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RESEARCH ARTICLE

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Direct and indirect effects of pine silviculture on the larval occupancy and breeding of declining amphibian species

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Abstract

1. Plantation silviculture is increasing globally and is particularly intensive in temperate coniferous forests, where densely planting trees requires practices common to non-conifer systems that can alter forest floor microhabitat, and potentially threaten amphibian persistence. Most declining amphibian species depend on specific forest microhabitats as terrestrial refugia, but amphibian extirpation associated with tree harvest alone appears unlikely, suggesting that impacts of planting forests on groundcover might better predict recent declines in amphibian occupancy.
2. We repeatedly sampled larval presence or absence of 10 amphibian species native to temperate coniferous forest in the Southeastern United States for one year at 62 isolated wetlands, located in either naturally regenerating or planted forest (plantation). We assessed three direct ways that planted forests might reduce amphibian breeding site occupancy by: (a) increasing conifer densities, (b) decreasing groundcover, and (c) an indirect pathway, whereby increased tree densities at plantations might reduce groundcover and thus amphibian site occupancy.
3. After controlling for wetland traits and accounting for differences in detection, breeding site occupancy for 8/10 amphibian species was dependent upon whether forests were planted surrounding wetlands (within 300 m). Herbaceous groundcover, not canopy, most commonly influenced occupancy and increased occupancy for declining surface active or fossorial amphibians.
4. Path analyses showed that, by directly and indirectly reducing groundcover (via conifer densities), plantations had significantly lower occupancy of two declining surface active or fossorial frog species, whereas two common aquatic frog species were tolerant to planting conifers. Among declining species, salamanders showed a greater reduction in occupancy than anurans, likely because of greater vulnerability to the drier forest floor conditions of plantation than naturally regenerating forests.
5. *Synthesis and applications*. Direct negative impacts of coniferous plantation on amphibians can be addressed by limiting groundcover and soil impacts, including switching from high intensity practices, such as mechanical chopping vegetation or bedding soil, to lower intensity site preparation treatments that are less likely to

significantly disturb groundcover. Indirect negative effects of dense canopy cover at planted forests could be lowered by periodically thinning canopies prior to final harvest, thus increasing intact forest groundcover and the conservation of both common and declining amphibians.

KEYWORDS

extirpation, forest floor, forest management, habitat specialist, land use, longleaf pine, path analysis

1 | INTRODUCTION

Amphibians are disappearing over a thousand times faster than natural background extinction rates (McCallum, 2007), and forest management is a major global determinant of habitat complexity (Puettmann, Coates, & Messier, 2009), ultimately influencing the abiotic conditions and microhabitat available to declining amphibians (August, 1983; Aussenac, 2000; Rothermel, 2004). As poikilotherms with very permeable skin, amphibians are highly vulnerable to changes in abiotic conditions of terrestrial forests (Lannoo, 2005). Timber harvest (logging) can reduce amphibian abundance by removing the canopy layer and thus increasing temperature and moisture stress for amphibians via insolation (Gardner, Barlow, & Peres, 2007; Harpole & Haas, 1999; Semlitsch et al., 2009), but a recent review suggested that such impacts alone appear unlikely to cause their extirpation (Tilghman, Ramee, & Marsh, 2012). Yet globally, planted coniferous forests are increasing in both acreage and intensity (FAO, 2000; Fox, Jokela, & Allen, 2004; Payn et al., 2015), and use practices (other than logging) that can alter forest floor microhabitat, and potentially impact amphibian occupancy of forests (Earl & Semlitsch, 2015; Moseley, Castleberry, & Ford, 2004; Rittenhouse, Harper, Lelande, & Semlitsch, 2008).

Coniferous forests are typically dominated by a few *Pinus* (pine) spp. in the canopy, but habitat complexity at the forest floor can include a particularly rich groundcover of herbaceous plants that buffer forest floor microclimates and provide microhabitat for a diverse community of surface active and fossorial amphibians (Walker & Peet, 1984; Wright & Wright, 1949). Additionally, herbaceous plant abundance and forest floor microhabitats in coniferous forest could buffer juvenile amphibians from insolation, wind, and thus desiccation risk (Haggerty, Crisman, & Rohr, 2019), and herbaceous plant diversity can increase the abundance of insects that serve as a food source for many amphibians (Hahn & Orrock, 2015). In contrast, groundcover complexity at pine plantations (trees planted in rows at unnaturally high densities) is often impacted by common forestry practices that pose a conservation concern for amphibian communities (Bergeron & Harvey, 1997; Means & Means, 2005; Puettmann et al., 2009). These practices include mechanically chopping groundcover vegetation and logging debris, breaking up soil structure, and planting conifers at high densities that often shade any herbaceous plants for over a decade until the next harvest (Fox et al., 2004; Hartley, 2002). Such practices could alter soil moisture, microhabitats such as burrows used by fossorial amphibians (Roznik & Johnson, 2009; Wright & Wright, 1949), soil integrity, and accumulation of coarse woody debris (CWD), all of which can affect amphibian microhabitats and ultimately amphibian communities (Owens et al., 2008). Tree mortality, decomposition and abundance of larger snags on the forest floor at plantations are typically a fraction of that found at natural pine forest (McComb & Muller, 1983; USDA, 1993). CWD and subterranean cavities, including root channels of dead trees, contribute to moisture and temperature refugia, habitat heterogeneity and ultimately species richness of amphibian communities (Harmon, Franklin, & Swanson, 1986; Owens et al., 2008). Thus, because amphibians of pine forests are adapted to canopy dominance by *Pinus* spp. (Lannoo, 2005), it may be that forest groundcover loss, particularly near wetland breeding sites, better predicts recent amphibian declines (Enge & Marion, 1986; Russell, Hanlin, Wigley, & Guynn, 2002). Importantly, millions of hectares of former pine plantations are undergoing natural canopy regeneration (http://www.nfwf.org/longleaf/Pages/home.aspx) and could potentially increase occupancy of threatened amphibians if managed properly.

