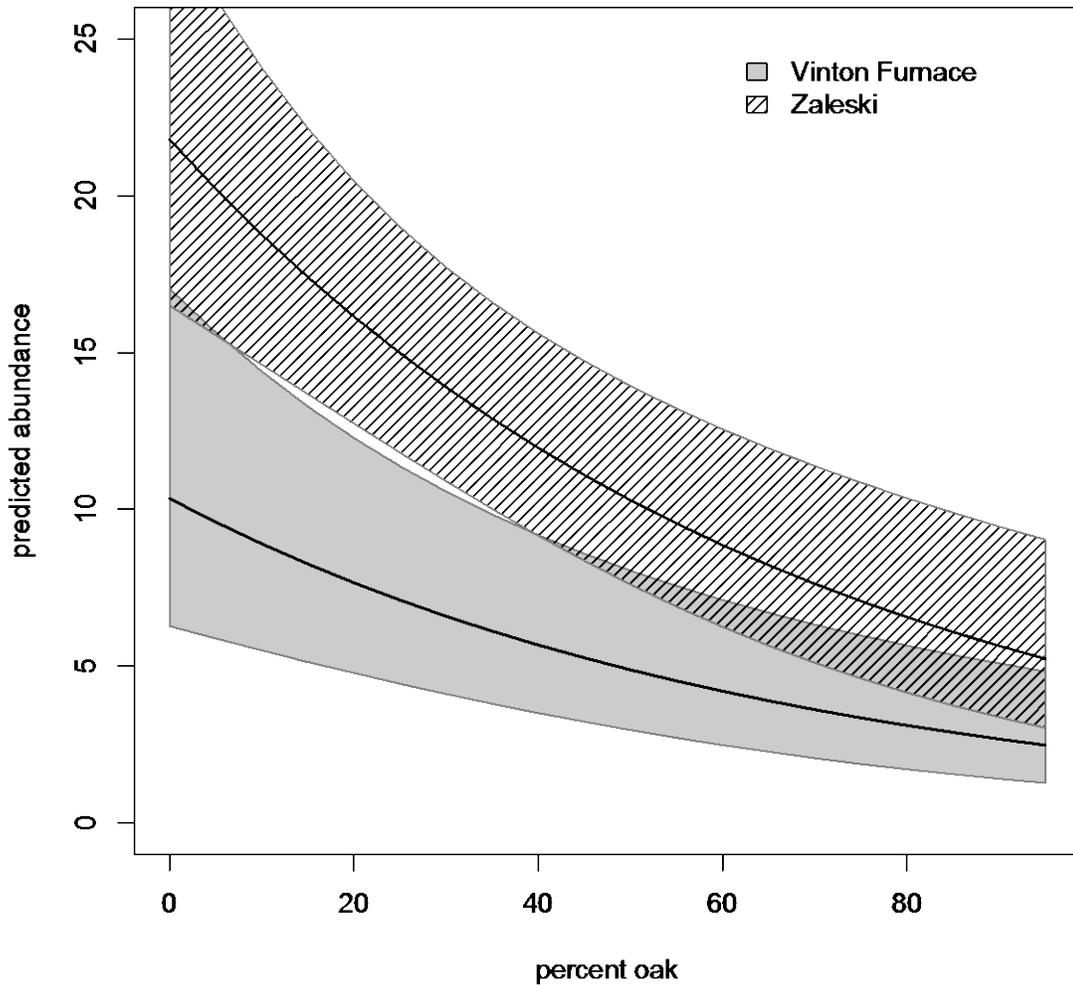


Figure 3.5. Predicted *Plethodon cinereus* abundance and 95% confidence intervals across the range percent overstory trees (> 10 cm dbh) that are genus *Quercus* as predicted by the 2014 $p(\text{humidity}+\text{temp}+\text{temp}^2)\cdot\lambda(\text{oak}+\text{rep})$ model. Vinton Furnace State Experimental Forest and Zaleski State Forest replicates plotted separately.

