Knowing your limits: estimating range boundaries and co-occurrence zones for two competing plethodontid salamanders

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Abstract. Understanding threats to species persistence requires knowledge of where species currently occur. We explore methods for estimating two important facets of species distributions, namely where the range limit occurs and how species interactions structure distributions. Accurate understanding of range limits is crucial for predicting range dynamics and shifts in response to interspecific interactions and climate change. Additionally, species interactions are increasingly recognized as an important but not well-understood predictor of range shifts. Our objective was to predict range limits and contact zones for two plethodontid salamanders, the highly range-restricted Shenandoah salamander (*Plethodon shenandoah*) and the wide-ranging red-backed salamander (*Plethodon cinereus*). Using detection/non-detection data, we assess four methodological decisions when estimating species' distributions: (1) accounting for imperfect detection, (2) covariates to predict species occurrences, (3) accounting for species interactions, and (4) the inclusion of spatial autocorrelation. We found that Shenandoah salamander and red-backed salamander co-occurrence would have been underestimated and the range edge misidentified had we not accounted for incomplete detection. Covariates related to habitat were not sufficient to explain species' range boundaries. Models that included spatial autocorrelation (i.e., a conditional autoregressive random effect) performed better than models that included just species interactions (i.e., detection and occurrence were conditional on the other species being present) and models that included both spatial autocorrelation and species interactions. Further, we found that the breadth of primary contact zones was typically 60–170 m, which is greater on average than previous estimates. In addition, we frequently observed secondary, disjunct contact zones along the range boundary. Understanding the extent to which species co-occur and how the range boundaries are shaped is crucial to conservation efforts. Our work indicates that accounting for detection is crucial for accurately characterizing range edges and that spatial models may be especially effective in modeling distributions at the boundary.

Key words: conditional autoregressive models; conditional occupancy; detection probability; joint species distribution model; range limit; red-backed salamander; Shenandoah salamander.

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INTRODUCTION

Knowledge of current species range limits is important for measuring current limits, forecasting future range shifts, predicting future conservation needs, and prioritizing spatial allocation of management (Hulme 2005, Elith and Leathwick 2009). Understanding factors determining species range

limits is also necessary to assess broad threats to species persistence and monitor shifts in local dynamics (Anderson et al. 2009). Despite the far-reaching importance of identifying species' range limits, there are unique challenges that occur when estimating these boundaries.

An underlying basic yet critical assumption for determining higher resolution range limits is that the presence and absence of a species is known without error. Given this is rarely the case, the ability to estimate detection errors is dependent on methodologies used to survey and model species distributions (Sastre and Lobo 2009, Rocchini et al. 2011, Stolar and Nielsen 2015) in addition to species' characteristics that impact their detectability by observers (Pellet and Schmidt 2005, Comte and Grenouillet 2013). Researchers often aggregate data from multiple studies, each with their own survey methodologies (and potential biases), to inform species range models. These data may lead to estimates of species distributions that are not as statistically robust due to inconsistent historical sampling or analytical approaches (Bailey et al. 2004, Tingley and Beissinger 2009), variation in detection of target taxa (Grant 2014), or because ranges have shifted over time with changing environmental pressures or altered population dynamics. While identifying the factors underlying species occurrence is inherently challenging, these difficulties are exacerbated at range edges where species presence fades to absence and abundance is assumed to be lower than at the core of a species' distribution (Hengeveld and Haeck 1982, Sagarin et al. 2006). Occupancy modeling is an important advancement in species range modeling as it corrects for variability in latent (unobservable) processes and accounts for imperfect detection of species (MacKenzie et al. 2006). By using a robust sampling design that allows us to account for imperfect species detection during surveys, a finer resolution of species occupancy at difficult to map areas (e.g., range edges) can be achieved.

In addition to the inclusion of detection probability, understanding distributional patterns at the range edge requires accurately estimating the spatial configuration of where species occur (Johnson et al. 2013, Ver Hoef et al. 2018). As with all species distribution models, covariates related to climate, topography, geology, and land cover can be used to model the spatial configuration of species occurrence (MacKenzie et al. 2006, Tingley and Beissinger 2009). However, variables that do well in explaining large-scale geographic patterns of occurrence may be less informative when predicting the fine-scale extent of a range limit. Spatially explicit models are another tool that may be used to better estimate the range boundaries of species' distributions. Spatial models can capture similarities in species occupancy driven by the proximity of spatial units to one another (i.e., neighboring units are more likely to be similarly occupied or not occupied as compared to those that are far apart; Dormann 2007). By incorporating autocorrelated spatial effects that may explain variation in species occupancy, variables driving patterns at the range boundary may be identified and fewer spurious associations may be made (Lichstein et al. 2002, Dormann 2007). Spatial autocorrelation may also better capture abiotic and biotic characteristics that covary over space and contribute to patterns in species occupancy (Legendre 1993, Lichstein et al. 2002).

Understanding species range limits, especially on a local scale, may also require accounting for species interactions (Louthan et al. 2015). Range models have historically focused on the role of climate as a primary ecological filter determining species distributions (Grinnell 1917, Menge and Olson 1990), but an increasing number of studies (Gilman et al. 2010, Pigot and Tobias 2012, HilleRisLambers et al. 2013, Yackulic et al. 2014) highlight the importance of species interactions in delimiting species ranges and influencing population dynamics. Several studies indicate these interactions provide a mechanistic explanation of patterns observed at the local scale (Pearson and Dawson 2003, Soberón 2007) and should be considered when creating conservation plans (Gilman et al. 2010). Parsing out the importance of species interactions and using them in modeling distributions may be of particular importance with rare, endangered, or specialist species when predicting range shifts (Preston et al. 2008, Bateman et al. 2012). Competitive interactions can shape ranges (Sexton et al. 2009), alter or exacerbate responses to climate (Gilman et al. 2010), and lead to local extinctions of species (Bengtsson 1989), complicating range models. Species can actively exclude one another, thus altering occupancy, but behavioral interactions can also

alter species' detectability and therefore bias conclusions about occurrence (Bailey et al. 2009, Miller et al. 2012). Joint species distribution models (JSDMs) are a broad category of models that account for relationships among species and aim to better attribute variance in patterns to abiotic or biotic factors (Ovaskainen et al. 2010, Richmond et al. 2010, Pollock et al. 2014). For one specific type of JSDM, occupancy models, species interactions can be estimated via their influence on the probabilities of species detection and occupancy (Richmond et al. 2010) and can thus better inform range-modeling efforts.

We used occupancy models to estimate the range boundary of a high-elevation, range-restricted plethodontid salamander, the Shenandoah salamander (*Plethodon Shenandoah*; Highton and Worthington 1967), and the more widely distributed red-backed salamander (*Plethodon cinereus*; Green 1818) at the intersection of their ranges. Plethodontid salamanders are a diverse group with complex patterns of speciation and hybridization across space, and competition is frequently invoked in explaining their distributions (Hairston 1987). We aimed to determine the value of habitat covariate information, spatial autocorrelation, and species interactions in generating accurate estimates of species occupancy at the range boundary for these two species. Incorporating estimates of species interactions in explaining range limits in this system is especially interesting due to previous research suggesting competitive exclusion defines range boundaries for these two species and other plethodontid salamanders where their range boundaries intersect (Hairston 1987). Research on this system has purported that red-backed salamanders exert strong competitive exclusion on Shenandoah salamanders in locations where the two meet (Jaeger 1970, Griffis and Jaeger 1998), but, despite decades of research, the specific mechanism leading to competitive exclusion at the range edge is unknown (Jaeger et al. 2016). In addition, surface activity and thus detectability is known to vary with environmental conditions for terrestrial salamanders (Hairston 1987, Petranka and Murray 2001), and occupancy modeling can provide a valuable tool in this system where detection is imperfect (Bailey et al. 2004).