To investigate mechanisms by which pine plantation practices surrounding wetlands affect amphibian occupancy, we repeatedly sampled amphibian larvae of 10 species, including seven with relatively stable population dynamics, and three species that are currently in decline (Krysko, Enge, & Moler, 2011). We performed occupancy analyses for all 10 species to determine how occupancy varied with pine plantation practices surrounding wetlands, and path analyses for the three declining species to discriminate two hypotheses of direct mechanisms by which pine silviculture could reduce amphibian occupancy: (a) increase tree densities, and (b) directly reduce groundcover. We also hypothesized a third and indirect mechanism that entails pine silviculture increasing the densities of pines, which reduces herbaceous groundcover that causes amphibian declines.

In addition to hypotheses regarding the mechanisms by which pine silviculture practices might affect amphibians, we had hypotheses regarding which types of amphibians might be most adversely affected by pine silviculture. Specifically, we hypothesized that the effect of pine plantation silviculture on amphibian occupancy would be dependent upon amphibian microhabitat preference (Table 1). We expected that surface active and fossorial amphibians, including all three declining species (Table 1), would be most adversely affected by pine plantation operations because common practices in these operations cause intense soil disturbance that can alter

TABLE 1 Adult microhabitat use of 10 amphibian species found at >5 sites in the study as reported by Lannoo (2005) and their ranges for all analyses

Common name	Scientific name	Adult microhabitat	Range
Frogs			
Southern cricket frog	*Acris gryllus dorsalis*	Aquatic	ALL
Pig frog	*Lithobates grylio*	Aquatic	ALL
Southern leopard frog	*Lithobates sphenocephala*	Aquatic	ALL
Pine woods treefrog	*Hyla femoralis*	Arboreal	ALL
Barking treefrog	*Hyla gratiosa*	Arboreal/subterranean	ALL
Ornate chorus frog	*Pseudacris ornata**	Arboreal/subterranean	SMN, ANF
Little grass frog	*Pseudacris ocularis*	Vegetation/litter	ALL
Gopher frog	*Lithobates capito**	Subterranean	OCA, JEN, GOT
Salamanders			
Dwarf salamander	*Eurycea quadridigitata*	Vegetation/litter	SM, ANF
Striped newt	*Notophthalmus perstriatus**	Subterranean	OCA, JEN, GOT

Note: An asterisk (*) by a scientific name denotes a declining species. All species can successfully breed at the <2 ha temporary or isolated wetlands that we sampled with the exception of the pig frog (*L. grylio*).
Abbreviations: ALL, all sites; ANF, Apalachicola Nat. Forest; GOT, Goethe State Forest; JEN, Jennings State Forest; OCA, Ocala Nat. Forest; SMN, St. Marks Nat. Wildlife Refuge.

soil moisture, destroy animal burrows and uproot herbaceous plant microhabitat. We hypothesized that arboreal and aquatic species would be least impacted because they can utilize tree or wetland microhabitats within plantations, respectively, that are less affected by silviculture practices (with the exception of clear cutting) than are the soil and understory. Among the three declining species, we hypothesized that the salamander *Notophthalmus perstriatus* would be more adversely affected by plantation operations than the two anuran species because of its greater vulnerability to low soil moisture, the latter of which is known to decrease with planted tree density. We also hypothesized that occupancy of surface active or fossorial amphibians would be related to conifer density primarily by its indirect effects on groundcover. We grouped species by adult microhabitat in part because (a) there is not enough space within the manuscript to present life histories of 10 species and (b) we would ideally like our findings on the relative importance of forest canopy and groundcover habitat to apply broadly to species in other regions with similar microhabitat preferences as those studied here.

2 | MATERIALS AND METHODS

2.1 | Site selection

This study was conducted in temperate coniferous forest of the Southeastern United States (SEUS; Figure 1), which is a fire-adapted *Pinus* (pine) spp. system rich in herbaceous plants and now among the most intensively managed planted conifer forests in the world (Oswalt, Smith, Miles, & Pughes, 2014). We categorized forests as either naturally regenerated or planted coniferous forest, using the Florida Cooperative Land Use, Cover Classification System (FLUCCS) Map (http://myfwc.com/research/gis/applications/articles/Cooperative-Land-Cover) in ArcMap v9.3 to select FLUCCS classes 'Pine Flatwoods' and 'Longleaf Pine – Xeric Oak', which are both naturally regenerated (open canopy) pine forest, and FLUCCS class "Coniferous Plantation". Raster coverage with a 10 × 10 m resolution and focal statistics were then used to estimate the percent cover of forest types (FT) within 300 m of each cell to identify forest areas with >50% coverage of either naturally regenerated pine forests or pine plantation. This percentage cutoff was to determine which FT composed the majority of the area surrounding each study site. Plantation forests in our study were planted ≥15 years ago and used practices typical of short-rotation pulpwood generation as described above. Finally, National Wetland Inventory (NWI) data from the US Fish & Wildlife Service (http://www.fws.gov/wetlands/data/data-download.html) were used to identify approximately 30 small (<2 ha), freshwater wetlands isolated within each of the two FTs (62 total sites). At each site, we recorded the maximum water depth (m) and used Google Earth imagery to estimate wetland size (ha), and distance to the nearest neighbouring wetland (m).

