



A meta-analysis of biodiversity responses to management of southeastern pine forests—opportunities for open pine conservation



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ABSTRACT

Open canopy conditions in southeastern pine (*Pinus* spp.) forests were historically maintained by frequent fire and other disturbances, without which midstory hardwoods create closed canopy conditions limiting value of pine stands for many endemic, disturbance-adapted species. Intensively managed pine forests, which comprise 19% of forests in the southeastern U.S., can emulate historical open pine conditions, providing appropriate vegetation structure and composition for many endemic species. However, exact mechanisms for producing and maintaining open pine conditions and subsequent effects on biodiversity have not been examined across regions and stand ages. To better inform managers about options for providing open pine conditions in intensively managed pine stands, we used meta-analyses to examine biodiversity and open pine focal species responses to 5 stand establishment intensities and 4 mid-rotation practices (prescribed fire, selective herbicide, fire and herbicide combination, and thinning). We calculated 1742 biodiversity and 169 open pine focal species effect sizes from 42 publications of manipulative studies at 14 unique study sites in managed loblolly pine (*P. taeda* L.) forests in the Atlantic and Gulf Coastal Plains of the southeastern U.S. We quantified diversity and abundance responses by taxa and management practices for vegetation, birds, amphibians, reptiles, small mammals, and invertebrates. Diversity and abundance responses generally decreased as stand establishment intensity increased, but those reductions appeared to be short-term (<3 years). Birds and open pine focal species responded positively to chemical stand establishment relative to a mechanically-prepared control. Thinning elicited positive diversity and abundance responses from reptiles and small mammals. Effects of prescribed fire, selective herbicide, and their combination on biodiversity responses varied by taxa (e.g., following fire, vegetative and avian diversity increased but amphibian and invertebrate diversity decreased). Further research is warranted on under-represented taxa (e.g., herpetofauna and invertebrates) in literature and long-term effects of forest management on biodiversity. Understanding how silvicultural management practices produce and maintain open pine forest conditions and influence biodiversity responses is necessary to inform opportunities for open-pine wildlife communities in working forested landscapes.

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1. Introduction

Pine (*Pinus* spp.) forests of the southeastern Coastal Plain were historically described as open pine woodlands and savannahs with low canopy coverage, variable tree age classes, and floristically rich understories that supported diverse wildlife communities

(Mitchell and Duncan, 2009; Van Lear et al., 2005). However, widespread fire suppression following European settlement transitioned many open pine communities to hardwood-encroached, closed-canopy forests followed by subsequent declines in many species of disturbance-adapted wildlife (Mitchell and Duncan, 2009).

Currently, open pine forests occur throughout the southeastern U.S. with most natural and planted pine forests held in private ownership (Oswalt et al., 2014), making them susceptible to fragmentation, parcelization, and land use conversion (Wear and

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Greis, 2012; Zhang and Polyakov, 2010). Connecting open pine forests and increasing area of open pine conditions across the region could benefit myriad open pine species and help meet conservation goals (Gulf Coastal Plains and Ozarks Landscape Conservation Cooperative, 2012). Working forest landscapes can provide open pine conditions during portions of a typical, 25–35 year rotation (e.g., Jones et al., 2009b). Because planted pine comprises approximately 19% (~15.8 million hectares; Wear and Greis, 2012) of forestland in the southeastern U.S., there is potential for it to provide substantial open pine conditions when appropriately managed. However, a comprehensive investigation of how well forest management practices achieve open pine structural and biodiversity conditions is lacking. Thus, there is a need to evaluate potential for managed pine systems to provide habitat conditions conducive to open pine-adapted species.

Managed pine systems provide a dynamic mosaic of vegetation structure and composition across landscapes, ranging from early successional communities following tree harvest, to canopy closure, to post-thin open stands. Managed pine forests receiving at least some mid-rotation management (e.g., thinning, herbicides, burning) can provide habitat for wildlife species adapted to and favoring open pine conditions by altering forest structure and plant community composition (e.g., Iglay et al., 2014b; Burger, 2005; Singleton et al., 2013; Wilson and Watts, 1999). In publications we reviewed, thinned stands receiving some mid-rotation management (e.g., prescribed fire and/or selective herbicide) had basal areas of 68–78 ft² ac⁻¹ (15.6–18.0 m² ha⁻¹; Smith, 2004; Ulyshen et al., 2012), limited midstory hardwood encroachment and shrub cover (Albaugh et al., 2012; Cain and Shelton, 2003; Sladek et al., 2008), and abundant ground cover by graminoids and forbs (Iglay et al., 2014b; Jones et al., 2009a) with total herbaceous understory coverage ranging from 55% under a thin-only regime (Miller et al., 2004) to 97.7% when prescribed fire follows thinning (Cain and Shelton, 2003). These values of stand structure in managed loblolly pine forests are consistent with pine and hardwood basal area values in old-growth longleaf pine (*P. palustris* Mill.) stands in Alabama and Mississippi (Kush and Meldahl, 2000, Schwarz 1907 as cited in Landers and Boyer, 1999). As managed stands transition from dense, closed-canopy conditions toward open woodland conditions following thinning, avian community composition also shifts toward open woodland and pine-grassland species (Iglay, 2010; Singleton et al., 2013), suggesting that commercially managed pine stands may provide conditions equivalent to open pine for at least part of typical rotations. In addition, young pine stands (2–6 years following establishment) provide early successional conditions, such as dense graminoid bunches, diverse forbs, and singing perches (Hanberry et al., 2013a; Jones et al., 2009a; Lane et al., 2011b), that are used by avian species associated with pine-grasslands (Lane et al., 2011a).