We compared estimates from single-species occupancy models that independently calculate species occupancy and detection probabilities (MacKenzie et al. 2004) to two-species conditional occupancy models that model dependency between occupancy and detection probabilities of potentially interacting species (e.g., dependencies that may result from competition, avoidance, or from distinct habitat preferences; Richmond et al. 2010). We also assessed improvement in modeling the range edge when incorporating a spatial element to single- and two-species conditional occupancy models via the inclusion of a conditional autoregressive (CAR) random effect to explain spatial patterns in occupancy unrelated to measured biotic or abiotic covariates (Bled et al. 2013, Johnson et al. 2013, Ver Hoef et al. 2018). All models included substrate covariates to assess whether occupancy patterns could be largely modeled using only metrics of local microhabitat (as these were originally identified as critical to the competition-driven distribution of *Plethodon shenandoah*; Jaeger 1970). Cross-validation of these different model permutations allowed us to then evaluate the importance of species interactions and spatial structure in setting the species range limit. Understanding how changing climate and competition are affecting the range boundaries for these species requires a precise understanding of where the current and future range limits occur. With management plans relying on such basic information as knowing the current distribution of species and what factors contribute to their range limits, accounting for species detection in combination with choices about how to model distributions can greatly affect our ability to create accurate species distribution models.

METHODS

Study system

The Shenandoah salamander is a small-bodied, terrestrial salamander endemic to Shenandoah National Park, Virginia, USA (Highton and Worthington 1967). The species occurs on only three mountaintops at elevations over 850 m (Highton and Worthington 1967, Jaeger 1970) and is federally listed as an endangered species (54 CFR 34464; U.S. Fish and Wildlife Service 1994). As such, we maintained all geo-spatial relationships in analyses and results, but exact geographic locations and location names are not

published herein. The species range is restricted, and little is known about the abundance and population dynamics of the species (National Park Service 2015). In contrast, the red-backed salamander is more broadly distributed, occurring across most of the northeastern United States and Canada (Green 1818) in the deeper soil and leaf litter of forested habitats (Jaeger 1970). Shenandoah salamanders occur in rocky, talus habitats on north-facing slopes where it is hypothesized that more extreme moisture and temperature regimes exclude the red-backed salamander (Jaeger 1971a). Red-backed salamanders surround these talus slopes (Jaeger 1970) and are posited to be competitively superior (Jaeger 1970, Griffis and Jaeger 1998), leading to little overlap in the observed species' ranges. Laboratory-based and in situ manipulative experiments suggest red-backed salamanders are capable of outcompeting Shenandoah salamanders for space in deeper soil habitats (Griffis and Jaeger 1998) that are less physiologically stressful for both species (Jaeger 1971a, b). Laboratory experiments and species removal studies have shown that red-backed salamanders may exclude Shenandoah salamanders by outcompeting them for microhabitat (Jaeger 1971b, Griffis and Jaeger 1998) and food (Jaeger 1972, Dallalio et al. 2017). Previous research suggests interactions between the two species are responsible for the formation of the lower elevational range limit of the Shenandoah salamander postglaciation (Jaeger 1970, 1971b, Highton 1995, Griffis and Jaeger 1998).

Field sampling

We surveyed four study areas along the lateral range boundaries for both Shenandoah and red-backed salamanders using parallel transects spaced 50 m apart. We established transects based on historical range maps and recent USGS and NPS observations of both species near suspected co-occurrence zones, that is, areas of expected intersection of the species' ranges. In establishing transects, we aimed to begin surveying in one species' territory, pass through the co-occurrence zone, and continue into the other species' territory while maintaining a constant bearing and thus elevation (e.g., moving from north-facing to south-facing slopes). Transects were surveyed in consecutive 50-m segments using transect tape and a compass, and tree tags were placed every 50–100 m on initial surveys to mark transects for subsequent surveys. Total transect lengths surveyed during any individual visit varied due to physical obstacles (e.g., cliffs), time constraints, and a lack of surface-active animals or suitable habitat (e.g., surveying stopped if no animals were found in 100 m). Two to three transects were established at each of the four study areas (11 transects in total), with most transects surveyed in 2015 and 2016 (t = 6–9 surveys across spring, early summer, and fall; Appendix S2: Table S1). We surveyed approximately 270 m per transect on average (but transect length varied between 200 and 400 m).

During the first survey, we surveyed transects starting in the Shenandoah salamander range and working toward the red-backed salamander range. Subsequent surveys were randomized to start in either species territory. For each transect, observers checked all cover objects within 2 m of each side of the transect tape. Detected salamanders were captured by hand and placed in new plastic sandwich bags for immediate species identification (based on Highton and Worthington 1967) and measurement. Any uncertainty in species identification required verification by a second observer, and any individual that could not be definitively identified was noted and subsequently removed from our analyses. Animals were immediately returned to cover objects where captured, and we recorded the site of capture (5 × 4 m segment of the transect) for use in subsequent analyses. We categorized percent substrate type for each site for all transects during spring 2017 using four categories: rock (exposed expanses of talus, boulder, and cobble), soil/wood (fallen woody debris and open stretches of ground), moss/leaf (thick, moist ground cover), and other (none of the above, e.g., large fallen trees or roots that could not be checked underneath and manmade alterations such as campfire residue and trails).

Data analysis

We estimated patterns of occurrence for both species at all sites (i.e., 5 × 4 m sections of the overall transect). Detection histories for each site, i, were analyzed using four parameterizations of single- and two-species occupancy models (MacKenzie et al. 2004, 2006) fit in a Bayesian

framework. We assessed the relative importance of different model parameterizations in generating accurate predictions. We used a static occupancy formulation that assumes occupancy (i.e., presence or absence) was constant at sites across all surveys. Thus, we estimated the probability each site was occupied at any point during our study.

For our first model, we simultaneously fit single-species occupancy models for both red-backed (species A) and Shenandoah (species B) salamanders where species occupancy and detection probabilities were independent of the other species (MacKenzie et al. 2004, 2006). We defined the latent true site occupancy for species A at site i, z_i^A, to be 1 when species A was present and 0 when absent. The probability that the site was occupied (i.e., $z_i^A = 1$) was denoted as ψ_i^A, where $z_i^A \sim$ Bernoulli (ψ_i^A). The probability of detecting a salamander at site i during visit t was conditional on true species occupancy at a site as well as the detection probability at that survey such that

$$\text{Prob}(y_{it}^A = 1) = \begin{cases} 0 & \text{if} \quad z_i^A = 0 \\ p_t^A & \text{if} \quad z_i^A = 1 \end{cases} \quad (1)$$

where $y_{it}^A = 1$ if the species is detected and 0 if it is not detected during a visit. We used a prior of $p_t^A \sim$ Uniform (0, 1).

Our base model included only covariates for the fixed effects of substrate type at each site.

$$\begin{aligned} \text{logit}(\psi_i^A) = &\beta_1 \times \text{Rock}_i + \beta_2 \times \text{SoilWood}_i \\ &+ \beta_3 \times \text{MossLeaf}_i \\ &+ \beta_4 \times \text{Other}_i \end{aligned} \quad (2)$$

Substrate values were the proportion of the total area of each site that consisted of that substrate and sum to 1 for each site. We set the priors for substrate regression coefficients to be approximated by $\beta_k \sim$ Normal (0, 100). Boundary conditions (i.e., estimates of ψ at 0 or 1) became an issue later when we added the spatial random effect, so we made two additional constraints to priors for all models. First, we bounded the β values between −7 and 7. Second, we bounded ψ_i^A between 0.0001 and 0.9999. Occupancy and detection probabilities for species B, ψ_i^B and p_t^B, were estimated in the same manner as species A.

For our second model, we further modified the substrate covariate-only model to fit a two-species conditional occupancy model that

calculated probabilities of detection and occurrence for species B conditional upon the occupancy and detection of species A (Richmond et al. 2010). Similar to the single-species model, we estimated the effect of substrate covariates on ψ_i^A and ψ_i^B using Eq. 2. However, for the two-species model, ψ_i^B was also conditional on whether $z_i^A = 1$ (Richmond et al. 2010), resulting in two estimates of occurrence probability, ψ_i^{BA} (occupancy of B given A is also present at a site) and ψ_i^{Ba} (occupancy of B given A is absent at a site). We modified Eq. 2 to estimate ψ_i^B by including the intercept term $\alpha^{BA} \times z_i^A$, which adjusts for the difference between ψ_i^{Ba} and ψ_i^{BA}. We used a prior of $\alpha^{BA} \sim$ Normal (0, 100).

