BIODIVERSITY RESEARCH

Mountaintop removal mining alters stream salamander population dynamics

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Abstract

Aim: Population dynamics are often tightly linked to the condition of the landscape. Focusing on a landscape impacted by mountaintop removal coal mining (MTR), we ask the following questions: (1) How does MTR influence vital rates including occupancy, colonization and persistence probabilities, and conditional abundance of stream salamander species and life stages? (2) Do species and life stages respond similar to MTR mining or is there significant variation among species and life stages?

Location: Freshwater and terrestrial habitats in Central Appalachia (South-eastern Kentucky, USA).

Methods: We conducted salamander counts for three consecutive years in 23 headwater stream reaches in forested or previously mined landscapes. We used a hierarchical, N-mixture model with dynamic occupancy to calculate species- and life stage-specific occupancy, colonization and persistence rates, and abundance given occupancy. We examined the coefficients of the hierarchical priors to determine population variation among species and life stages.

Results: Over 3 years, reference sites had greater salamander abundances and were occupied at a much higher rate than streams impacted by MTR. At sites impacted by MTR mining, most salamander species and life stages exhibited reduced initial occupancy, colonization rates, persistence rates and conditional abundance relative to reference stream reaches. Furthermore, the rates in MTR sites showed low variance, reinforcing that species and life stages were responding similar to MTR.

Main conclusions: Salamander populations in landscapes modified by MTR mining exhibited significantly reduced vital rates compared to reference sites. Yet, similarity in responses across species suggests that management or restoration may benefit the entire salamander assemblage. For example, reforestation could reduce landscape resistance, repair altered hydrologic regimes and allow for higher rates of colonization and persistence in streams impacted by MTR.

KEYWORDS
abundance, Appalachia, coal mining, colonization, persistence, valley fill

1 | INTRODUCTION

Human-induced landscape modification is a primary driver of species loss and population declines (Sala et al., 2000). Human-modified landscapes are often characterized by a reduction, elimination, or enhanced patchiness of native vegetation and increased land use intensity, which collectively degrade or subdivide habitat for many species (Fischer & Lindenmayer, 2007; McIntyre & Hobbs, 1999; Sala et al., 2000). The probability of long-term survival of populations in human-modified landscapes is tied to both colonization and persistence (or conversely extinction) rates; this is especially apparent for species exhibiting metapopulation structure or patchy distributions (Irizarry, Collazo, & Dinsmore, 2016; Schroeder, Ranius, Ekbom, & Larsson, 2007; Snäll, Ehrlén, & Rydin, 2005). Patch-dependent species within human-modified landscapes may have decreased persistence rates due to reduced patch size, variable resource dynamics and/or changes to microhabitat conditions (Thomas, 1994). Colonization via dispersing individuals from neighbouring populations, however, may stabilize declining populations or re-establish locally extinct populations (Brown & Kodric-Brown, 1977; Erős & Grant, 2015).

Mountaintop removal mining (MTR) is a form of landscape modification common to the central Appalachian region of the eastern United States that impacts both aquatic and terrestrial environments (Bernhardt & Palmer, 2011; Wickham et al., 2013). Mountaintop removal mining involves the removal of overlain geologic material (i.e., tops of mountains) to access the coal seams underneath (Palmer et al., 2010). The overburden material is often disposed into adjacent valleys, burying streams and creating a valley fill (VF, Palmer et al., 2010; Bernhardt & Palmer, 2011). Unweathered rock in the VF alters physical and chemical conditions of streams (Bernhardt et al., 2012; Griffith, Norton, Alexander, Pollard, & LeDuc, 2012; Lindberg et al., 2011; Negley & Eshleman, 2006). In addition to the removal of mountaintops, terrestrial impacts of MTR include forest loss and fragmentation (Wickham et al., 2013). Native vegetation is typically slow to recolonize mined landscapes due to soil compaction required by the Surface Mining Control and Reclamation Act to increase land stability and return the land to an approximate original contour (Office of Surface Mining, 1977). Also, thin topsoil or topsoil substitutes and the prevalence of non-native invasive plant species, many of which are planted as a mandated restoration measure (Zipper et al., 2011), slow natural succession. In general, MTR landscapes are vastly different from the mesic forests that typically dominate the central Appalachian landscape. The landscape modifications arising from MTR and VF restrict the distribution and reduce the abundance of the region's rich fauna (i.e., Becker, Wood, Strager, & Mazzarella, 2015; Hopkins & Roush, 2013; Pond, 2010; Warren & Haag, 2005; Williams, Brown, & Wood, 2017).