Herpetofauna and small mammal diversity, abundance, and activity have been correlated with changes in microhabitat features such as leaf litter depth, soil moisture, and vegetation structure (deMaynadier and Hunter, 1995; Schurbon and Fauth, 2003), and amount and distribution of coarse woody debris following forest management (Davis et al., 2010; Loeb, 1999; Owens et al., 2008; Riffell et al., 2011). However, few studies address responses of herpetofauna or small mammals to specific management activities with appropriate control stands and these studies have not been pooled for region-wide analysis and management recommendations.

To address our knowledge gap and cohesively examine results of multiple studies, we conducted a comprehensive meta-analysis to evaluate how a gradient of stand establishment practices (mechanical vs. chemical site preparation, banded vs. broadcast herbicide, and number of herbicide applications) and mid-rotation management (thinning, prescribed fire, selective herbicide, and fire and

herbicide combination) affect biodiversity (e.g., plants, birds, amphibians, reptiles, small mammals, invertebrates) and open pine focal species within managed loblolly pine (*P. taeda* L.) forests in the Atlantic and Gulf Coastal Plains of the southeastern U.S. We expected biodiversity responses to decrease as stand establishment intensity increased and for ground-nesting birds, herpetofauna, and small mammals to decrease in diversity and abundance in response to the most intense stand establishment practices (i.e., mechanical and chemical site preparation with broadcast herbicide for one or two years). Prescribed fire and thinning are frequently promoted to improve wildlife habitat quality (e.g., Sladek et al., 2008; Thompson, 2002; Wigley et al., 2000; Woodall, 2005), and thus, we expected their application to increase total biodiversity and the diversity and abundance of plants, birds, and small mammals. We expected herbicide to have similar effects as prescribed fire and their combination to have a somewhat additive effect.

2. Materials and methods

We conducted a systematic literature search for publications that compared biodiversity responses to various practices in managed forests. We restricted our literature search to managed, naturally regenerating or planted forests dominated by loblolly pine in the Atlantic and Gulf Coastal Plains due to similarities in management practices and physiographic characteristics (e.g., soil classification) across this region. We searched 11 databases including Wildlife and Ecology Studies Worldwide, USDA Forest Service Tree-search, and Google Scholar for relevant publications. Response variables of interest included diversity metrics (species richness, alpha diversity, and evenness) and abundance of taxa, guilds, and individual species for vegetation, birds, amphibians, reptiles, small mammals, and invertebrates. We searched titles, abstracts, and keywords using 189 combinations of search terms including forestry, biodiversity, taxa, and a list of open pine focal species (Table 1). We supplemented database searches by manually examining references cited in publications from our literature search.

Because responses to forest management can vary substantially among taxa, guilds, and species within a taxon, we considered different biodiversity metrics (e.g., richness, equitability, abundance) from the same publication to be independent effects (Bender et al., 1998; Riffell et al., 2011). We also separated effects by season to account for migration and seasonal differences in activity (Bender et al., 1998; Riffell et al., 2011). For publications presenting data for multiple years, we calculated mean effect and pooled variance across all years or for year subsets according to treatment application frequency (e.g., fire return interval). Most publications compared more than one treatment to the same control. To account for this lack of independence, we calculated cumulative effect sizes for each taxon across all manipulations and for each manipulation type (Borenstein et al., 2009). We contacted authors to obtain standard deviations or raw data to calculate statistics whenever unavailable in the published literature.

Several publications (e.g., Singleton et al., 2013) noted that mid-rotation management appeared to drive a shift in community composition toward species adapted to open canopy, pine-grassland conditions. This shift may occur concomitant to changes in diversity and abundance metrics. Therefore, we evaluated individual open pine wildlife species (Table 1) responses to stand establishment and mid-rotation manipulations using meta-analysis techniques identical to our biodiversity analyses.

We conducted all meta-analyses in MetaWin 2.0 (Rosenberg et al., 2000). We calculated effect sizes (i.e., values that reflect magnitude of a treatment effect) using means, standard deviations, and sample sizes for experimental and control groups. Meta-analyses used log response ratios as an effect size index with log response

Table 1

Open pine focal species included in literature search terms to understand effects of management actions during stand establishment and after thinning on biodiversity within intensively managed pine stands in the southeastern United States. Species with data included in meta-analysis are indicated by +. Source: Gulf Coastal Plains & Ozarks Landscape Conservation Cooperative (GCPO LCC) Integrated Science Agenda, Appendix 2: Representative Species Pool for Priority Systems of the GCPO LCC, Open Pine Woodland and Savanna.