In the two-species conditional model, the probability of detecting a salamander was conditional on true species occupancy of both species at a site as well as whether the other species was detected during the survey (sensu Richmond et al. 2010) such that

$$\text{Prob}(y_{it}^A = 1) = \begin{cases} 0 & \text{if} \quad z_i^A = 0 \text{ and } z_i^B = 0 \\ p_t^A & \text{if} \quad z_i^A = 1 \text{ and } z_i^B = 0 \\ 0 & \text{if} \quad z_i^A = 0 \text{ and } z_i^B = 1 \\ r_t^A & \text{if} \quad z_i^A = 1 \text{ and } z_i^B = 1 \end{cases} \quad (3)$$

$$\text{Prob}(y_{it}^B = 1) = \begin{cases} 0 & \text{if} \quad z_i^A = 0 \text{ and } z_i^B = 0 \\ 0 & \text{if} \quad z_i^A = 1 \text{ and } z_i^B = 0 \\ p_t^B & \text{if} \quad z_i^A = 0 \text{ and } z_i^B = 1 \\ r_t^{BA} & \text{if} \quad z_i^A = 1, y_i^A = 1, \\ & \text{and } z_i^B = 1 \\ r_t^{Ba} & \text{if} \quad z_i^A = 1, y_i^A = 0, \\ & \text{and } z_i^B = 1 \end{cases} \quad (4)$$

We used p to denote detection probabilities when the second species was not present and r when the second species was present (Richmond et al. 2010). For species B, we separately estimated the probability of detecting species B given that species A was present and also detected (r_t^{BA}) vs. when species A was present but not detected (r_t^{Ba}). We similarly allowed all detection parameters to vary among visits using a uniform prior from 0 to 1. Priors for all other parameters follow single-species model specifications.

For the third and fourth models, we further modified the single-species (model 1) and two-species conditional occupancy models (model 2),

respectively, by adding a site- and species-specific CAR random effect (ρ_i^A and ρ_i^B) to Eq. 2. The CAR random effect assumes that the probability of site occupancy along the transect is correlated to neighboring sites and allows this information to be shared through a random effect structure (Johnson et al. 2013). Neighboring sites were defined as sites immediately preceding or following each current site along the transect. Terminal sites of each transect possessed only one neighbor. All neighbors were weighted equally. We approximated ρ_i^A using an intrinsic Gaussian CAR prior distribution (car.normal in WinBUGS) with a precision term, τ^A. We set the prior for $\tau^A = 1/(\sigma^A)^2$ where $\sigma^A \sim$ Uniform (0, 5). We estimated ρ_i^B using the same parameterization as for ρ_i^A.

All four models were fit using WinBUGS via the R2WinBUGS package (Sturtz et al. 2005). We used the spdep package (Bivand and Piras 2015) to create neighborhood matrices for the CAR analyses. All model code can be found in Appendix S1. Model convergence was determined visually from traceplots and Gelman-Rubin statistics ($\hat{R} < 1.05$; Gelman and Rubin 1992).

Model comparisons

Using fivefold Bayesian cross-validation to test the predictive accuracy of our models, we randomly removed 20% of the data prior to model fitting and then calculated model likelihood and deviance based on values predicted by each model (Hooten and Hobbs 2015, Miller and Grant 2015). We repeated this removal process for each of the remaining 20% segments of data (i.e., generating five test datasets each with 20% missing observations) and summed calculated deviances for each test dataset across all five model fits. To better isolate where each model did better or worse, we calculated model likelihoods for each species individually and for both species together using (1) all test data (i.e., overall), (2) test data where information on both species was removed (i.e., both species data were removed at the same site), and (3) test data where only one or the other species information was removed. This allowed us to determine overall fit but also isolate parts of the dataset where one model did measurably better than another. Deviance was calculated as $-2[\Sigma(\ln(\mathcal{L}(\text{test data}))]$. Removal of both species

information for a single-species occupancy model was the same as removing information on just a single species as these models do not share a conditional relationship between species occupancy; however, we calculated deviance where observations for both species were missing in order to use the same removed 20% across all models.

We also compared predicted co-occurrence zones of all models to determine how model choice affected conclusions about range limits. Occupancy probabilities ($\psi_i^A \times \psi_i^B$ for single-species models assuming independence or ψ_i^{BA} for two-species models assuming conditional dependence) were mapped to each site. These values were then summed across each site and the next two immediate sites (or three 5×4 m sites = 60 m² area used) of a transect to identify areas of consistent species occurrence. Male red-backed salamanders use a maximum area of 62.1 m² (averaged spring and autumnal space-use estimates; Muñoz et al. 2016) surrounding a resident territory, and we therefore used this area to infer resident animals vs. potential dispersers (assuming the same territory size for both species). Summed values of $\psi_i^A \times \psi_i^B$ or ψ_i^{BA} could equal a maximum value of 3. We considered a high probability of co-occurrence to be any site where the likelihood of co-occurrence across 15 m (3 sites) was equal to or greater than one (e.g., at least two of the three sites had a 0.5 or greater co-occurrence probability). For defining zones of co-occurrence, we considered two types of co-occurrence. Primary and secondary contact zones were both areas with a high probability of resident animals of both species co-occurring, but we defined primary zones as the longest stretch of continuous co-occurrence in a given transect. Secondary contact zones were narrower than primary zones, representing a second area of potentially dispersing or transient individuals (e.g., a very short length of co-occurrence) or a disjunct pocket of resident animals (e.g., a longer length of co-occurrence nearly equivalent to the primary contact zone).

RESULTS

We used data from 1954 red-backed salamander and 654 Shenandoah salamander detections for all analyses and tests. The naïve (i.e., unadjusted for detection probability) spatial overlap

of detected salamanders varied among surveys. Observations of co-occurrences at individual sites were relatively uncommon during a single survey, but, when summarized across all surveys, we observed a larger area of overlap between the two species (Fig. 1; Appendix S2: Fig. S1). Number of detected salamanders of each species peaked toward the center of each species' respective territory but was not consistently highest where only a single-species was detected (Appendix S2: Fig. S2). Substrate maps showed a trend of higher proportion of rock in Shenandoah salamander territory and a higher proportion of soil/wood in red-backed salamander
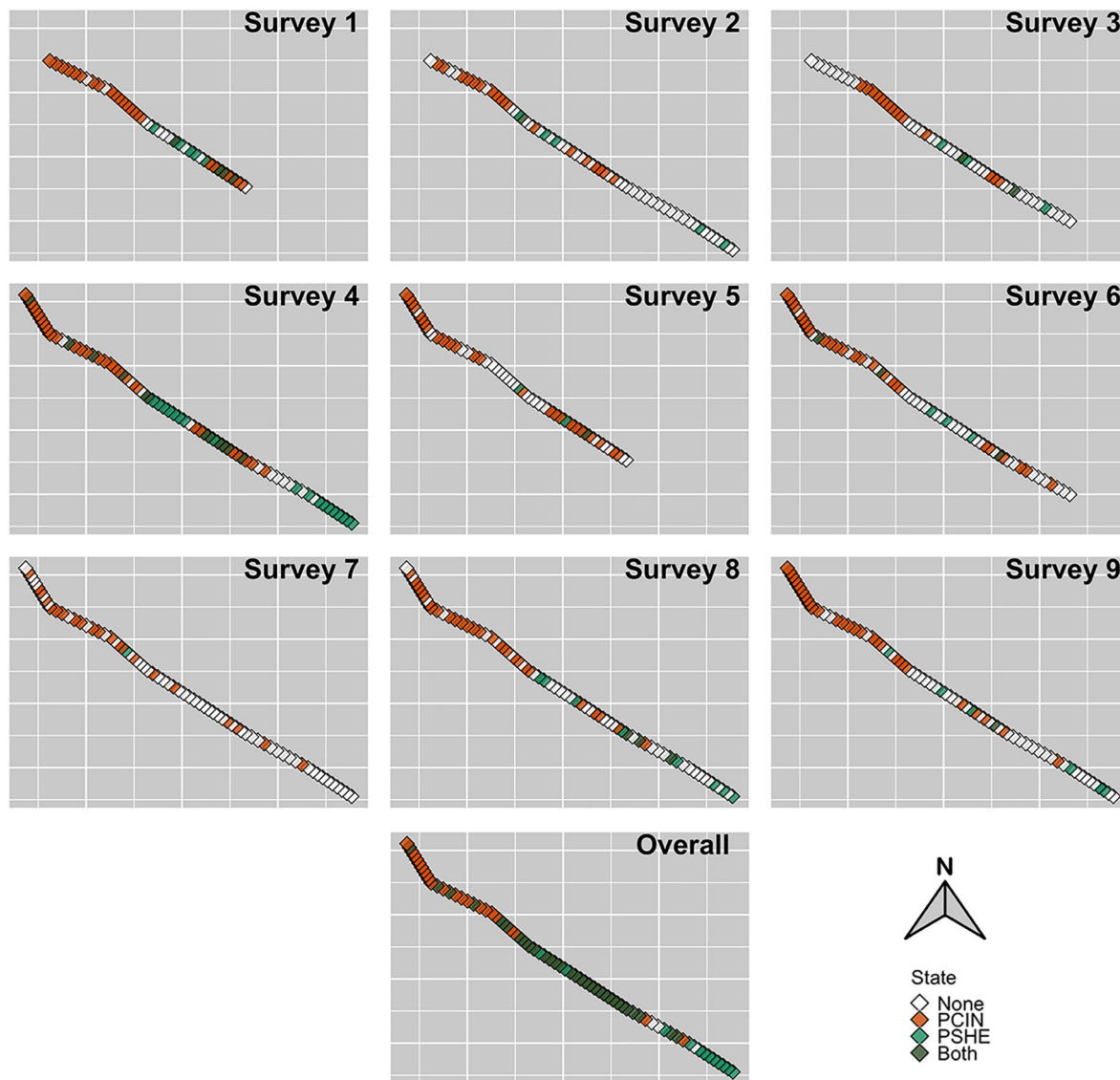