Stream-breeding salamanders are abundant components of Appalachian landscapes, where populations reach their greatest population densities in low-order streams with forested watersheds and intact riparian zones (see Nowakowski & Maerz, 2009; Peterman, Crawford, & Semlitsch, 2008). Stream salamander metapopulations

in undisturbed, forested landscapes tend to exhibit interannual stability (Green, 2003; Hairston, 1986) due to relatively high adult survival (Organ, 1961; Price, Eskew, Cecala, Browne, & Dorcas, 2012) coupled with the use of multiple dispersal pathways (Grant, Nichols, Lowe, & Fagan, 2010). Conversely, in human-modified landscapes, stream salamander populations often exhibit reduced occupancy rates (Price, Cecala, Browne, & Dorcas, 2011). Decreased colonization and persistence rates, due to changes in the permeability of the upland habitat (i.e., matrix) and deterioration of within-stream habitat conditions, may lead to changes in occupancy (Price et al., 2011).

Recent studies of stream salamander populations within MTR landscapes have shown reduced occupancy, abundance and species richness compared to reference streams (Muncy, Price, Bonner, & Barton, 2014; Price, Muncy, Bonner, Drayer, & Barton, 2016; Wood & Williams, 2013a). Mechanisms responsible for these patterns in MTR landscapes are likely multi-faceted; however, one hypothesis suggests that changes in the terrestrial matrix and subsequent deterioration of local stream habitat may reduce colonization and persistence rates within streams affected by MTR and VF (see Muncy et al., 2014; Price et al., 2016; Wood & Williams, 2013a). Using count data from three consecutive years and a hierarchical, dynamic model of occupancy and abundance, we test this hypothesis by asking the following questions: (1) How does MTR mining influence occupancy, colonization and persistence probabilities, and conditional abundance of individual stream salamander species and life stages over three years? (2) Do species and life stages respond similar to MTR mining or is there significant variation among species and life stages?

2 | METHODS

2.1 | Study area

We conducted salamander counts in 23 headwater streams in Breathitt and Knott Counties in south-eastern Kentucky, USA (see Figure S1A). Eleven streams were located on the reclaimed Laurel Fork surface mine, active from the late 1990s to the early 2000s. The headwaters of these streams were valley-filled, but otherwise the stream geomorphology and riparian zone were apparently unaltered from mining activities. Vegetation on the Laurel Fork surface mine included American sycamore (*Platanus occidentalis*), autumn olive (*Elaeagnus umellate*), the nitrogen fixing herb sericea lespedeza (*Lespedeza cuneata*), tall fescue (*Schedonorus arundinaceus*), Virginia pine (*Pinus virginiana*), black locust (*Robinia pseudoacacia*) and white oak (*Quercus alba*) (Fritz et al., 2010). Approximately 34% of the surface mine was covered in deciduous, coniferous or mixed forest types typical of the region, yet most forested areas were restricted small, isolated, unmined patches or the riparian zones of streams (including our study streams). The remaining land cover (approximately 65%) was considered mined or reclaimed land and dominated by grassland, shrub, barren lands and smaller percentages of developed land, such as roads (J. Yang, pers. comm.).

The 12 reference streams were located in the University of Kentucky's Robinson Forest, a mixed mesophytic, second-growth

forest (i.e., approximately 80 years old) located directly north-east of the Laurel Fork surface mine. Common vegetation in Robinson Forest included Eastern hemlock (*Tsuga canadensis*), white oak (*Quercus alba*), chestnut oak (*Q. prinus*) and tulip poplar (*Liriodendron tulipifera*) (Phillippi & Boebinger, 1986). Average forest cover within reference stream catchments was 99%, and the matrix habitat was also almost entirely forested. For additional study site details, see Muncy et al. (2014) and Price et al. (2016).

2.2 | Data collection

We conducted time-constrained salamander count surveys in 10-m reaches within streams on MTR and reference landscapes. First, we identified reaches downstream of the VF in MTR landscapes. Then, we selected reaches at Robinson Forest to coincide with reach widths and depths at MTR sites. Thus, reaches were similar in terms of width and depth and each reach contained riffle, run and pool microhabitats (see Muncy et al., 2014).

Stream reaches were sampled three times per year in 2013, 2014 and 2015 (approximately monthly from April through June) at base flow conditions during daylight hours. Prior to sampling, we recorded environmental conditions that may have influenced our ability to detect salamanders (e.g., number of cover objects, number of days since last precipitation event, see Price et al., 2016). We used dipnetting and active search methods to locate adult and larval salamanders. Dipnetting entailed one observer moving from downstream to upstream actively netting under cover objects and within detritus to capture salamanders. Dipnetting was restricted to 30 min. We also conducted 15-min active searches in the riparian zone adjacent to streams, which involved examining cover objects within 1 m from the wetted stream width for stream salamanders. Captured individuals were counted and classified to species and life stage (i.e., larvae and adults). We released all individuals into the sampling reach after counts were taken. See Muncy et al. (2014) and Price et al. (2016) for additional details on sampling methods.