2.2 | Amphibian and vegetation sampling

We sampled each of the 62 wetlands repeatedly for the presence or absence of amphibian larvae, using a Ward's 12″ D-frame 1,000 µm dip net, including one winter (January–February), spring (March–May), and summer (May–August) sampling period in 2014, permitting three sampling occasions per species. We performed 1-m net sweeps at approximately 30 randomly located points per ha of wetland size, as

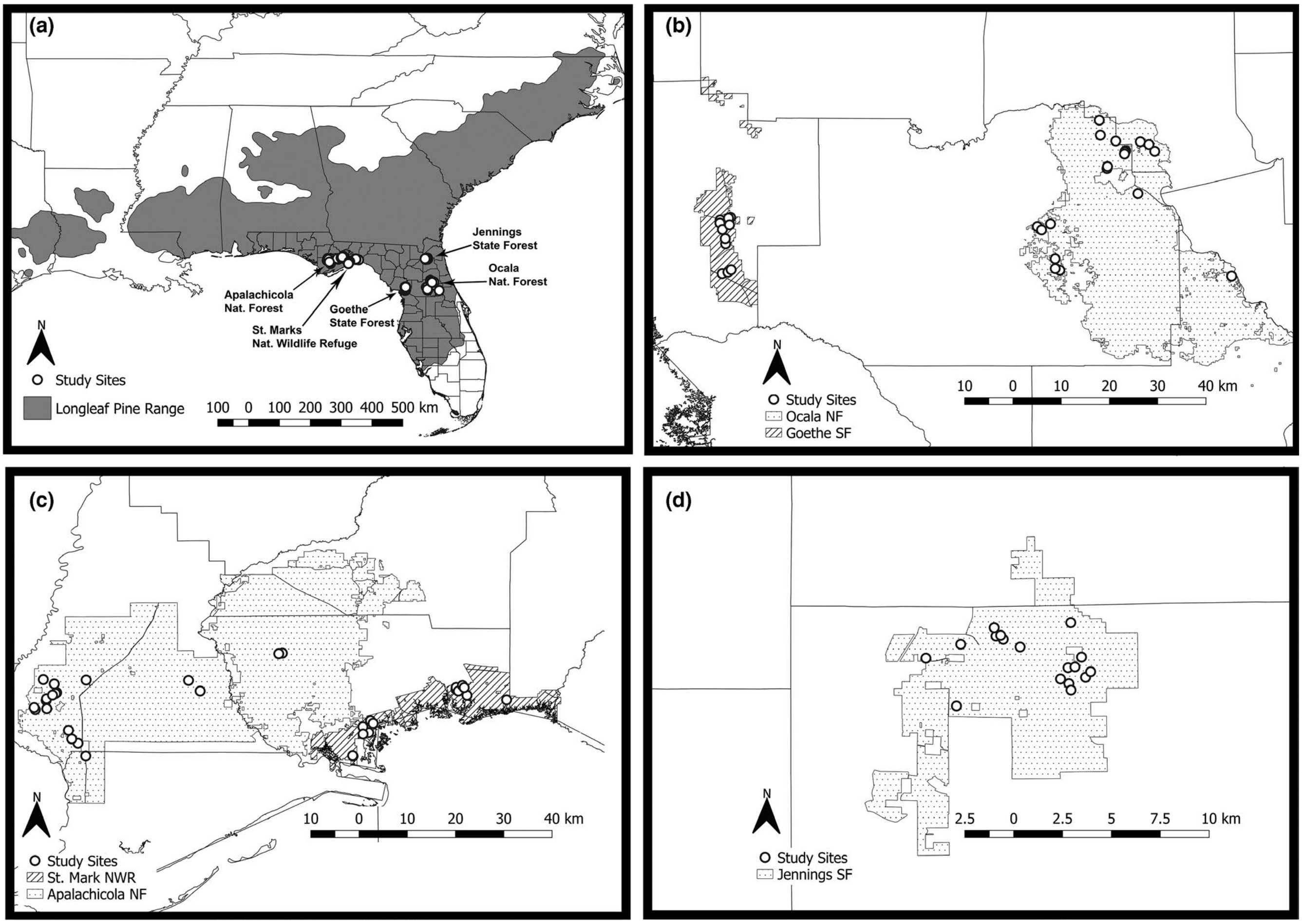

FIGURE 1 Map of study site locations in historic longleaf-wiregrass range (a), and detailed maps for Goethe State Forest (SF) and Ocala National Forest (NF) (b), Apalachicola NF and St. Marks National Wildlife Refuge (c), and Jennings SF (d)

quantified previously using NWI data. In total, over 12,200 1-m net sweeps (χ = 65 per visit per site) were performed in the study, and all sites held sufficient water in both seasons to support amphibian larvae. Among the 10 amphibian species that we sampled (Table 1), adult microhabitat requirements ranged from species that are predominantly found in (a) aquatic habitats (n = 3), (b) forest canopy (n = 1), (c) a combination of canopy and subterranean habitats (n = 2), (d) surface vegetation or litter (n = 2), or (e) surface and subterranean habitats (n = 2).