Fig. 1. Based on raw detection data, Shenandoah (*Plethodon shenandoah*, PSHE; green) and red-backed (*Plethodon cinereus*, PCIN; orange) salamanders did not frequently co-occur (dark green) at a site (5 × 4 m square) during a single survey but did overlap across a larger area when summarizing information from all surveys (Overall). Species non-detections (None; white) show the importance of accounting for detection probabilities. Data shown are for a single transect at study area one. Meters surveyed varied by visit.

territory (Appendix S2: Fig. S3). Moss/leaf had large variation among transects in no consistent pattern while other substrate types occurred sporadically.

Model comparison

We calculated model likelihoods and deviances using multiple criteria to compare how each model performed in modeling the range limit between red-backed and Shenandoah salamanders (Table 1). The best-supported overall model for all data and for both species was our third model, the single-species occupancy model with a CAR random effect (deviance = 486.20). When we considered different subsets of data, in most cases this model was the best-supported model except where test data were restricted to only cases where both species detection histories were not included in the dataset used to fit the model. When test data where information on both species was removed, the two-species conditional occupancy model with CAR random effect was best supported (deviance = 96.94) as compared to

Table 1. Model likelihood results from fivefold Bayesian cross-validation with 20% data removed.

Model	Overall	Both	One species removed
Red-backed salamander (*Plethodon cinereus*)			
Single-species	386.18	88.95	297.23
Single-species CAR	312.22	68.32	243.90
Two-species	348.94	72.49	276.46
Two-species CAR	366.66	66.28	300.38
Shenandoah salamander (*Plethodon shenandoah*)			
Single-species	204.55	36.65	167.91
Single-species CAR	173.99	30.35	143.64
Two-species	196.20	38.05	158.15
Two-species CAR	183.15	33.81	149.34
Both species			
Single-species	590.73	125.60	465.14
Single-species CAR	486.20	98.67	387.54
Two-species	545.15	110.54	434.61
Two-species CAR	549.81	100.09	449.72

Notes: CAR, conditional autoregressive. Model likelihoods were calculated separately for each species and combined for additional comparison of model performance. Model likelihood was assessed using deviance calculated as $-2[\Sigma(\ln(\mathcal{L}(\text{test data})))]$. Three deviances were calculated based on the test data used: Overall (using all test data), both (using test data where both species information was removed), and one species removed (using test data where only one or the other species' detection histories remained).

the next best-supported model (single-species occupancy model with CAR random effect, deviance = 98.67). Models with CAR random effects resulted in occupancy estimates that were smoothed across space with peak areas of species occupancy, showing similar spatial patterns between the single-species and the two-species conditional occupancy models with CAR random effects (Fig. 2). Models without CAR random effects and only substrate covariates showed no clear spatial pattern.

We calculated model deviance separately for each species for each model, and all models had a lower deviance for Shenandoah salamander parameters than red-backed salamander parameters (Table 1). For the best-supported species occupancy model with CAR random effect, model deviance calculated for red-backed salamander estimates was 243.90 as compared to 143.64 for Shenandoah salamander estimates. When data were removed for only one species or the other, we obtained smaller deviances from models when only red-backed salamander data were present rather than when only Shenandoah salamander data were available. For the top-supported single-species occupancy model with CAR random effect, deviance using only red-backed salamander data was 143.64 while deviance was 243.90 when using only Shenandoah salamander data.

Detection probabilities for red-backed salamanders were higher than those for Shenandoah salamanders for all models and all surveys (Fig. 3). From the single-species occupancy model with the CAR random effect, mean detection probability of red-backed salamanders was over twice that of Shenandoah salamanders (p^A = 0.564 compared to p^B = 0.241, Table 2). For the two-species conditional model with the CAR random effect, mean detection probability of red-backed salamanders was higher where Shenandoah salamanders did not co-occur (p^A = 0.763 compared to r^A = 0.415). Shenandoah salamanders were detected fairly similarly with or without the co-occurrence or detection of red-backed salamanders (p^B = 0.259, r^{BA} = 0.212, r^{Ba} = 0.200). Occupancy models with and without CAR random effects predicted similar detection probabilities.

Based on our best model, the single-species occupancy model with CAR random effect, substrate use differed between the two species
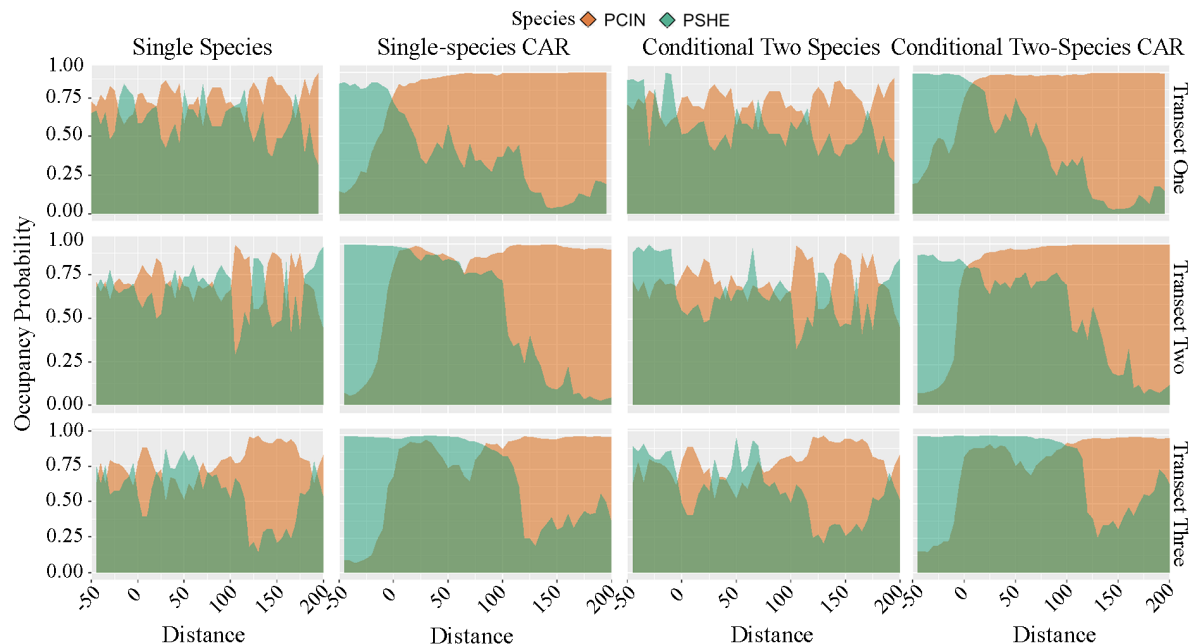
Fig. 2. Model comparison of occupancy probabilities for study area two. Occupancy probability at each site for Shenandoah (*Plethodon shenandoah*, PSHE; green) and red-backed (*Plethodon cinereus*, PCIN; orange) salamanders for each transect (row) and model type (column). Distance was measured in meters. Origins of transects were marked as 0 m with added segments toward red-backed salamander territory being marked as positive meters and added segments toward Shenandoah salamander territory being marked as negative meters.