Scientific name	Common name	Taxon
<i>Aimophila aestivalis</i> ⁺	Bachman's sparrow	Birds
<i>Ammodramus henslowii</i>	Henslow's sparrow	Birds
<i>Caprimulgus carolinensis</i>	Chuck-will's-widow	Birds
<i>Caprimulgus vociferous</i>	Whip-poor-will	Birds
<i>Coccyzus americanus</i> ⁺	Yellow-billed cuckoo	Birds
<i>Colinus virginianus</i> ⁺	Northern bobwhite	Birds
<i>Dendroica discolor</i> ⁺	Prairie warbler	Birds
<i>Dendroica dominica</i> ⁺	Yellow-throated warbler	Birds
<i>Dryocopus pileatus</i> ⁺	Pileated woodpecker	Birds
<i>Falco sparverius paulus</i>	Southeastern American kestrel	Birds
<i>Geococcyx californianus</i>	Greater roadrunner	Birds
<i>Grus canadensis pulla</i>	Mississippi sandhill crane	Birds
<i>Melanerpes erythrocephalus</i> ⁺	Red-headed woodpecker	Birds
<i>Meleagris gallopavo</i> ⁺	Wild turkey	Birds
<i>Picoides borealis</i>	Red-cockaded woodpecker	Birds
<i>Picoides villosus</i> ⁺	Hairy woodpecker	Birds
<i>Pipilo erythrophthalmus</i> ⁺	Eastern towhee	Birds
<i>Sitta pusilla</i> ⁺	Brown-headed nuthatch	Birds
<i>Geomys pinetis</i>	Southeastern pocket gopher	Mammals
<i>Crotalus adamanteus</i>	Eastern diamondback rattlesnake	Reptiles
<i>Gopherus polyphemus</i>	Gopher tortoise	Reptiles
<i>Pituophis melanoleucus</i>	Northern pine snake	Reptiles
<i>Pituophis ruthveni</i>	Louisiana pine snake	Reptiles

ratio being a mean outcome in experimental versus control groups (Hedges et al., 1999). For stand establishment meta-analyses, we used mechanically-prepared sites as the control, the least intensive manipulation consistently used and often designated as a “control” for included publications. For mid-rotation manipulations (e.g., prescribed fire, selective herbicide, prescribed fire and selective herbicide in combination, and thinning), we used the untreated forest stand as the control. Response ratios were centered on 1.00 (e.g., negative treatment responses < 1.00). We used bias-corrected bootstrap confidence intervals (alpha = 0.05, iterations = 999) and considered responses significant if confidence intervals did not include 1.00. Because large studies with significant results may be published more often than small studies with non-significant results, we used graphical techniques (i.e., weighted histogram, funnel plot, normal quantile plot) and formal statistical tests (i.e., fail-safe numbers) to assess how our results may be affected by publication bias, missing non-significant studies, and small sample sizes. We used Rosenberg's (2005) method for calculating fail-safe numbers, the number of non-significant, unpublished, or missing studies that would need to be added to meta-analysis in order to change significant meta-analysis results to non-significance. In some cases, very few effect sizes (*n*) and publications (*k*) were available to assess effects of one or more manipulations on a particular taxon. We report meta-analysis results for these sub-groups despite small sample sizes because meta-analysis provides superior quantitative estimates than other summary methods, but results should be treated with caution (Bender et al., 1998; Borenstein et al., 2009).

Due to the great number of effect sizes for avian species, we conducted additional analyses for avian guilds. Therefore, we assigned species to nesting (Hamel, 1992), migratory (Texas Parks and Wildlife, 2015), and Conservation Priority Score (Beissinger et al., 2000) guilds. We calculated Conservation Priority Scores based on regional population trend, regional threats to breeding, and global breeding distribution using data from Partners in Flight following Nuttle et al. (2003). We had guild

assignment externally reviewed by two open pine avian taxa specialists working in the southeastern Coastal Plains.

3. Results

3.1. General results

We found 42 of 47 relevant publications (*k*) on 14 study sites suitable for meta-analyses (provided means, standard deviations, and sample sizes) with the following experimental manipulations: prescribed fire (“fire”), selective herbicide (“herbicide,” typically imazapyr), prescribed fire and selective herbicide (“fire + herbicide”), thinning, and five stand establishment intensities [(1) chemical with banded herbicide, (2) mechanical with broadcast herbicide, (3) combination of mechanical and chemical with 1-year banded herbicide, (4) 1-year broadcast herbicide, and (5) 1-year and 2-year broadcast herbicide applications]. We included 21 peer-reviewed publications and 21 thesis/dissertation chapters not published elsewhere. These 42 publications provided 1742 biodiversity effect sizes: 322 diversity, 178 total abundance, and 1242 individual species responses (Table 2). Of individual species responses, we used 1011 effect sizes from 10 publications for avian guild meta-analyses, and we used 169 effect sizes from 11 publications for meta-analyses of 11 open pine focal bird species (Table 1). Publications generally followed biodiversity responses for fewer than 4 years following stand establishment or mid-rotation manipulation. Notable exceptions include Hanberry (2007) (6 years) and Lane (2010) (8 years) at stand establishment and Iglay (2010) (9 years with 3-year fire return interval) at mid-rotation.