To characterize vegetation in October 2014, we generated 10 random points within a 200 m buffer landward from the edge of each wetland study site polygon. At each random point, we recorded pine basal area (BA) using a BA factor 10 prism, and canopy cover using a spherical densiometer. Within 7 m of each random point, we used previously described methods (OBVM, 2007) to position three 1 m^2 quadrats and recorded percent cover of herbaceous plants (OBVM, 2007). Drooping wiregrass was held vertically by hand when estimating the percent herbaceous cover.

2.3 | Forest inventory dataset

To assess the relationship between stand age and pine BA at plantation versus naturally regenerating forest, we used the Forest Inventory Analysis (FIA) dataset provided by the Southern Research Station (http://www.srs.fs.fed.us/pubs/). The FIA program compiles data on habitat structure of forest lands throughout the United States, which are available for analyses online (http://www.fia.fs.fed.us/tools-data/) using plot methodology described by Burrill et al. (2017). We used state-level data for Florida, USA to encompass our study region, and selected the FTs 141 and 142, which constitutes the majority of natural and planted pine lands, respectively (Burrill et al., 2017). Finally, we used the FIA attribute STDORGCD to determine whether forests were planted or naturally regenerated.

2.4 | Statistical analyses

All statistical analyses were performed in R-2.13 (https://www.cran.r-project.org/). To quantify pine canopy differences at our plantation and second growth study sites, we performed a linear mixed effects model using the *lme4* package for average pine BA using a categorical fixed predictor for FT, and a random effect of study site. To determine pine BA impacts on groundcover regeneration, we used the *glmmTMB* package to perform a negative binomial model using a fixed effect of pine BA and random effect of site. Finally, we used FIA data described above to investigate stand age impact on

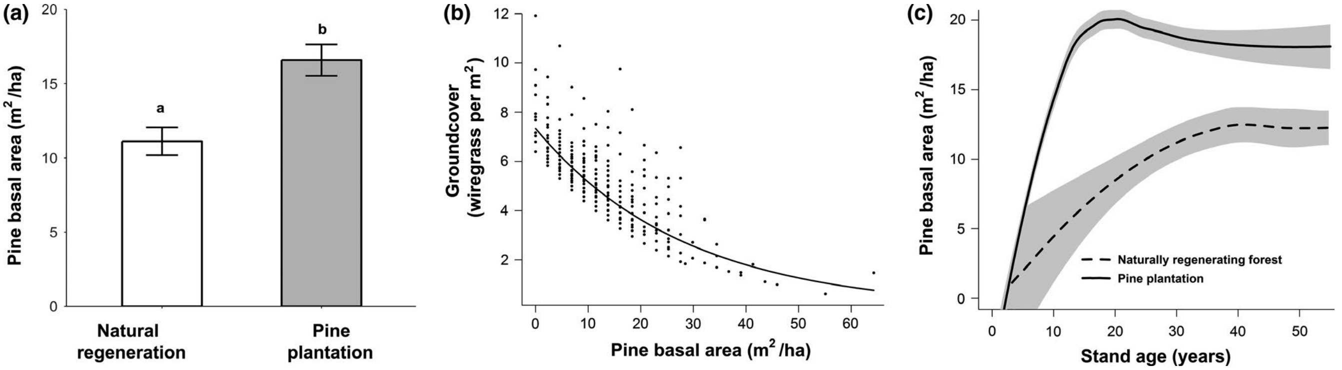

FIGURE 2 Average pine basal area (m^2/ha) at naturally regenerating and plantation forest study sites using Tukey's post hoc comparisons shown with 95% confidence intervals (CI) (a), wiregrass cover (per m^2) predicted using pine basal area (m^2/ha) in a zero-inflated negative binomial model with a random site effect (b), and local polynomial regression fit using loess function in R for pine basal area predicted by stand age using Forest Inventory Analysis (FIA) data for plantation and natural forest with 95% CIs (c)

pine BA at planted and second growth forests. Given that pine BA increases after planting to an asymptote (Zhao & Kane, 2012), we regressed BA against a quadratic predictor for stand age (in years) and a binary predictor defining planted or natural stands. To examine wetland differences among FTs, we used a two sample t test to compare wetland depth (cm), size (ha), and distance to the nearest neighbour (m) between FTs. Given that none of these wetland variables differed between the two FTs (see Results), we focused strictly on forest rather than wetland traits for our site occupancy and path analyses described below.