(Fig. 4, Table 3). Red-backed salamander occupancy was high in all substrates categories, with rock and soil/wood being the most important (3.606 [2.129, 5.006] and 3.380 [1.432, 5.465], respectively). Shenandoah salamander occupancy increased most strongly with greater rock cover (2.597 [0.879, 4.401]) and increased with all other substrates except soil/wood (−1.085 [0.757, 0.462]). Occupancy estimates from both models with a CAR random effect showed a trend of higher occupancy for red-backed salamanders in areas with increased amounts of soil and wood substrate and higher Shenandoah salamander occupancy in areas with increased rock substrate (Fig. 5; Appendix S2: Fig. S4). Substrate patterns were similar in less supported models except that occupancy probabilities were lower in rock than other substrates for the red-backed salamander when the CAR random effect was not included in the model (Fig. 4; Appendix S2: Table S2). True occupancy (z^A and z^B) varied little across the different models except toward the ends of each transect (Appendix S2: Fig. S5).

When mapping overlap of each species' range, extent of primary and secondary contact zones varied by model (Fig. 6). Contact zones from models incorporating a CAR random effect corresponded to peaks in predicted occupancy probabilities rather than the low-level background co-occurrence rate estimated from models using only substrate covariates (Fig. 6). For the top-supported single-species occupancy model with CAR random effect, primary zones of co-occurrence varied by study area and transect (Fig. 7), with the extent varying between 60 and 170 m (mean = 101.82 m, standard deviation [SD] = 37.51 m, Table 4; Appendix S2: Fig. S6). Secondary contact zones were present for five of the eleven transects and varied between 5 and 60 m (mean = 32 m, SD = 24.14 m, Table 4; Appendix S2: Fig. S6). However, the smallest secondary contact zone of 5 m was at the very end of a surveyed transect, indicating that co-occurrence may have extended past the end of the transect. The next smallest secondary contact zone was 10 m in length.
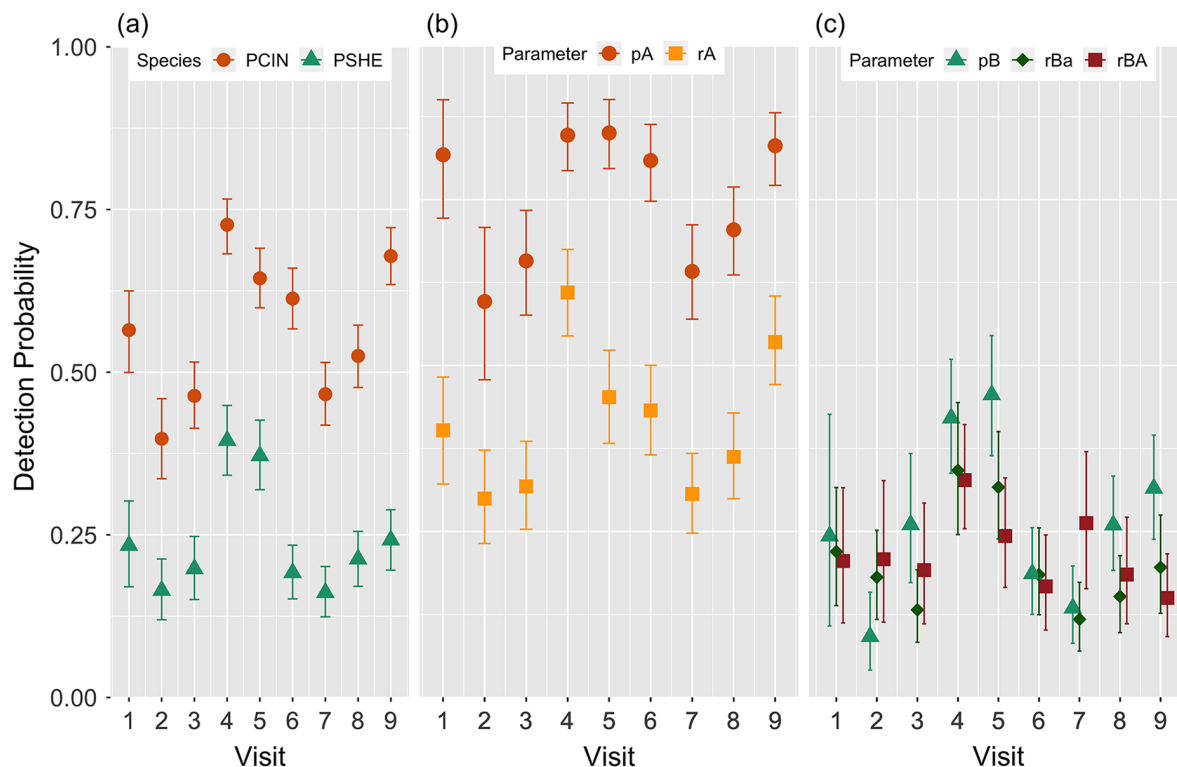
Fig. 3. Detection probabilities across all transects from (a) single-species and (b, c) two-species conditional occupancy models with conditional autoregressive (CAR) random effects. Models without a CAR random effect had similar probabilities to those shown. Detection probabilities were estimated for each survey but were either (a) estimated separately for each species or (b, c) were conditional upon the other species. Conditional probabilities include the probability of (b) detecting red-backed salamander (*Plethodon cinereus*, PCIN) given that either Shenandoah salamander (*Plethodon shenandoah*, PSHE) is absent (p^A) or PSHE and PCIN are both present (r^A) and (c) detecting PSHE given either PCIN is absent (p^B), both species are present and PCIN is also detected (r^{BA}), or PCIN is not also detected (r^{Ba}).

Discussion

An understanding of species range limits and the factors establishing these constraints is germane to critical ecological and management questions. Here, we used substrate information as a starting model to assess the importance of accounting for species interactions and spatial autocorrelation in occupancy models to best predict the range limits of an endangered plethodontid salamander. We found that correcting for detection probability was essential to understand both Shenandoah and red-backed salamander range boundaries and the breadth of their co-occurrence. If we had relied on only a single or limited number of surveys and the assumption

we had observed all occurrences along transects without error, we would have underestimated the breadth of contact zones in every transect (Appendix S2: Fig. S1).

After correcting for false absences, we were better able to evaluate the potential influence of local-level substrate information and species interactions on species occupancy in order to understand the intersection of these two species' ranges. The single-species occupancy model with CAR random effect was almost always best supported in modeling red-backed and Shenandoah salamander range limits, suggesting that explicitly including a conditional relationship between the two species did not improve estimation of the range limits in our study. Additionally,

Table 2. Detection probabilities from single-species occupancy model with conditional autoregressive random effect, the top-supported model, for each species for each survey occasion ($t = 9$).

Parameter	Mean	SD	2.5%	50%	97.5%
$p^A[1]$	0.565	0.033	0.500	0.565	0.625
$p^A[2]$	0.398	0.031	0.336	0.397	0.459
$p^A[3]$	0.464	0.026	0.414	0.464	0.516
$p^A[4]$	0.727	0.022	0.682	0.727	0.766
$p^A[5]$	0.644	0.024	0.599	0.645	0.690
$p^A[6]$	0.613	0.023	0.567	0.613	0.660
$p^A[7]$	0.466	0.024	0.419	0.466	0.515
$p^A[8]$	0.525	0.024	0.476	0.525	0.572
$p^A[9]$	0.678	0.022	0.635	0.679	0.722
$p^B[1]$	0.234	0.033	0.170	0.233	0.302
$p^B[2]$	0.164	0.024	0.120	0.164	0.213
$p^B[3]$	0.198	0.025	0.151	0.197	0.248
$p^B[4]$	0.395	0.028	0.342	0.395	0.449
$p^B[5]$	0.371	0.027	0.319	0.371	0.426
$p^B[6]$	0.192	0.022	0.152	0.191	0.234
$p^B[7]$	0.161	0.019	0.124	0.161	0.201
$p^B[8]$	0.213	0.021	0.171	0.212	0.255
$p^B[9]$	0.242	0.024	0.196	0.242	0.289

Notes: A, red-backed salamander; B, Shenandoah salamander. Standard deviation (SD) and 2.5%, 50%, and 97.5% percentiles are included.

spatially explicit, autoregressive models better captured patterns of occupancy across the range boundary than models solely relying on substrate covariates. Conditional autoregressive and other spatial models can provide a spatially smoothing approach to estimating range boundaries by sharing information among neighboring sites, thus improving model fit due to the spatially structured nature of most ecological data (Dormann 2007, Ver Hoef et al. 2018). Gradients in environmental characteristics along the range boundary such as temperature and humidity may help pattern species occupancy due to known differences in physiological tolerances between these salamander species (Jaeger 1971*a*, Dallalio et al. 2017). These autoregressive effects that share information from neighboring sites can better incorporate such patterns of spatial variation in abiotic and biotic gradients (Dormann 2007).