As stand establishment intensity increased relative to a mechanical control, there was a general decline in total biodiversity and the diversity and abundance of all taxa and most avian guilds (Table 3). However, birds and open pine focal species responded positively to chemical stand establishment relative to a mechanically-prepared control for all biodiversity metrics. Effects of mid-rotation management varied by taxa and manipulation (Table 4). Thinning elicited positive diversity and abundance responses from reptiles and small mammals (Fig. 1). Plants, birds, and focal species had positive and neutral responses to fire, herbicide, and fire + herbicide, but amphibians, reptiles, and invertebrates generally had negative responses. We expected fire and herbicide to have an additive effect when combined, but insufficient sample sizes prevented a direct test of our hypothesis.

When we evaluated data for publication bias, we found that a relatively large number (i.e., at least $5 \times (\text{number of studies}) + 10$; Rosenberg, 2005) of non-significant, unpublished, or missing studies would need to be added to our meta-analysis to change our significant results to non-significance even when the alpha-level was reduced from 0.05 to 0.01. However, meta-analysis subgroups that had few effect sizes and studies (e.g., effect of thinning on small mammals) did not pass the fail-safe number test and results for these subgroups should be treated with caution as they could be unduly influenced by additional studies.

3.2. Vegetation responses

We found 75 vegetation responses (effect sizes) from 5 stand establishment publications (4 study sites; Table 3) and 79 responses from 7 publications involving mid-rotation manipulations (3 study sites; Table 4). Most studies measured plant diversity for two to five years following management (e.g., Miller and Chamberlain, 2008). Plant diversity decreased with increasing stand establishment intensity, but total abundance (e.g., stem counts) increased following chemical stand establishment. Plant diversity increased following fire. Although not significant, fire

Table 2

Summary of publications used for meta-analysis of effects of forest management on biodiversity in managed loblolly pine forests within the southeastern United States. Distinction is made for publications that analyzed amphibians and reptiles separately or together (“herpetofauna”).

Publication	Location	Taxa	Effect sizes ^a
Burke et al. (2008); see also Burke (2006) ^b	Louisiana	Invertebrates	0, 4, 0
Campbell (2011) ^b	Mississippi	Birds, vegetation	48, 4, 0
Carroll (2004) ^b	Mississippi	Amphibians, reptiles, small mammals	42, 21, 102
Chritton (1988) ^b	Texas	Birds, vegetation	6, 2, 0
Darden et al. (1990); see also Darden (1980) ^{b,c}	Mississippi	Birds	8, 0, 0
Duda (2003) ^b	Louisiana	Birds	3, 3, 0
Edwards (2004); see also Edwards et al. 2004; Jones et al. 2009a ^b	Mississippi	Small mammals	4, 4, 20
Hanberry (2005) ^b	Mississippi	Birds	12, 4, 304 ⁺
Hanberry (2007); see also Hanberry et al. (2012, 2013a, 2013b) ^b	Mississippi	Birds, small mammals	12, 11, 389 ⁺
Hawkes (1995) ^b	South Carolina	Invertebrates	0, 2, 8
Hood (2001); see also Hood et al. (2002) ^b	Mississippi	Herpetofauna, small mammals	23, 15, 48
Igley (2008) ^b	Mississippi	Invertebrates	6, 52, 17
Igley (2010); see also Igley et al. (2010, 2012a, 2012b, 2014a, 2014b) ^b	Mississippi	Birds, herpetofauna, invertebrates, small mammals, vegetation	71, 9, 138 ⁺
Lane (2010); see also Lane et al. (2011a, 2011b, 2013) ^b	North Carolina	Birds, small mammals, vegetation	21, 6, 0
Mihalco (2004) ^b	North Carolina	Birds, small mammals, vegetation	24, 12, 63
Miller and Chamberlain (2008) ^b	Louisiana	Vegetation	2, 6, 5
Mitchell (1992); see also Mitchell et al. (1995) ^b	North Carolina	Small mammals	3, 0, 0
O’Connell and Miller (1994) ^b	South Carolina	Birds, small mammals, vegetation	10, 3, 9
Schaeffbauer (2000) ^b	Georgia	Birds	0, 8, 16 ⁺
Singleton (2008); see also Singleton et al. (2013) ^b	Mississippi	Birds, vegetation	1, 1, 50 ⁺
Sladek (2006); see also Sladek et al. (2006, 2008) ^b	Mississippi	Birds	1, 1, 41 ⁺
Sutton (2010); see also Sutton et al. (2013, 2014) ^d	Alabama	Amphibians, reptiles	0, 5, 40
Thompson (2002) ^b	Mississippi	Birds, vegetation	18, 6, 210 ⁺
Woodall (2005) ^b	Mississippi	Birds, vegetation	15, 3, 105 ⁺

^a Effect sizes: diversity, taxon/guild abundance, species abundance.

^b Forest type: Loblolly plantation.

^c Forest type: Loblolly-shortleaf forest.

^d Forest type: Loblolly-hardwood forest.

⁺ Species abundance includes open pine focal species.

+ herbicide and herbicide subgroups had more negative response ratios than fire alone.