Site occupancy analysis uses repeated-measures of the binary response of species presence to create a latent variable for occupancy as a function of both the probability of detecting a species (p) and sampling covariates that ultimately reduce the error of false absences (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). To estimate amphibian site occupancy (Ψ), we used the R package *unmarked*, which fits occupancy models based on zero-inflated binomial models (MacKenzie et al., 2003; Royle & Dorazio, 2008). We performed a single-season Ψ model each for the 10 amphibian species and compared four nested models where Ψ was linearly predicted by either forest groundcover, canopy cover, both canopy and groundcover, or no covariates (constant occupancy). For each species, we included only forests within its range having documented populations within the past 15 years (Krysko et al., 2011; Table 1). We ranked models by AIC values corrected for small sample size (AICc) using the *AICcmodavg* package, and considered the best model as that with the lowest number of parameters (N_{par}) if ΔAICc ≤ 2 for multiple models per species. For the three declining species, we then used PRESENCE 12.21 (https://www.usgs.gov/software/presence) to provide beta-estimates of the effect of groundcover forest structure on species occupancy and performed an empirical Bayes estimate to find the proportion of sites occupied with 90% confidence intervals (Fiske & Chandler, 2011). To determine if our model fit observed data, we performed a bootstrap with 1,000 replicates based on the parameter estimates of our fitted models and used a chi-squared test to assess goodness-of-fit (Bailey & MacKenzie, 2004; Table S6).

For declining amphibian species, a path analysis in the R package *lavaan* was used to investigate whether the effect of pine plantation on amphibian occupancy was direct or indirect. Path analysis generates a path diagram with coefficients that are interpreted analogously to multiple regression, and is a useful method to discriminate relative significance of direct and indirect effects (Shipley, 2002). For each declining species, we began with the same global path model using a categorical factor where forests were either plantation or second growth (Plantation Y/N), a latent variable for canopy (which included pine BA and a metric canopy closure), and a latent variable for groundcover (which included herbaceous and wiregrass cover). There were pathways from FT, canopy, and groundcover to amphibian occupancy, pathways from FT to canopy and groundcover, and a pathway from canopy to groundcover (Figure S2). We sequentially dropped the least significant paths until all paths had $p < .10$ and used diagonally weighted least squares (DWLS) to estimate path analysis parameters. DWLS is a test statistic for model fit when using categorical and binary outcome variables in *lavaan* (Katsikatsou, Moustaki, Yang-Wallentin, & Joreskog, 2012), and all models we present had $p > .05$ suggesting a model well-fitting the observed data. In addition to the DWLS test statistic to assess model fit, we also examined potential missing pathways using modification indices. We employed a one-tailed test for the effect of canopy cover on groundcover because canopy trees shade the forest floor (Hartley, 2002).

3 | RESULTS

3.1 | Wetland and forest vegetation metrics

Average wetland size, depth, and distances to the nearest neighbouring wetlands (Table S5) did not vary between plantation and naturally regenerating forest. All of the studied wetlands supported aquatic vegetation and lacked pine trees or visible signs of plantation operations. Forested wetlands composed 41% and 59% of plantation and naturally regenerating study sites, respectively

TABLE 2 Summary of occupancy model selection for 10 species with >5 detections

Lithobates capito	N_{par}	AICc	ΔAICc	***Lithobates sphenocephala***	N_{par}	AICc	ΔAICc
Ψ (groundcover)	4	74.81	0.00	Ψ (.)	2	185.68	0.00
Ψ (all covariates)	6	79.28	4.47	Ψ (all covariates)	6	186.71	1.03
Ψ (.)	2	81.43	6.62	Ψ (groundcover)	4	188.49	2.81
Ψ (canopy)	4	84.15	9.34	Ψ (canopy)	4	188.65	2.97
Pseudacris ornata	N_{par}	**AICc**	**ΔAICc**	***Hyla gratiosa***	N_{par}	**AICc**	**ΔAICc**
Ψ (groundcover)	4	38.89	0.00	Ψ (all covariates)	6	70.67	0.00
Ψ (.)	2	45.06	6.17	Ψ (groundcover)	4	73.38	2.71
Ψ (canopy)	4	45.33	6.44	Ψ (canopy)	4	76.44	5.77
Ψ (all covariates)	6	53.17	14.28	Ψ (.)	2	80.28	9.61
Eurycea quadridigitata	N_{par}	**AICc**	**ΔAICc**	***Hyla femoralis***	N_{par}	**AICc**	**ΔAICc**
Ψ (groundcover)	4	53.85	0.00	Ψ (all covariates)	6	77.30	0.00
Ψ (all covariates)	6	62.51	8.66	Ψ (canopy)	4	84.42	7.12
Ψ (.)	2	63.91	10.06	Ψ (.)	2	100.34	23.04
Ψ (canopy)	4	67.66	13.81	Ψ (groundcover)	4	100.47	23.17
Notophthalmus perstriatus	N_{par}	**AICc**	**ΔAICc**	***Lithobates grylio***	N_{par}	**AICc**	**ΔAICc**
Ψ (canopy)	4	38.15	0.00	Ψ (groundcover)	4	85.56	0.00
Ψ (groundcover)	4	40.21	2.06	Ψ (.)	2	87.31	1.75
Ψ (all covariates)	6	43.22	5.07	Ψ (canopy)	6	91.05	5.49
Ψ (.)	2	43.95	5.80	Ψ (all covariates)	4	92.50	6.94
Pseudacris ocularis	N_{par}	**AICc**	**ΔAICc**	***Acris gryllus***	N_{par}	**AICc**	**ΔAICc**
Ψ (all covariates)	6	53.23	0.00	Ψ (all covariates)	6	144.21	0.00
Ψ (groundcover)	4	54.24	1.01	Ψ (canopy)	4	146.76	2.55
Ψ (.)	2	57.97	4.74	Ψ (groundcover)	4	148.82	4.61
Ψ (canopy)	4	60.52	7.29	Ψ (.)	2	153.80	9.59

Note: Occupancy was fitted as either constant (Ψ (.)) or as a linear function of either all covariates (saturated model), groundcover or canopy covariates alone. ΔAICc is the difference in AICc values compared with the top-ranked model and N_{par} is the number of parameters.