2.3 | Dynamic occupancy and abundance modelling

We applied a hierarchical, N-mixture model with dynamic occupancy to examine species and site-type-specific occupancy, colonization and persistence rates, and abundance given occupancy. The basic model combined a dynamic occupancy model (Royle & Kéry, 2007) with the hurdle model of abundance (Dorazio, Martin, & Edwards, 2013) allowing for imperfect detection of individuals. Populations at each stream reach were assumed to be independent and closed each year, implying that no individuals entered or exited the stream reaches between sampling occasions within the same year. The hierarchical framework allowed us to draw strength from the similarities among species and to estimate mean effects across species while still drawing inference from each species separately.

The basic model for occupancy, denoted by $O_{s,j,y}$ for species, s, at site, j, in year, y, was parameterized in terms of three probabilities: (1) initial occupancy or the probability that site j was occupied by species s in year 1 (denoted by $\psi_{s,j}$), (2) colonization or the probability that species s is present at site j in year $y + 1$ given that it did not occupy site j in year y ($\gamma_{s,j,y}$) and (3) persistence or the probability that site j remained occupied by species s in year $y + 1$ given that site j was occupied in year y ($\varphi_{s,j,y}$). Conditional on occupancy, abundance was modelled as a zero-truncated Poisson distribution with species, site- and year-specific rate parameters ($\lambda_{s,j,y}$). Finally, detection was modelled as a binomial process assuming that individuals from species s occupying site j in year y were detected on visit v independently and with the same probability ($p_{s,j,y,v}$).

We first separated salamander count data by life stage (i.e., gilled larvae or adult) for five stream salamander species. Due to few adult captures, we did not separate life stage for the spring salamander (*Gyrinophilus porphyriticus*, Green, 1827) or the northern red salamander (*Pseudotriton ruber*, Sonnini de Manoncourt and Latreille, 1801). We had sufficient individuals to separate southern two-lined salamander (*Eurycea cirrigera*, Green, 1831) adults and larvae. For the northern dusky salamander (*Desmognathus fuscus*, Rafinesque, 1820) and seal salamander (*D. monticola*, Dunn, 1916), we analysed adults separately but combined larvae into a singular "*Desmognathus* larvae" category due to difficulties identifying larvae (a solution also used in Muncy et al., 2014 and Price et al., 2016).

To examine how MTR mining affected salamander population dynamics, we modelled the base parameters in the occupancy and abundance models as functions of site type for the study stream reaches. Specifically, we modelled the initial occupancy, colonization and persistence probabilities as linear functions of site type (i.e., MTR or reference) on the logistic scale, such that the initial occupancy probability of species s at site j in the first year was modelled as:

$$\text{logit}\left(\psi_{s,j}\right) = \beta_{s,0}^{(\psi)}\left(1 - \text{MTR}_j\right) + \beta_{s,1}^{(\psi)}\text{MTR}_j \tag{1}$$

where MTR_j equalled 1 if site j was a MTR site and 0 otherwise. Colonization and persistence were modelled similarly so that for species s at site j in year y:

$$\text{logit}\left(\gamma_{s,j,y}\right) = \beta_{s,0}^{(\gamma)}\left(1 - \text{MTR}_j\right) + \beta_{s,1}^{(\gamma)}\text{MTR}_j \tag{2}$$

$$\text{logit}\left(\phi_{s,j,y}\right) = \beta_{s,0}^{(\phi)}\left(1 - \text{MTR}_j\right) + \beta_{s,1}^{(\phi)}\text{MTR}_j. \tag{3}$$

The rate parameter for abundance conditional on occupancy was modelled such that:

$$\log\left(\lambda_{s,j,y}\right) = \beta_{s,0}^{(\lambda)}\left(1 - \text{MTR}_j\right) + \beta_{s,1}^{(\lambda)}\text{MTR}_j. \tag{4}$$

Previous studies have found that salamanders become more difficult to detect when both the availability of shelter and the amount of water in the system increase (Connette, Price, & Dorcas, 2011; Kleeberger, 1985; Orser & Shure, 1975). To account for these effects, we modelled the detection probabilities as a function of the number of cover objects, which varied by site and year, and the number of days since last precipitation event, which varied by site, year and date:

$$\text{logit } (p_{s,j,y,v}) = \beta_{s,0}^{(p)} + \beta_{s,1}^{(p)} \text{Cover}_{j,y} + \beta_{s,2}^{(p)} \text{Precip}_{j,y,v}. \tag{5}$$

We did not allow for a difference in the detection probability between the MTR and reference sites to avoid the confounding effects of site type on both vital rates and detection probabilities.

