January 2017

Natural Environmental Gradients Predict The Microhabitat Use, Fine-Scale Distribution, And Abundance Of Three Woodland Salamanders In An Old-Growth Forest

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Recommended Citation

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NATURAL ENVIRONMENTAL GRADIENTS PREDICT THE MICROHABITAT USE, FINE-SCALE DISTRIBUTION, AND ABUNDANCE OF THREE WOODLAND SALAMANDERS IN AN OLD-GROWTH FOREST

BY

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Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
December, 2017

ACKNOWLEDGEMENTS

I would like to thank Jake Hutton & Emily Baker for the countless hours they volunteered in the summer and on weekends to work in the field; Kelley Hoefer for her technical assistance and beautiful maps; and David Brown & Brad Ruhfel for serving as members on my graduate advisory committee. Most importantly, I thank my advisor, Stephen Richter, whose leadership, patience, and sage wisdom, made this academic endeavor possible. This research was funded by the Society for the Study of Amphibians and Reptiles Field Research Grant in Herpetology, the Kentucky Academy of Science Marcia Athey Fund, the Eastern Kentucky University Division of Natural Areas Student Grant-in-Aid Program, and the Eastern Kentucky University Department of Biological Sciences.

ABSTRACT

Woodland salamanders (Plethodonidae: *Plethodon*)—a group of sensitive, direct developing, lungless amphibians—are particularly responsive to gradients in environmental conditions. Because of their functional dominance in terrestrial ecosystems, woodland salamanders are responsible for the transformation of nutrients and translocation of energy between highly desperate levels of trophic organization (detrital food webs and high-order predators). However, the spatial extent of woodland salamanders' role in the ecosystem is likely contingent upon the distribution of their biomass throughout the forest. Therefore, a better understanding of woodland salamander spatial population dynamics is needed to further understand their role in terrestrial ecosystems. The objectives of this study were to determine if natural environmental gradients influence the microhabitat use, fine-scale distribution, and abundance of three species of woodland salamander—*Plethodon richmondi, P. kentucki*, and *P. glutinosus*. These objectives were addressed by assessing microhabitat conditions and constructing occupancy, co-occurrence, and abundance models from temporally-replicated surveys ($N = 4$) at forty 0.08-ha sample plots within a ca. 42 ha old-growth forest in the Cumberland Plateau region of southeastern Kentucky. This study finds that patterns of microhabitat use, occupancy, and abundance of *P. richmondi* and *kentucki* reflected physiological restraints associated with desiccation vulnerability and thermo-osmoregulatory requirements of small to mid-sized salamanders. *Plethodon richmondi* occupied markedly cooler microhabitats, had the most restricted fine-scale distribution (mean occupancy probability [$\hat{\bar{\psi}}$] = 0.737), and exhibited variable abundance, from <250 to >1000 $\mathrm{N \cdot ha^{-2}}$, associated with increased soil moisture and reduced solar exposure due to slope face. While more ubiquitously distributed ($\hat{\bar{\psi}} = 0.95$),

P. kentucki abundance varied from >1000 to <400 $\mathrm{N \cdot ha^{-2}}$ in association with increased solar exposure from canopy disturbance and landscape convexity. *Plethodon glutinosus* displayed a dramatic tolerance to thermal environments by preferentially occupying warm microhabitats and relying only minimally upon subterranean refugia for thermo-osmoregulation (temporary vertical emigration). Given the critical role that woodland salamanders play in the maintenance of forest health, regions which support large populations of woodland salamanders, such as those highlighted in this study (mesic forest stands on north-to-east facing slopes with dense canopy and abundant natural cover) may provide enhanced ecosystem services and support the stability of the total forest.

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CHAPTER I

INTRODUCTION

Observations of biological patterns along physical gradients form the foundation of modern ecology and biogeography (e.g. Hutchinson 1957, MacArthur & Pianka 1966, MacArthur & Wilson 1967, Simberloff 1974), and a functional understanding of the mechanisms responsible for these patterns is crucial for the preservation of biodiversity (Gaston 2000, Willig *et al.* 2003). Furthermore, analyzing the distribution and abundance of species along environmental gradients yields invaluable information about their niche requirements (Costa *et al.* 2008), population dynamics (Peterman & Semlitsch 2013), and biotic interactions (Maestre *et al.* 2009), and can even inform decisions about the management and restoration of landscapes for species conservation (Peterson 2006). However, human-altered landscapes may not provide the spectrum of environmental conditions necessary to fulfill the collective niche requirements of a community (Oksanen & Minchin 2002, Estavillo *et al.* 2013). In unaltered landscapes, the distribution of species is a function of natural environmental gradients, which include abiotic factors (e.g. surface temperature, moisture, topographic relief, water and soil chemistry, and solar radiation) and biotic factors (e.g. vegetative structure and presence of predators, prey, and mates). Taxa likely to exhibit strong responses to such natural gradients are those with limited dispersal capabilities (Cushman 2006), low reproductive success (Elton 2000), and acute sensitivity to environmental conditions (Buckley & Jetz 2007).

One such group, amphibians, is particularly responsive to environmental gradients (Araújo *et al.* 2007, Werner *et al.* 2007, Semlitsch *et al.* 2015). Because of their highly permeable skin, amphibians are acutely sensitive to the chemical environment (Boone *et al.* 2007, Willson *et al.* 2012), thermal and hydrologic regimes (Walls *et al.* 2013, Semlitsch *et al.* 2015), and the microbiome (i.e. emerging pathogenic diseases; Carey *et al.* 2003, Collins *et al.* 2003). As carnivorous ectotherms, amphibian population dynamics are closely tied to landscape structure (Hecnar & M'Closkey 1996, Rothermel & Semlitsch 2002) as well as prey availability (Greene *et al.* 2008), making them especially sensitive to habitat destruction and degradation (Brooks *et al.* 2002). These characteristics likely explain why amphibians are currently experiencing unprecedentedly precipitous declines on a global scale (Houlahan *et al.* 2000, Alford *et al.* 2001, Stuart *et al.* 2004). Nevertheless, amphibians' hypersensitivity to environmental conditions translates into an effective taxonomic indicator of ecosystem integrity (Welsh & Ollivier 1998, Welsh & Droege 2001).

Despite this sensitivity, amphibians represent a tremendous component of biomass in aquatic (Gibbons *et al.* 2006), terrestrial (Burton & Likens 1975b, Petranka & Murray 2001), and riparian (Peterman *et al.* 2008) ecosystems. Because the life history of many amphibians involves movement between and among aquatic and terrestrial ecosystems (Regester *et al.* 2006), they are responsible for the transformation (Burton & Likens 1975a) and translocation (Capps *et al.* 2014, Luhring *et al.* 2017) of substantial quantities of energy throughout the landscape. However, the role of energy transformation is not unique to biphasic organisms.

Terrestrial woodland salamanders (Caudata: Plethodontidae: *Plethodon*), which lack aquatic larval stages (i.e. have direct development), are among the most abundant vertebrate animals in eastern deciduous forests of North America (Petranka & Murray

2001, Semlitsch *et al.* 2014)—reaching densities between 0.73 and 18.46 individuals per m^2 (Semlitsch *et al.* 2014, O'Donnell & Semlitsch 2015). They also act as predators of detrital food webs (Best & Welsh 2014, Hutton *et al.* 2017, Davic & Welsh 2004) and represent a prey resource for a wealth of vertebrate and invertebrate predators (for a taxonomic review of *Plethodon* predators, see Semlitsch 2014). As such, woodland salamanders are hypothesized to serve as a key energetic intermediary between highly disparate levels of trophic organization in terrestrial ecosystems (detrital communities and high-order vertebrate predators; Burton & Likens 1975b) and exert a significant, top-down, regulatory force upon detrital food webs, leaf litter decomposition, and organic material retention (Burton & Likens 1975a, Hairston 1987). Therefore, woodland salamanders may significantly influence the direction and magnitude of energy flow through ecosystems (Davic & Welsh 2004).

Wyman (1998) found that, through predation of detrital food webs, woodland salamanders (*Plethodon cinereus,* eastern red-backed salamander) can indirectly reduce leaf-litter processing rates by 11–17%, aiding in the retention of organic carbon in forests, and perhaps even reducing gaseous carbon fluxes into the atmosphere via heterotrophic decomposition of organic material. Additional studies with terrestrial salamanders (Plethodontidae) have found that the strength and sign of top-down effects on leaf litter decomposition and detrital communities is subject to variation (Walton 2005, Walton & Streckler 2005, Walton *et al.* 2006, Homyack *et al.* 2010, Best & Welsh 2014). Recent evidence suggests that variation in the effects of terrestrial salamanders on forest floor dynamics is likely correlated with spatio-temporal variability in environmental conditions (Walton 2013) and the abundance of salamander predators

(Hickerson *et al.* 2017). Walton (2013) found that patterns in leaf litter mass and moisture predicted the effects of terrestrial salamanders on detrital food webs; increasing litter mass may amplify the predatory effect of salamanders on invertebrate prey, while increasing litter moisture may buffer such predatory effects. Hickerson *et al.* 2017 found that increased salamander abundance corresponded with slower rates of leaf litter decomposition, which contributes to higher organic material retention in terrestrial ecosystems (Aerts 1997). Therefore, the nature of woodland salamanders' role in terrestrial ecosystem nutrient cycling is likely contingent upon the spatial distribution of their biomass within the ecosystem (Hickerson *et al.* 2017, Semlitsch *et al.* 2014), which is influenced by spatial patterns in environmental conditions and resource availability (Walton 2013, Peterman & Semlitsch 2013, Milanovich & Peterman 2016).

Numerous studies have found the distribution of woodland salamanders to be influenced chiefly by terrestrial ecosystem features such as soil moisture (Jaeger 1971a, Wyman 1988, Peterman & Semlitsch 2013), availability of natural cover (i.e. coarse woody debris, rocky cover, and leaf litter; McKenny *et al.* 2006, O'Donnell *et al.* 2014), and forest composition/canopy structure (Gibbs 1998, Peterman & Semlitsch 2013). Furthermore, presence of heterospecifics has been found to influence microhabitat usage (Keen 1982, Farallo & Miles 2016), distribution (Hairston 1950, Jaeger 1970, 1971a, 1972b), and abundance (Hairston 1951) of individual species. Thus, the species-specific contribution of woodland salamanders to terrestrial ecosystem processes may be modified through population-level effects of interspecific competition. Due to the diversity and endemism of woodland salamanders, particularly in Appalachian forests, where their diversity is greatest (Dodd 2004), community structure varies dramatically across physiographic regions. Therefore, community interactions are likely geographically nuanced and not easily generalizable from any single region.

With the desire to further understand the inherent complexity of woodland salamander ecology in Appalachian forests, descriptions of veritable detail have been repeatedly published for well over a century (e.g. Cope 1870, Brimley 1912, King 1939, Hairston 1949, Highton 1972, 1995, Dodd 2004), and these observations are paramount to our knowledge of woodland salamander natural history and ecology. However, many studies used occurrence records, either from field surveys or natural history collections, and count indices to approximate the distribution and abundance of woodland salamanders (Anderson 2001; although see McKenny *et al.* 2006, Peterman & Semlitsch 2013, Semlitsch *et al.* 2014). Certain aspects of woodland salamander natural history, such as subsurface migration (temporary emigration) and crypsis, when combined with the ability (or inability) of observers to detect a species, allow salamanders to occupy a patch without being detected (Hyde & Simons 2001, Bailey *et al.* 2004). Therefore, a lack of detection does not always imply absence. Likewise, in many circumstances the perceived abundance of a species is confounded by numerous variables, including some biological (e.g. crypsis, emigration, foraging and breeding behavior; Durso *et al.* 2011, O'Donnell & Semlitsch 2015), some environmental (e.g. precipitation, season, surface temperature, abundance of cover items; Hyde & Simons 2001, Guzy *et al.* 2014), and some human (observer experience, visual/auditory acuity, search vigor; Simons 2007). Therefore, species counts often serve insufficiently as indices of abundance. Central to these issues is the concept of imperfect detection (Gu & Swihart 2004): detection is seldom perfect and often covaries predictably with certain factors. Fortunately, modeling the distribution and abundance of species while accounting for imperfect detection is now possible without the implementation of invasive and expensive capture-mark-recapture methods through the use of hierarchical models of occupancy and abundance (MacKenzie *et al.* 2002, Royle 2004, Pellet & Schmidt 2005, Kéry & Royle 2016). Hierarchical models allow the estimation of population parameters (distribution and population density), while simultaneously incorporating heterogenous detection probabilities.

Studies of the spatial population dynamics of woodland salamander species occurring in syntopy, which incorporate imperfect detection, are needed to further understand the role of these animals in terrestrial ecosystems. Furthermore, woodland salamander populations in lower elevation Appalachian forests, like those of central Appalachia, have not been studied as thoroughly as in regions with greater topographic relief and higher proportions of land allocated for conservation (i.e. Piedmonts, Blue Ridge, southwestern Appalachia). Therefore, this study examines the population dynamics of an assemblage of woodland salamanders—*P. richmondi, P. kentucki,* and *P. glutinosus*—within an old-growth forest in the Cumberland Plateau region of Appalachia.

The objectives of this study were to (1) determine if natural environmental gradients associated with the transition from mesic to xeric forest habitat within Appalachian forest influence the microhabitat use, fine-scale distribution, and abundance of woodland salamanders, (2) determine if those relationships vary among species. These objectives were addressed by assessing the microhabitat of woodland salamanders and constructing models of occupancy and abundance, incorporating imperfect detection, from temporally-replicated surveys within an old-growth forest in eastern Kentucky.