(Table S5). All three declining species in our study utilize both forested and non-forested isolated wetlands for breeding (Krysko et al., 2011) and were detected at both wetland types during our surveys.

Pine BA was significantly greater at plantations than at naturally regenerating forests (Figure 2a). FIA data indicated that pine BA increased with stand age ($R^2 = 0.13$, $F_{1/3536} = 139.90$, $df = 1$, $p < .001$) and that pine BA at stands left to regenerate naturally after logging increased slower and reached an asymptote at a lower canopy density than at plantations (Figure 2c; Table S3). Further, comparison of 95% confidence intervals revealed that pine BA of plantations was significantly greater than naturally regenerating stands 6–7 years after planting, with differences increasing over time (Figure 2c). Importantly, as pine BA increased in our study, herbaceous groundcover cover declined (Figure 2b), consistent with canopy trees shading out groundcover vegetation ($\chi^2 = 23.1$ $df = 1$, $p < .001$).

3.2 | Amphibians detected

We captured eight frog and two salamander species (Table 1), including three species experiencing recent population declines: the ornate chorus frog (*Pseudacris ornata*), gopher frog (*Lithobates capito*), and striped newt (*N. perstriatus*). During this study, all wetlands held water from winter 2014 into the following summer sampling period, permitting three sampling occasions per species. Eight of 10 species were found less frequently in plantation than in naturally regenerating forest (Table S7).

3.3 | Amphibian occupancy

For site occupancy models accounting for detection probability, forest groundcover was the best single predictor of amphibian occupancy (4/10 species), followed by canopy cover (1/10 species). Among species that use surface or subterranean habitat in coniferous forest (Table 1), groundcover positively predicted occupancy for two frogs (*L. capito*, *P. ornata*) and two salamanders (*Eurycea quadridigitata* and *N. perstriatus*). Thus, canopy cover was a predictor of occupancy only for *N. perstriatus* (Table 2), but its strong negative effect was roughly similar to the positive impact of forest groundcover (ΔAICc = 2.06; Table 2). In contrast, amphibians that are aquatic as adults, *Lithobates grylio* and *Lithobates sphenocephala*, tended to occupy wetlands independent of forest structure (Ψ (.) within <2 ΔAICc of top model; Table 1). No single metric of forest structure was clearly most important for frogs that are arboreal or use wetland margins (*Pseudacris ocularis*, *Hyla gratiosa*, *Hyla femoralis* and *Acris gryllus*; Table 2). Among sympatric declining species, frogs (*L. capito*) occupied sites with lower groundcover than salamanders (*N. perstriatus*; Figure 3).

3.4 | Path analysis

A path model incorporating our measures of forest structure (Table S1) was a good fit to observed data for all declining amphibians (*L. capito* ($R^2 = 0.50$, DWLS = 2.4, $df = 15$, $p = .94$), *N. perstriatus* ($R^2 = 0.96$, DWLS = 2.2, $df = 15$, $p = .82$), and *P. ornata* ($R^2 = 0.35$, DWLS = 2.3, $df = 5$, $p = .94$)), and model fit indices suggested that all paths were important in our models (Figure 4). All models had Comparative Fit Index (relative to a null independence model) = 1.00, RMSEA = 0.00, and $p > .80$ for RMSEA.

As predicted, site occurrence of the declining salamander (*N. perstriatus*) was more adversely affected by pine silviculture than site occurrence of the two declining frog species. In fact, 96% of the variance in *N. perstriatus* occupancy was accounted for by planted conifer operations, whereas these values were <51% for the other two declining species (Figure 4). Also as predicted, *N. perstriatus* appeared to be affected mostly by the direct pathway from planted forest to occupancy, which should reflect effects of silviculture practices on soil disturbances and CWD, whereas the effects of planted forests on frogs (*L. capito* and *P. ornata)* were always mediated by forest groundcover (Figure 4). For both declining frogs (*L. capito* and *P. ornata*), the models supported planted forest practices directly reducing groundcover, which was associated with declines in occupancy. However, for *L. capito*, the models also suggested that occupancy was reduced by the indirect pathway of silviculture increasing canopy trees that reduced the abundance of groundcover (Figure 4).