The model was fit in the Bayesian framework via Markov chain Monte Carlo (MCMC) sampling implemented in the program JAGS 4.2.0 accessed through R (version 2.15.1; R Development Core Team, 2010). Three Markov chains were run in parallel starting at diffuse parameter values generated by fitting initial models assuming fixed occupancy and abundance under three sets of conditions: maximal (i.e., all sites occupied with abundance equal to five times the maximum count for each species), minimal (sites only occupied if a species was detected and abundance equal to the highest count for each species, site, and year) and medium (occupancy at sites where a species went undetected determined by a coin-flip and abundance equal to twice the highest count for that species, site and year). We ran each chain for an adaptive phase of 5,000 iterations plus 100,000 further sampling iterations. Convergence was assessed via the Brooks–Gelman–Rubin diagnostic (Brooks & Gelman, 1998) and visual assessment of the traceplots. We used common priors with unknown parameters (i.e., hyperparameters) for each set of βs that varied by species. For example, the parameters modelling the initial occupancy at reference sites were assigned priors:

$$\beta_{s,k}^{(\psi)} \sim \text{Normal} \left(\mu_k^{(\psi)}, \sigma_k^{(\psi)^2} \right) \tag{6}$$

where the hyperparameters were assigned further priors (called hyperpriors) such that:

$$\mu_k^{(\psi)} \sim \text{Normal} \left(0, 1.67^2 \right) \tag{7}$$

$$\sigma_k^{(\psi)} \sim \text{Half} - t_3 (2) \tag{8}$$

for $k = 0, 1$. The standard deviation of 1.67 in the prior for $\mu_k^{(\psi)}$ produces a prior distribution for the median of $\psi_{s,j}$ that is approximately uniform for both the reference and MTR-VF sites. The half-t_3(2) represents the distribution over the positive real line that is proportional to a t-distribution with three degrees of freedom scaled by a factor of 2 and recommended as a default prior by Gelman (2006). This same structure was repeated for the priors of the parameters in the models of $\gamma_{s,j}$, $\Phi_{s,j}$ and $p_{s,j,y}$. The prior structure for the coefficients of the conditional abundance was defined similarly with the exception that:

$$\mu_k^{(\lambda)} \sim \text{Normal}(0, 1000) \tag{9}$$

as $\lambda_{s,j}$ is not restricted to be between 0 and 1.

The hierarchical model is the Bayesian analogue of a classical random effects model and can be seen to serve two purposes. First, the hierarchical model can borrow strength across the species, providing more precise estimates than by modelling each species alone while still allowing for variation between species. Second, the

hierarchical model provides information about the variation of the different parameters across the groups. Given a fixed value of the mean in the normal hyperprior for one of the coefficients, the variance represents the similarity between the values of this coefficient for different species and life stages. For example, $\sigma_0^{(\psi)}$ models the variation in $\beta_{s,0}^{(\psi)}$, the log-odds that a reference site is initially occupied by species s given $\mu_0^{(\psi)}$, or the overall average log-odds. If $\sigma_0^{(\psi)}$ is small, then the values of $\beta_{s,0}^{(\psi)}$ will tend to be close to one another, and if $\sigma_0^{(\psi)}$ is large, the values of $\beta_{s,0}^{(\psi)}$ will vary more. Unfortunately, variation in the log-odds can provide misleading results about the relative variation of parameters on the natural scale (i.e., the unit interval for probabilities or the positive real line for abundance). The reason is that the degree of variation on these scales depends on both the mean and the variance of the normal hyperpriors. Instead, we compare the relative variation in the base demographic parameters $\psi_{s,j}$, $\gamma_{s,j,y}$, $\varphi_{s,j,y}$ and $\lambda_{s,j,y}$ for the reference and MTR-VF sites by computing their variation through numerical integration on each iteration of the MCMC sampling algorithms.

3 | RESULTS

Despite equal search efforts between site types, MTR-VF streams accounted for only 11% (97/903), 12% (97/818) and 12% (98/850) of all captures from 2013, 2014 and 2015, respectively. *Eurycea cirrigera*, *D. fuscus* and *D. monticola* were the most commonly detected species in both site types. We found that over the three years of sampling, estimated percentage occupancy of salamanders on reference sites was much greater than occupancy of MTR-VF sites, although the rates of occupancy were more uncertain for MTR-VF sites (Figure 1). For instance, adult *D. fuscus* occupancy rates averaged 37.2% lower in MTR-VF streams (54.5% (95% CI = 51.52%–60.61%) than reference streams (91.7% (95% CI = 91.7% to 91.7%). Similarly, reference sites had higher average abundances across all site type-by-year combinations for all species and life stages (Figure 2). For example, estimated mean *G. porphyriticus* abundance over all 3 years was 8.45 (95% CI = 5.33–14.15) in reference sites and 0.66 (95% CI = 0.39–1.09) in MTR-VF sites. Effects of number of cover objects and date of last precipitation significantly affected detection rates for several species, with both positive and negative responses to these covariates (see Figure S2A).