CHAPTER II

METHODS

Study Site

This study was conducted at Lilley Cornett Woods Appalachian Ecological Research Station (LCW), which contains 102-ha of old-growth forest (Figure 1). Lilley Cornett Woods is a stable mixed mesophytic forest in the Cumberland Plateau region of southeastern Kentucky. The dissected topography of this region greatly modifies local climate and generates a gradient of soil moisture, depth, and complexity, resulting in high botanical diversity (Braun 1950, Chapman & McEwan 2013). Martin (1975) described nine upland forest communities in LCW, composed chiefly of several beech communities, as well as oak, sugar maple-basswood-tulip poplar, and hemlock communities. Generally, mesic habitats are found on north-to-east facing slopes with minimal convexity and feature deep soils, rich with organic matter; xeric habitats are represented on most south-to-west facing slopes and ridge tops, and contain shallow soil horizons dominated by clay (pers. obs., Martin 1975). With no history of timber harvest the old-growth forest at LCW has experienced virtually no substantial anthropogenic disturbance with the exception of understory livestock grazing, which ended in the 1950s. Of the three tracts of old-growth forest at LCW, one tract, “Shop Hollow”, (Figure 1, panel E) currently experiences little disturbance from human recreation (only guided hiking on an established trail) and invasive plants (J. Peters, unpubl. data), and was therefore chosen as the location for this study. Shop Hollow features 57 permanent 0.08-ha circular sample plots, originally established by Martin (1975). Sample plots are stratified by aspect and slope (lower [< 345 m], middle [345–410 m], upper [411–467 m], and ridge [> 467 m]; Figure 2). Data collection occurred at all sample plots free of intersecting streams (N=40; Figure 1), and plots contained relatively minimal understory vegetation.

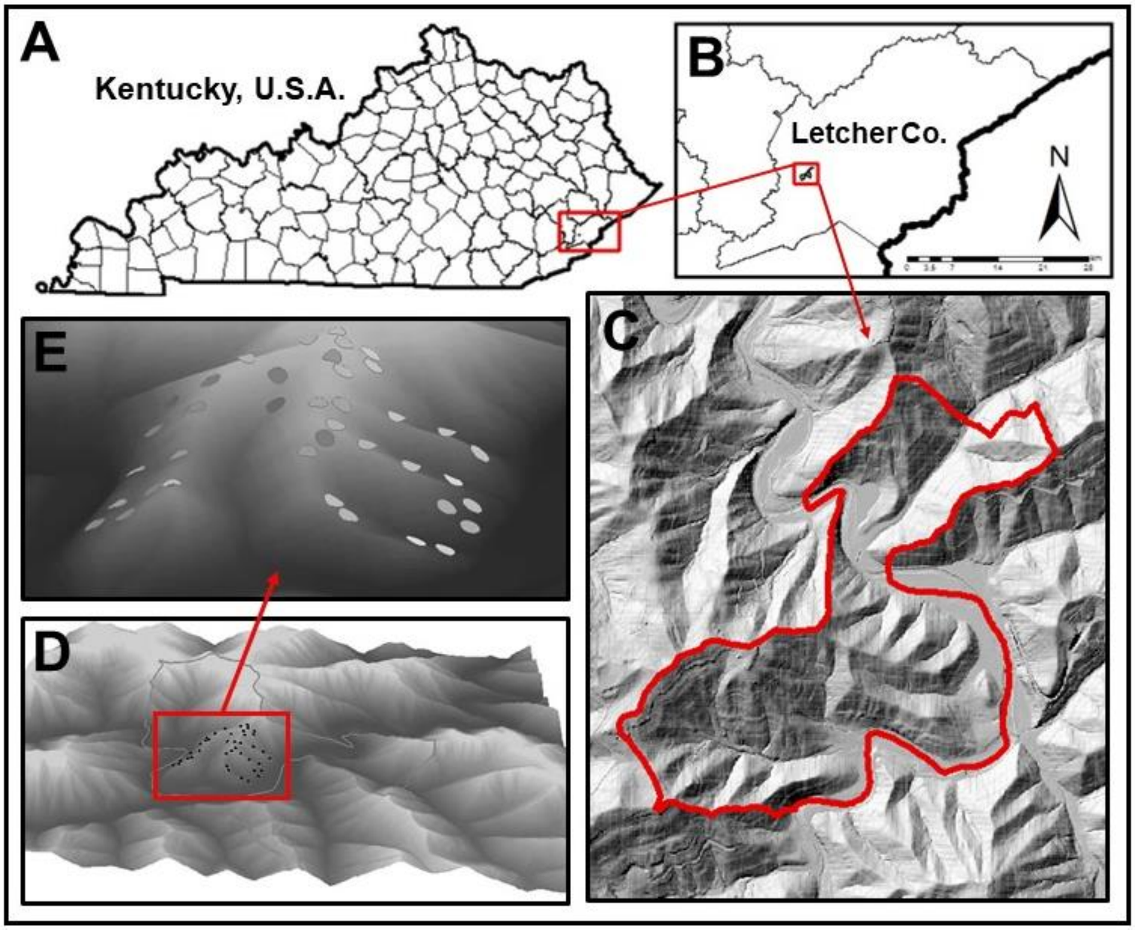

Figure 1. Study location: Lilley Cornett Woods Appalachian Ecological Research Station. (A) County map of Kentucky, USA, (B) Letcher County, KY, (C) Boundary of old-growth forest at Lilley Cornett Woods Appalachian Ecological Research Station (LWC), (D) Terrain map of LCW; points represent amphibian sampling locations (N=40), (E) 0.08-ha circular sample plots in the Shop Hollow stand of LCW.

Amphibian Sampling

LCW features three species of *Plethodon* (Caudata: Plethodontidae) salamander found throughout much of the Cumberland Plateau region: *Plethodon glutinosus* (northern slimy salamander, Green 1838), *P. kentucki* (Cumberland Plateau salamander, Mittleman 1951), and *P. richmondi* (southern ravine salamander, Netting & Mittleman 1938). Additional genera (*Desmognathus*, *Pseudotriton*, *Gyrinophilus*, *Eurycea*, and *Ambystoma*) were not captured frequently enough to merit further analysis.

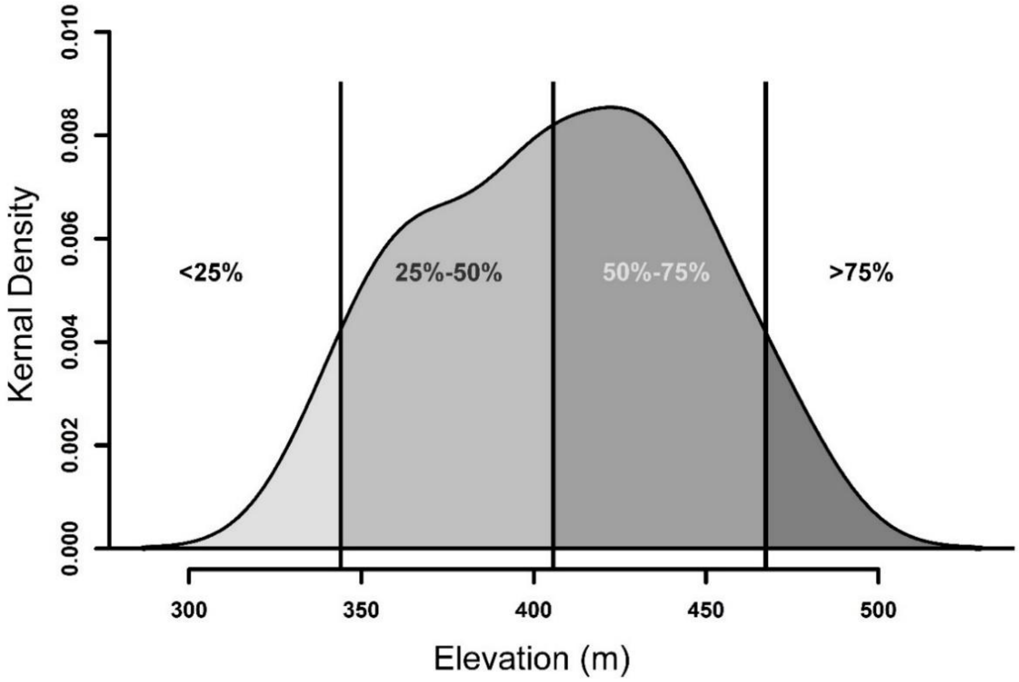

Figure 2. Kernel density plot of the elevational distribution of amphibian sampling plots (N=40) in Shop Hollow at Lilley Cornett Woods Appalachian Ecological Research Station, Letcher County, Kentucky, USA.

This study relied upon visual encounter surveys (VES) to detect species, and therefore all observations resulted from hand captures during standardized searching. Sampling events consisted of four two-day intervals occurring from 15 October to 13 November 2016. Surveys were conducted along a linear 3-m x 36-m transect through the center point of each 0.08-ha circular sample plot. To eliminate sampling bias and ensure plots were sampled thoroughly, the direction of VES transects during every sampling event was determined by randomly selecting a bearing between 0° and 180°, with the midpoint of all transects pivoting at the geometric center of the circular sample plot. In LCW, woodland salamanders are found primarily by searching under coarse woody debris, rocks, and other natural cover on the forest floor. Moist leaf litter may also provide suitable habitat, but preliminary surveys with comparable effort yielded substantially fewer captures. During surveys, all coarse woody debris and rocky cover within the 96 m^2 were flipped, and microhabitats beneath were examined for the presence of salamanders before replacing cover items to their exact position. Microhabitat temperature was recorded temperature under every cover item within the sampling transect using a handheld infrared thermometer (Kintrex, model: IRT0421). Microhabitats inhabited by salamanders were noted to allow for a comparison of temperatures between inhabited, uninhabited, and inhabited + uninhabited (ambient) microhabitats. Microhabitat moisture was recorded only under cover objects inhabited by salamanders using a moisture probe (Decagon Devices, model: Pro Check). Once captured, snout-to-vent length (SVL) and tail length (TL) were measured by placing the animal in a clean plastic bag and measuring from the tip of the snout to the posterior edge of the vent (accuracy = 1 mm), and mass was recorded using 10-g or 20-g PESOLA scale (accuracy = 0.1 g and 0.2 g, respectively). Following data collection animals were returned to their precise capture location. All protocols for the use and handling of amphibians were approved by the Eastern Kentucky University Animal Care and Use Committee (IACUC protocol # 05-2015).

Site Covariates

Soil moisture of each sampling plot was measured during every survey at five equidistant points along the transect using a Pro Check moisture probe (Decagon Devices, Inc.). Moisture data were then averaged across sites and surveys to obtain an accurate estimate of site-level variation in soil moisture within the sampling season. Quantification of forest canopy openness was achieved using hemispherical canopy photography (Herbert 1987, Frazer *et al.* 1997; Baldwin *et al.* 2006). Canopy structure was captured with a 24-megapixel digital single lens reflex camera (Nikon D7100), fitted with a 180° lens (Nikon AF DX Fisheye-Nikkor 10.5 mm f/2.8G ED; Nikon Instruments, Melville, NY, U.S.A.). The camera was adjusted using a leveling tripod, and photographs were taken on automatic settings with the camera angled vertically at the underside of the canopy. All photographs were taken during the fall of 2016, just prior to leaf off. Percent canopy openness was calculated by converting images into binary color (black pixels = closed canopy, white pixels = open canopy) using a binarization algorithm provided by the Auto Threshold Plugin for ImageJ software (Abramoff *et al.* 2004, Rasband 2014), and then calculating the percent of white pixels in each frame.

A GIS and remotely sensed data were used to gather several reportedly useful covariates for modeling population parameters of woodland salamanders: aspect, elevation, slope, topography, canopy, and solar radiation (Hairston 1951, Ford *et al.* 2002, Peterman & Semlitsch 2013, Semlitsch *et al.* 2014). See Table 1 for a description of all site covariates. A 1.11-m^2 digital elevation model was used to derive the following layers: aspect, slope, Topographic Position Index, and Direct Solar Radiation. Aspect was scaled into a linear variable ranging from 0 (xeric, southwest-facing slopes) to 2 (mesic, northeast-facing slopes) using the Beers transformation (Beers *et al.* 1966, O'Donnell *et al.* 2015a). Topographic Position Index (TPI) is the slope position of sample plots relative to surrounding landscape. It was calculated using a neighborhood function, which calculates changes in DEM cells within a chosen, 150-m, buffer of the sample site (Guisan & Weiss 1999, Weiss 2001). Direct Solar Radiation, a component of the total solar radiation, represents the quantity of solar radiation remaining after a fraction is absorbed by the atmosphere (diffuse solar radiation) or reflected off of the earth's surface (reflected solar radiation). Normalized Difference Vegetation Index (NDVI) is a measure of vegetative cover (range: -1.0 [barren] to 1.0 [heavily vegetated]), and was derived using imagery from the National Agriculture Imagery Program. All data were gathered and analyzed with ArcGIS 10.3 (ESRI 2011).

Table 1: Description and summary statistics of covariates used in occupancy and N-mixture models of three species of woodland salamanders surveyed in 2016 at Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., Kentucky, U.S.A.). Covariates quantify two important processes: "sampling" (detectability) and "site" (species occupancy or population size).

Covariate	Parameterization	Covariate description	Unit	$\bar{x}$	Q_1	Q_3
Sampling (p: conditional capture probability, effective detection probability)	p(CWD, ...)	*Abundance of coarse woody debris* †	qty.	3.05	1.00	4.00
	p(DAY, ...)	*Day of the year survey occurred*	Julian date	306.50	300.80	312.20
	p(LLD, ...)	*Leaf litter depth* †	cm	5.45	4.45	6.75
	p(LUX, ...)	*Luminous flux* †	$\text{lumen}\cdot\text{m}^{-2}$	510.40	175.00	740.00
	p(ROC, ...)	*Abundance of rocky cover* †	qty.	5.00	1.00	7.00
	p(TOD, ...)	*Time of day survey occurred*	24 hour time	1310.00	1102.00	1518.00
Site (occupancy and conditonal occupancy probabilities, ψ; esimated population size, λ)	ψ,λ(ASP, ...)	*Beers-transformed aspect* ‡	range (0,2)	1.19	0.33	1.87
	ψ,λ(CAN, ...)	*Canopy openness* † §	% *	0.26	0.20	0.28
	ψ,λ(ELV, ...)	*Elevation* ‡	m	407.40	375.40	436.40
	ψ,λ(MST, ...)	*Soil moisture* †	% **	0.14	0.11	0.17
	ψ,λ(RAD, ...)	*Direct Solar Radiation* ‡	$\text{Watts}\cdot\text{hr}^{-1}\cdot\text{m}^{-2}$	746124.00	677918.00	846907.00
	ψ,λ(TPI, ...)	*Topographic Position Index* ‡	***	14.20	4.05	23.55
	ψ,λ(VEG, ...)	*Normalized Difference Vegetation Index* ‡§	****	126.60	123.80	130.40

†—collected *in situ* , ‡—spatially derived metric, §—competing metric, *—expressed as: (open pixles/closed pixels)x100,
—expressed as: $(m^3\cdot m^{-3})$x100, *—measure of slope position relative to surroundings ("+"=ridges, "-"=valleys, "0"=flat)
****—measure of vegetative density (range: -1.0 = barren, 1.0 = heavily vegetated)

Sampling Covariates

The quantity of fallen coarse woody debris larger than 20 cm in diameter (Muller and Liu 1991) and rocky cover within each VES transect were counted. Leaf-litter depth was measured with a metric ruler at five equidistant points within each survey transect. Solar conditions during surveys were quantified by measuring the ambient luminous flux (perceived power of light) at breast height with a digital illuminance light meter (TekPower, model: LX1330B). Finally, date and time of day of each survey was recorded. See Table 1 for a description of all sampling covariates.