3.3. Bird responses

Bird publications accounted for 40% of our search results. We found 611 bird responses from 8 publications involving stand establishment (3 study sites; Table 3) and 554 responses from 10 publications involving mid-rotation manipulations (6 and 3 study sites for bird and guild analyses, respectively; Table 4). Species

abundance and guild responses were based on 65 species. Bird diversity, total abundance, and species abundance increased following chemical site preparation with 1-year banded herbicide relative to mechanical site preparation, but all responses declined as stand establishment intensified (Table 3). Bird guild responses to stand establishment also had an inverse relationship between abundance and management intensity, but magnitude of responses differed among guilds. Birds associated with open canopy conditions declined more severely than closed canopy species as stand establishment intensity increased. Ground-shrub nesters exhibited greatest declines in abundance following mechanical + chemical preparation with one and two years of broadcast herbicide (Fig. 2). Neotropical migrant abundance had a greater negative response than resident and short-distance migrant species based on migratory guild response ratios. However, we did not directly test (e.g., pairwise comparisons) differences between guild members (e.g., neotropical vs. short-distance migrants). Cavity nesters and Conservation Priority Score 4 (high concern) guilds were the only guilds without a negative response to the most intense management. Two species [loggerhead shrike (*Lanius ludovicianus*) and common ground dove (*Columbina passerina*)] were within the Conservation Priority Score 4 guild.

Bird diversity, total bird abundance, and species abundance had positive and neutral responses to mid-rotation fire, fire + herbicide, and herbicide (Table 4). Ground-shrub (response ratio [RR] = 1.13), tree (RR = 1.02), and cavity (RR = 1.01) nesters had increased abundance following fire + herbicide. Indigo bunting (*Passerina cyanea*) increased in abundance following thinning, but eastern towhee (*Pipilo erythrophthalmus*) and cavity nesters decreased.

We calculated 72 effect sizes from 4 stand establishment publications and 97 effect sizes from 7 mid-rotation publications (on 2 and 3 study sites, respectively) for open pine focal bird species. Responses of focal bird species to stand establishment were similar to bird responses in the overall biodiversity meta-analysis. Open pine focal birds responded positively to chemical stand establishment compared to a mechanical control and responded negatively to more intense establishment manipulations (Fig. 3). Focal birds had slightly greater abundance following fire + herbicide and herbicide applications. Focal bird species abundance had a non-significant response ratio for the thinning subgroup, but only 4 effect sizes for eastern towhee and pine warbler (*Setophaga pinus*) responses to thinning were available.

3.4. Herpetofauna response

We found 5 publications on 2 study sites involving herpetofauna responses to mid-rotation manipulations and no publications for stand establishment. Of the 108 herpetofauna responses, 42 were amphibians, 51 reptiles, and 15 combined all herpetofauna. Amphibians responded negatively to fire, fire + herbicide, and herbicide for almost all biodiversity metrics (Table 3). Reptile diversity decreased in response to fire + herbicide, but reptiles exhibited neutral responses to independent fire or herbicide applications. Reptile abundance increased in response to thinning when we considered total species and individual species abundance (Fig. 2). Combined herpetofauna data reflected decreased diversity in response to fire + herbicide and increased total and species abundance in response to thinning (Table 3). Few effect sizes were available for evaluating effect of mid-rotation manipulations on amphibian and reptile total abundance, and results may be biased toward site-specific conditions of the included publications.

3.5. Small mammal response

We found 72 responses from 4 publications on 3 study sites involving small mammal responses to stand establishment.

Table 3
Summary response ratios from meta-analysis of the effects of stand establishment in loblolly pine forests on biodiversity by taxa and manipulation type. Stand establishment intensities as follows: chemical with 1-year banded herbicide (1), mechanical with 1-year broadcast herbicide (2), and mechanical and chemical with 1-year banded herbicide (3), 1-year broadcast herbicide (4), or 2-year broadcast herbicide (5). Mechanically-prepared stands with 1-year banded herbicide were used as the control plots.