Site type had strong and consistent effects on population vital rates for most species and life stages. First, we found lower initial occupancy probabilities in MTR stream reaches for most individual species and life stages (except *P. ruber*) as indicated by the mean difference in $\beta_{1,1}^{(\psi)} - \beta_{1,2}^{(\psi)}$ between reference and MTR-VF sites (Figure 3, Table 1). Also, all species and stages showed decreased colonization rates on MTR-VF sites, with significant differences exhibited for adult *D. fuscus* and *D. monticola*, adult and larval *E. cirrigera*, and *P. ruber* (Figure 3, Table 1). In contrast to colonization rates, differences in persistence rates were less consistent among species and life stages, yet adult *D. fuscus* and *D. monticola* and larval *E. cirrigera* were less likely to persist in MTR-VF streams than those in our
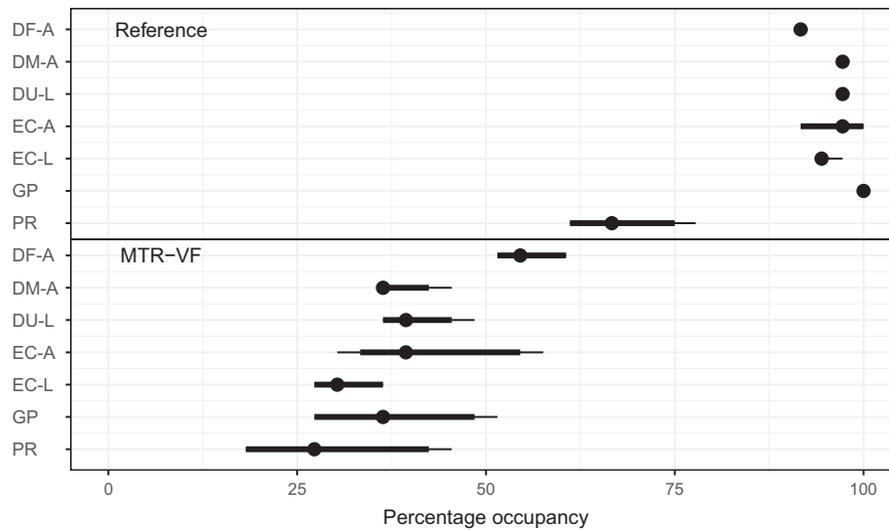
FIGURE 1 Estimated percentage occupancy over 3 years by salamanders in streams on a reference (forested) landscape or a landscape impacted by mountaintop removal mining and valley filling (MTR-VF). For each species and life stage, the points represent the posterior mean; the thick and thin bars represent the extents of the highest posterior density 90% and 95% credible intervals, respectively. Groups are denoted as adult *Desmognathus fuscus* (DF-A), adult *D. monticola* (DM-A), larval *Desmognathus* spp. (DU-L), adult *Eurycea cirrigera* (EC-A), larval *E. cirrigera* (EC-L), *Gyrinophilus porphyriticus* (GP) and *Pseudotriton ruber* (PR). We combined counts of adult and larval forms of GP and PR as all but one of the captures of these two species were larvae
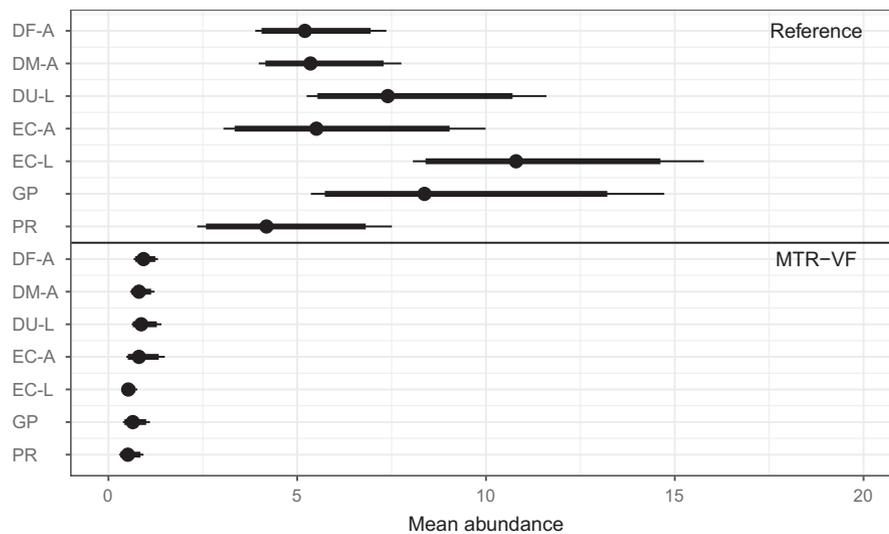

FIGURE 2 Estimated mean abundance over 3 years by salamanders in streams on a reference (forested) landscape or a landscape impacted by mountaintop removal mining and valley filling (MTR-VF). For each species and life stage, the points represent the posterior mean; the thick and thin bars represent the extents of the highest posterior density 90% and 95% credible intervals, respectively. Groups are denoted as adult *Desmognathus fuscus* (DF-A), adult *D. monticola* (DM-A), larval *Desmognathus* spp. (DU-L), adult *Eurycea cirrigera* (EC-A), larval *E. cirrigera* (EC-L), *Gyrinophilus porphyriticus* (GP) and *Pseudotriton ruber* (PR). We combined counts of adult and larval forms of GP and PR as all but one of the captures of these two species were larvae

reference landscape (Figure 3; Table 1). Finally, estimated conditional abundances were significantly lower at MTR-VF streams for all species and life stage (Figure 3; Table 1).