Data Analysis

To test the hypothesis that microhabitat use differs among the three species of woodland salamanders at LCW, the average temperature and soil moisture content of each species' refugia was compared using a two-way ANOVA ($\alpha = 0.05$), and if differences were detected, multiple comparisons were made using a Tukey's honest significant difference (HSD) test. The hypothesis that salamanders are selecting microhabitats with temperatures that differ from ambient microhabitat temperature was tested by comparing average temperatures of microhabitats occupied by each species with the average temperature of all available microhabitat (occupied + unoccupied) within the transect using independent *t*-tests ($\alpha = 0.05$). Additionally, an ordinary least squares regression was used to determine if salamander body mass adjusted for SVL predicted microhabitat temperature ($\alpha = 0.05$). A two-way ANOVA ($\alpha = 0.05$), followed by a Tukey HSD test, was used to determine differences in salamander body masses by species. All statistical procedures were performed in the R programming environment (v. 3.4.1; R Core Team 2017).

Because detection probabilities of salamanders were assumed <1, hierarchical models (HMs) were used to approximate woodland salamander distributions and population size from repeated surveys of unmarked animals (MacKenzie & Royle 2005). One of the most restrictive assumptions of HMs is population closure. In the context of HMs used for occupancy (occupancy models), the state parameter—whether a species is present or absent—must remain static during and between surveys (i.e. closed to migration, extinction, and colonization). The population closure assumption for HMs of abundance (*N*-mixture models) restricts any net flux in population size, and therefore populations must remain closed to births, deaths, migration, extinction, and colonization. While exhaustive, these assumptions can be met by conducting field surveys in rapid succession, minimizing the duration between surveys (MacKenzie & Royle 2005, MacKenzie *et al.* 2006). Therefore, the sampling design of this study satisfied these assumptions.

Although occupancy and *N*-mixture models both require an estimate of detectability to compute state parameters, the specific components of detection used by each are surprisingly different (O’Donnell and Semlitsch 2015). Most occupancy models, including the model used in this study, estimate the “conditional capture probability” ($\hat{p}_{\psi}$), defined as the probability of capture, given the individual is present (capture probability | availability). For these terms, availability is defined as 1 – (temporary emigration). *N*-mixture models estimate a form of detection which combines a term for the ability of the observer to capture an individual that is present (conditional capture probability) with a term for the individual’s availability for capture (expressed as:

availability x conditional capture probability), and is thus referred to as an “effective detection probability” (p_λ).

Occupancy models (MacKenzie *et al.* 2002) were used to estimate the probability that a species occupied a given site (ψ), while *N*-mixture models (Royle 2004) were used to estimate species true population size (λ). Fitting occupancy and *N*-mixture models followed a stepwise procedure (Kendall *et al.* 2009, Scherer *et al.* 2012, Peterman & Semlitsch 2013, O’Donnell *et al.* 2015b; see Figure 3 for workflow diagram): (1) models were constructed to estimate detection probabilities by holding the state parameters, ψ and λ, constant (Appendices 1–6); (2) the model-averaged effects ($\hat{\hat{\beta}}$) of each p covariate was calculated using multi-model inference (Burnham & Anderson 2002, Mazerolle 2006) to determine importance; (3) models with a single site covariate were then constructed to estimate ψ and λ using p covariates selected from the previous step; (4) from the resulting models, $\hat{\hat{\beta}}$ was calculated for each site covariate to determine which was important in explaining ψ and λ; (5) if two or more site covariates featured significant $\hat{\hat{\beta}}$ estimates (95% CI not containing “0”), models containing two site covariates were run and $\hat{\hat{\beta}}$ recalculated; (6) all models were ranked and multi-model inference was used to make predictions across all models. Models failing to converge or exhibiting signs of instability (producing inflated confidence intervals, arbitrarily large standard errors, or non-numeric predictions) were discarded.

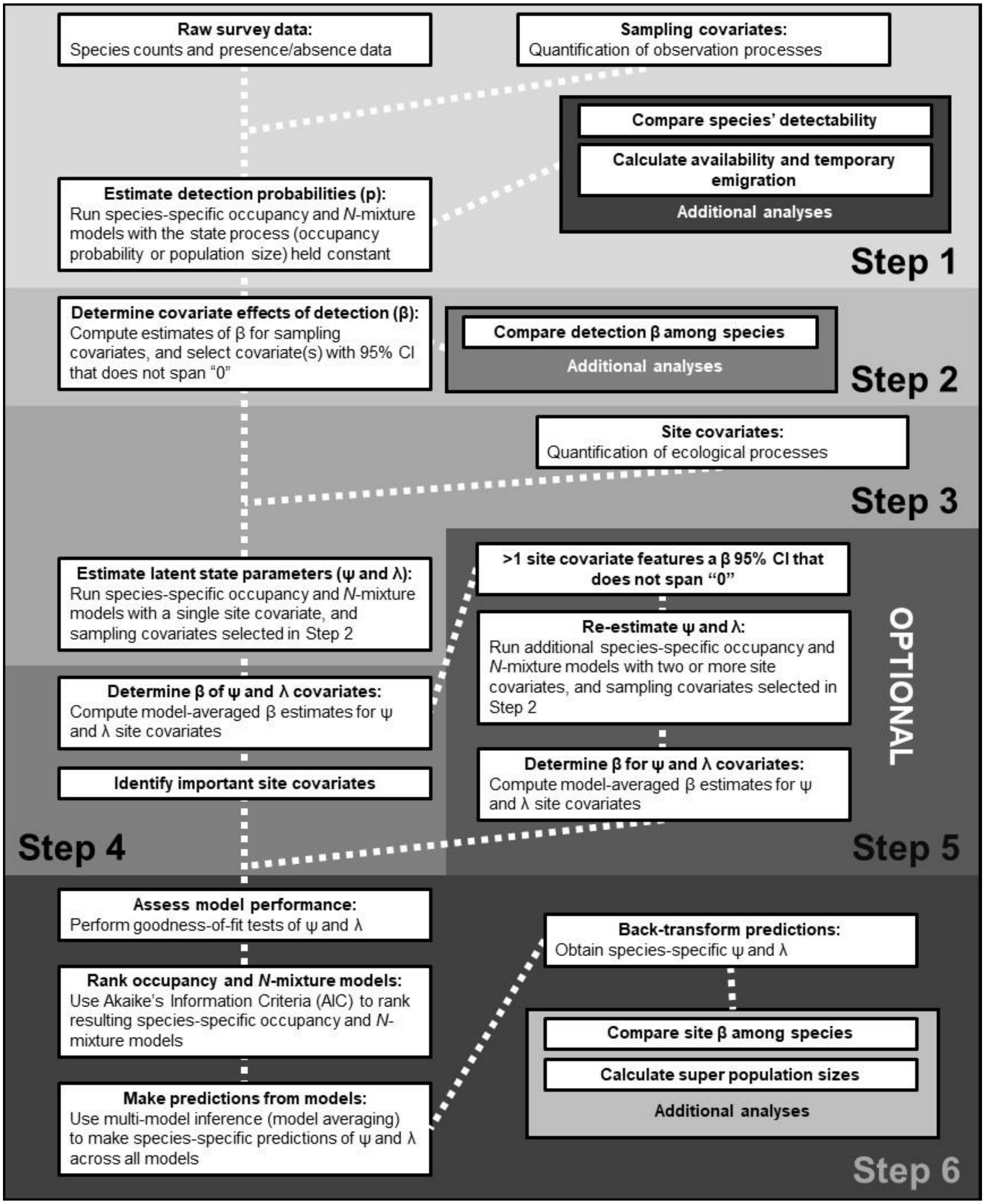

Figure 3. Diagrammatic representation of the workflow process of modeling population parameters: detectability metrics, occupancy probability, and abundance in *Plethodon* salamanders at Lilley Cornett Woods Appalachian Ecological Research Station, Letcher County, Kentucky, USA.

Prior to fitting, all site and sampling covariates were standardized to a mean of zero and unit variance by subtracting the arithmetic mean and dividing by the standard deviation (as recommended by Fiske & Chandler 2011, 2017). Occupancy and *N*-mixture models were fitted using a maximum-likelihood approach with package "unmarked" (Fiske & Chandler 2011), in the R programming environment (v. 3.4.1; R Core Team 2017). Goodness-of-fit tests with 10,000 parametric bootstrap iterations on a Chi-square discrepancy were performed on the most highly parameterized (global) occupancy and *N*-mixture models of each species to assess model adequacy and check for overdispersion, as recommended by Kéry & Royle (2016). These tests confirmed that each species' occupancy and *N*-mixture models, barring one, performed well under standard parameterization, with little or no evidence of lack of fit ($p > 0.05$, $\hat{c} \approx 1$; Table 2). Perhaps due to sparse detections, the *N*-mixture model for *P. glutinosus* was moderately overdispersed ($\hat{c} = 1.92$, Table 2; Kéry & Royle. 2016). Alternative negative binomial (NB) and zero-inflated Poisson (ZIP) distribution models were both fitted and compared to the Poisson distribution model originally created. Additional goodness-of-fit tests determined a ZIP distribution produced the least over-dispersed model ($p = 0.226$, $c = 1.357$), surpassing that of NB ($p = 0.231$, $c = 1.380$), and therefore ZIP distributions were used for all *N*-mixture models of *P. glutinosus*. All resultant occupancy and *N*-mixture models were ranked with AIC (Appendices 1–6), model-averaged, and back-transformed to obtain predictions. Multi-model inference, back-transformations, and goodness-of-fit tests were all executed using R package "AICcmodavg" (Mazerolle 2015).

Table 2: Results from 10,000 parametric bootstrap goodness-of-fit tests of global occupancy and N-mixture models (fitted with Poisson distributions) of three species of Plethodon salamanders surveyed in 2016 at Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., Kentucky, USA).

Species	**ψ**			**λ**		
	χ^2	**ĉ**	**p**	χ^2	**ĉ**	**p**
P. richmondi	15.96	1.18	0.263	144.12	0.96	0.583
P. kentucki	15.28	1.14	0.299	169.40	1.13	0.148
P. glutinosus	6.71	0.83	0.393	139.12	1.92	0.099

ψ = conditional occupancy probability, λ = estimated population size,
χ^2 = Pearson chi-square statistic, ĉ = overdispersion estimate, p = p-value

It was further hypothesized that (1) the distribution of woodland salamanders in LCW is modified behaviorally through interspecific competition and territoriality, and (2) the pattern of co-occurrence of woodland salamanders varies along natural environmental gradients. To test these hypotheses, two-species occupancy models were used to investigate patterns of co-occurrence (MacKenzie *et al.* 2004). The necessarily complex parameterization scheme of co-occurrence models featuring *P. glutinosus*, which was infrequently detected during this study, resulted in lack of model convergence. Therefore, co-occurrence models were only performed on *P. richmondi* and *P. kentucki*. The two-species occupancy model—an extension of the MacKenzie *et al.* (2002) single-species occupancy model—estimates the probability of two species occupying a patch simultaneously, while accounting for species-specific detection probabilities. To integrate effects from environmental gradients (i.e. site covariates) into the models of co-occurrence, an alternate parameterization of the MacKenzie (2004) model developed by Richmond *et al.* (2010) was used (known as the "conditional two-species occupancy model"). As opposed to the single-species occupancy model, this model allows for estimation of many additional population parameters, including the two-species joint conditional occupancy probability, or co-occurrence probability—the probability of a given species, S_A, occupying a site or sites wherein another species, S_B, is known to be present. Under the null hypothesis, the pattern and frequency of species co-occurrence does not vary across environmental gradients. This hypothesis was tested by comparing a null model of co-occurrence, wherein the pattern in which species co-occur at sites is unrelated to environmental conditions (essentially random), to models of co-occurrence which predict co-occurrence patterns relating to environmental gradients. Using the co-occurrence probability (ψ_{AB}), a "Species Interaction Factor", or φ, can also be obtained (MacKenzie 2004, Richmond *et al.* 2010). For species A and B, φ is defined as:

$$\varphi = \frac{\psi_{AB}}{\psi_A \cdot \psi_B};$$

where ψ_A and ψ_B are the independent occupancy probabilities of species A and B, and ψ_{AB} represents the co-occurrence probability of species A and B. Under the null hypothesis, $\varphi = 1$, species populations exist independently and the pattern and frequency of species co-occurrence is assumed to be random. If $\varphi > 1$, species co-occur more frequently than expected from chance; likewise, $\varphi < 1$ indicates species occur less frequently than chance.

Conditional two-species occupancy models (hereafter referred to as "co-occurrence models") were constructed to investigate if populations of *P. richmondi* and *P. kentucki* experience competition and if co-occurrence patterns vary across environmental gradients. Co-occurrence models were parameterized using the site and sampling covariates previously identified as important in single-species occupancy models (Appendices 1–6). Candidate models were fitted within the maximum-likelihood framework provided by program PRESENCE (v. 11.7; Hines 2006) under a ψ_{Ba}-parameterization (Richmond *et al.* 2010) and ranked using AIC (Appendix 7).

CHAPTER III

RESULTS

Repeated surveys of woodland salamanders at LCW resulted in the capture of 55 *P. richmondi*, 46 *P. kentucki*, and 8 *P. glutinosus*, with an average of 27.25 captures per survey. *Plethodon glutinosus* were only detected at 7 of 40 sites (naïve proportion of area occupied [POA] = 0.18), while *P. richmondi* and *P. kentucki* were detected at 25 and 26 of the total 40 sites surveyed, respectively (POA: *P. richmondi* = 0.63, *P. kentucki* = 0.65). An average of 2.73 salamanders were detected at each site (inter-quartile range [IQR] = 1.00–5.00), with a maximum of 11 detections and nine sites with zero detections.