	Stand establishment intensity					All establishment manipulations
	1	2	3	4	5	
<i>Vegetation</i>						
Diversity	0.95 ^a (n = 16)	0.95 ^a (n = 9)	0.87 ^a (n = 19)	0.87 ^a (n = 18)	0.87 ^a (n = 10)	0.91 ^a (n = 73)
Abundance	1.21 ^a (n = 2)	– (n = 0)	– (n = 0)	– (n = 0)	– (n = 0)	1.21 ^a (n = 2)
Species	– k = 2	– k = 2	– k = 3	– k = 3	– k = 1	– k = 5
<i>Birds</i>						
Diversity	1.23 ^a (n = 14)	0.95 ^a (n = 3)	0.95 ^a (n = 10)	0.87 ^a (n = 10)	0.73 ^a (n = 7)	0.97 ^a (n = 44)
Abundance	1.41 ^a (n = 5)	0.93 ^a (n = 6)	0.87 ^a (n = 10)	0.88 ^a (n = 10)	0.64 ^a (n = 4)	0.90 ^a (n = 34)
Species	1.22 ^a (n = 155) k = 6	1.00 ^a (n = 16) k = 2	0.99 ^a (n = 127) k = 6	0.97 ^a (n = 127) k = 6	0.85 ^a (n = 127) k = 4	1.00 ^a (n = 533) k = 8
<i>Small mammals</i>						
Diversity	0.87 ^a (n = 3)	0.86 ^a (n = 3)	0.86 ^a (n = 5)	0.73 ^a (n = 5)	0.83 ^a (n = 2)	0.83 ^a (n = 18)
Abundance	0.90 ^a (n = 2)	– (n = 0)	0.90 ^a (n = 2)	– (n = 0)	0.82 ^a (n = 2)	0.87 ^a (n = 6)
Species	1.00 ^a (n = 14) k = 3	– (n = 0) k = 2	0.93 ^a (n = 11) k = 4	0.99 ^a (n = 12) k = 4	0.85 ^a (n = 11) k = 2	0.96 ^a (n = 48) k = 4
<i>All taxa</i>						
Diversity	1.05 ^a (n = 33)	0.93 ^a (n = 15)	0.92 ^a (n = 33)	0.86 ^a (n = 34)	0.81 ^a (n = 19)	0.92 ^a (n = 135)
Abundance	1.26 ^a (n = 9)	0.93 ^a (n = 6)	0.87 ^a (n = 12)	0.87 ^a (n = 10)	0.70 ^a (n = 6)	0.90 ^a (n = 44)
Species	1.20 ^a (n = 169) k = 8	1.00 ^a (n = 16) k = 6	0.99 ^a (n = 138) k = 13	0.96 ^a (n = 139) k = 13	0.85 ^a (n = 118) k = 7	1.00 ^a (n = 580) k = 15

n = number of effect sizes; k = number of publications;

^a Bootstrap confidence interval does not include 1.00.

Although response measurements ranged from 3 to 8 years post-establishment, effect sizes were skewed toward responses in the first 3–4 years following initial site preparation. Small mammal diversity and total abundance decreased as stand establishment intensity increased relative to mechanical site preparation (Table 3), but unlike birds, no intensity of stand establishment generated a positive small mammal response.

We found 151 small mammal responses from 4 publications on 2 study sites involving mid-rotation manipulations (Table 4). Captures were dominated by hispid cotton rat (*Sigmodon hispidus*), *Peromyscus* spp., house mouse (*Mus musculus*), and golden mouse (*Ochrotomys nuttalli*). Abundance slightly decreased following herbicide application, but the response ratio indicated that differences between managed and control stands were negligible. Small mammal diversity increased in response to thinning, but results were based on a single publication (Fig. 2). Most publications of small mammal responses to mid-rotation management were limited to the first two years post-application (Carroll, 2004; Hood et al., 2002; Mitchell et al., 1995), and thus, they were unable to assess effects of repeated disturbances from mid-rotation to harvest. However, continued surveys of stands used in Hood et al. (2002) and Carroll (2004) did not find persistent effects from repeated disturbances, indicating that small mammal responses may be short-term (Iglay, 2010).

3.6. Invertebrate response

We found 89 invertebrate responses from 3 publications on 3 study sites involving mid-rotation manipulations (Table 4) and no stand establishment publications. Invertebrate diversity decreased in response to fire, fire + herbicide, and herbicide. Species abundance decreased following fire + herbicide, but increased following herbicide alone.

4. Discussion

Meta-analyses revealed potential for intensively managed forests to maintain biodiversity and promote open-pine and pine-grassland associated avian species among stand rotation combinations of low to moderate intensity stand establishment practices and mid-rotation thinning followed by fire with or without herbicide. Vegetation, bird, and small mammal responses were positive and neutral to all mid-rotation practices. Minimal and negative responses of most herpetofauna and invertebrates may be a function of limited vagility, behavioral responses to habitat alteration, or small sample sizes. Small sample sizes for herpetofauna and invertebrates makes any meta-analysis of responses to vegetation structure or management susceptible to bias. However,

Table 4

Summary response ratios from meta-analysis of the effects of mid-rotation manipulations in loblolly pine forests on biodiversity by taxa and manipulation type. Mid-rotation manipulations include prescribed fire ("fire"), selective herbicide ("herbicide"), combination of fire and herbicide ("fire + herbicide"), and thinning.