Previous research on the competitive interactions of Shenandoah and red-backed salamanders has focused on laboratory-based experiments or in situ manipulations (Jaeger 1970, 1971*a, b*, Griffis and Jaeger 1998), but an understanding of the current, natural dynamics of populations in their native range is required for creating targeted management plans. Past studies have suggested that red-backed salamanders exhibit a near perfect competitive ability to exclude Shenandoah salamanders and create sharply delineated range boundaries (Jaeger 1970, Griffis and Jaeger 1998), corresponding to abrupt changes in microhabitat variables that comprise discrete talus habitats. The fact we do not observe a hard transition zone with little overlap between species may be a product of three factors. First, range overlap may be increasing as a result of pressures such as climate or the effects of invasive species within the system that may have changed in the course of three decades (Webb et al. 1995, Young et al. 2000, Grant et al. 2012), altering competitive dynamics in this system. Second, the past assumptions of near perfect competitive exclusion in the wild may be an artifact of historical survey methods or those not correcting for imperfect species detection (Tingley and Beissinger 2009, Comte and Grenouillet 2013). Whether or not each species was observed at a given site varied greatly from survey to survey (Fig. 1; Appendix S2: Fig. S1), and both species were rarely detected under the same cover object. This confirms research elsewhere regarding the inconsistency of plethodontid surface activity (Bailey et al. 2004) and also the importance of designing survey methods to account for imperfect detection, especially for those species that are rare, cryptic, or temporally unavailable for detection (Gu and Swihart 2004, Durso et al. 2011, Kéry et al. 2013). Lastly, the importance of species interactions in species distribution modeling may be scale-dependent (Huston 1999, Pearson and Dawson 2003, Guisan and Thuiller 2005). At the scale of the individual, behaviors such as microhabitat selection or foraging may be impacted by the presence of the other species (Jaeger 1971*b*, Jaeger 1972, Levin 1992, Griffis and Jaeger 1998, Dallalio et al. 2017). Interspecific aggression may influence cover object selection, surface activity, or occupancy at a smaller resolution but not manifest itself as differences in occupancy at a larger spatial scale.

We found consistently higher detection probabilities for red-backed salamanders in single-species models. When species interactions were considered in models, Shenandoah salamander
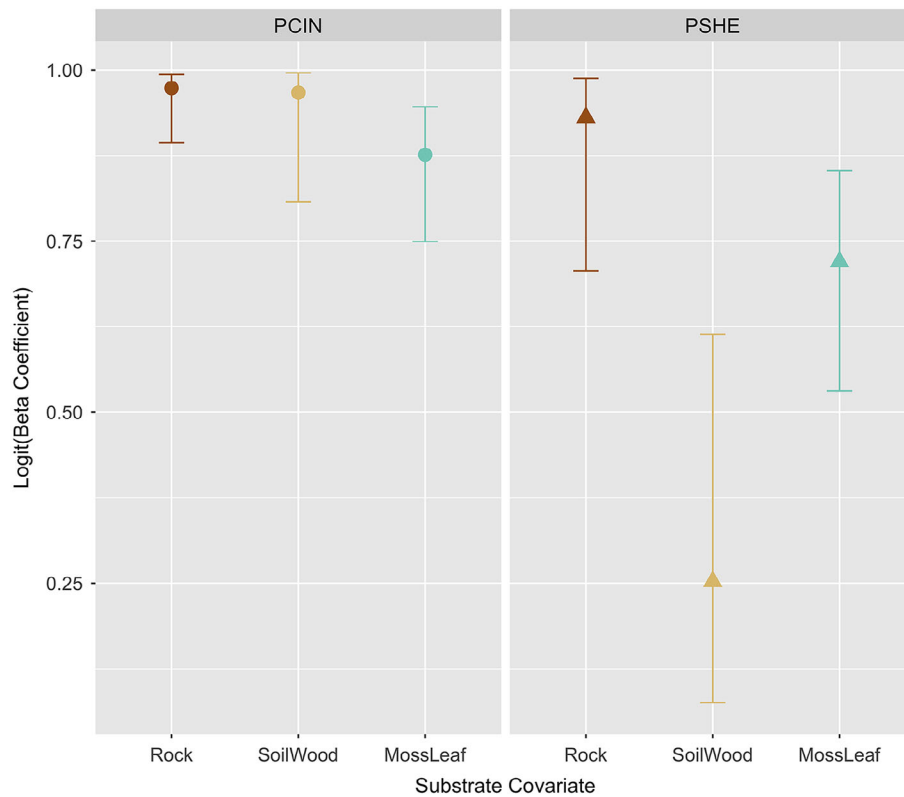
Fig. 4. Logit-transformed beta coefficients for substrate covariates for the red-backed (*Plethodon cinereus*, PCIN) and Shenandoah (*Plethodon shenandoah*, PSHE) salamander. Other substrate not shown as it represented a minimal proportion of the transect substrate sampled. Substrate coefficients and 2.5% and 97.5% credible intervals are from single-species occupancy model with conditional autoregressive random effect.

Table 3. Beta estimates from the top-supported single-species occupancy models with conditional autoregressive random effect.

Parameter	Mean	SD	2.5%	50%	97.5%
Red-backed salamander (*Plethodon cinereus*)					
Rock	3.606	0.734	2.129	3.635	5.006
SoilWood	3.380	1.015	1.432	3.353	5.465
MossLeaf	1.956	0.457	1.095	1.951	2.868
Other	2.822	2.449	−2.351	2.944	6.751
Shenandoah salamander (*Plethodon shenandoah*)					
Rock	2.597	0.911	0.879	2.570	4.401
SoilWood	−1.085	0.757	−2.503	−1.087	0.462
MossLeaf	0.944	0.424	0.126	0.940	1.759
Other	1.388	2.317	−2.815	1.283	6.136

Note: Substrate covariates including standard deviation (SD) and 2.5%, 50%, and 97.5% percentiles are shown for each species.