Body Size and Microhabitat Usage

Some differences were found between the body size (defined as salamander mass adjusted for snout-to-vent [SVL] length) of each species ($F_{2,104} = 5.954$, $p < 0.004$). *Plethodon glutinosus* was 3.7–7.2 $g \cdot cm^{-2}$ greater than *P. kentucki* ($p = 0.043$) and 4.9–8.4 $g \cdot cm^{-2}$ greater than *P. richmondi* ($p = 0.004$), however no differences were found between body sizes of *P. richmondi* and *P. kentucki* ($p = 0.192$; Figure 4). Body size was considered as a predictor of microhabitat moisture and temperature. Volumetric moisture content of microhabitats inhabited by each species did not vary significantly ($F_{2,100} = 0.7942$, $p = 0.4548$; IQR = 0.174–0.211 $m^3 \cdot m^{-3}$). However, body size was a significant predictor of microhabitat temperature ($F_{1,105} = 10.533$, $p = 0.002$, $R^2 = 0.09$), suggesting that large bodied *Plethodon* tolerate higher temperatures (Figure 4).

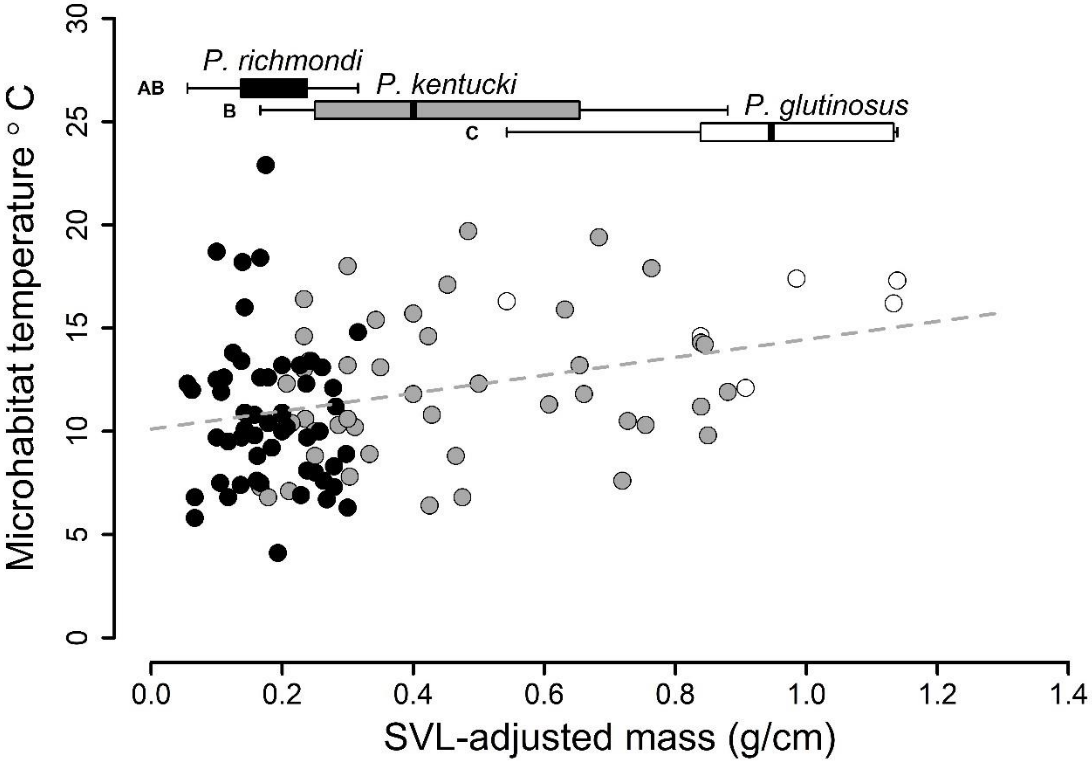

Figure 4: Relationship of salamander mass adjusted for snout-to-vent (SVL) length (grams per centimeter) and surface microhabitat temperature (degrees Celsius) of *Plethodon richmondi* (black), *P. kentucki* (grey), and *P. glutinosus* (white) in an old-growth forest of Lilley Cornett Woods Appalachian Ecological Research Station (data collected 15 October to 13 November 2016). Dotted line represents a least squares regression of microhabitat temperature and SVL-adjusted biomass ($F_{1,105} = 10.533$, p = 0.002). Horizontal boxplots above regression display summaries of SVL-adjusted biomass by species; letters beside boxplots denote statistically significant groups (Tukey HSD) from a two-way ANOVA ($F_{2,104} = 5.954$, $p < 0.004$).

Temperature of microhabitats inhabited by *P. richmondi*, *P. kentucki*, and *P. glutinosus* differed significantly ($F_{2,104} = 5.954$, p = 0.004). *Plethodon glutinosus* inhabited microhabitats 1.34–8.39 ℃ warmer (Tukey 95% CI) than *P. richmondi* (p = 0.004) and 0.09–7.22 ℃ warmer than *P. kentucki* (p = 0.043). There was no evidence to suggest that *P. richmondi* and *P. kentucki* inhabited microhabitats with different temperatures (p = 0.191). While microhabitat temperature of *P. kentucki* did not differ from ambient microhabitat conditions ($t = -1.157$, d.f. = 55.37, p = 0.271), *P. richmondi* and *P. glutinosus* were significantly different from ambient temperature. Microhabitats inhabited by *P. richmondi* were 0.79–2.78 ℃ cooler than ambient temperature (*t* = -3.590, d.f. = 61.86, p < 0.001) and those of *P. glutinosus* were 0.97–5.18 ℃ warmer (*t* = 3.705, d.f. = 5.24, p = 0.013; Figure 5).

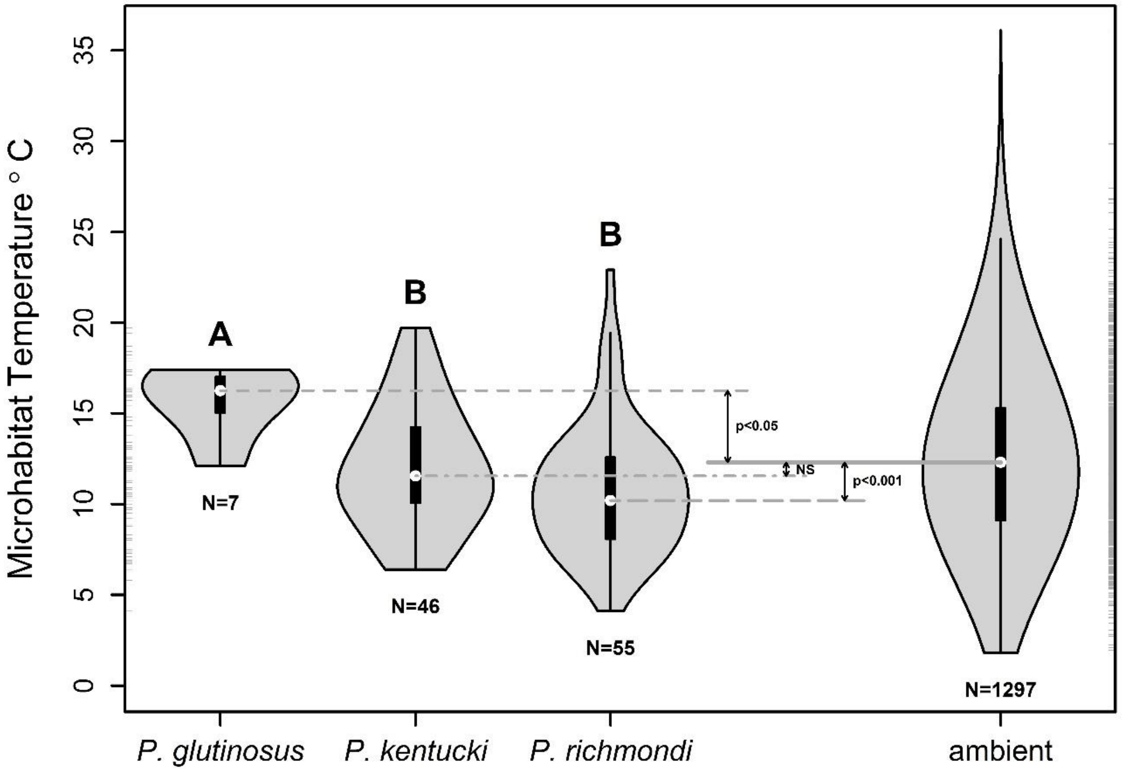

Figure 5: Temperature differentials of microhabitats inhabited by *Plethodon* salamanders and ambient (inhabited + uninhabited) in an old-growth forest of Lilley Cornett Woods Appalachian Ecological Research Station from 15 October to 13 November 2016. Lateral boundaries of boxplots represent kernel density estimates. Letters above boxplots denote statistically significant groups (Tukey HSD) from a two-way ANOVA (α = 0.05) of microhabitat temperature between three species of *Plethodon*. P-values accompanying each line segment drawn between plots are resultant from independent *t*-tests (α = 0.05) of microhabitat occupied by each *Plethodon* species and ambient microhabitat. NS indicates a statistical test with p > 0.05. Left-sided rug marks (in gray) represent values of observations from inhabited microhabitats and right-sided represent those of ambient microhabitats with 10% thinning to increase visibility.

Detection, Availability, and Temporary Emigration

All detection probability estimates reported herein are model-averaged across the full candidate set of models. *Plethodon richmondi* and *P. kentucki* exhibited moderately low detection probabilities, while detection of *P. glutinosus* was extremely low (Table 3). Additionally, for *P. richmondi* and *P. kentucki*, $\hat{\bar{p}}_{\psi}$ far exceeded $\hat{\bar{p}}_{\lambda}$. On the contrary, *P. glutinosus* $\hat{\bar{p}}_{\psi}$ was approximately equivalent to $\hat{\bar{p}}_{\lambda}$, suggesting availability ≈ 1. For *P. richmondi*, time of day ("TOD") in which the survey occurred was the most important covariate for estimating conditional capture probability ($\hat{\bar{\beta}}_{\psi}$ = -0.42 [95% unconditional CI: -0.83, -0.01]) and effective detection probability ($\hat{\bar{\beta}}_{\lambda}$ = -0.43 [-0.75, -0.12]). Availability of coarse woody debris ("CWD") was the most important covariate in explaining both detectability parameters of *P. kentucki* ($\hat{\bar{\beta}}_{\psi}$ = -0.42 [-0.83, -0.01, $\hat{\bar{\beta}}_{\lambda}$ = -0.43 [95% CI: -0.75, -0.12]). Two covariates, TOD and CWD, explained the conditional capture probability ($\hat{\bar{\beta}}_{\psi,\text{ TOD}}$ = 1.45 [0.41, 2.49], $\hat{\bar{\beta}}_{\psi,\text{ CWD}}$ = 1.41 [0.48, 2.33]) and effective detection probability ($\hat{\bar{\beta}}_{\lambda,\text{ TOD}}$ = 1.19 [0.33, 2.05], $\hat{\bar{\beta}}_{\lambda,\text{ CWD}}$ = 1.14 [0.47, 1.82]) of *P. glutinosus*; however, to avoid model nonconvergence due to over-parameterization, models were parameterized with a maximum of one covariate per parameter (all occupancy and *N*-mixture models have $K \leq 4$). Therefore, the covariate with the smallest $\hat{\bar{\beta}}$ 95% unconditional CI was used to estimate state parameters (CWD for ψ, TOD for λ).

Table 3: Model-averaged predictions of metrics of conditional capture probability and effective detection probability of three species of *Plethodon* salamanders from repeated (N=4) surveys in 2016 at Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., Kentucky, USA). Table includes estimates and 95% CI. All values are an average of N=40 sites.

Species	Conditional capture probability† ($\hat{p}_\psi$)	95% CI lower	95% CI upper	Effective detection probability‡ ($\hat{p}_\lambda$)	95% CI lower	95% CI upper
P. richmondi	0.355	0.245,	0.486	0.058	0.024,	0.136
P. kentucki	0.243	0.159,	0.349	0.050	0.015,	0.154
P. glutinosus	0.045	0.016,	0.113	0.043	0.001,	0.420

† defined as (capture prob.)|(availability), ‡ defined as (conditional capture prob.) x (availability)

By exploiting the relationship between effective detection probability and conditional capture probability, a population's availability for capture and temporary emigration (probability an animal is alive, but unavailable for capture), can be obtained mathematically (Table 4). Derivations from two components of detectability estimated within this study reveal that *P. richmondi* and *P. kentucki* both exhibit relatively low availability for capture and relatively high temporary emigration when compared to *P. glutinosus* (Table 4).

Table 4: Estimates of availability and temporary emigration derived from model-averaged estimated detectability parameters of three species of *Plethodon* salamanders from repeated (N=4) surveys in 2016 at Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., Kentucky, USA). All values are an average of N=40 sites.

Species	Conditional capture probability ($\hat{p}_\psi$)	Effective detection probability ($\hat{p}_\lambda$)	Availability†	Temporary Emigration‡
P. richmondi	0.355	0.058	0.164	0.836
P. kentucki	0.243	0.050	0.204	0.796
P. glutinosus	0.045	0.043	0.962	0.038

† derived using the formula: (effective detecton prob.)/(conditional capture prob.), ‡ defined as 1 - (availability)

Occupancy

Plethodon richmondi was predicted to have the most restricted distribution, with a model-averaged estimate of occupancy probability, $\hat{\psi}$, of 0.737 (95% CI: 0.35, 0.89). Comparatively, *P. kentucki* and *P. glutinosus* were distributed more ubiquitously ($\hat{\psi}_{kentucki}$

= 0.947 [0.11, 1.0], $\hat{\psi}_{glutinosus}$ = 0.984 [0.0, 1.0]), although the error surrounding estimates of *P. glutinosus* occupancy were large (Table 5).

Table 5: Model-averaged predictions from occupancy and N-mixture models of three species of *Plethodon* salamanders from repeated (N=4) surveys in 2016 at Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., Kentucky, USA). Table includes estimates and unconditional 95% confidence intervals of occupancy probability and density. All values are an average of N=40 sites.