When we considered all salamander species and stages together, we found MTR consistently affects salamander species and life stages by decreasing rates of initial occupancy, colonization, persistence and abundance (Figure 3). Furthermore, these results suggest that most species and life stages responded in a similar manner

to site type. For example, the mean values for initial occupancy at reference stream reaches were quite similar among species, with most species having mean values quite similar to the mean value across species (Table 1).

The posterior distributions of the variance in initial occupancy, colonization and persistence probabilities as predicted by the hierarchical model for both the reference and MTR-VF sites were much lower than would be expected under pure random sampling from
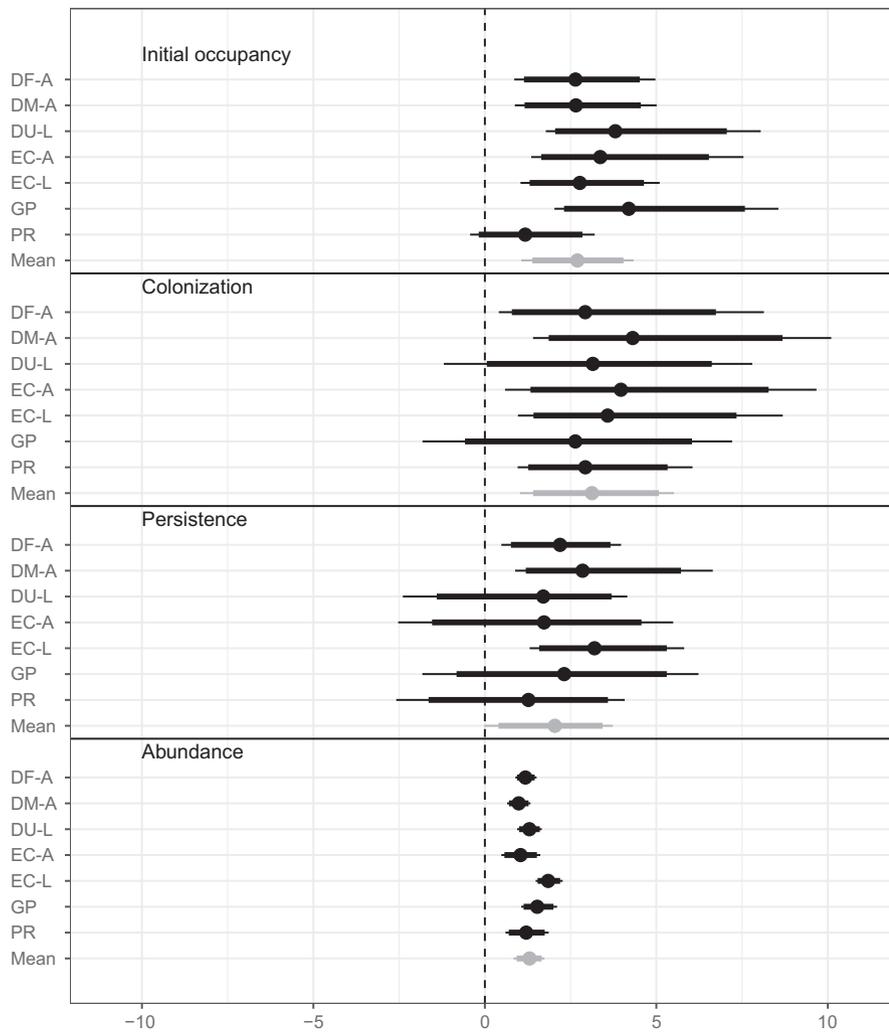
FIGURE 3 Effect of site type (i.e., reference vs. mined) on occupancy, colonization, persistence and abundance of stream salamander species and life stages. For each species and life stage, the points represent the posterior mean; the thick and thin bars represent the extents of the highest posterior density 90% and 95% credible intervals, respectively. Groups are denoted as adult *Desmognathus fuscus* (DF-A), adult *D. monticola* (DM-A), larval *Desmognathus* spp. (DU-L), adult *Eurycea cirrigera* (EC-A), larval *E. cirrigera* (EC-L), *Gyrinophilus porphyriticus* (GP) and *Pseudotriton ruber* (PR). We combined counts of adult and larval forms of GP and PR as all but one of the captures of these two species were larvae. Mean values (grey bars) represent all salamander species and stages considered together

the uniform distribution between 0 and 1 (see Figures S3A and S4A). Despite having low precision because of the small number of species and life stages, the models suggested that each of these probabilities is more variable across species at the reference sites than at the MTR-VF sites (see Figure S3A). Similarly, the estimated variance in the rate of abundance conditional on occupancy indicated that the mean abundance is also more variable between species and life stages at the reference sites than at MTR-VF sites (see Figure S4A). This lack of variation seen at MTR sites indicates similarity in salamander responses (i.e., low initial occupancy and low abundances across species).

