Ecological Applications, 29(3), 2019, e01870

Effects of forestry-driven changes to groundcover and soil moisture on amphibian desiccation, dispersal, and survival

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Citation: Haggerty, C. J. E., T. L. Crisman, and J. R. Rohr. 2019. Effects of forestry-driven changes to groundcover and soil moisture on amphibian desiccation, dispersal, and survival. Ecological Applications 29(3):e01870. 10.1002/eap.1870

Abstract. Over 80% of amphibian species that are declining are forest dependent. Forestry practices are a major cause of forest alterations globally, and it is well documented that clearcutting can contribute to amphibian declines. However, there might be adverse effects of forestry practices other than clearcutting. For example, planting overstory trees in rows (plantations) can change groundcover microhabitats and soil moisture levels, but the effects of this common practice on amphibian populations are not well studied. We compared the impacts of common intensive pine plantation operations to naturally regenerated pine forests on the desiccation, movement rates, behavior, and survival of >900 juvenile southern toads (*Anaxyrus terrestris*). Pine plantations had significantly more accumulation of conifer needles and less exposed soil, herbaceous groundcover, broadleaf litter, and soil moisture than natural pine forests despite the greater canopy cover at plantations. Litter cover explained 85% of groundcover microhabitat variance among forest types and predicted minimum soil moisture levels. When toads were held in small outdoor enclosures that constrained microhabitat selection, 24-h desiccation rates and 72-h mortality were significantly greater in pine plantation than in naturally regenerated pine forest because of lower soil moisture, especially during low rainfall periods. In large outdoor pens where juvenile amphibians could select microhabitats, movement was strongly directed down slope and increased with precipitation. However, initial speeds were positively associated with pine density, likely because toads were trying to evacuate from the drier high-pine-density areas. High-intensity silviculture practices that eliminate herbaceous or vegetative groundcover, such as roller chopping and scalping, increase amphibian desiccation because planted conifers dry the upper soil layer. Our study highlights the importance of prioritizing lower intensity silviculture practices or lower pine densities to retain groundcover microhabitat that serves as amphibian refugia from dry conditions that are predicted to increase in frequency with climate change.

Key words: *enclosure; groundcover; land use; management; movement; permeability; silviculture.*

Introduction

Habitat alteration is a major cause of amphibian declines (Collins and Storfer 2003), and over 80% of rapidly declining amphibians depend on forest structure, including trees and ground cover (Stuart et al. 2004). Less than one-quarter of global forest is considered intact without significant human transformation and only 12% of these forests are protected (Wirth 2009, Potapov et al. 2017). Forest alteration near wetland breeding sites can lower amphibian population persistence by modifying terrestrial microhabitats used by juvenile amphibians to avoid desiccation and potentially mortality during feeding and maturation (Rittenhouse et al. 2008). Forest structure also influences amphibian habitat selection and movement within forests that link populations breeding at wetlands, lowering both extirpation and extinction risk (Cushman 2006). Indeed, forest alteration has been suggested as the biggest cause of amphibian declines (Dodd and Smith 2003), and the main cause of forest alteration globally is timber production and intensive silviculture (the growth and cultivation of trees; Potapov et al. 2017).

While it is well documented that intensive timber harvest can cause rapid amphibian declines (Tilghman et al. 2012), the pre-harvest phase of plantation is unnaturally dense for decades and can more gradually change groundcover biotic and abiotic conditions, but their effects on amphibian populations are less studied (Means and Means 2005, Hansen et al. 2013). Moreover, the retention of forest groundcover microhabitat can mediate the negative impacts of canopy removal on

Manuscript received 29 October 2018; revised 13 December 2018; accepted 14 January 2019. Corresponding Editor: Trenton W. J. Garner.

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amphibian biomass (Todd and Rothermel 2006, Patrick et al. 2008, Popescu et al. 2012, Harper et al. 2015), and could increase amphibian persistence in planted forests by influencing desiccation risk (Rittenhouse et al. 2008, Rohr and Palmer 2013) or behavior (Harpole and Haas 1999). Previous work has also suggested amphibian behavioral avoidance of inhospitable habitat created by forestry practices as one contributor to biodiversity loss (Semlitsch et al. 2008, Popescu and Hunter 2011). Amphibian susceptibility to desiccation (Rittenhouse et al. 2008), their ability to locate suitable forest conditions (Todd and Rothermel 2006, Tilghman et al. 2012), and availability of diverse microhabitats within the forest groundcover of temperate and boreal *Pinus* spp. forests were key to conservation of declining amphibians (Hart and Chen 2006).

Coniferous trees are the most common timber species on plantations (Brown 2000), and their intensive management can eliminate herbaceous or vegetative groundcover seen at sites supporting imperiled amphibians (Walker and Peet 1983, Lannoo 2005), yet the value of retaining some forest groundcover to reduce amphibian declines on timber lands is understudied (Fox et al. 2004, Lannoo 2005, Jones et al. 2010). In the one case where this has been studied, groundcover loss associated with intensive silviculture practices was linked to declines of the imperiled striped newt (*Notophthalmus perstriatus*), and declines might be accelerated by drought (Means and Means 2005). Predicted increases in xeric (dry) conditions globally during the next 100 yr (Solomon et al. 2007) will likely influence amphibian survival and dispersal (Reichling 2008, Rittenhouse et al. 2008) and increase the importance of forest floor microhabitats in the future management of planted forests (Mason et al. 2012). Given that increased canopy density at plantations should be negatively associated with insolation and thus thermoregulation stress for amphibians (Popescu and Hunter 2011, Cole and Newton 2015), we focused our study on moisture physiology and refuge-seeking behavior. Knowledge of amphibian survival and behavioral selection of habitat in planted forests relative to reference (close to pristine) forests is key to determining whether forest management and current human reintroduction efforts for imperiled amphibian species are likely to sustain populations (Means and Means 2005).

This study combined the use of small- and large-scale experimental enclosures to investigate the importance of intact groundcover microhabitat on desiccation risk, behavior, and survival of >900 juvenile southern toads (*Anaxyrus terrestris*) in three forest conditions: even-aged pine plantation (PP), partially regenerated pine forest (PRP) with one-half the groundcover of reference condition pine forest, and fully regenerated pine forest (FRP) with "reference condition" groundcover. We constrained juvenile amphibians to specific microhabitats within known-fate enclosures to observe desiccation rates and survival across habitat types, and created large runway enclosures to determine whether amphibians behaviorally orient or increase movement according to groundcover microhabitats. *A. terrestris* was selected as a model organism for this study, because it behaviorally selects among forest floor microclimates to minimize physiological costs (Jaeger 1980). We hypothesized that, despite the greater canopy cover in pine plantations, water loss and mortality in small enclosures would be higher than in naturally regenerated pine forest because of less herbaceous or vegetative groundcover. When placed in large runway enclosures at each forest type, we hypothesized that toads would orient in directions of greater groundcover and increase their movement to avoid the drier habitat associated with more dense pine trees.