Species	$\hat{\psi}$	95% CI		$\hat{\lambda} \cdot m^{-2}$	95% CI	
		lower	upper		lower	upper
P. richmondi	0.737	0.348,	0.895	0.060	0.025,	0.151
P. kentucki	0.947	0.105,	0.997	0.061	0.019,	0.206
P. glutinosus	0.984	0.001,	1.000	0.036	< 0.001,	14.808

$\hat{\psi}$ = estimated occupancy probability, $\hat{\lambda}$ = estimated abundance (expressed as density per m^{-2})

Percent soil moisture (“MST”), NDVI (“VEG”), and elevation (“ELV”) were all important covariates in estimating occupancy of *P. richmondi* ($\hat{\beta}_{MST}$ = 2.27 [0.11, 4.43]), $\hat{\beta}_{VEG}$ = 1.04 [0.07, 2.01], $\hat{\beta}_{ELV}$ = -1.27 [-2.46, -0.08]; Figure 6). Like *P. richmondi, P. kentucki* and *P. glutinosus* occupancy was also correlated with % soil moisture and NDVI (Figure 7), but the directions of the covariates’ effects were heterogeneous (*P. kentucki*: $\hat{\beta}_{MST}$ = 0.90 [-2.07, 3.89], $\hat{\beta}_{VEG}$ = 2.04 [-0.89, 4.97]; *P. glutinosus*: $\hat{\beta}_{MST}$ = -0.81 [-3.89, 2.28], $\hat{\beta}_{VEG}$ = 0.52 [-2.19, 3.22]; Figures 6 and 7). The remaining covariates included in models of occupancy produced heterogeneous effects and were therefore not considered to be reliable predictors of woodland salamander distributions in LCW (Figure 6).

Co-occurrence

Co-occurrence models determined the overall probability of *P. richmondi* co-occurring with *P. kentucki*, $\hat{\psi}_{ric\,|\,ken}$, was 0.72 (95% CI: 0.53, 0.86). Models of co-occurrence featuring covariates that represent environmental gradients were better at predicting patterns of co-occurrence (cumulative Akaike model weight [$\Sigma\omega_{ij}$] = 0.971) than null models ($\Sigma\omega_{ij} = 0.029$; Appendix 7). Co-occurrence probabilities were positively influenced by percent soil moisture and NDVI (Figure 8). The relationship of $\hat{\bar{\psi}}_{ric \mid ken}$ with NDVI was nearly linear, with a gradual positive slope. Co-occurrence exhibited a steep positive slope where percent soil moisture <15%, plateauing at approximately 20%. These results provide evidence that species co-occurrence patterns are non-random and vary along natural environmental gradients. However, the Species Interaction Factor, or φ, of *P. richmondi* and *P. kentucki* was equal to 1 ($\hat{\varphi} = 1.00$; 95% CI = 0.984, 1.016), which provides evidence that populations of *P. kentucki* and *P. richmondi* occur independently and do not experience competition.

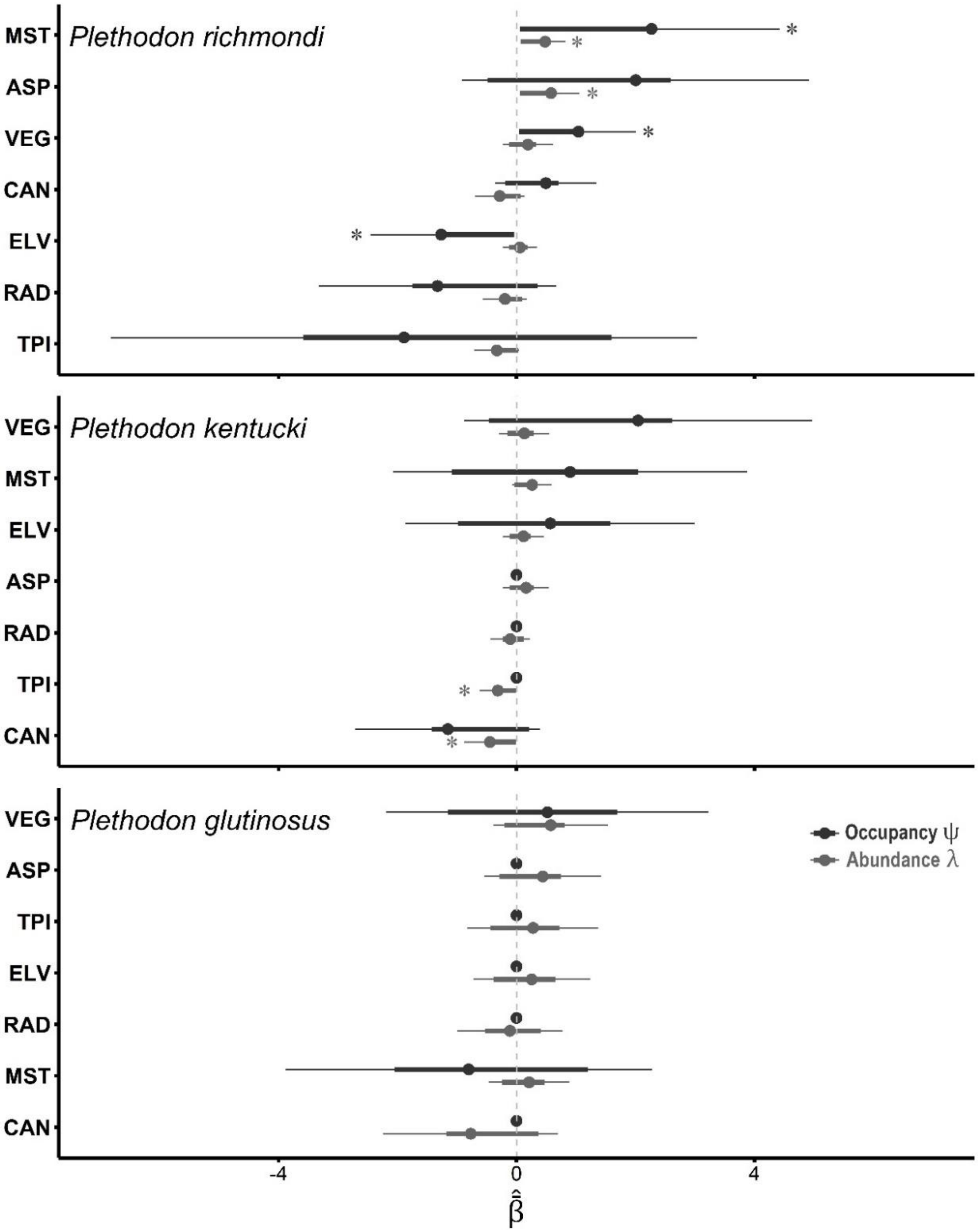

Figure 6. Model-averaged estimates of effect sizes, $\hat{\bar{\beta}}$, of covariates used in occupancy (ψ, dark grey) and *N*-mixture models (λ, light grey) of *Plethodon richmondi* (top), *kentucki* (middle), and *glutinosus* (bottom) surveyed at Lilley Cornett Woods Appalachian Ecological Research Station, Letcher County, Kentucky, USA in Fall 2016**.** "VEG" = Normalized Difference Vegetation Index, "ASP" = Beers-transformed aspect, "TPI" = Topographic Position Index, "ELV" = Digital Elevation Model, "RAD" = direct solar radiation, "MST" = volumetric soil moisture, "CAN" = percent canopy openness. Covariates with $\hat{\bar{\beta}}$ values centered at zero were not estimated due to non-convergent model or model instability, and are therefore represented as having zero effect sizes.

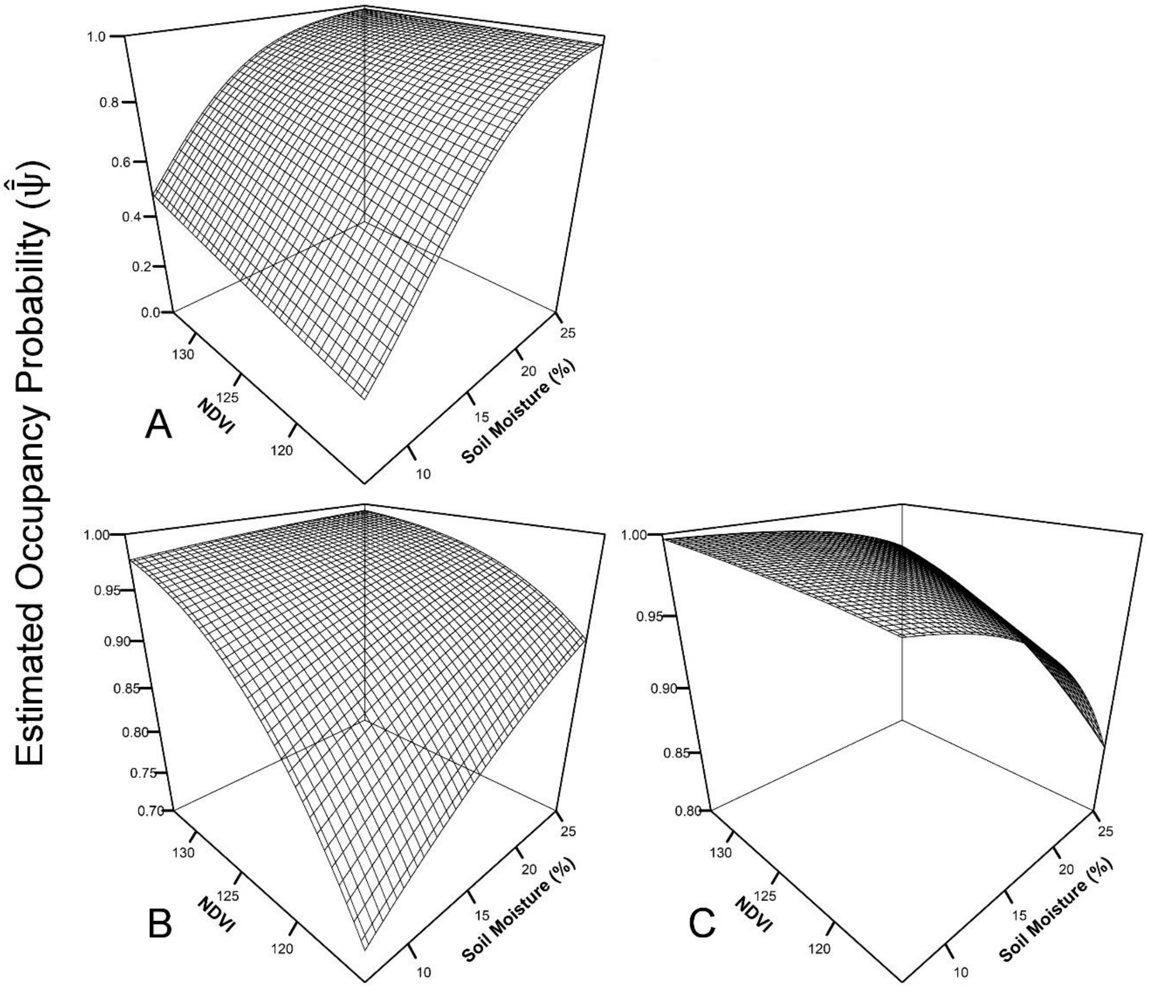

Figure 7. Model-averaged estimates of occupancy probability ($\hat{\bar{\psi}}$) of *Plethodon richmondi* (A), *P. kentucki* (B), and *P. glutinosus* (C) in old-growth forest at Lilley Cornett Woods Appalachian Ecological Research Station, Letcher County, Kentucky, USA in Fall 2016**.** Surfaces of three-dimensional plots represent patterns of predicted occupancy probability with respect to percent soil moisture and NDVI (Normalized Difference Vegetation Index), an estimate of canopy density gathered from NAIP imagery. Note: change in scale of $\hat{\bar{\psi}}$ across species.

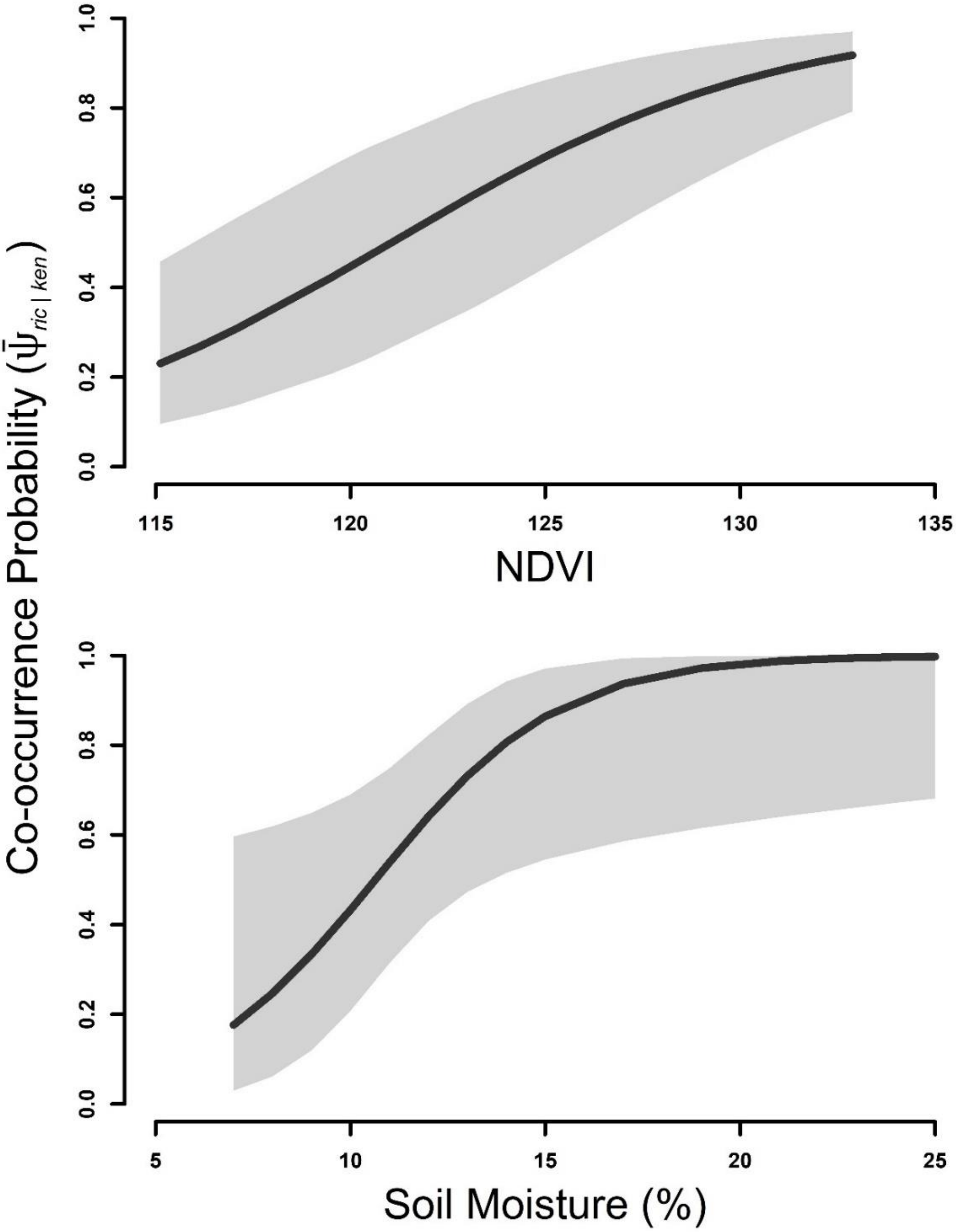

Figure 8. Estimates of *P. richmondi* and *P. kentucki* co-occurrence from conditional two-species occupancy models of salamanders surveyed in an old-growth forest at Lilley Cornett Woods Appalachian Ecological Research Station, Letcher County, Kentucky, USA in Fall 2016**.** Curves model relation of co-occurrence probability with percent soil moisture (bottom) and Normalized Difference Vegetation Index (NDVI, top). Gray regions represent 95% confidence intervals.