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Appendix A: Supplemental Materials

Table A.1 Summary of the habitat variables at each replicate and treatment, including mean and standard deviation. Habitat variables were percent canopy openness, volume of coarse woody debris, total number of saplings, percent of *Quercus* trees in the overstory, and total number of woody stems. Replicates were Vinton Furnace State Experimental Forest and Zaleski State Forest. The treatment sequence was a mid-story thinning during the winter of 2000-2001, followed by prescribed burns in April 2001, 2005, and 2010, prior to leaf-out.

	openness (%)		CWD (m)		saplings		oak (%)		stems	
	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
Vinton Furnace control	3	1	1.16	1.29	40	22	34	35	139	132
Vinton Furnace thin/burn	14	16	0.89	1.13	50	58	40	34	216	203
Zaleski control	2	1	0.27	0.30	23	21	17	17	162	67
Zaleski thin/burn	10	5	1.22	1.91	106	79	58	38	441	215

Table A.2. Eigenvalues and their contribution to the correlations in principal component analyses for all 20 sites as well as the two reduced scenarios used in the redundancy analysis. Sites and habitat variables occur with similar strength along the axis in all three scenarios.

	PC1	PC2	PC3	PC4	PC5
All 20 sites					
Eigenvalue	2.718	1.026	0.633	0.389	0.233
Proportion explained	0.544	0.205	0.127	0.078	0.047
Cumulative proportion	0.544	0.749	0.876	0.953	1.000
Vinton Furnace control removed—15 sites					
Eigenvalue	2.941	0.995	0.594	0.348	0.121
Proportion explained	0.588	0.199	0.119	0.070	0.024
Cumulative proportion	0.588	0.787	0.906	0.975	1.000
Vinton Furnace control removed—12 sites					
Eigenvalue	3.111	1.084	0.539	0.158	0.109
Proportion explained	0.622	0.217	0.108	0.032	0.022
Cumulative proportion	0.622	0.839	0.947	0.978	1.000

Table A.3. Results of pseudo-F tests, utilizing 1000 permutations, on the global redundancy analysis model as well as the first two axes for 2013, 2014, and both years combined.

	d.f.	var	F	p
2013 RDA				
Global test	5	0.140	2.77	0.051
RDA1	1	0.109	10.80	0.008
RDA2	1	0.018	1.79	0.167
residual	6	0.061		
2014 RDA				
Global test	5	0.127	4.901	0.001
RDA1	1	0.091	17.593	0.002
RDA2	1	0.020	3.857	0.006
residual	9	0.046		
2013 and 2014 combined				
Global test	5	0.092	2.211	0.092
RDA1	1	0.069	8.329	0.016
RDA2	1	0.012	1.433	0.251
residual	6	0.050		