4 | DISCUSSION

Within landscapes modified by MTR mining, we found that stream salamander populations exhibit low initial occupancy and abundance and reduced colonization and persistence rates compared to reference streams. On the one hand, our findings support our hypothesis that reduced colonization rates, and for some species, reduced rates of persistence, may be the mechanisms responsible for reductions in salamander occupancy rates in streams impacted by MTR. On the

other hand, we found that stream salamanders maintained relatively high occupancy rates and abundances in undisturbed, forested landscapes. High persistence estimates for reference stream reaches suggest local extinction of stream salamander metapopulations in minimally disturbed, low-order, central Appalachian streams is rare. Yet, if extinctions do occur, relatively high salamander colonization rates will preclude long-term reductions in occupancy. These results provide additional evidence for Green's (2003) suggestion regarding interannual stability of stream salamander metapopulations, albeit this is the first study on stream salamander population dynamics in central Appalachian landscapes.

Reduced colonization rates suggest that dispersal may be limited in MTR landscapes. Recent studies indicate that overland dispersal is critical to maintaining population connectivity among stream salamander metapopulations (Grant et al., 2010; Miller, Snodgrass, & Gasparich, 2015). Newly metamorphosed, juvenile salamanders are the primary dispersal agents (Grant et al., 2010). Dispersal ability is tightly linked to the physiological limits of salamanders (Feder, 1983; Rothermel & Luhring, 2005) and behaviour (Cecala, Noggle, & Burns, 2017). Research on matrix permeability shows greater movement through matrix types that are more similar to species' preferred habitats (Erős & Grant, 2015). Therefore, land use disturbances within

TABLE 1 Mean and 95% credible intervals (95% CI) for the initial occupancy, colonization and persistence rates of salamanders at mountaintop removal and valley fill (MTR-VF) and reference (i.e., forest) streams located in the interior rugged section of the Cumberland Plateau, Kentucky. Salamander abbreviations: DF-A = *Desmognathus fuscus* adult, DM-A = *D. monticola* adult, DU-L = *Desmognathus* spp. unknown larvae, EC-A = *Eurycea cirrigera* adult, EC-L = *E. cirrigera* larvae, GP = *Gyrinophilus porphyriticus* and PR = *Pseudotriton ruber*

	Initial Occupancy				Colonization				Persistence			
	MTR-VF mean	95% CI	Reference mean	95% CI	MTR-VF mean	95% CI	Reference mean	95% CI	MTR-VF mean	95% CI	Reference mean	95% CI
All	0.4	0.24–0.57	0.91	0.68–0.98	0.17	0.06–0.37	0.82	0.44–0.97	0.7	0.45–0.92	0.95	0.81–0.98
DF-A	0.45	0.27–0.71	0.92	0.73–0.99	0.29	0.11–0.66	0.88	0.54–1.00	0.62	0.36–0.83	0.94	0.80–0.98
DM-A	0.45	0.27–0.71	0.92	0.73–0.99	0.09	0.00–0.26	0.85	0.36–1.00	0.68	0.41–0.89	0.97	0.90–1.00
DU-L	0.39	0.20–0.60	0.96	0.82–1.00	0.17	0.05–0.38	0.82	0.06–1.00	0.79	0.49–1.00	0.96	0.87–0.99
EC-A	0.4	0.19–0.64	0.95	0.77–1.00	0.12	0.01–0.33	0.85	0.24–1.00	0.83	0.54–1.00	0.96	0.87–1.00
EC-L	0.42	0.24–0.66	0.92	0.74–0.99	0.15	0.03–0.34	0.85	0.37–1.00	0.5	0.13–0.78	0.96	0.86–0.99
GP	0.33	0.08–0.53	0.96	0.82–1.00	0.24	0.09–0.56	0.82	0.06–1.00	0.77	0.45–0.99	0.97	0.90–1.00
PR	0.36	0.13–0.56	0.63	0.32–0.90	0.15	0.02–0.37	0.75	0.42–0.97	0.69	0.27–0.99	0.9	0.55–0.99

matrices have the potential to disrupt overland dispersal pathways used by stream salamanders (i.e., Grant et al., 2010; Miller et al., 2015). In our study, the MTR landscape was dominated by grasslands and shrubs; these land cover types are characterized by reduced microhabitat availability and warmer and drier microclimatic conditions compared to Appalachian forests (Wickham et al., 2013; Wood & Williams, 2013b). Thus, our findings suggest that land use composition on MTR landscapes, particularly the reduction in forest cover and subsequent changes to temperature, moisture and light may limit overland dispersal, leading to low colonization rates and ultimately reduced occupancy. However, investigations that focus on microhabitat conditions within the matrix and those examining how the terrestrial matrix type influences movement rates are the next steps needed to investigate the role of the matrix on dispersal rates.