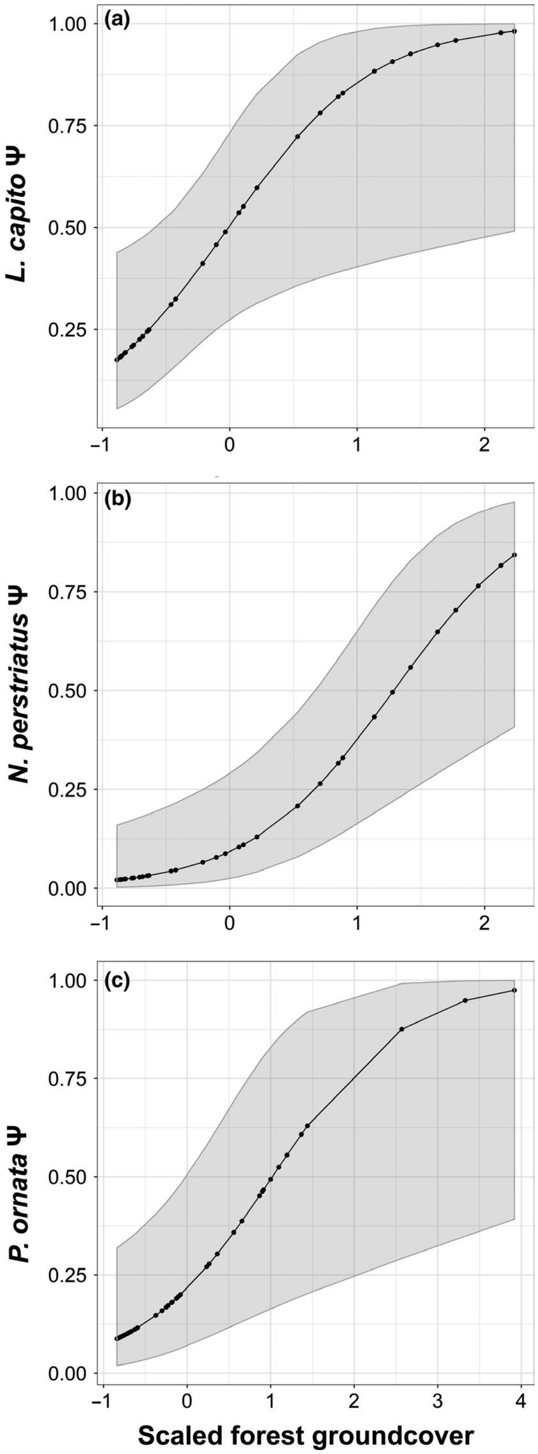

FIGURE 3 Relationship between groundcover (wiregrass) and occupancy (95% confidence interval shaded region) for three declining amphibian species (*Lithobates capito* (a), *Notophthalmus perstriatus* (b), and *Pseudacris ornata* (c))

4 | DISCUSSION

Accounting for non-significant differences in traits of wetland study sites, occupancy variation for amphibian species in decline appeared to be driven by whether the forest surrounding wetlands was planted or naturally regenerating. We do not have data to support that greater wetland loss in plantations than naturally regenerating forests is driving this difference in occupancy because all study sites supported amphibian breeding and the wetland's nearest neighbour distances were comparable between these two FTs, suggesting similar wetland densities. Loss of forest groundcover, not increased pine density, at plantations was the most significant negative predictor of amphibian occurrence for surface active or fossorial frogs and thus, pine density effects seem to

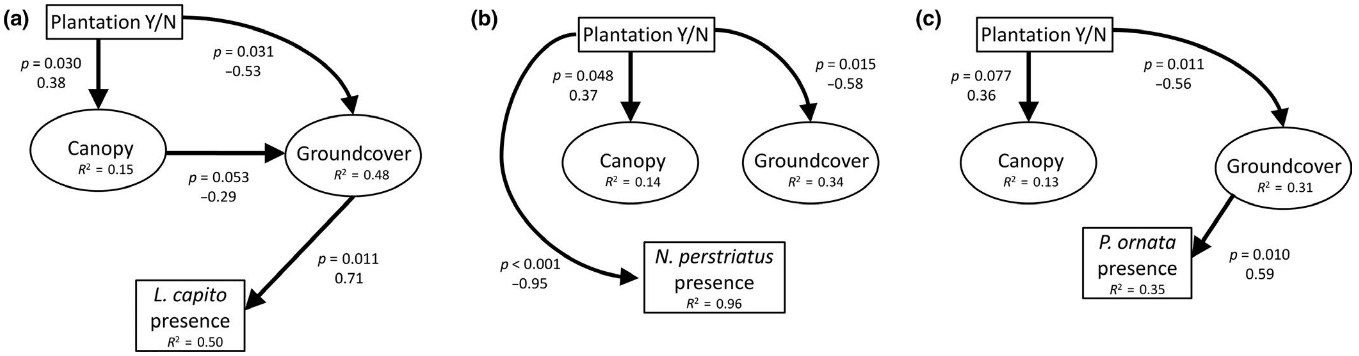

FIGURE 4 Path model analysis for presence of three declining amphibian species (*Lithobates capito* (a), *Notophthalmus perstriatus* (b) and *Pseudacris ornata* (c)) using average vegetation metrics per site. For each species, we began with a saturated model (upper left) and then dropped non-significant regression paths sequentially to reach a final model. For each significant pathway in the final models, we provide standardized path coefficients and *p*-values next to that regression pathway. All path models used the same predictors for latent canopy (pine basal area and canopy closure) and groundcover (herbaceous cover and wiregrass cover) variables and provided a good fit to observed data for *L. capito* (R^2 = 0.50, DWLS = 2.4, *df* = 15, *p* = .94), *N. perstriatus* (R^2 = 0.96, DWLS = 2.2, *df* = 15, *p* = .82), and *P. ornata* (R^2 = 0.35, DWLS = 2.3, *df* = 5, *p* = .95). Missing paths from our models were not statistically significant and all models had Comparative Fit Index = 1.00, RMSEA = 0.00, and *p* > .80 for RMSEA

be largely indirect by significantly reducing forest groundcover. However, forest floor disturbance appears to be the most important predictor of occupancy for the fossorial salamander species *N. perstriatus*. Our results are consistent with documented absences of declining amphibian species at forest plantations (Means & Means, 2005; Means, Palis, & Baggett, 1996), but contribute uniquely by both estimating the relative importance of various silviculture practices to these declines in amphibian occupancy and highlighting that site preparation practices that profoundly disturb forest groundcover and soil might be just as important contributors to amphibian declines as planting trees in high densities and harvesting these trees (Tilghman et al., 2012).