METHODS

Study site

This study was conducted at the Citrus Tract of the Withlacoochee State Forest in Citrus County, Florida, United States (28°42′13.4″ N, 82°24′43.9″ W). This forest mostly occurs on xeric (dry) well-drained, sandy soils and predominately consists of second growth pine (*Pinus* spp.) with a groundcover dominated by wiregrass (*Aristida* spp.). We studied three forest conditions: even-aged pine plantation (PP) planted approximately 25 yr ago (1988) on a former clearcut, partially regenerated pine forest (PRP) with one-half the groundcover of reference condition pine forest, and fully regenerated pine forest (FRP) with an open canopy and abundant herbaceous groundcover considered to be in "reference condition" for our region (Florida Natural Areas Inventory 2009). All regeneration occurred naturally and thus was managed to mimic natural disturbance regimes (Myers and Ewel 1990). Specifically, fires occurred at PP, PRP, and FRP stands 5, 8, and 10 times in the past 15 yr, respectively, and generally encourage canopy gaps and herbaceous plant cover (Myers and Ewel 1990). Importantly, PRP and FRP sites lacked practices that reduce groundcover, whereas at the PP site, roller chopping was used before planting to reduce herbaceous cover. Roller chopping is a common site preparation treatment in planted *Pinus* spp. forests that mechanically destroys non-merchantable plant material and can reduce herbaceous groundcover and fossorial cavities that are potential microhabitats for amphibians during dry periods (Lannoo 2005, Reichling 2008, Fritts et al. 2015).

Desiccation experiment

Field methods.—To quantify amphibian susceptibility to desiccation according to forest structure, 30 enclosures were constructed, with 10 enclosures placed in each of our three forest categories described above (Table 1). Each desiccation enclosure was made of 1-mm mesh fiberglass screen formed into a 15 cm diameter by 45 cm tall cylinder. Soil disturbance was minimized by

Table 1. List of response and predictor variables with model error distributions.

Response variable(s)	Fixed effects (s)	Crossed predictors	Random effects	Error distribution/ model
VWC, air temperature, humidity	FT, temporal block, time of day	NA	visit, enclosure	Gaussian
Vegetation structure	FT	NA	NA	beta-binomial
Precipitation	FT	NA	NA	Kruskal-Wallis test
24-h water loss (proportion)	FT, temporal block, time of day, VWC, precipitation	NA	visit, enclosure	Gaussian
24 and 72 h survival	FT, time of day, VWC, understory	NA	enclosure	binomial
Toads observed (proportion)	precipitation, slope	FT × direction	batch	binomial
Toads in pitfalls (proportion)	precipitation, slope	FT × direction	batch	binomial
Movement rate	precipitation, slope, understory	FT × direction	batch	Gaussian
VWC (minimum)	PCA axis 1	NA	NA	Gaussian
24-h water loss	PCA axis 1	NA	enclosure	Gaussian
72-h survival	PCA axis 1	NA	batch	Gaussian

Notes: VWC, soil volumetric water content; FT, forest type; GLMER, generalized linear mixed effects regression; LMER, linear mixed effects regression; PCA, principal coordinates analysis. Twenty four hour water loss and movement rate were logit- and log-transformed, respectively.

installing each enclosure by hand using a spade to a depth of 6 cm. This design allowed light and wind to enter the enclosures.

Two pairs of southern toads in amplexus were collected on 16 July 2015 at an isolated wetland in Chassahowitzka, Florida adjacent to our study sites. Fertilized egg masses were placed into plastic bins, and upon hatching, tadpoles were placed into wading pools under partial shade. Tadpoles were fed rabbit chow until metamorphosis began on 6 August, with daily collection of individuals undergoing metamorphosis for one week. All individuals were placed onto moist paper towels inside 15-L plastic bins maintained at 25°C and fed fruit flies every other day until release into enclosures (within one week).

To ensure that each toad was hydrated fully at the start of the trial, juvenile southern toads were placed on moist towels for 4 h before being weighed to 0.001 g, then randomly assigned to an enclosure. During each trial, enclosures were visited after 24 h in the same order as release to keep exposure times comparable among habitats. At 24 h, toads were weighed and returned to their respective enclosure. Final masses of all toads were obtained after 72 h in enclosures, after which all were released into the forest before beginning the next temporal block. If a toad exceeded 30% mass loss, it was recorded as dead and immediately rehydrated to reduce unnecessary vertebrate death. In total, we conducted six consecutive 72 h trials or temporal blocks during May–June 2015. To assess differences in environmental conditions among the three forest categories (Table 1), we used a Vegetronix VH400 and DHT-22 sensor to record air temperature, humidity, and soil moisture in the top 15 cm of soil during each enclosure visit (±2% accuracy). Additionally, we visually estimated percent cover of pine litter, oak litter, bare ground, and herbaceous cover within each desiccation enclosure.

Statistical methods.—To compare the environmental conditions among the forests through time, we conducted linear mixed effects models (LME) in *R* (using the lme4 package) treating the abiotic factors (air temperature, humidity, and soil moisture) as dependent variables with normal errors, forest type and temporal block as categorical fixed effects, time of day as a continuous fixed effect, and visit and enclosure as random effects. Differences in rainfall among forests were assessed with a Kruskal-Wallis test given that a linear model showed non-normality of residuals. We performed a principal components analysis (PCA) in R (function prcomp) to reduce dimensionality of the forest floor structure (cover with pine or oak litter, bare ground, or herbaceous plants), and used the first PCA axis (85% of variance explained) as an independent variable (square transformed) in a linear regression model with minimum soil moisture level as the response variable. The prcomp function was used to plot both individual enclosures, grouping those with similar vegetation cover profiles, and forest cover variables. Variables pointing in the same general direction in a PCA plot were positively correlated, whereas those pointing in opposite directions were negatively correlated. The PCA plot was produced in the factoextra R package.

To evaluate how forest type affected toad water loss, we conducted an LME model treating the proportion of mass (water) lost in 24 h (logit-transformed) as a Gaussian response variable, forest type, rainfall, and temporal block as fixed effects, and visit and enclosure as random effects. Tukey post-hoc tests (using the lsmeans package) were used to test for differences in response variables among forest types. We also tested whether soil moisture was a significant predictor of water loss treating enclosure as a random effect (Table 1). Finally, to evaluate how forest type affected survival, we treated the number of toads alive at 24 and 72 h as the binomial response

TABLE 2. Pine basal area, herbaceous, wiregrass, and pine needle (duff) ground cover, volumetric water content (VWC) of soil, humidity, and air temperature in current pine plantation and former pine plantation that is partially or fully regenerated with pine in Florida.