detection probabilities did not differ from when red-backed salamanders did and did not co-occur yet red-backed salamander detection probabilities were higher when Shenandoah salamanders were not also present. Differences in detection probability may be a product of differential surface activity between the two species or differences in abundance. Red-backed salamanders potentially are more abundant than Shenandoah salamanders, helping to explain their higher detection probability. Disentangling these explanations requires further insight that could be obtained from using a mark–recapture study to better understand differences in density vs. individual capture rates. Jaeger (1974) found behavioral avoidance by red-backed salamanders in burrows when Shenandoah salamanders were also present, supporting the idea of interference competition between the two species that might also alter surface activity. This could
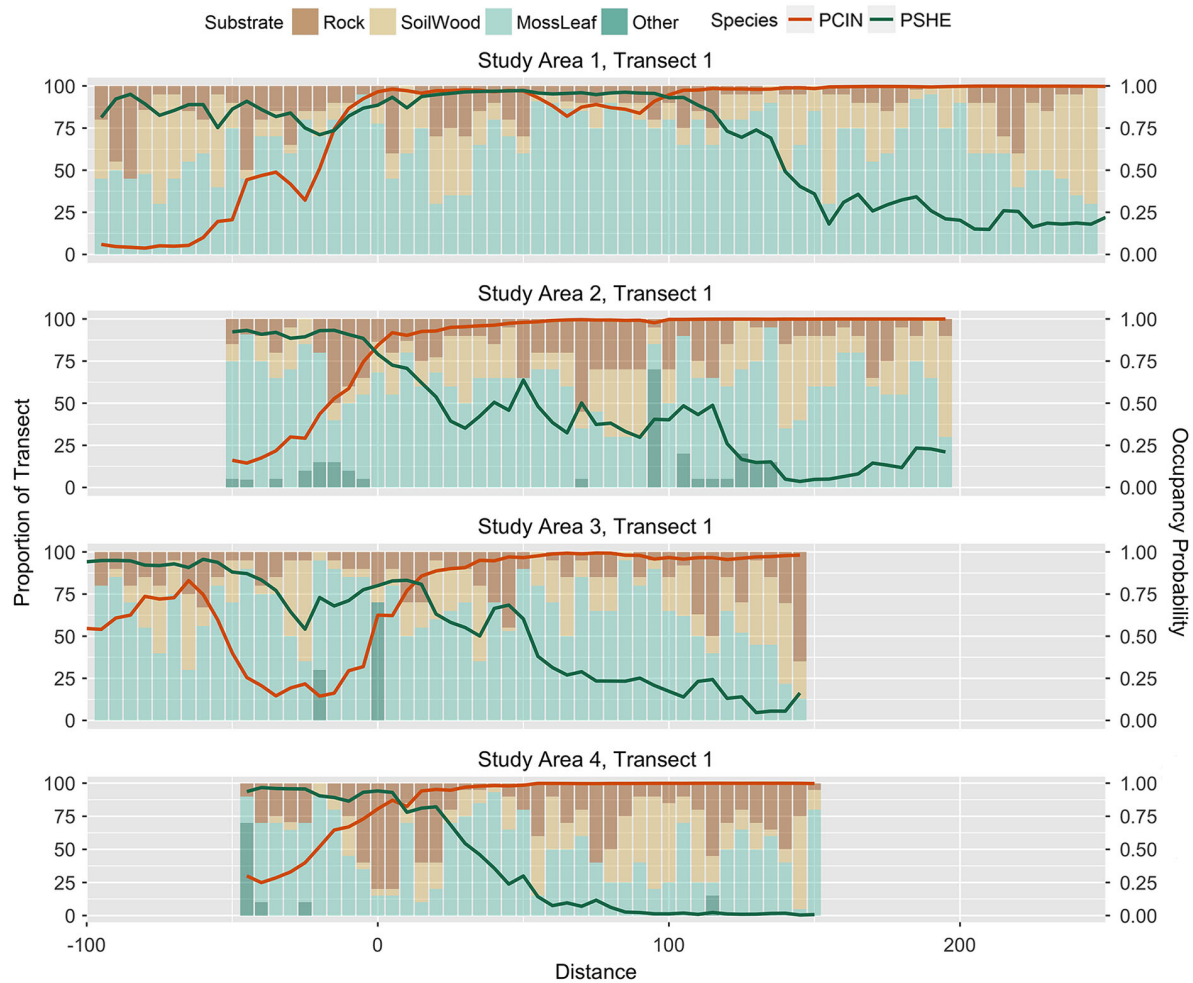
Fig. 5. Occupancy probability at each site for Shenandoah (*Plethodon shenandoah*, PSHE; green line) and red-backed (*Plethodon cinereus*, PCIN; orange line) salamanders with proportion of each substrate type at each site from best-supported single-species occupancy models with conditional autoregressive random effect. Values for the first transect for every study area shown. Distance was measured in meters. Origins of transects were marked as 0 m with added segments toward red-backed salamander territory being marked as positive meters and added segments toward Shenandoah salamander territory being marked as negative meters.

contribute to the limited number of occasions where both species were detected under the same cover object, but this difference in detectability does not appear to manifest itself in distributional patterns at the transect level.

When mapping the range limit, the shape and extent of the co-occurrence zone varied based on our model (Fig. 6), highlighting the importance of accounting for and testing these hypothesized relationships when modeling species distributions. From the single-species occupancy model with CAR random effect, we found range

overlap between the Shenandoah and red-backed salamander is currently wider than previously reported (<100 m; Jaeger 1972). Jaeger (1970) found coexistence was possible (though rare) within 20 m of the talus edge in soil but did not conduct surveys >30 m from the talus edge. Our results support an overlap of >100 m in about half of our transects. In addition, multiple transects showed secondary contact zones that do not necessarily coincide with talus slopes and may be proximate to primary zones (i.e., may not represent distinct metapopulations; Griffis
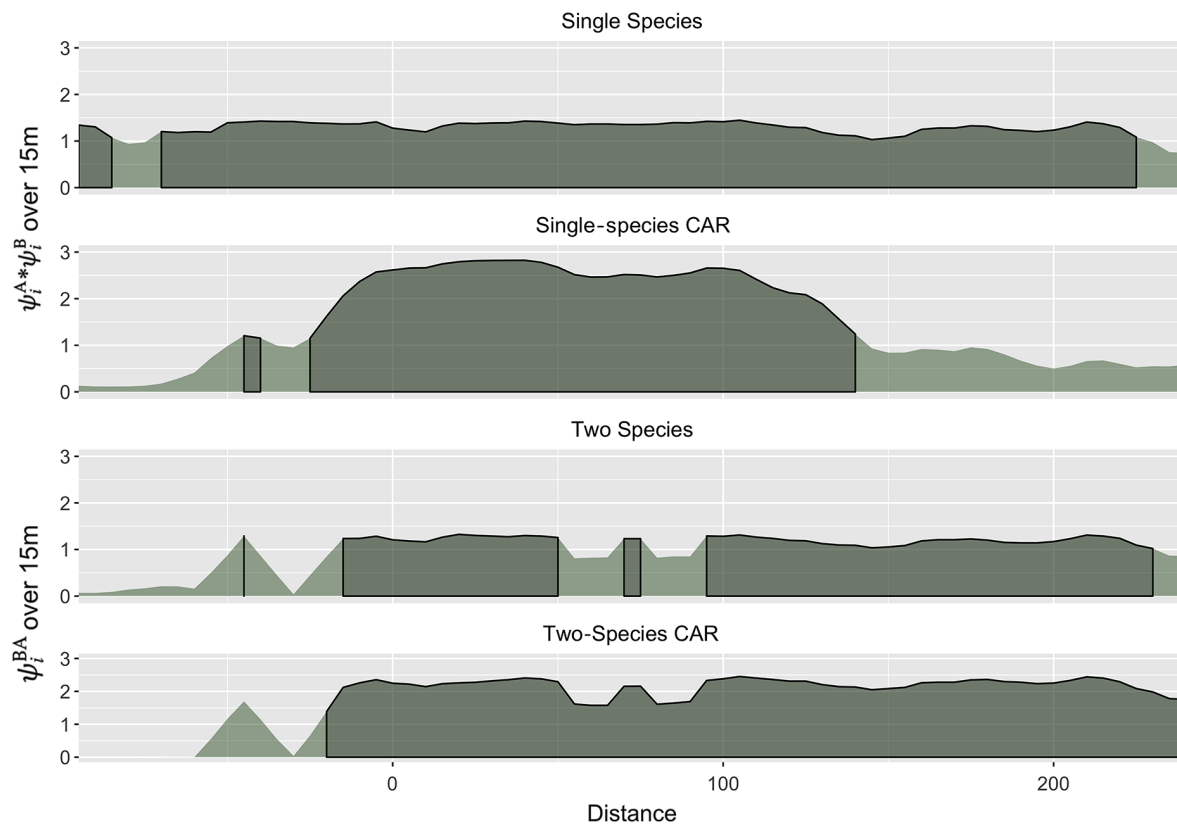
Fig. 6. Co-occurrence probabilities of both species for a single transect of a single study area based on each model of the four models with primary (and secondary) contact zone(s) highlighted in darker green. For single-species models, co-occurrence probability was calculated by multiplying $\psi_i^A \times \psi_i^B$. For two-species models, co-occurrence probability (ψ_i^{BA}) was calculated from our conditional Shenandoah model using only surveys where z^A was estimated to be 1. These values were then summed across each site and the next two immediate sites (three 5 × 4 m sites or 60 m^2 area used, Muñoz et al. 2016) of a transect to identify areas of consistent species occurrence (i.e., a contact zone). Single-species and two-species conditional occupancy models with only substrate covariates do not show a clear peak area of overlap but rather have low levels of co-occurrence across much of their length. Origins of transects were marked as 0 m with added segments toward red-backed salamander territory being marked as positive meters and added segments toward Shenandoah salamander territory being marked as negative meters.

and Jaeger 1998), highlighting that the range boundary is not as sharply delineated as previously suspected and that the red-backed salamander may not be able to completely exclude Shenandoah salamanders from its range.