	Fire	Fire + herbicide	Herbicide	Thinning	All manipulations
<i>Vegetation</i>					
Diversity	1.18 ^a (n = 21)	1.04 (n = 24)	0.96 (n = 22)	– (n = 0)	1.06 ^a (n = 68)
Abundance	– (n = 0)	0.96 (n = 6)	– (n = 0)	– (n = 0)	0.96 (n = 6)
Species	– (n = 0)	0.64 (n = 5)	– (n = 0)	– (n = 0)	0.64 (n = 5)
	k = 6	k = 7	k = 5	k = 0	k = 7
<i>Birds</i>					
Diversity	1.02 ^a (n = 15)	1.02 (n = 12)	1.03 (n = 12)	– (n = 0)	1.02 (n = 39)
Abundance	1.06 ^a (n = 6)	1.12 ^a (n = 7)	1.11 (n = 7)	0.98 (n = 8)	1.07 ^a (n = 28)
Species	1.00 (n = 137)	1.01 (n = 197)	1.00 (n = 137)	1.00 (n = 16)	1.00 (n = 487)
	k = 5	k = 6	k = 4	k = 2	k = 10
<i>Amphibians</i>					
Diversity	0.93 ^a (n = 4)	0.96 ^a (n = 4)	0.93 ^a (n = 4)	– (n = 0)	0.94 ^a (n = 12)
Abundance	0.94 ^a (n = 2)	0.97 ^a (n = 2)	0.94 ^a (n = 2)	– (n = 0)	0.95 ^a (n = 6)
Species	0.97 (n = 8)	0.97 (n = 6)	0.96 ^a (n = 6)	1.31 (n = 4)	0.97 (n = 24)
	k = 3	k = 2	k = 2	k = 1	k = 3
<i>Reptiles</i>					
Diversity	1.04 (n = 4)	0.95 ^a (n = 4)	1.02 (n = 4)	– (n = 0)	1.00 (n = 12)
Abundance	0.96 (n = 3)	0.99 (n = 2)	1.01 (n = 2)	1.78 ^a (n = 2)	1.02 (n = 9)
Species	0.97 (n = 10)	0.98 (n = 4)	0.99 ^a (n = 4)	1.53 ^a (n = 12)	0.99 (n = 30)
	k = 4	k = 2	k = 2	k = 2	k = 4
<i>All herpetofauna</i>					
Diversity	1.00 (n = 11)	0.95 ^a (n = 11)	0.98 (n = 11)	– (n = 0)	0.98 (n = 33)
Abundance	1.00 (n = 7)	1.01 (n = 6)	1.01 (n = 6)	1.78 ^a (n = 2)	1.01 (n = 21)
Species	0.98 (n = 18)	0.97 (n = 10)	0.98 ^a (n = 10)	1.48 ^a (n = 16)	0.98 ^a (n = 54)
	k = 8	k = 5	k = 5	k = 3	k = 5
<i>Small mammals</i>					
Diversity	0.96 (n = 13)	0.99 (n = 12)	0.98 (n = 12)	1.30 ^a (n = 3)	1.02 (n = 40)
Abundance	1.00 (n = 9)	1.01 (n = 6)	0.98 ^a (n = 6)	– (n = 0)	1.00 (n = 21)
Species	0.99 (n = 33)	1.00 (n = 31)	1.00 (n = 27)	– (n = 0)	1.00 (n = 91)
	k = 3	k = 3	k = 3	k = 1	k = 4
<i>Invertebrates</i>					
Diversity	0.91 ^a (n = 2)	0.81 (n = 2) ^a	0.91 ^a (n = 2)	– (n = 0)	0.88 ^a (n = 6)
Abundance	1.00 (n = 20)	1.01 (n = 19)	1.01 (n = 19)	– (n = 0)	1.01 (n = 58)
Species	0.98 (n = 6)	0.96 (n = 5) ^a	1.04 ^a (n = 14)	– (n = 0)	1.01 (n = 25)
	k = 3	k = 3	k = 3	k = 0	k = 3
<i>All taxa</i>					
Diversity	1.05 ^a (n = 64)	1.01 (n = 61)	0.98 (n = 59)	1.30 ^a (n = 3)	1.02 (n = 187)
Abundance	1.00 (n = 42)	1.02 (n = 44)	1.02 (n = 38)	1.05 (n = 10)	1.01 ^a (n = 134)
Species	1.00 (n = 194)	1.01 (n = 248)	1.00 (n = 188)	1.02 (n = 32)	1.00 (n = 662)
	k = 22	k = 22	k = 18	k = 5	k = 30

n = number of effect sizes; k = number of publications;

^a Bootstrap confidence interval does not include 1.00.

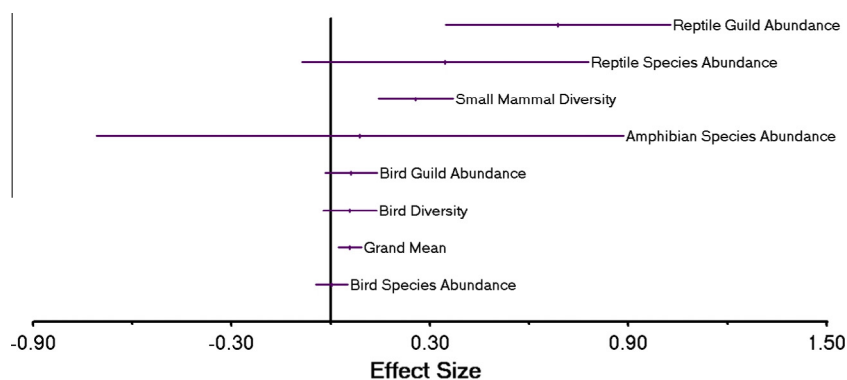


Fig. 1. Effects of thinning on biodiversity: mean effect sizes and 95% bootstrap confidence intervals. Grand mean is the effect of thinning on all biodiversity metrics and taxa.