Forest type	Pine basal area (m^2/ha)	Herbaceous cover (%)	Wiregrass cover (%)	Duff cover (%)	Soil water, VWC (%)	Humidity (%)	Air temperature (°C)	Precipitation (cm)
Fully regenerated pine	3.8 (0.52)^{a}	6.8 (0.7)^{a}	4.5 (0.55)^{a}	14.4 (4.7)^{a}	4.1 (0.10)^{a}	67.3 (0.8)^{a}	31.5 (0.3)^{a}	0.81 (0.10)^{a}
Partially regenerated pine	12.4 (1.71)^{b}	4.8 (1.1)^{a}	1.9 (0.36)^{b}	60.8 (7.1)^{b}	4.7 (0.10)^{a}	67.5 (0.9)^{a}	32.1 (0.3)^{a}	0.97 (0.10)^{a}
Pine plantation	15.6 (1.98)^{b}	0.5 (0.2)^{b}	0.0 (0.00)^{c}	97.0 (0.6)^{c}	3.6 (0.10)^{b}	63.2 (0.8)^{b}	32.3 (0.3)^{a}	0.61 (0.09)^{a}

Notes: Forest types that do not share letters are significantly different from one another ($P < 0.05$) based on a Tukey's post hoc multiple comparison test. Values are means with SE in parentheses.

variables (using the lme4 package), forest type, time, and soil moisture as fixed effects, and enclosure as a random effect. For models with a significant forest type effect, we then included fixed predictors for vegetation structure (Table 2) to test whether specific groundcover types predicted survival in small scale enclosures and used AIC and chi-square tests of nested models to drop nonsignificant terms. During analyses, significance of predictors was assessed using the ANOVA function in the car package.

Movement experiment

Field methods.—To evaluate whether amphibians move in response to groundcover, we built one large-scale runway enclosure at both PRP and FRP forest, each with four cardinal directions, that allows behavioral selection of habitat (Popescu and Hunter 2011). We did not install a runway at PP forest because herbaceous cover was absent and, therefore, could not vary among runway directions. We marked and released toads into the center of each enclosure during summer 2015 and tracked their distance moved and behavioral habitat selection for one month. The runway enclosures had four arms, each 50 × 2.5 m, that were arranged in the four cardinal directions and joined at the center (Fig. 1). The enclosures were constructed of silt fence stapled to wooden stakes. The walls were 0.45 m tall and buried 30 cm into the soil. Wooden baffles (2.5 cm wide) were placed on top of the walls to prevent toads escaping. In each runway direction, pitfalls were placed at 10 m, 20 m, and 30 m behind interior walls angled at 45° to capture only toads that reversed direction toward the release point (Fig. 1). At the center of these interior walls was a 3-L plastic shoebox with sides removed to encourage unidirectional movement. Pitfall traps were also placed at 50 m in each runway to capture individuals traveling the entire runway distance. Wooden covers were placed 5 cm above the bottom of all pitfall traps to provide refuge. A rain gauge was installed adjacent to each enclosure to record precipitation between visits.

At both the runway center and in each arm at 10, 20, 30, and 50 m, we quantified vegetation structure for each forest type using the Objective Based Vegetation Monitoring procedure (Florida Natural Areas Inventory and Commission 2007), which quantifies herbaceous cover in 1-m^2 quadrats, while canopy cover was measured with a densiometer at each point. For each arm of each enclosure, slope was measured from 0–10 m, 10–20 m, 20–30 m, and 30–50 m using mason string and a line level.

Juvenile toads collected as described previously were randomly divided into eight batches or temporal blocks of 40–50 toads, with each batch given a unique identification by clipping one toe on a front leg, after which they were released simultaneously in a given runway. The first batch of toads was released on 10 August 2015 in the center of each runway, and subsequent releases were made on the same night for all runways once at least one individual from the previous batch had reached 50 m. Toad initial masses were comparable among forest types (Appendix S1: Table S1), and all individuals per batch were released within an hour at all forest types. Runways were revisited daily when possible until 19 September 2015, and individuals that had reversed direction (captured in pitfalls) were identified to batch, weighed to 0.1 g, and removed from the experiment. All toads observed on the ground of enclosures were captured, identified to batch, weighed, their individual body patterns photographed, and released back into enclosures at the location and in the same orientation as they were found. Dispersal orientation was inferred from the cardinal direction chosen after passing an interior wall (Fig. 1). Unique toads were identified by body pigment patterns to estimate individual movement rates and total distance traveled per runway and direction.

Statistical methods.—We quantified four different types of behaviors in these trials: (1) the proportion of toads selecting each cardinal direction or arm of the enclosure, (2) the proportion of toads that changed their initial direction in an effort to return to the runway center (i.e., falling in pitfalls at 10, 20, or 30 m), (3) the speed of toad movements (distance/time), and (4) maximum distance traveled. For each analysis on a response variable that was a proportion, the error distribution was binomial (using the lme4 package), precipitation, slope, forest type (FT), direction, and an FT × direction