Abundance

Abundance estimates obtained from *N*-mixture models were substantially greater than counts uncorrected for effective detection probability, such that counts only represented 1.43–7.22 % (inter-quartile range) of the total estimated abundance of all three species of woodland salamanders. *Plethodon richmondi* and *P. kentucki* had similar estimated densities and were approximately twice as large as those of *P. glutinosus* (Table 4); although, 95% unconditional confidence intervals of *P. glutinosus* abundance were large and exceeded the upper limits of both *P. richmondi* and *P. kentucki*. When extrapolated to the total extent of the study area (44.25 ha), abundances of *Plethodon* species were estimated at $N_{richmondi}$ = 26570 (95% CI: 10895, 66897), $N_{kentucki}$ = 26848 (95% CI: 8552, 91098), and $N_{glutinosus}$ = 8461.61 (95% CI: 47.55, $2.75 \cdot 10^9$).

Percent soil moisture (“MST”) and Beers-transformed aspect (“ASP”) were the most important covariates when estimating abundance of *P. richmondi* ($\hat{\bar{\beta}}_{\mathrm{MST}} = 0.48$ [0.14, 0.82]), $\hat{\bar{\beta}}_{\mathrm{ASP}} = 0.58$ [0.1, 1.05]; Figure 6 and 9). *Plethodon richmondi* abundance exhibited marked, positive curvilinear responses to percent soil moisture and aspect. *Plethodon kentucki* abundance was most influenced most by Topographic Position Index (“TPI”) and percent canopy openness (“CAN”; $\hat{\bar{\beta}}_{\mathrm{CAN}} = -0.45$ [-0.88, -0.01]), $\hat{\bar{\beta}}_{\mathrm{TPI}} = -0.32$ [-0.63, -0.01]; Figure 9). The abundance of *P. kentucki* exhibited gradually dampened negative responses to both Topographic Position Index and percent canopy openness, with inflated upper limits. *Plethodon glutinosus* exhibited heterogenous responses among all site covariates (Figure 6), and therefore only total abundances are reported (Table 4).

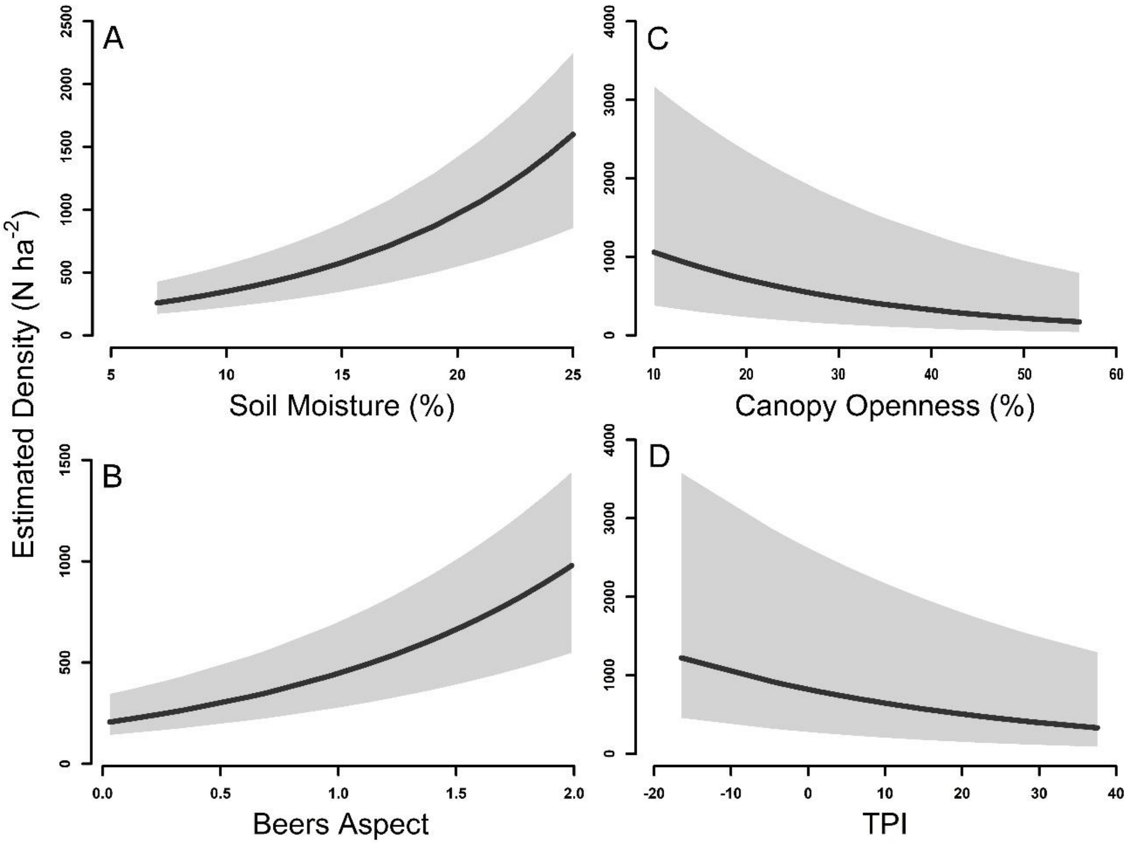

Figure 9. Model-averaged abundance estimates from *N*-mixture models (extrapolated to 1 ha) of woodland salamanders in an old-growth forest at Lilley Cornett Woods Appalachian Ecological Research Station, Letcher County, Kentucky, USA in Fall 2016**.** Panels A – B depict estimated abundance per ha of *Plethodon richmondi* with respect to: (A) percent soil moisture and (B) Beers-transformed aspect and *P. kentucki* with respect to: (C) percent canopy openness and (D) Topographic Position Index. Gray regions represent 95% unconditional confidence intervals.

CHAPTER IV

DISCUSSION

Microhabitat Associations

In undisturbed Appalachian forests, the thermal and hydric properties of surface refugia found under natural cover items—coarse woody debris (CWD) and rocky cover—are influenced by many of the forest's characteristics which modify local climate, including slope-aspect, elevation, soil depth, understory vegetation, and canopy density. Therefore, potential surface microhabitat conditions exhibit myriad complexity across natural environmental gradients, providing amphibians with a buffer from ambient conditions (Rittenhouse *et al.* 2008) and ample opportunity for niche differentiation among species (Whitfield & Pierce 2005, Farallo & Miles 2016).

As fossorial ectotherms, *Plethodon* salamander physiology is intimately related to soil conditions, and surface microhabitats are key thermo-osmoregulatory components of their home ranges (Spotila 1972, O'Donnell *et al.* 2014). In LCW, three species of *Plethodon* salamanders—*P. richmondi*, *P. kentucki*, and *P. glutinosus*—displayed thermal differentiation in their use of surface microhabitats (Figure 4); however, moisture of microhabitats did not vary among species. *P. glutinosus* was found to prefer microhabitats warmer than those selected by *P. richmondi* and *P. kentucki*, and warmer than ambient microhabitat conditions. Conversely, microhabitat thermal preferences of *P. richmondi* were cooler than that of *P. glutinosus* and ambient conditions. *Plethodon* salamanders are generally known to use subterranean refugia for desiccation avoidance and thermal regulation (Jaeger 1980, Grover 1998), and *P. richmondi* and *P. kentucki* have been regularly documented retreating into underground refugia during drought and extreme seasonal temperatures (Nagel 1979, Green & Pauley 1987, Bailey & Pauley 1993, Marvin 1996). Such responsiveness to daily or seasonal temperature and moisture extremes have not been documented in *P. glutinosus* (although see Bishop 1941 for notes about for burrowing behavior).

Results from this study suggest differential utilization of microhabitat temperatures by *P. richmondi*, *P. kentucki*, and *P. glutinosus* in LCW. Thermal preferences of *Plethodon* salamanders at LCW may correspond to species-specific physiological responses of woodland salamanders to the thermal environment (Riddell & Sears 2015, Peterman & Semlitsch 2014). Ectotherms regulate their body temperature behaviorally, and therefore, animals with low surface area-to-volume ratio are generally more capable of buffering their internal body temperature under extreme thermal conditions than animals with high surface area-to-volume ratios (Spight 1968, Peterman *et al.* 2013). This study found that body size of *Plethodon* salamanders is a clear indicator of thermal tolerance, and general body sizes of species corresponded with their previously identified thermal preferences. Specifically, *P. glutinosus,* a large-bodied salamander, occupied the warmest microhabitats and *P. richmondi*, a small-bodied salamander, occupied the coolest environments. Although this study identifies a physiological relationship between *Plethodon* salamanders and thermal preferences of microhabitats, there may be additional factors contributing to their thermal preferences. For instance, species' thermal preferences may result from thermal stratification of microhabitats in an effort ameliorate competitive pressure for resources (territories and prey) among heterospecifics (Schoener 1974, Farallo & Miles 2016). This hypothesis is supported by Jaeger (1971b), which determined that in microhabitats containing abundant soil, *P. cinereus* prohibits the presence of *P. richmondi* through competitive exclusion. However, empirical estimates of the frequencies with which *P. richmondi* interact with *P. kentucki* (Species Interaction Frequency) in LCW suggest that competition does not occur at the site-level (see "Co-occurrence" section of discussion for more detail about competition and species interactions). Further research incorporating field and laboratory studies are needed to test if, in fact, competition does influence thermal preferences of *Plethodon* salamanders in LCW.

Detectability, Availability, and Temporary Emigration

Unless all individuals in a population are available for capture during a survey (availability = 1), it is important to distinguish between conditional capture probability (probability of capturing an animal given availability = 1) and effective detection probability (probability of capturing an animal given availability ≤ 1). Given that *Plethodon* are known to migrate between surface and subsurface refugia frequently (Bailey *et al.* 2004), their availability—the probability of an individual being alive and present on the soil surface during a survey—should be much less than 1 (availability = 1 – [temporary emigration]; O'Donnell *et al.* 2015), and therefore estimates of effective detection probability should be much less than that of the conditional capture probability.

Estimates of temporary emigration suggests that *P. glutinosus* utilize subterranean refugia much less than *P. richmondi* and *P. kentucki* in LCW. Additionally, results from microhabitat usage of *Plethodon* salamanders in this study indicated that *P. glutinosus* tolerates greater surface temperatures than both *P. richmondi* and *P. kentucki*, which may further corroborate the notion that *P. glutinosus* rely less upon subterranean refugia for thermal regulation or desiccation avoidance. Further research involving the spatiotemporal dynamics of temporary emigration in *Plethodon* salamanders may elucidate predictable patterns in population availability, which could expand known natural history, inform future study design, and improve methods for estimating population parameters (e.g. distribution, abundance, extinction/colonization likelihood).

Plethodon richmondi

The fine-scale distribution (i.e. occupancy) of *P. richmondi* in LCW is restricted to forest stands with moist soil and robust canopy coverage, occurring primarily in elevations below exposed ridge-tops. *Plethodon richmondi* abundance was also positively related to forest soil moisture. However, factors affecting the fine-scale distribution of *P. richmondi* did not necessarily affect local abundance. For instance, aspect was found to be a key predictor of the abundance at a given site, but did not influence the likelihood of that site being occupied. Contrarily, elevation was an important factor influencing the occupancy of *P. richmondi*, but not abundance. These results suggest that factors which govern the fine-scale occurrence (i.e. colonization, extinction) and local abundance (i.e. productivity, recruitment) of *P. richmondi* in LCW may be functions of different gradients of environmental conditions. Further research incorporating alternative population models (multi-season models of occupancy, co-occurrence, and abundance), which incorporate parameters for colonization and local extinction, could perhaps be useful in exploring these patterns (MacKenzie *et al.* 2003).