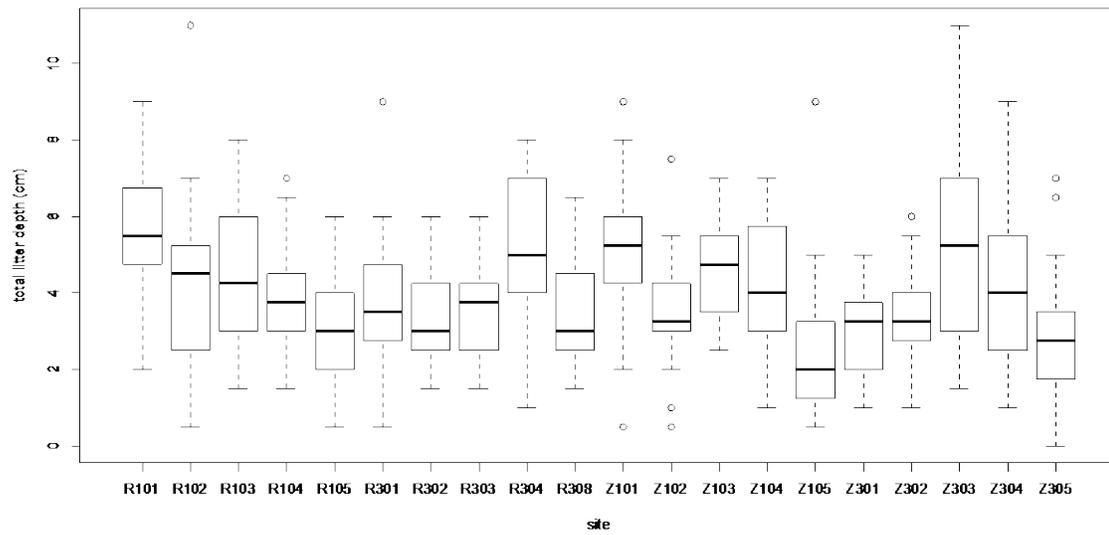
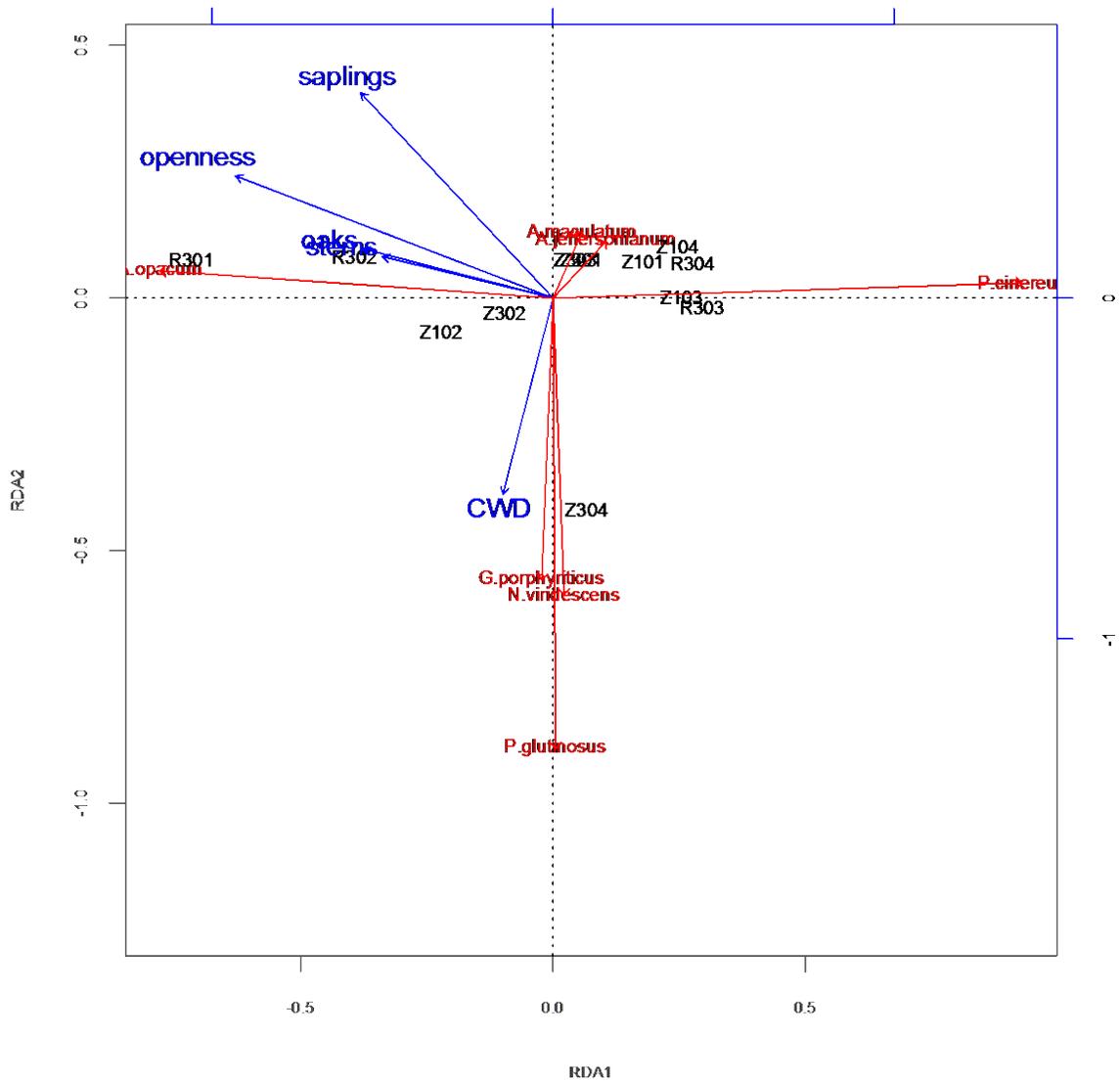


Figure A.1. Boxplot of 24 leaf litter depths at each site.