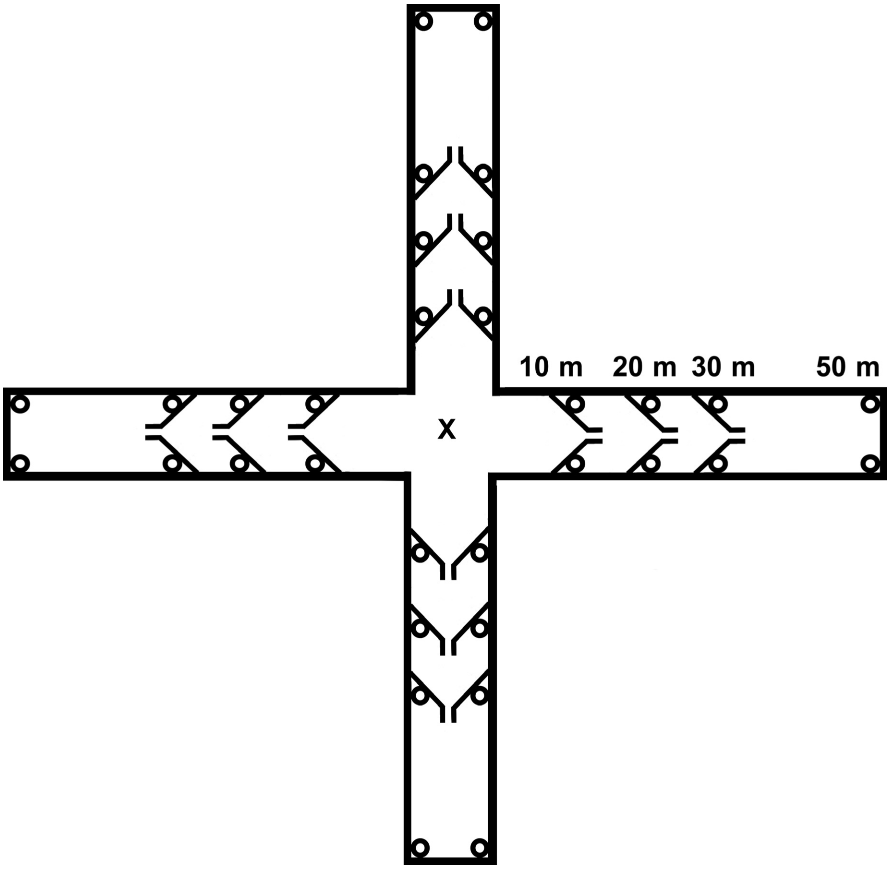

FIG. 1. Design of runway enclosures with shoeboxes to reduce reversals and pitfall traps (circles) at 10, 20, 30, and 50 m from the runway center (x).

interaction were fixed effects and batch ID was treated as a random effect (Table 1). To estimate movement rate among habitats, a log-transformation of distance traveled before the first observation of an individual (m) divided by time since batch release (d) was the response variable with precipitation, slope, FT, direction, and an FT × direction interaction as fixed effects. Distance traveled before the first observation was used because the majority of toad movement occurred between release and the first observation. During analyses, significance of predictors was assessed using the ANOVA function in the car package. For models with significant direction effects after controlling for ground slope and precipitation, we then included fixed predictors for vegetation structure (Table 2) to test whether specific understory predicted movement and used AIC and chi-square tests of nested models to drop non-significant terms.

RESULTS

Comparison of the abiotic and biotic traits of the forest types

Pine basal area was significantly greater in PP and PRP than in FRP forest, and silviculture treatments in PP eliminated native herbaceous plant microhabitat, including wiregrass, with groundcover being replaced by coniferous litter (Table 2). Herbaceous and wiregrass cover was also 30% and 42% lower, respectively, at PRP than at FRP forest (Table 2). Soil moisture was lowest at PP forest ($\chi^2 = 46.5$, df = 2, $P < 0.001$), despite non-significant differences in air temperature ($\chi^2 = 3.4$, df = 2, $P = 0.201$) and precipitation ($\chi^2 = 0.22$, df = 2, $P = 0.903$; Table 2) among forest types. Pine plantation also held less humidity near the forest floor than the other forest types ($\chi^2 = 16.4$, df = 2, $P < 0.001$). It had an average volumetric water content (VWC) of approximately 4 percent during all trials (Fig. 2A), and had the lowest soil moisture during 80% of site visits – up to 46% less than at enclosures in nearby FRP forest (Appendix S1: Fig. S2). Partially and fully regenerated pine forests averaged soil moisture levels >4 percent VWC for all trials (Fig. 2A) except one following 6 d without rainfall. Minimum VWC values were 1.2 for PP, and ranged from 2.4 to 2.7 for PRP and FRP.

PCA axis 1 accounted for 85% of the variation in forest groundcover among the enclosures (Fig. 3A; Appendix S1: Table S9), with pine litter and bare sand cover as the largest contributing factors to PCA axis 1 (Fig. 3B). These differences in groundcover appeared to drive the difference in the soil moisture among forest types, as PCA axis 1 was a significant predictor of minimum soil moisture ($F_{2,26}$ = 8.35, df = 1, P = 0.008; Fig. 3C).

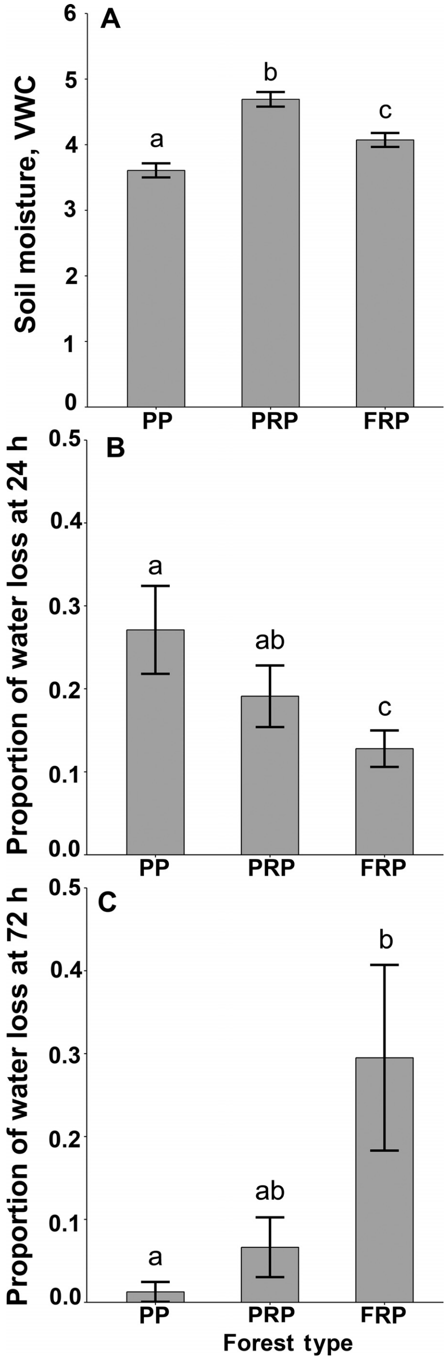

FIG. 2. (A) Mean (±SE) soil volumetric water content (VWC) of desiccation enclosures (%), (B) proportion water loss in 24 h, and (C) proportional water loss at 72 h across the three forest types. Different lower case letters indicate significant differences based on Tukey's post hoc multiple comparison tests (P < 0.05). Forest types are PP (pine plantation), PRP (partially regenerated pine), and FRP (fully regenerated pine).

Desiccation experiment

While juvenile southern toads experienced water loss in all forest types, losses were greatest in PP and decreased with increasing natural pine regeneration (Fig. 2B). In fact, 24 h mass (water) loss in PP was more than double that in FRP (χ^2 = 7.3, df = 2, P = 0.020; Appendix S1: Table S3). Precipitation events lowered water losses (χ^2 = 5.21, df = 1, P = 0.022), but juvenile desiccation increased dramatically at VWC < 4, which was above the average values observed at PP (Table 2).