Plethodon kentucki

This study found that abundance of *P. kentucki* varied along natural environmental gradients within the old-growth forest of LCW, while occupancy patterns exhibited heterogeneous responses. Specifically, abundance was negatively impacted by canopy disturbance (openness). Moreover, canopy disturbance impacted the abundance of *P. kentucki* with a greater magnitude than canopy closure, soil moisture, and aspect—gradients which all positively influenced abundance of *P. richmondi*. These data suggest that, among the environmental conditions which typically promote local *Plethodon* salamander population viability (e.g. moist soil, dense canopy, low solar exposure; Ford *et al.* 2002, Peterman & Semlitsch 2013, Semlitsch 2014), canopy disturbance exerts a greater governing force on *P. kentucki* abundance in LCW. Canopy disturbance in LCW can be caused by wind throw, which results in either mechanical removal of leaves and branches, or, in rare circumstances, complete root upheaval. Senescence or indirect damage from adjacent fallen trees may also result in minor canopy disturbance. However, *Adelges tsugae* (Hemlock Woolly Adelgid), an invasive pest to Hemlock trees in eastern deciduous forests, have caused overwhelmingly accelerated mortality of *Tsuga canadensis* (Eastern Hemlock) in LCW. Tree mortality associated with *A. tsugae* is predicted to result in declines of *Setophaga virens* (Black-throated Green Warbler) in LCW and surrounding Appalachian forests in southeast Kentucky (Brown & Weinkam 2014). It follows that through alterations to canopy characteristics, *A. tsugae*, and other invasive pests in LCW (e.g. *Agrilus planipennis*, Emerald Ash Borer) could negatively impact *Plethodon* salamanders, which lack the vagility to evacuate habitats that have undergone dramatic transformation (Welsh & Droege 2001). Further research into the mechanisms responsible for canopy loss in LCW may provide a more meaningful interpretation of *P. kentucki* occupancy and abundance dynamics. Future surveys and analyses should incorporate data pertaining to tree age, diameter, canopy density, and prevalence of pest-related damage.

Plethodon glutinosus

This study found little evidence suggesting that the fine-scale distribution of *P. glutinosus* varies across natural environmental gradients in the old-growth forest of LCW. Abundance of *P. glutinosus* did however exhibit substantial variation, albeit heterogenous, among gradients of canopy density and aspect. However, *P. glutinosus* was sparsely detected during this study and we therefore cautiously interpret predictions of occupancy, abundance, and detectability (and thus, temporary emigration and availability), which feature large confidence intervals and estimates of error. These results are perhaps corroborated by the microhabitat usage patterns and vertical migration patterns found in this study. *Plethodon glutinosus* was found to select warm microhabitats, exceeding the temperatures of those inhabited by *P. richmondi* and *P. kentucki*. The large body size and low surface area relative to body size (Spight 1968, Peterman *et al.* 2013) of *P. glutinosus* likely confers tolerance to thermal conditions otherwise uninhabitable by smaller species of *Plethodon.* Furthermore, starkly reduced vertical emigration relative to *P. richmondi* and *P. kentucki* suggests *P. glutinosus* relies upon physiology to tolerate environmental conditions, rather than retreating to underground refugia. Together, these results suggest *P. glutinosus* exhibits increased tolerance to environmental conditions, relative to *P. richmondi* and *P. kentucki*. Future investigations of *P. glutinosus* population dynamics should incorporate a study design that allows the observer to monitor animals within subterranean refugia (i.e. passive integrated transponders). Such an approach may enable investigators to calibrate estimates of whole-population temporary emigration frequency, as well as conduct analyses to determine if emigration is in fact used as a strategy for avoiding desiccation or extreme thermal environments.

Co-occurrence

The degree of overlap in the fine-scale distributions of *P. richmondi* and *P. kentucki* within LCW corresponded strongly with natural environmental gradients. The probability of *P. richmondi* and *P. kentucki* co-occurring in a given forest stand at LCW was positively correlated with soil moisture and canopy density. More specifically, co-occurrence was more common between *P. richmondi* and *P. kentucki* in mesic habitats, where stress associated with desiccation avoidance and thermoregulation is minimal; co-occurrence was much less common in xeric habitats with dry, clay-dominated soils and sparse canopy coverage, where physical stress is likely most apparent. However, there is no evidence to suggest that the occurrence of one species is influenced by the presence of another; their populations likely occur independently. Perhaps observed patterns in co-occurrence of *P. richmondi* and *P. kentucki* are artifacts of the individual occurrence pattern of *P. richmondi*, given that the occupancy probabilities of *P. kentucki* were almost uniformly equal to 1.

If *P. richmondi* and *P. kentucki* populations do in fact experience interspecific competition and are not independent, it is possible that the methods applied in this study were insufficient to detect such phenomena. For instance, if *Plethodon* salamanders ameliorate competitive pressure through spatial reorganization of territories, which can occur on scales equivalent to the cumulative area of the focal individuals' home ranges (Marvin 1988), it is possible that the spatial scale of this study is too coarse to quantify such fine-scale interactions. To test this hypothesis, future research should incorporate field surveys with hierarchically organized sampling which could allow for comparisons of species interactions across several spatial scales (Rizkalla & Swihart 2006).

Another potential explanation of the observed patterns of co-occurrence may be related to mating behavior of *P. kentucki*. Marvin (1998) found that populations of *P. kentucki* in this region exhibit territoriality associated with mate pairing. In southeast Kentucky, the breeding period of *P. kentucki* begins late June to mid August and lasts until mid-to-late October (Baecher pers. obs., Marvin & Hutchison 1996). Although unrelated to interspecific competition, it is possible that territoriality associated with *P. kentucki* breeding behavior was not observed during the timeframe of this study (15 October to 13 November 2016). To test this hypothesis, future research should feature survey periods within and outside breeding periods to test for seasonal patterns in species interactions.

Conclusions

This study found that natural environmental gradients created by dynamic ecosystem processes inherent in old-growth forest influence the habitat use, fine-scale distribution, and abundance of three species of woodland salamanders—*P. richmondi, P. kentucki*, and *P. glutinosus*. Species-specific responses to gradients of soil moisture and temperature, solar exposure from canopy structure, and slope position reflected physiological restraints associated with desiccation vulnerability and thermal avoidance of small to mid-sized salamanders relative to large-bodied salamanders. Although patterns in co-occurrence of *P. richmondi* and *P. kentucki* do vary along gradients of canopy density and soil moisture, little evidence was found to support the hypothesis that populations of woodland salamanders experience interspecific competition.

Additionally, this study found that the pattern of distribution and abundance of woodland salamanders throughout the landscape can be non-random—a finding that may seem intuitively simple and unworthy of contemplation. However, given that the nature of woodland salamanders' effects on forest floor dynamics (detrital food webs, organic material retention) can change due to variation in environmental conditions (Walton 2005, Walton 2013), it likely that the spatial extent of woodland salamander's influence on the ecosystem is non-random and varies dramatically across natural environmental gradients (Semlitch 2014). Thus, the role that woodland salamanders play in the maintenance of forest health, biodiversity, and ecosystem services (Davic & Welsh 2004), is likely contingent upon the inherent inhabitability of the system. Therefore, regions within a forest which support large populations of woodland salamanders, such as those highlighted in this study—mesic forest stands on north-to-east facing slopes with dense canopy—may provide enhanced ecosystem services and support stability in the total forest ecosystem (Davic & Welsh 2004).

Results from this study also support the contention that studies using methods that do not account for imperfect detection underestimate true distribution and abundance of organisms (Anderson 2001, MacKenzie *et al.* 2002, Royle 2004, Pellet & Schmidt 2005). Estimates of woodland salamander occurrence and abundance that incorporate detection probability likely provide a more well-informed view of species population dynamics (Bailey *et al.* 2004, Peterman & Semlitsch 2013, O'Donnell & Semlitsch 2015).

An important consideration, this study takes place in a stable old-growth forest (Martin 1975), virtually undisturbed by human activity (with the exception of light recreation from guided hiking). Because woodland salamanders in this study exhibited such marked responses to natural disturbances associated with forested ecosystems (e.g. isolated canopy perforation and soil desiccation due to solar exposure), population-level responses to non-natural disturbances (e.g. timber harvest and residential/commercial development) are hypothesized to be much more substantial. A large body of literature exists documenting the impact of anthropogenic disturbance regimes on woodland salamanders (for reviews, see deMaynadier & Hunter 1995, Welsh and Droege 2001, Highton 2005). Among the most detrimental to woodland salamanders are silviculture (e.g. Pentranka et al. 1993), urbanization (e.g. Scheffers and Paszkowski 2012), habitat fragmentation (e.g. Wyman 1990), and extraction of natural resources (e.g. Drohan et al. 2012). Despite the unassuming nature of these small, cryptic animals, the diverse services they provide to terrestrial ecosystems are disproportionately great in size (Davic & Welsh 2004). Therefore, more research is needed to generate reliable and biologically relevant criteria by which to structure land management guidelines, such as those proposed for pond breeding amphibians (Semlitsch & Bodie 2002), with the express purpose of bolstering woodland salamander populations and the ecosystem services they provide.

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APPENDICES

APPENDIX 1:

AIC table of *N*-mixture models of *P. richmondi* counts from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016

AIC table of *N*-mixture models of *P. richmondi* counts from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016. Detection models are parameterized with sampling covariates, and the state parameter, λ, is held constant. Abundance models are parameterized with sampling covariates and site covariates. A poisson mixture was used for all models.

Parameterization		**K**	**AIC**	**ΔAIC**	**ω_i**
Detection					
p(CWD+TOD)	, λ(.)	4	240.42	0.00	0.489
p(TOD)	, λ(.)	3	242.10	1.68	0.212
p(TOD+DAY)	, λ(.)	4	243.78	3.36	0.091
p(ROC+TOD)	, λ(.)	4	244.06	3.64	0.079
p(CWD)	, λ(.)	3	245.68	5.25	0.035
p(ROC+LUX+DAY+CWD+TOD+LLD)	, λ(.)	8	247.04	6.61	0.018
p(CWD+LUX)	, λ(.)	4	247.30	6.88	0.016
p(CWD+DAY)	, λ(.)	4	247.37	6.95	0.015
p(ROC+CWD)	, λ(.)	4	247.62	7.20	0.013
p(.)	, λ(.)	2	247.93	7.51	0.011
p(LUX)	, λ(.)	3	249.28	8.85	0.006
p(LLD)	, λ(.)	3	249.78	9.36	0.005
p(DAY)	, λ(.)	3	249.86	9.44	0.004
p(ROC)	, λ(.)	3	249.92	9.49	0.004
Abundance					
p(TOD)	, λ(TPI+ASP)	5	223.91	0.00	0.250
p(TOD)	, λ(ASP+MST)	5	224.43	0.52	0.200
p(TOD)	, λ(MST)	4	225.92	2.01	0.093
p(TOD)	, λ(RAD+MST)	5	226.22	2.31	0.080
p(TOD)	, λ(CAN+ASP)	5	226.55	2.64	0.068
p(TOD)	, λ(CAN+MST)	5	226.76	2.85	0.061
p(TOD)	, λ(VEG+MST)	5	226.86	2.95	0.058
p(TOD)	, λ(ELV+MST)	5	227.53	3.62	0.042
p(TOD)	, λ(ASP)	4	227.73	3.82	0.038
p(TOD)	, λ(TPI+MST)	5	227.89	3.98	0.035
p(.)	, λ(MST)	3	229.13	5.22	0.019
p(TOD)	, λ(VEG+ASP)	5	229.45	5.54	0.016
p(TOD)	, λ(ELV+ASP)	5	229.67	5.75	0.014
p(TOD)	, λ(RAD+ASP)	5	229.70	5.79	0.014
p(TOD)	, λ(CAN+MST+ELV+ASP+VEG+RAD+TPI)	10	232.08	8.17	0.004
p(TOD)	, λ(RAD)	4	233.44	9.52	0.002
p(TOD)	, λ(CAN)	4	233.65	9.73	0.002
p(.)	, λ(ASP)	3	234.55	10.64	0.001
p(TOD)	, λ(VEG)	4	235.83	11.92	0.001
p(TOD)	, λ(TPI)	4	237.17	13.25	0.000
p(.)	, λ(RAD)	3	239.01	15.09	0.000
p(.)	, λ(VEG)	3	241.03	17.12	0.000
p(.)	, λ(CAN)	3	241.10	17.19	0.000
p(.)	, λ(TPI)	3	241.89	17.98	0.000
p(TOD)	, λ(.)	3	242.10	18.19	0.000
p(TOD)	, λ(ELV)	4	243.94	20.03	0.000
p(.)	, λ(.)	2	247.93	24.02	0.000
p(.)	, λ(ELV)	3	249.76	25.85	0.000

K = # parameters, AIC = Akaike's Information Criteria, ΔAIC = AIC_i - $AIC_{top\ model}$, ω_i = model weight

APPENDIX 2:

AIC table of occupancy models of *P. richmondi* presence/absence data from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016

AIC table of occupancy models of *P. richmondi* presence/absence data from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016. Detection models are parameterized with sampling covariates, and the state parameter, ψ, is held constant. Occupancy models are parameterized with sampling covariates and site covariates.

Parameterization		**K**	**AIC**	**ΔAIC**	**ω_i**
Detection					
p(TOD)	, ψ(.)	3	183.24	0.00	0.231
p(ROC+TOD)	, ψ(.)	4	183.52	0.28	0.201
p(CWD+TOD)	, ψ(.)	4	184.62	1.38	0.116
p(TOD+DAY)	, ψ(.)	4	184.95	1.71	0.098
p(.)	, ψ(.)	2	185.22	1.99	0.086
p(ROC)	, ψ(.)	3	186.23	2.99	0.052
p(CWD)	, ψ(.)	3	186.36	3.12	0.049
p(LUX)	, ψ(.)	3	187.00	3.77	0.035
p(LLD)	, ψ(.)	3	187.06	3.82	0.034
p(DAY)	, ψ(.)	3	187.18	3.95	0.032
p(ROC+CWD)	, ψ(.)	4	187.82	4.59	0.023
p(CWD+LUX)	, ψ(.)	4	188.19	4.96	0.019
p(CWD+DAY)	, ψ(.)	4	188.24	5.00	0.019
p(ROC+LUX+DAY+CWD+TOD+LLD)	, ψ(.)	8	191.26	8.02	0.004
Occupancy					
p(TOD)	, ψ(MST)	4	175.55	0.00	0.382
p(TOD)	, ψ(ASP)	4	176.85	1.30	0.199
p(.)	, ψ(MST)	3	177.41	1.85	0.151
p(TOD)	, ψ(CAN)	4	178.59	3.04	0.084
p(TOD)	, ψ(VEG)	4	179.92	4.37	0.043
p(TOD)	, ψ(RAD)	4	180.45	4.90	0.033
p(.)	, ψ(ASP)	3	180.55	5.00	0.031
p(.)	, ψ(CAN)	3	181.10	5.54	0.024
p(.)	, ψ(VEG)	3	182.25	6.70	0.013
p(.)	, ψ(RAD)	3	182.91	7.36	0.010
p(TOD)	, ψ(.)	3	183.24	7.68	0.008
p(TOD)	, ψ(TPI)	4	183.45	7.89	0.007
p(TOD)	, ψ(ELV)	4	183.94	8.39	0.006
p(.)	, ψ(TPI)	3	184.81	9.25	0.004
p(.)	, ψ(.)	2	185.22	9.67	0.003
p(.)	, ψ(ELV)	3	185.92	10.36	0.002

K = # parameters, AIC = Akaike's Information Criteria, ΔAIC = $AIC_i - AIC_{\text{top model}}$, ω_i = model weight

APPENDIX 3:

AIC table of *N*-mixture models of *P. kentucki* counts from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016

AIC table of *N*-mixture models of *P. kentucki* counts from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016. Detection models are parameterized with sampling covariates, and the state parameter, λ, is held constant. Abundance models are parameterized with sampling covariates and site covariates. A poisson mixture was used for all models.