Reduced colonization rates may also be related to the in-stream habitat conditions in MTR-VF stream reaches. Within-stream dispersal is an additional pathway used by juvenile stream salamanders that enhances population stability (Grant et al., 2010; Lowe, 2003). Most species, including four of our focal species, have been shown to disperse from downstream to upstream sections of streams (See Cecala, Price, & Dorcas, 2009; Grant et al., 2010; Lowe, 2003). Although some factors (i.e., increased light levels, Cecala et al., 2017) may reduce colonization rates along riparian corridors, alterations to stream discharge rates in mined landscapes might also affect in-stream dispersal rates. Streams impacted by MTR mining often have higher and more sustained baseflow (Nippgen, Ross, Bernhardt, & McGlynn, 2017). Furthermore, reduced infiltration, from compaction and reduction in forest cover in catchments, increases run-off and discharge rates in MTR-VF stream reaches (Negley & Eshleman, 2006). Thus, increased run-off and higher baseflow rates may displace individuals and decrease colonization probability (i.e., Barrett, Helms, Guyer, & Schoonover, 2010).

The altered state of the stream environment also has consequences for salamander persistence in streams impacted by MTR-VF. In this study, adult *D. fuscus* and *D. monticola* and larval *E. cirrigera* were less likely to persist in MTR streams than those in our reference landscape. High peak flows reduce survival of larval *E. cirrigera* in urban streams (Barrett et al., 2010). Therefore, changes to stream geomorphology on mined land may further reduce persistence, especially for species that require structurally complex, intermittent streams for larval development. Jaeger (2015) notes that increased sediment loads, increased bedrock exposure and deeper maximum channel depths characterize streams on mined lands; these conditions are negatively correlated with salamander abundances (Smith & Grossman, 2003). Finally, MTR-VF streams are characterized by elevated levels of specific conductance, which are known to reduce species richness and abundance of certain aquatic macroinvertebrates (Boehme, Zipper, Schoenholtz, Soucek, & Timpano, 2016; Pond, 2010, 2012; Pond et al., 2014). Aquatic macroinvertebrates represent an important prey source for stream salamanders (Hutton, Price, & Richter, 2018; Martof & Scott, 1957; Trice, Rosemond, & Maerz, 2015), and reduced aquatic macroinvertebrate populations

may decrease stream salamander growth, body condition and, ultimately, population persistence (Johnson & Wallace, 2005).

When we considered mean responses across all salamander species and stages, we found a consistent difference between MTR-VF and reference sites in terms of rates of initial occupancy, colonization, persistence and abundance. If our study sites are representative of other surface mines in the region, our findings suggest that MTR-VF has the potential to influence salamander population dynamics throughout central Appalachia, a region broadly dissected by surface mines (Wickham et al., 2013). More broadly, salamanders, due to their small body size and high densities, play a valuable role in stream nutrient retention, secondary productivity and the density of emerging aquatic invertebrates, which affects aquatic–terrestrial connectivity (See Davic & Welsh, 2004; Keitzer & Goforth, 2013; Peterman et al., 2008; Petranka & Murray, 2001); the altered state of entire assemblages will likely impact both aquatic and terrestrial ecosystems in MTR landscapes.

Similarity in responses across species, as seen from estimated vital rates and the posterior distributions of their variances, suggests that management or restoration may benefit the entire salamander assemblage. For example, the Forestry Reclamation Approach (Angel, Davis, Burger, Graves, & Zipper, 2005) focuses on restoring native forests on MTR sites. The FRA approach recommends, in part, reducing compaction and the preparation of suitable soils or soil substitutes (i.e., weathered overburden) for reestablishment and growth of native vegetation. Sena, Barton, Angel, Agouridis, and Warner (2014) found that weathered overburden, as a topsoil substitute, reduced hydrologic impacts through improved tree growth and water utilization. Thus, soil restoration and reforestation have the potential to repair hydrologic regimes and reduce landscape resistance, which may allow for higher rates of salamander persistence and colonization in landscapes modified by MTR mining.

DATA ACCESSIBILITY

Salamander count data and site and sampling covariates are available from Dryad Digital Repository.

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BIOSKETCH

The research team consists of applied ecologists with broad interests in conservation and management of aquatic and semi-aquatic species, quantitative ecology and restoration of degraded landscapes. Much of their research is conducted in the Central Appalachians. More information can be found at: http://pricelab.ca.uky.edu/.

Author contributions: S.J. Price, S.B. Freytag and C.D. Barton designed the study; S.J.P., S.B.F., B. L. Muncy and A.N. Drayer conducted the fieldwork; S.J.P., S.B.F., J. M. Hutton and S.J. Bonner analysed the data; and all authors contributed to the interpretation of the results and the writing of the final version of the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.