Toad survival among forest types was similar at 24 h (χ^2 = 0.42, df = 2, P = 0.810) but differed by forest type at 72 h (χ^2 = 11.27, df = 2, P = 0.004; Fig. 2C). The proportion of toads surviving to 72 h was approximately five to six times lower in PP (mean ± SE, 0.03 ± 0.02) than in either PRP (0.20 ± 0.05) or FRP forests (0.15 ± 0.05; Fig. 2C). Soil moisture positively predicted juvenile amphibian survival to both 24 h and 72 h (Appendix S1: Table S4), and survival was <50% at 24 h when soil moisture was <4 VWC. Within 1–3 d following precipitation, PP forest floor dried faster than PRP or FRP floors (Appendix S1: Fig. S2), and during these periods (VWC levels approximately 4) toad survival at FRP was significantly greater than at PP (Fig. 4B). During the day, toads exhibited water conservation behavior as they were regularly burrowed into the soil with their permeable ventral surfaces positioned toward the ground. PCA axis 1 was a significant predictor of 72 h survival (Fig. 4A), indicating that groundcover differences among the forests were associated with the survival differences (see Appendix S1: Table S4 for relationships between individual traits of the groundcover and survival).

Movement experiment

Of the approximately 740 toads released into runway enclosures (equal number released per forest type), 225 were recaptured, and the number of recaptured individuals was similar in PRP (129) and FRP forest (96). The proportion of toads recaptured in runway arms did not vary significantly by habitat (χ^2 = 0.16, df = 1, P = 0.690), runway direction (χ^2 = 0.80, df = 3, P = 0.852), or the interaction between the two (Appendix S1: Table S5). Precipitation (χ^2 = 6.45, df = 1, P = 0.011) positively predicted the number of toads observed in runways. The number of toads reversing direction, as indicated by pitfall captures, did not vary significantly between habitats (χ^2 = 0.38, df = 1, P = 0.545), runway direction, or with precipitation (Appendix S1: Table S6). Fewer toads were observed in runway arms upslope than downslope from the release point (χ^2 = 5.25, df = 1, P = 0.022; Appendix S1: Fig. S1).

At least one individual reached 50 m in all cardinal directions of both PRP and FRP forests Appendix S1: Fig. S2, and the average proportion (±SE) of toads

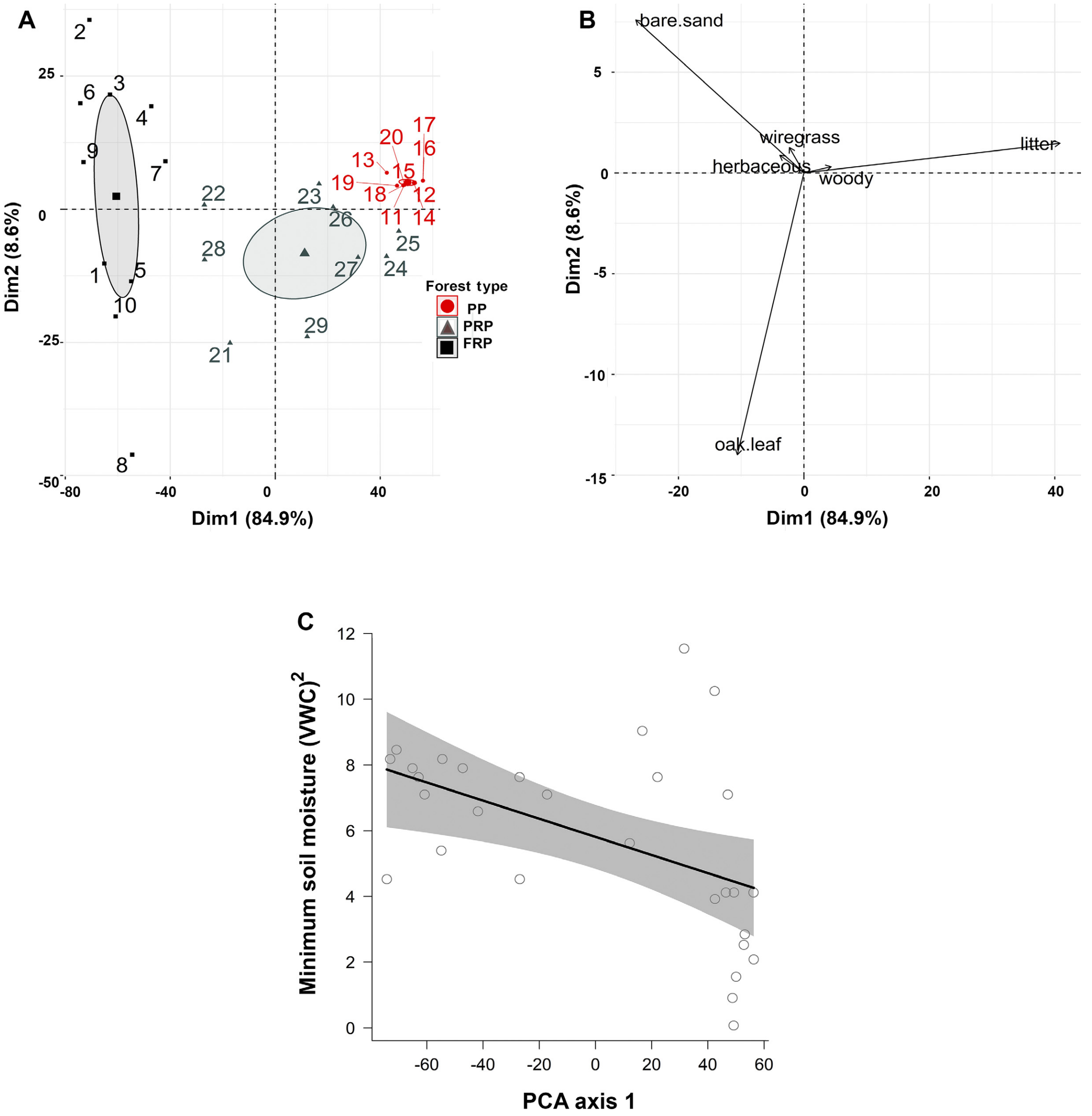

FIG. 3. Principal components analysis (PCA) of individual desiccation enclosures grouped by (A) forest type, (B) forest floor cover metrics accounting for PCA axes, and (C) regression of minimum soil moisture upon PCA axis 1 ($P < 0.05$).

moving 50 m was 0.48 ± 0.006 and 0.48 ± 0.007, respectively. Direction of travel was specific to forest type (Appendix S1: Table S7), and toads directed more of their movements down than upslope (Appendix S1: Fig. S1). Toad speed varied among cardinal directions ($\chi^2 = 8.24$, df = 3, $P = 0.041$), was negatively related to slope ($\chi^2 = 60.49$, df = 1, $P < 0.001$; Fig. 5A), and was positively related to both precipitation ($\chi^2 = 19.10$, df = 1, $P < 0.001$) and PCA axis 1 ($\chi^2 = 15.04$, df = 1, $P < 0.001$; Fig. 5B, see Appendix S1: Table S8 for associations with groundcover types). In addition, accounting for ground slope, toad speed was higher in PRP than FRP forest ($\chi^2 = 8.39$, df = 1, $P = 0.004$), specifically increasing in runway directions where pine density was greatest (Fig. 5C).