Parameterization		**K**	**AIC**	**ΔAIC**	**ω_i**
Detection					
p(ROC+CWD)	, λ(.)	4	210.71	0.00	0.666
p(CWD)	, λ(.)	3	213.85	3.14	0.138
p(CWD+TOD)	, λ(.)	4	215.60	4.89	0.058
p(CWD+DAY)	, λ(.)	4	215.72	5.01	0.054
p(CWD+LUX)	, λ(.)	4	215.83	5.12	0.052
p(ROC+LUX+DAY+CWD+TOD+LLD)	, λ(.)	8	217.64	6.93	0.021
p(ROC)	, λ(.)	3	220.48	9.77	0.005
p(ROC+TOD)	, λ(.)	4	222.32	11.61	0.002
p(.)	, λ(.)	2	223.06	12.35	0.001
p(DAY)	, λ(.)	3	224.32	13.62	0.001
p(TOD)	, λ(.)	3	224.96	14.26	0.001
p(LLD)	, λ(.)	3	224.99	14.28	0.001
p(LUX)	, λ(.)	3	225.00	14.29	0.001
p(TOD+DAY)	, λ(.)	4	226.32	15.62	0.000
Abundance					
p(CWD)	, λ(CAN+TPI)	5	207.47	0.00	0.478
p(CWD)	, λ(CAN)	4	208.82	1.35	0.243
p(CWD)	, λ(TPI)	4	209.40	1.94	0.182
p(CWD)	, λ(MST)	4	212.80	5.33	0.033
p(CWD)	, λ(CAN+MST+ASP+ELV+VEG+TPI+RAD)	10	214.11	6.65	0.017
p(CWD)	, λ(ASP)	4	215.11	7.64	0.010
p(CWD)	, λ(VEG)	4	215.11	7.64	0.010
p(CWD)	, λ(RAD)	4	215.41	7.94	0.009
p(CWD)	, λ(ELV)	4	215.46	7.99	0.009
p(.)	, λ(CAN)	3	216.96	9.49	0.004
p(.)	, λ(TPI)	3	218.38	10.91	0.002
p(.)	, λ(MST)	3	220.13	12.67	0.001
p(.)	, λ(ASP)	3	222.86	15.40	0.000
p(.)	, λ(VEG)	3	222.96	15.50	0.000
p(.)	, λ(.)	2	223.06	15.59	0.000
p(.)	, λ(ELV)	3	224.23	16.76	0.000
p(.)	, λ(RAD)	3	224.26	16.79	0.000

K = # parameters, AIC = Akaike's Information Criteria, ΔAIC = AIC_i - $AIC_{top\ model}$, ω_i = model weight

APPENDIX 4:

AIC table of occupancy models of P. *kentucki* presence/absence data from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016

AIC table of *N*-mixture models of *P. glutinosus* counts from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016. Detection models are parameterized with sampling covariates, and the state parameter, λ, is held constant. Abundance models are parameterized with sampling covariates and site covariates. A poisson mixture was used for all models.

Parameterization		**K**	**AIC**	**ΔAIC**	**ω_i**
Detection					
p(CWD+TOD)	, λ(.)	4	48.04	0.00	0.800
p(CWD+DAY)	, λ(.)	4	51.80	3.76	0.120
p(ROC+LUX+DAY+CWD+TOD+LLD)	, λ(.)	8	53.38	5.34	0.055
p(CWD)	, λ(.)	3	56.80	8.76	0.010
p(ROC+CWD)	, λ(.)	4	58.62	10.58	0.004
p(CWD+LUX)	, λ(.)	4	58.72	10.68	0.004
p(TOD+DAY)	, λ(.)	4	59.24	11.20	0.003
p(TOD)	, λ(.)	3	60.05	12.00	0.002
p(DAY)	, λ(.)	3	60.35	12.31	0.002
p(ROC+TOD)	, λ(.)	4	61.13	13.09	0.001
p(LLD)	, λ(.)	3	64.79	16.75	0.000
p(.)	, λ(.)	2	69.45	21.41	0.000
p(ROC)	, λ(.)	3	70.46	22.42	0.000
p(TOD)	, λ(.)	4	61.59	0.00	0.202
Abundance					
p(TOD)	, λ(CAN)	5	61.63	0.04	0.197
p(TOD)	, λ(VEG)	5	62.31	0.73	0.140
p(TOD)	, λ(ASP)	5	62.75	1.17	0.113
p(TOD)	, λ(MST)	5	63.23	1.64	0.089
p(TOD)	, λ(TPI)	5	63.30	1.71	0.086
p(TOD)	, λ(ELV)	5	63.31	1.73	0.085
p(TOD)	, λ(RAD)	5	63.53	1.94	0.077
p(TOD)	, λ(CAN+MST+ASP+ELV+VEG+TPI+RAD)	11	69.81	8.22	0.003
p(.)	, λ(.)	3	71.22	9.63	0.002
p(.)	, λ(CAN)	4	71.38	9.79	0.002
p(.)	, λ(ASP)	4	71.48	9.89	0.001
p(.)	, λ(VEG)	4	71.65	10.06	0.001
p(.)	, λ(TPI)	4	72.71	11.12	0.001
p(.)	, λ(MST)	4	72.92	11.34	0.001
p(.)	, λ(RAD)	4	73.06	11.47	0.001
p(.)	, λ(ELV)	4	73.21	11.62	0.001
p(LUX)	, λ(.)	3	71.03	22.99	0.000

K = # parameters, AIC = Akaike's Information Criteria, ΔAIC = AIC_i - $AIC_{top\ model}$, ω_i = model weight

APPENDIX 5:

AIC table of *N*-mixture models of *P. glutinosus* counts from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016

AIC table of *N*-mixture models of *P. glutinosus* counts from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016. Detection models are parameterized with sampling covariates, and the state parameter, λ, is held constant. Abundance models are parameterized with sampling covariates and site covariates. A poisson mixture was used for all models.

Parameterization		**K**	**AIC**	**ΔAIC**	**ω_i**
Detection					
p(CWD+TOD)	, λ(.)	4	48.04	0.00	0.800
p(CWD+DAY)	, λ(.)	4	51.80	3.76	0.120
p(ROC+LUX+DAY+CWD+TOD+LLD)	, λ(.)	8	53.38	5.34	0.055
p(CWD)	, λ(.)	3	56.80	8.76	0.010
p(ROC+CWD)	, λ(.)	4	58.62	10.58	0.004
p(CWD+LUX)	, λ(.)	4	58.72	10.68	0.004
p(TOD+DAY)	, λ(.)	4	59.24	11.20	0.003
p(TOD)	, λ(.)	3	60.05	12.00	0.002
p(DAY)	, λ(.)	3	60.35	12.31	0.002
p(ROC+TOD)	, λ(.)	4	61.13	13.09	0.001
p(LLD)	, λ(.)	3	64.79	16.75	0.000
p(.)	, λ(.)	2	69.45	21.41	0.000
p(ROC)	, λ(.)	3	70.46	22.42	0.000
p(TOD)	, λ(.)	4	61.59	0.00	0.202
Abundance					
p(TOD)	, λ(CAN)	5	61.63	0.04	0.197
p(TOD)	, λ(VEG)	5	62.31	0.73	0.140
p(TOD)	, λ(ASP)	5	62.75	1.17	0.113
p(TOD)	, λ(MST)	5	63.23	1.64	0.089
p(TOD)	, λ(TPI)	5	63.30	1.71	0.086
p(TOD)	, λ(ELV)	5	63.31	1.73	0.085
p(TOD)	, λ(RAD)	5	63.53	1.94	0.077
p(TOD)	, λ(CAN+MST+ASP+ELV+VEG+TPI+RAD)	11	69.81	8.22	0.003
p(.)	, λ(.)	3	71.22	9.63	0.002
p(.)	, λ(CAN)	4	71.38	9.79	0.002
p(.)	, λ(ASP)	4	71.48	9.89	0.001
p(.)	, λ(VEG)	4	71.65	10.06	0.001
p(.)	, λ(TPI)	4	72.71	11.12	0.001
p(.)	, λ(MST)	4	72.92	11.34	0.001
p(.)	, λ(RAD)	4	73.06	11.47	0.001
p(.)	, λ(ELV)	4	73.21	11.62	0.001
p(LUX)	, λ(.)	3	71.03	22.99	0.000

K = # parameters, AIC = Akaike's Information Criteria, ΔAIC = AIC_i - $AIC_{top\ model}$, ω_i = model weight

APPENDIX 6:

AIC table of occupancy models of *P. glutinosus* presence/absence data from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016

AIC table of occupancy models of *P. glutinosus* presence/absence data from repeated surveys of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016. Detection models are parameterized with sampling covariates, and the state parameter, ψ, is held constant. Occupancy models are parameterized with sampling covariates and site covariates.

Parameterization		**K**	**AIC**	**ΔAIC**	**ω_i**
Detection					
p(CWD+TOD)	, ψ(.)	4	44.00	0.00	0.800
p(CWD+DAY)	, ψ(.)	4	48.46	4.46	0.086
p(ROC+LUX+DAY+CWD+TOD+LLD)	, ψ(.)	8	48.52	4.52	0.083
p(CWD)	, ψ(.)	3	52.52	8.52	0.011
p(ROC+CWD)	, ψ(.)	4	54.26	10.26	0.005
p(TOD+DAY)	, ψ(.)	4	54.48	10.48	0.004
p(CWD+LUX)	, ψ(.)	4	54.51	10.51	0.004
p(TOD)	, ψ(.)	3	54.84	10.84	0.004
p(DAY)	, ψ(.)	3	55.14	11.14	0.003
p(ROC+TOD)	, ψ(.)	4	55.98	11.98	0.002
p(LLD)	, ψ(.)	3	58.40	14.40	0.001
p(.)	, ψ(.)	2	61.50	17.50	0.000
p(ROC)	, ψ(.)	3	62.63	18.63	0.000
p(LUX)	, ψ(.)	3	63.28	19.28	0.000
Occupancy					
p(CWD)	, ψ(.)	3	52.52	0.00	0.880
p(CWD)	, ψ(MST+VEG)	5	56.45	3.94	0.120

K = # parameters, AIC = Akaike's Information Criteria, ΔAIC = AIC_i - $AIC_{top\ model}$, ω_i = model weight

APPENDIX 7:

AIC table of conditional two-species occupancy models of *P. richmondi* and *P. kentucki* co-occurrence in the old-growth forest of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016

AIC table of conditional two-species occupancy models of *P. richmondi* and *P. kentucki* co-occurrence in the old-growth forest of Lilley Cornett Woods Appalachian Ecological Research Station (Letcher Co., KY) in Fall 2016. Detection models are parameterized with sampling covariates, and the state parameter, ψ, is held constant. Co-occurrence models are parameterized with sampling covariates and site covariates. Below the double-line, terms in each model are defined according to Richmondi et al. (2010).

Parameterization		**K**	**AIC**	**ΔAIC**	**ω_i**
Detection					
p'(CWD), p"(CWD), r'(CWD), r"(CWD), r'"(CWD)	, ψ'(.), ψ"(.), ψ'"(.)	8	353.37	0.00	0.713
p'(CWD+TOD), p"(CWD+TOD), r'(CWD+TOD), r"(CWD+TOD), r'"(CWD+TOD)	, ψ'(.), ψ"(.), ψ'"(.)	9	355.36	1.99	0.264
p'(.), p"(.), r'(.), r"(.), r'"(.)	, ψ'(.), ψ"(.), ψ'"(.)	10	360.92	7.55	0.016
p'(TOD), p"(TOD), r'(TOD), r"(TOD), r'"(TOD)	, ψ'(.), ψ"(.), ψ'"(.)	9	362.77	9.40	0.007
Co-occurrence					
p'(CWD), p"(CWD), r'(CWD), r"(CWD), r'"(CWD)	, ψ'(MST), ψ"(MST), ψ'"(MST)	10	346.97	0.00	0.785
p'(CWD), p"(CWD), r'(CWD), r"(CWD), r'"(CWD)	, ψ'(VEG), ψ"(VEG), ψ'"(VEG)	10	349.88	2.91	0.183
p'(CWD), p"(CWD), r'(CWD), r"(CWD), r'"(CWD)	, ψ'(.), ψ"(.), ψ'"(.)	9	353.37	6.40	0.032

Parameterization explained

Term	Definition	Symbology Used
ψ'	Probability of occupancy for *P. kentucki*	ψ_{ken}
ψ"	Probability of occupancy for *P. richmondi*, given *P. kentucki* is present	$\psi_{ric \mid ken}$
ψ'"	Probability of occupancy for *P. richmondi*, given *P. kentucki* is absent	$\psi_{ric \mid \cancel{ken}}$
p'	Probability of detection for *P. kentucki*, given *P. richmondi* is absent	$p_{ken \mid \cancel{ric}}$
p"	Probability of detection for *P. richmondi*, given *P. kentucki* is absent	$p_{ric \mid \cancel{ken}}$
r'	Probability of detection for *P. kentucki*, given *P. richmondi* and *P. kentucki* are present	$p_{ken \mid ric+ken}$
r"	Probability of detection for *P. richmondi*, given both species are present and *P. kentucki is* detected	$p_{ric \mid ric+ken \times \underline{ken}}$
r'"	Probability of detection for *P. richmondi*, given both species are present and *P. kentucki* is not detected	$p_{ric \mid ric+ken \times ken}$

K = # parameters, AIC = Akaike's Information Criteria, ΔAIC = $AIC_i - AIC_{top\ model}$, ω_i = model weight