Red-backed salamanders did not demonstrate a preference for any measured substrate, but Shenandoah salamanders occupied areas with rocky substrate more often than those with soil and wood substrates (Jaeger 1971a, b). Talus slopes have been used as a proxy for moisture

and temperature regimes in which Shenandoah salamanders persist (on the three mountaintops at suitable elevations; Jaeger 1970, Grant et al. 2012), potentially explaining increasing Shenandoah salamander occupancy with rock substrate. Jaeger (1971b) indicated that experimental evidence supported the finding that red-backed salamanders were unable to persist in talus slopes and would thus not co-occur with Shenandoah salamanders, yet we observed no difference in substrate use for red-backed salamanders.
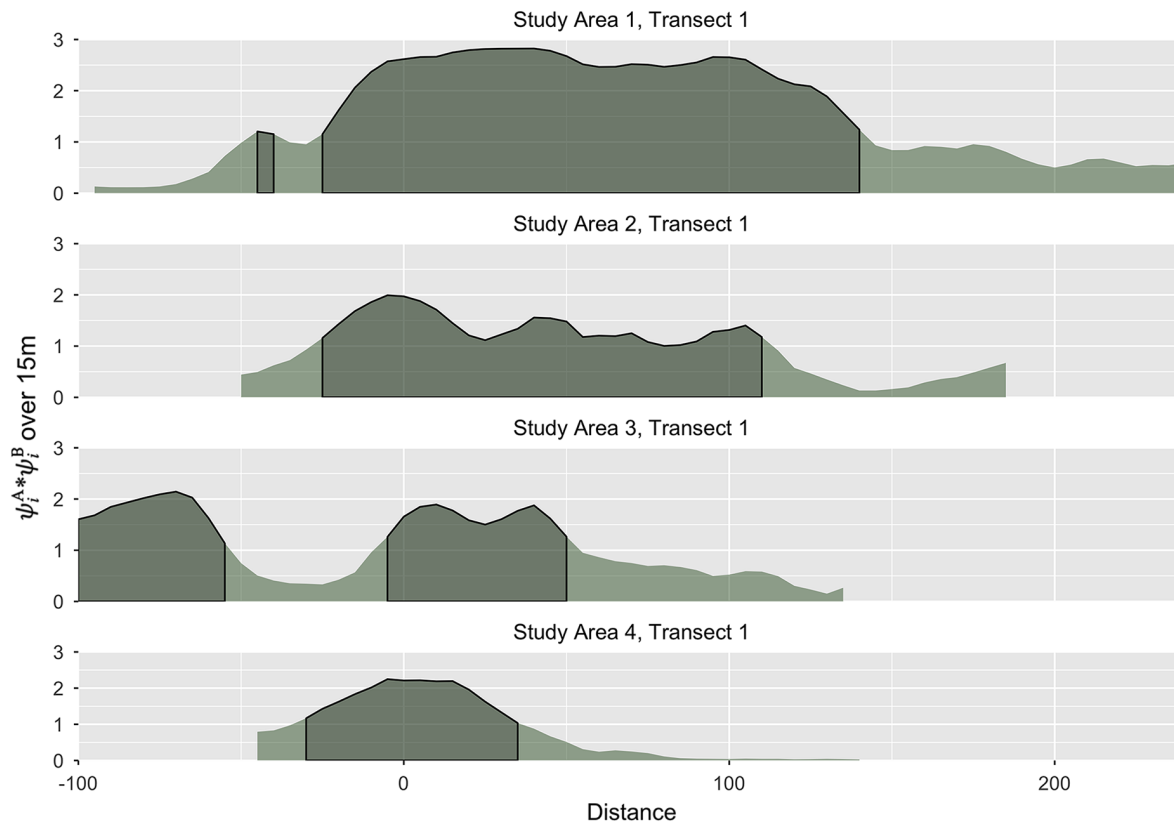
Fig. 7. Co-occurrence probabilities based on the single-species occupancy model with conditional autoregressive random effect for the first transect for every study area with primary (and secondary) contact zone(s) highlighted in darker green. Co-occurrence probabilities ($\psi_i^A \times \psi_i^B$) were summed across each site and the next two immediate sites (three 5×4 m sites or 60 m^2 area used, Muñoz et al. 2016) of a transect to identify areas of consistent species occurrence. We defined the co-occurrence zone as the area of overlap at the range edge of resident animals. Summarizing nearby sites by their occupancy allowed for the identification of core areas of overlap rather than including potentially dispersing or outlier animals. Distance was measured in meters. Origins of transects were marked as 0 m with added segments toward red-backed salamander territory being marked as positive meters and added segments toward Shenandoah salamander territory being marked as negative meters.

Substrate alone did not explain patterns in occupancy between the two species, though CAR models may also account for spatial patterns in habitat characteristics such as substrate and thus lessen the importance of substrate covariates alone in explaining occupancy patterns (Dormann 2007). Additionally, substrate measured at the 5×4 m spatial scale may not accurately reflect the importance of microhabitat refugia used by each species or broadscale associations that occur when considering larger scales.

Shenandoah salamanders are a range-restricted, endangered species that is currently threatened by the influence of changing climate on their montane ecosystems (Grant et al. 2012). The current conservation status of the salamander and vulnerability to range contractions under future climate change makes understanding the elements contributing to their range limits especially pressing. This is one of the first studies in this system to estimate these range boundaries using robust methodologies and to test the importance of different occupancy model structures on co-occurrence conclusions. The occupancy models we employed are amenable to the inclusion of abiotic and biotic covariates and

Table 4. Length of primary and secondary contact zones between red-backed and Shenandoah salamanders.

Parameter	Primary zone length	Secondary zone length	Distance between zones	Total length of transect
Study area one				
Transect 1	170	10	10	345
Transect 2	75	35	95	295
Transect 3	110			395
Study area two				
Transect 1	140			245
Transect 2	135			245
Transect 3	135	60	15	245
Study area three				
Transect 1	60	50	45	245
Transect 2	70	5†	70	195
Transect 3	80			195
Study area four				
Transect 1	70			195
Transect 2	75			295

Notes: We summed co-occurrence probabilities ($\psi_i^A \times \psi_i^B$) across each site and the next two immediate sites (three 5×4 m sites or 60 m^2 area used, Muñoz et al. 2016) of a transect to identify areas of consistent species occurrence. Primary zones represent the largest area of consistent overlap of both species ranges, while secondary zones were smaller, additional areas of overlap. All lengths are in meters.

† 5 m secondary contact zone was right at the end of transect sampling, indicating the contact zone likely continues outside of the area surveyed.

variations in occupancy and random effect structures, emphasizing their strength in such range-modeling questions (Kéry et al. 2013). Future analyses with additional seasons of data could fit dynamic occupancy models to better characterize temporal variation in range boundaries or seasonal variation in detection probabilities (Anderson et al. 2009, Kéry et al. 2013, Amburgey et al. 2018). Additional abiotic and biotic gradients that vary over space might influence occupancy of both species, and future work in this system could include the role of measured climate along these transects in order to fit climate by space models, allowing for estimates of turnover for both species and furthering our understanding of the ecology of these range boundaries. Further investigation of differences in detection probability or co-occurrence probabilities by individual species traits (e.g., striped vs. leadback dorsa; Moreno 1989) may also further explain the range boundary.

CONCLUSIONS

Delineation of species' range edges using robust modeling methodologies is important for management of a species (Rondinini et al. 2006), particularly those that are threatened, endangered, or range-restricted (Engler et al. 2004). Survey methods and modeling approaches that can accommodate uncertainty in species distribution models are important for conservation planning where biases can result in drastically different forecasts of range shifts (Wilson et al. 2005) or identification of management threats (Gu and Swihart 2004). Failure to incorporate spatial autocorrelation in models where it plays a part in species occupancy can lead to overestimation and inaccurate prediction of species distributions (Dormann 2007). Similarly, failure to test for conditional species relationships that integrate biotic interactions can lead to erroneous species distribution models (Guisan and Thuiller 2005) or conclusions about species co-occurrence (Bailey et al. 2009, Miller et al. 2012). We highlight the importance of testing the fit of a suite of range models in order to select reliable parameterizations for management and encourage validation of models to assess goodness of fit. Goals from a structured decision-making workshop for the Shenandoah salamander indicated a favorable attitude of managers toward active management for this species, as long as uncertainty of the cause of declines and responses to management can be quantified (Grant et al. 2012). In considering potential future initiatives, an approach such as occupancy modeling to understand range dynamics better addresses uncertainty and informs managers about how best to target management efforts.

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product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Data Availability

All data belong to the National Park Service, and public release of information on endangered species is not permitted. All R code for running occupancy models is available in Appendix S1. Additional Supporting Information may be found online.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2727/full