DISCUSSION

We provide the first experimental evidence that planted pine forests increase desiccation and mortality by lowering intact groundcover microhabitat that offers refuge from desiccation for juvenile amphibians in coniferous forest. Dry periods exacerbated soil moisture differences among forest types, increasing desiccation-related mortality where groundcover was lost. We further found that juvenile amphibians move more quickly

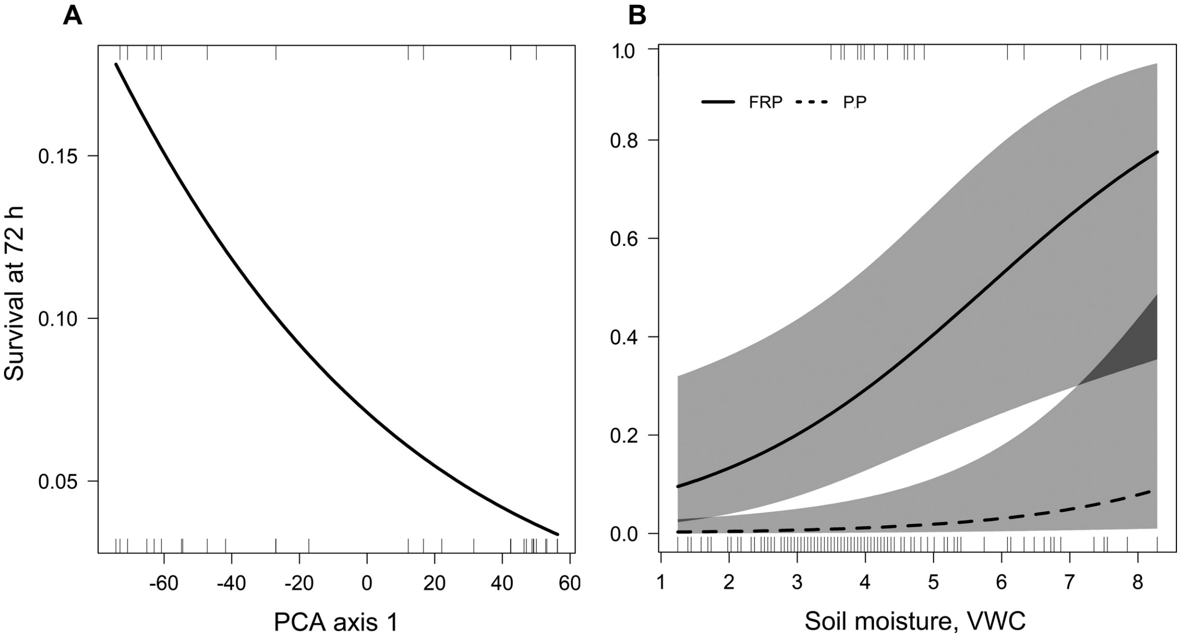

FIG. 4. (A) Seventy-two hour survival curves vs. PCA axis 1 and (B) 72 h survival for fully regenerated pine (FRP) and pine plantation (PP) forest types as a function of soil moisture (VWC) (%) with associated 95% confidence bands. An interaction term between forest type and VWC was not significant ($P > 0.05$).

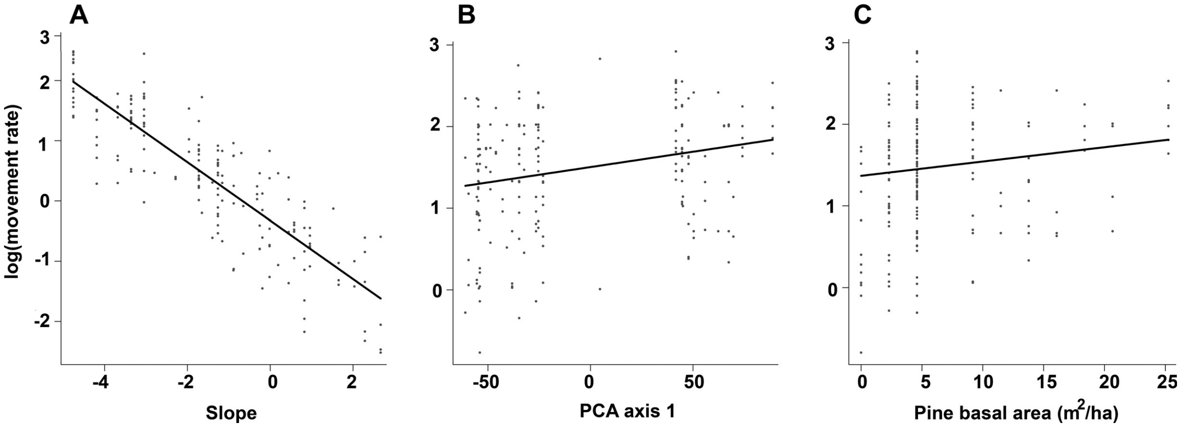

FIG. 5. Movement rate ($\log_{10}$-transformed) vs. (A) ground slope, (B) PCA axis 1, and (C) pine basal area (m^2/ha).

out of densely planted pine areas than fully regenerated pine forests with lower densities of pine. This may partially explain recent declines of imperiled amphibians associated with intensive silviculture and species absence at some open-canopy forests (Means and Means 2005, Farmer et al. 2017).

Pine plantations can limit groundcover vegetation and produce needle litter that covers the forest floor and lowers surface moisture levels (Jose et al. 2006). As conifers mature, canopies limit available light to the forest groundcover lowering both herbaceous plant abundance (Jose et al. 2006) and retention of moisture near the soil surface (Snedaker and Lugo 1972). The dominant *Pinus* species of the Southeastern United States (SEUS), longleaf pine (*Pinus palustris*), is shade intolerant, and this trait, together with frequent fires propagated by wiregrass (*Aristida* spp.), keeps the groundcover clear of thick needle cover (Jose et al. 2006). We found planted *Pinus* on sandy (well-drained) soils produced several millimeters of needle litter that typically lowered soil water content significantly below that of nearby naturally regenerated forests and below values considered “dry conditions” in the SEUS (Zotarelli et al. 2013). Increased periods of low rainfall could affect persistence of some amphibian species in all forests (Walls et al. 2013), even drying small isolated breeding wetlands within forests and increasing amphibian extinction rates (Walls et al. 2013). However, our results suggest that groundcover microhabitat within forests can help moderate such risks if they are not reduced by intensive forestry practices, such as roller chopping.