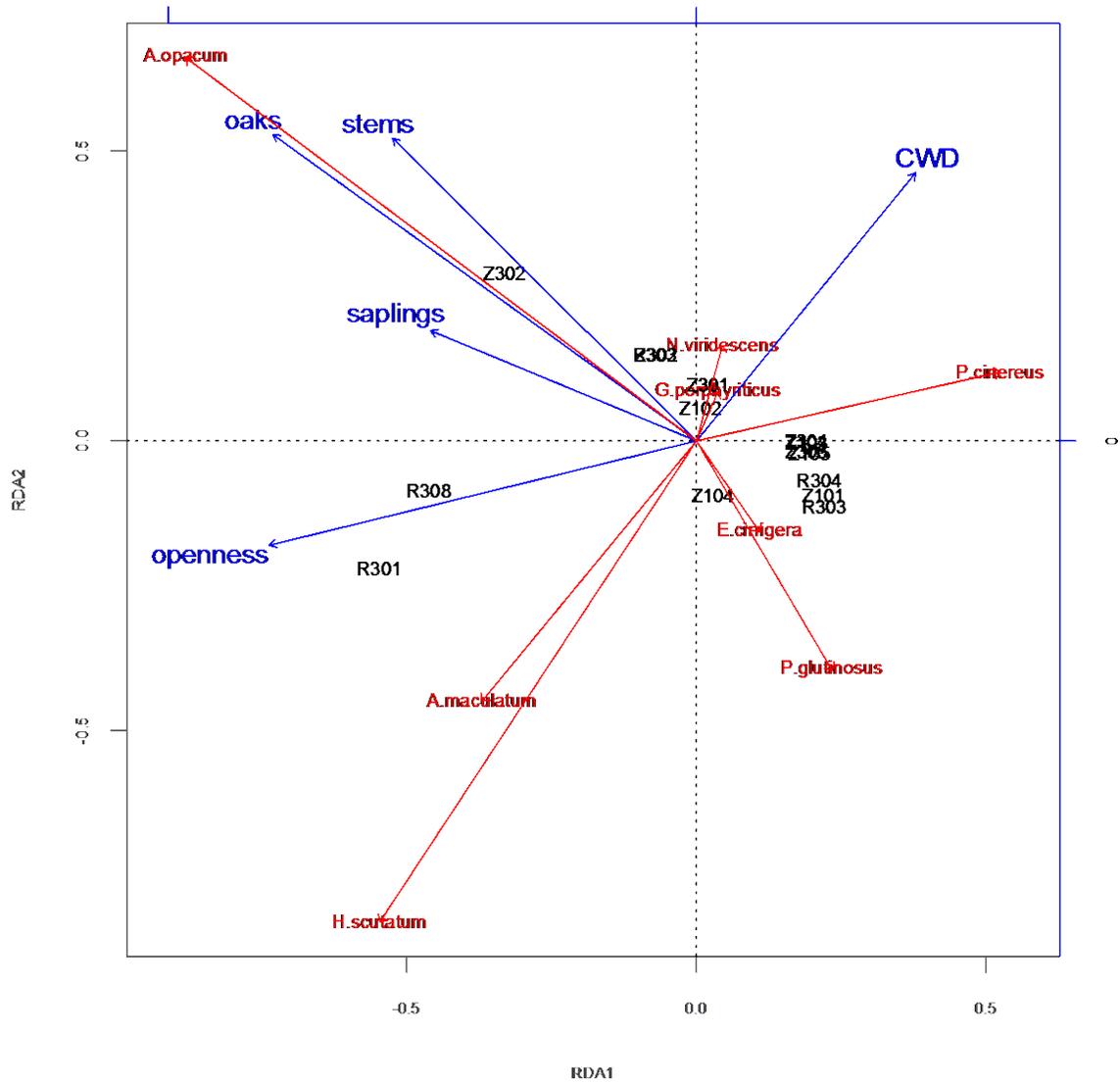


A. 2013

Continued

Figure A.2. Triplots of redundancy analysis for 2013 (a), and 2014 (b). Salamander abundance data in red, constrained by habitat variables, in blue. Sites plotted in black. The 2013 model explained 70% of variation, and the principal axis represented 54% of this variation. The 2014 model explained 73% of variation, and the principal axis represented 53% of this variation.

Figure A.2 Continued



B. 2014