4.1 | Direct and indirect impacts of canopy cover

The faster increase in pine BA with stand age in plantations versus naturally regenerating forest that we found using FIA data agrees with previous work (Dickens, Moorhead, Dangerfield, & Chapman, 2005; Zhao & Kane, 2012), and surface active or fossorial amphibians would not directly benefit from pine canopy microhabitats (Lannoo, 2005). Densely planted forest could lower soil moisture and soil microhabitats such as burrows used by fossorial amphibians (Roznik & Johnson, 2009; Wright & Wright, 1949). This may be why pine BA was a relatively stronger negative predictor of occupancy for *N. perstriatus* than other declining species. *N. perstriatus* is known to hide in the soil to avoid desiccation and declined faster than *L. capito* and *P. ornata* at wetlands isolated within one pine plantation (Means & Means, 2005), potentially because drier soil conditions associated with increased planted pine density (Jose, Jokela, & Miller, 2006). Salamanders are particularly vulnerable to desiccation risk because of their small size relative to surface area (Rohr & Madison, 2003). Overall, the negative influence of dry conditions on soil dwelling salamanders is likely not unique to *N. perstriatus* (Walls, Barichivich, Brown, Scott, & Hossack, 2013). Greater pine canopy cover can also lower soil moisture by rain interception and leaf transpiration (Jose et al., 2006), which could play a role in amphibian declines at plantations. Canopy cover may also indirectly affect amphibians by shading and therefore limiting groundcover microhabitats used by surface active or fossorial amphibians (Wright & Wright, 1949). Overall, the potential benefits of canopy closure to amphibian communities, for example by lowering direct sun exposure and thus amphibian desiccation risk (Earl & Semlitsch, 2015), did not outweigh the negative indirect effect of canopy cover on amphibian occupancy by reducing groundcover habitat (Jose et al., 2006; Walker & Peet, 1984) in our study.

4.2 | Direct impacts of groundcover

Coniferous forest groundcover often includes herbaceous vegetation that provides amphibian microhabitat at the surface and below-ground including root channels and herbivorous animal burrows near live or dead vegetation (Brown & Means, 1984; Deckert, 1915; Franz, 1986; Wright & Wright, 1949). Herbaceous plants can improve soil structure, moisture retention, and fire propagation that increases the abundance and diversity of coniferous forest plant species (Walker & Peet, 1984). In our study, use of plantation site preparation practices (i.e. FT) appeared most detrimental to *N. perstriatus*, a salamander of conservation concern (Lannoo, 2005; Means et al., 2011), likely in part because of the adverse impact of these practices on the microhabitat of this salamander. While the terrestrial microhabitats used by *N. perstriatus* remain poorly known, it appears to use habitats comparable to other surface- and subterranean-dwelling salamanders, including soil burrows, leaf litter, and herbaceous plant root channels (Lannoo, 2005). The relative importance of intact forest groundcover to buffer forest floor microclimates from change for amphibians is likely applicable to coniferous forest beyond our study region (Morneault, Naylor, Schaeffer, & Othmer, 2004), and future studies should investigate what proportion of groundcover in surrounding forest permits the presence of surface active amphibians, preferably using a long-term BACI study design (Homyack & Haas, 2009).

4.3 | Conservation and management applications

Forest management near wetlands provide important opportunities for amphibian conservation (Schotthoefer et al., 2011; Semlitsch, 1998), and we found that planted forest impacts to forest groundcover, not canopy, were likely key drivers of lower occupancy of three threatened amphibian species at coniferous plantations. Thus, switching from high to low or moderate intensity site preparation treatments that do not cause major soil disturbances for pine plantations could promote persistence and recovery of declining amphibian species (Outcalt, 1993). While conifer BA was a weaker predictor of amphibian occurrence in our study, it should not be ignored because of its indirect negative impact on intact forest groundcover that can persist for decades at pine plantations (Hedman, Grace, & King, 2000; Kirkman, Goebel, Palik, & West, 2004). Thinning conifer canopies when planted stands reach 10–15 years old can increase soil moisture, economic returns, tree health (Demers & Andreu, 2016), and the recovery of herbaceous groundcover species that provide amphibian microhabitats (Clewell, 1989; Jose et al., 2006). The indirect effect of canopy density on groundcover that we documented has been demonstrated to be independent of prescribed fire regime (Walker, Silletti, & Cohen, 2010). Thus, repatriation efforts of threatened amphibians might be more successful by reducing canopy densities, using site preparation techniques that cause less permanent groundcover and soil disturbances, particularly within 300 m of wetlands in planted forests (FNAI, 2009; USFWS, 2011).

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AUTHORS' CONTRIBUTIONS

C.J.E.H. conceived and conducted the study. J.R.R. assisted with the statistical analyses. C.J.E.H. drafted the manuscript and J.R.R. and T.L.C. contributed to its editing.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.3cc2702 (Girard, Shea, & Fisher, 2018).

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SUPPORTING INFORMATION

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

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