Juvenile amphibians experience high natural mortality in terrestrial forests (Todd et al. 2014) and seek moist microhabitats to survive dry conditions (Rittenhouse et al. 2008, Rohr and Palmer 2013), including live herbaceous vegetation or exposed sandy soils in which to burrow (Fritts et al. 2015). Juvenile toads burrow to avoid water loss (Lannoo 2005) and position the thin moist skin of their ventral surface toward cool and moist soil (Pough et al. 1983). While toads were observed burrowing in all forest types, lack of soil moisture increased 72-h juvenile mortality at PP forest by a factor of five to six relative to reference forests (FRP) where groundcover microhabitat held significantly greater soil moisture. Non-significant differences in survival among other forest types (PRP vs. FRP) agree with previous studies (Popescu and Hunter 2011), and indicate that forests allowed to regenerate naturally provide diurnal refugia from desiccation (Fritts et al. 2015). Greater amphibian survival differences among forest types at 72 vs. 24 h suggest that duration of dry conditions will increase juvenile amphibian vulnerability to complete loss of forest floor microhabitat (PP). Similarly, soil moisture, amphibian water loss, and mortality were strongly predicted by a principal components analysis of coniferous forest groundcover, suggesting that forestry-driven objectives that regenerate groundcover microhabitat increase juvenile amphibian vitality during dry periods. Air speed is one determinant of desiccation rate we did not quantify (Riddell et al. 2017); however, it is likely to be confounded with cover of herbaceous plants that intercept both light and wind, influencing microclimate at the forest floor (Snedaker and Lugo 1972, Jose et al. 2006).

The ability to move between wetlands lowers risk of population declines in the forest landscape (Cushman 2006), and amphibians seek microhabitats that minimize water loss, including ground cover (Patrick et al. 2006, Roznik and Johnson 2009). However, ground cover does not appear to be as strong a predictor of juvenile movement rates or habitat permeability (Graeter et al. 2008) as precipitation (Rothermel 2004, Semlitsch et al. 2009). In our study, toad speed increased during or soon after rainfall and, given that precipitation occurred periodically throughout our experiment, abiotic constraints on movement appear to have been temporary. We found that amphibians directed movement downslope, consistent with moisture seeking behavior (Rohr and Madison 2003), which may explain why orientation is not consistently toward mature forest in experimental studies (Rothermel 2004). While previous studies reported that physical resistance to movement can lower amphibian speed (Cline and Hunter 2014), open-canopy forest in our study had far less pine litter and greater bare ground that should facilitate rapid movements. However, we found that toads moved faster where herbaceous groundcover was low and pine densities were higher, consistent with toads attempting to rapidly evacuate from pine plantations to more suitable forest habitats containing sufficient groundcover (Semlitsch et al. 2008).

Conservation and Forest Management Implications

Sustainable forest management requires balancing economic benefits of intensive silvicultural practices with conservation of wildlife native to *Pinus* forests (Lannoo 2005, Means and Means 2005), which comprise the majority of global plantations (Brown 2000). Recent extirpation of imperiled amphibian species, especially those adapted to xeric habitats (Farmer et al. 2017), could be prevented or reversed where habitat degradation does not limit survival or behavior (Means and Means 2005, Rittenhouse et al. 2008, Semlitsch et al. 2009). High-intensity silviculture practices, such as roller chopping and scalping, can eliminate forest groundcover, increasing amphibian desiccation as conifers dry the upper soil layer. Thus, we recommend prioritizing lower intensity roller chopping or lower pine densities to retain groundcover microhabitat found at reference condition forest given that PRP permitted comparable juvenile survival to FRP forest. Behavioral avoidance of dry conditions favored use of habitat with greater herbaceous groundcover, which increases with prescribed fire frequency. Our results suggest that the cumulative impacts of forestry operations on forest groundcover should be strongly considered, and benefits of retaining patches of intact forest groundcover near amphibian breeding sites, vs. stand-wide groundcover modification, on amphibian persistence should be investigated. Given that moisture is fundamental to amphibian biology (Veysey et al. 2009) and their distribution (Riddell et al. 2017), and that dry periods are predicted to increase in frequency in the next 100 yr (Carey and Alexander 2003, Li et al. 2013, Chaudhary et al. 2016), our experimental study demonstrates that forest management practices that maintain groundcover habitat complexity should promote persistence of amphibian populations within highly managed forest and across changing climates.

Acknowledgments

We would like to thank Brian Composano of the Florida Forest Service, and the staff at Withlacoochee State Forest for their letter of authorization to conduct research on property. The techniques used in this study were approved under Institutional Animal Care and Use Committee permit # IS00000009 and FWC Scientific Collecting Permit: LSSC-12-00090. The authors declare no conflict of interest.

Literature Cited

Brown, C. 2000. The global outlook for future wood supply from forest plantations. Working paper no: GFPOS/WP/03. http://www.fao.org/docrep/003/x8423e/x8423e00.htm

Carey, C., and M. A. Alexander. 2003. Climate change and amphibian declines: Is there a link? Diversity and Distributions 9:111–121.

Chaudhary, A., Z. Burivalova, L. P. Koh, and S. Hellweg. 2016. Impact of forest management on species richness: global meta-analysis and economic trade-offs. Scientific Reports 6. doi: 10.1038/srep23954

Cline, B. B., and M. L. Hunter. 2014. Different open- canopy vegetation types affect matrix permeability for a dispersing forest amphibian. Journal of Applied Ecology 51:319–329.

Cole, L., and M. Newton. 2015. Relationships between radiation and canopy closure estimates in streamside buffers in western Oregon. Forest Science 61:559–569.

Collins, J. P., and A. Storfer. 2003. Global amphibian declines: sorting the hypotheses. Diversity and Distributions 9:89–98.

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

Dodd, C. K. Jr, and L. L. Smith. 2003. Habitat destruction and alteration. Historical trends and future prospects for amphibians. Pages 94112 in R. D. Semlitsch, editor. Amphibian Conservation. Smithsonian Institution Press, Washington, D.C., USA.

Farmer, A., K. Enge, J. B. Jensen, D. J. Stevenson, and L. L. Smith. 2017. A range-wide assessment of the status and distribution of the striped newt (*Notophthalmus perstriatus*). Herpetological Conservation and Biology 12:595–598.

Florida Natural Areas Inventory. 2009. Reference natural communities geodatabase. http://www.fnai.org/reference-natural-communities.cfm

Florida Natural Areas Inventory and Florida Fish and Wildlife Commission. 2007. Vegetation monitoring standard operating procedure. https://myfwc.com/media/17529/obvm-sop-2018-revision-final.pdf

Fox, T. R., E. J. Jokela, and H. L. Allen. 2004. The evolution of pine plantation silviculture in the Southern United States. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Fritts, S. R., S. M. Grodsky, D. W. Hazel, J. A. Homyack, S. B. Castleberry, and C. E. Moorman. 2015. Quantifying multiscale habitat use of woody biomass by southern toads. Forest Ecology and Management 346:81–88.

Graeter, G. J., B. B. Rothermel, and J. W. Gibbons. 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. Journal of Wildlife Management 72:473–482.

Hansen, M. C., et al. 2013. High-resolution global maps of 21st-century forest cover change. Science 342:850.

Harper, E. B., D. A. Patrick, and J. P. Gibbs. 2015. Impact of forestry practices at a landscape scale on the dynamics of amphibian populations. Ecological Applications 25:2271–2284.

Harpole, D. N., and C. A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management 114:349–356.

Hart, S. A., and H. Y. H. Chen. 2006. Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25:381–397.

Jaeger, R. G. 1980. Microhabitats of a terrestrial forest salamander. Copeia 1980:265–268.

Jones, P. D., B. B. Hanberry, and S. Demarais. 2010. Managing the southern pine forest—retained wetland interface for wildlife diversity: research priorities. Wetlands 30:381–391.

Jose, S., E. J. Jokela, and D. L. Miller. 2006. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer Science & Business Media, New York, New York, USA.

Lannoo, M. 2005. Amphibian declines the conservation status of United States species. First edition. University of California Press, Oakland, California, USA.

Li, Y., J. M. Cohen, and J. R. Rohr. 2013. Review and synthesis of the effects of climate change on amphibians. Integrative Zoology 8:145–161.

Mason, W. L., M. Peter, and S. Bathgate. 2012. Silvicultural strategies for adapting planted forests to climate change: from theory to practice. Journal of Forest Science 58:265–277.

Means, D. B., and R. C. Means. 2005. Effects of sand pine silviculture on pond-breeding amphibians in the woodville karst plain of North Florida. Page 317 *in* W. E. J. Meshaka and K. J. Babbitt, editors. Amphibians and reptiles: status and conservation in Florida. Krieger Publishing, Melbourne, Florida, USA.

Myers, R. L., and J. J. Ewel. 1990. Ecosystems of Florida. University of Florida Press, Gainesville, Florida, USA.

Patrick, D. A., M. L. Hunter, and A. J. K. Calhoun. 2006. Effects of experimental forestry treatments on a Maine amphibian community. Forest Ecology and Management 234:323–332.

Patrick, D. A., A. J. K. Calhoun, and M. L. Hunter. 2008. The importance of understanding spatial population structure when evaluating the effects of silviculture on spotted salamanders (*Ambystoma maculatum*). Biological Conservation 141:807–814.

Popescu, V. D., and M. L. Hunter. 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. Ecological Applications 21:1283–1295.

Popescu, V. D., D. A. Patrick, M. L. Hunter, and A. J. K. Calhoun. 2012. The role of forest harvesting and subsequent vegetative regrowth in determining patterns of amphibian habitat use. Forest Ecology and Management 270:163–174.

Potapov, P., et al. 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances 3:e1600821.

Pough, F. H., T. L. Taigen, M. M. Stewart, and P. F. Brussard. 1983. Behavioral modification of evaporative water loss by a Puerto Rican frog. Ecology 64:244–252.

Reichling, S. B. 2008. Reptiles & amphibians of the southern pine woods. University Press of Florida, Gainesville, Florida, USA.

Riddell, E. A., E. K. Apanovitch, J. P. Odom, and M. W. Sears. 2017. Physical calculations of resistance to water loss improve predictions of species range models. Ecological Monographs 87:21–33.

Rittenhouse, T. A. G., E. B. Harper, R. R. Lelande, and R. D. Semlitsch. 2008. The role of microhabitats in the desiccation and survival of anurans in recently harvested oak-hickory forest. Copeia 4:807–814.

Rohr, J. R., and D. M. Madison. 2003. Dryness increases predation risk in EFTS: support for an amphibian decline hypothesis. Oecologia 135:657–664.

Rohr, J. R., and B. D. Palmer. 2013. Climate change, multiple stressors, and the decline of ectotherms. Conservation Biology 27:741–751.

Rothermel, B. B. 2004. Migratory success of juveniles: A potential constraint on connectivity for pond-breeding amphibians. Ecological Applications 14:1535–1546.

Roznik, E. A., and S. A. Johnson. 2009. Canopy closure and emigration by juvenile gopher frogs. Journal of Wildlife Management 73:260–268.

Semlitsch, R. D., C. A. Conner, D. J. Hocking, T. A. G. Rittenhouse, and E. B. Harper. 2008. Effects of timber harvesting on pond-breeding amphibian persistence: testing the evacuation hypothesis. Ecological Applications 18: 283–289.

Semlitsch, R. D., et al. 2009. Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. BioScience 59:853–862.

Snedaker, S. C., and A. E. Lugo. 1972. Ecology of the Ocala national forest. Volume 24. USDA Forest Service Southern Region Publication, Atlanta, Georgia, USA.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, and M. Tignor. 2007. Climate change 2007—the physical science basis. Cambridge University Press, Cambridge, UK.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

Tilghman, J. M., S. W. Ramee, and D. M. Marsh. 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biological Conservation 152:1–9.

Todd, B. D., and B. B. Rothermel. 2006. Assessing quality of clearcut habitats for amphibians: Effects on abundances versus vital rates in the southern toad (*Bufo terrestris*). Biological Conservation 133:178–185.

Todd, B. D., S. M. Blomquist, E. B. Harper, and M. S. Osbourn. 2014. Effects of timber harvesting on terrestrial survival of pond-breeding amphibians. Forest Ecology and Management 313:123–131.

Veysey, J. S., K. J. Babbitt, and A. Cooper. 2009. An experimental assessment of buffer width: Implications for salamander migratory behavior. Biological Conservation 142:2227–2239.

Walker, J., and R. K. Peet. 1983. Composition and species diversily of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55:163–179.

Walls, S. C., W. J. Barichivich, M. E. Brown, D. E. Scott, and B. R. Hossack. 2013. Influence of drought on salamander occupancy of isolated wetlands on the southeastern coastal plain of the United States. Wetlands 33:345–354.

Wirth, C., G. Gleixner, and M. Heimann, editors. 2009. Old-growth forests function, fate and value. Springer-Verlag, Berlin, Germany.

Zotarelli, L., M. D. Dukes, and M. Paranhos. 2013. Minimum number of soil moisture sensors for monitoring and irrigation purposes. University of Florida, Institute of Food and Agricultural Sciences, Gainesville, Florida, USA.

SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1870/full

DATA AVAILABILITY

Data are available on the Dryad Digital Repository: https://doi.org/10.5061/dryad.1619515.