Graeter et al. (2008) found contrasting movement patterns, habitat selection, and responses to short-term environmental cues among three pond-breeding amphibians in managed pine forests,

suggesting that some herpetofauna may not move into suitable open pine conditions due to habitat permeability constraints. Therefore, spatial distribution of open-canopy conditions in

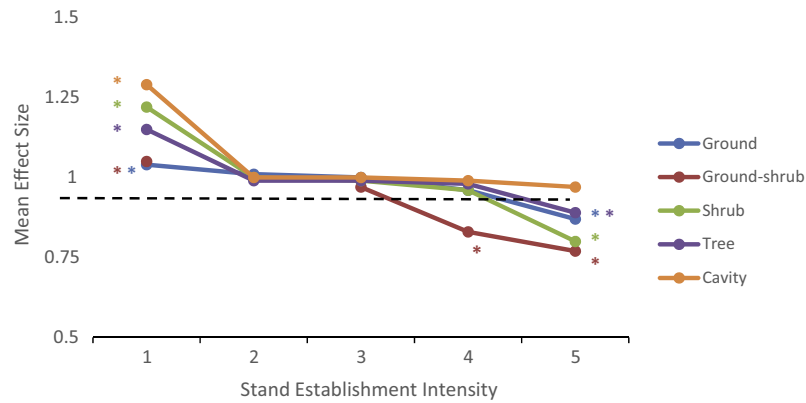


Fig. 2. Effect of stand establishment intensity on abundance by avian nesting guild. Stand establishment intensities range from 1 (chemical site preparation; least intense) to 5 (mechanical and chemical site preparation with two broadcast herbicide applications; most intense). Asterisks denote significant response ratios (confidence intervals do not include 1.00).

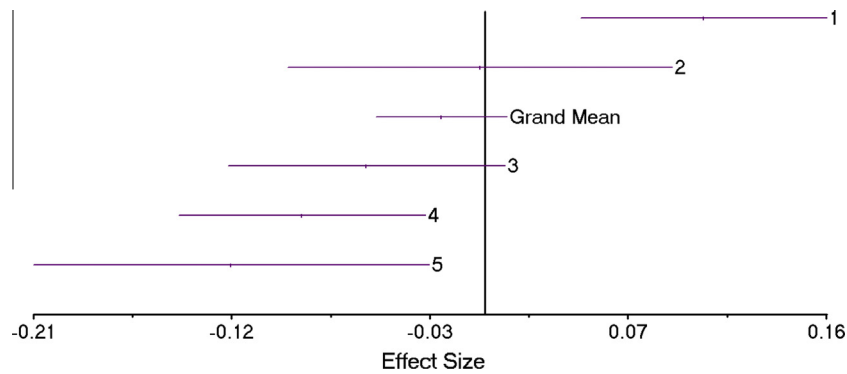


Fig. 3. Effect of stand establishment intensity on open pine focal species abundance (birds): mean effect sizes and 95% bootstrap confidence intervals. Stand establishment intensities range from 1 (chemical site preparation with 1-year banded herbicide; least intense) to 5 (mechanical and chemical site preparation with 2-year broadcast herbicide applications; most intense). Grand mean is the mean effect of all stand establishment intensities on open pine focal bird abundance.

managed pine landscapes warrants investigation, as aggregating open-pine conditions may have benefits for associated species that are less mobile or area-sensitive. If open pine acreage increased throughout the southeastern U.S., by applying some of the practices herein, connectivity would possibly begin to facilitate dispersal of some open pine and less mobile species.

Stand establishment intensity is a primary influence on wildlife responses in regenerating stands (Iglay et al., 2012b; Lane et al., 2013; Mihalco, 2004). Plant and small mammal diversity, richness, and abundance have been found to be greater in mechanically-prepared stands than in stands receiving more intense site preparation in combination with herbaceous weed control (Lane et al., 2011b, Mihalco 2004). Many studies have documented short-term reductions in plant and small mammal diversity and abundance following chemical stand establishment, but negative effects associated with establishment practices usually disappear within the first five years post-establishment (Keyser et al., 2003; Lane et al., 2013; O'Connell and Miller, 1994). We were unable to investigate temporal variation in our responses due to assumptions imposed by our meta-analysis (Borenstein et al., 2009). However, a repeated measures design could differentiate responses across years since establishment if data were available.

Thinning, the initial step toward mid-rotation open pine, can positively affect biodiversity. Thinning reduces canopy coverage allowing more sunlight to reach the forest floor and influence understory vegetation (Peitz et al., 2001), increase basking sites and facilitate changes in soil surface temperatures benefitting reptiles (Russell et al., 2002), and promote general changes in

vegetation structure, attracting bird species such as indigo buntings, pine warblers, and brown-headed nuthatches (Chritton, 1988; Wilson and Watts, 1999). Although our meta-analysis detected positive and neutral biodiversity responses to thinning, few studies were available comparing thinned and unthinned stands without confounding factors (e.g., stand age). We were unable to differentiate effects of thinning intensity or changes in wildlife communities over time since thinning. Information regarding these responses could help develop future recommendations among a range of thinning intensities and timing of mid-rotation management (e.g., 1–2, 3–4, or 5–6 years after thinning).

Prescribed fire with or without herbicide during mid-rotation generally elicited positive effects on vegetation and bird communities. Fire has been shown to promote increased understory plant diversity in southeastern pine forests (e.g., Masters et al., 1993; Sparks et al., 1998; Thomas et al., 1999). Using herbicide with fire has resulted in mixed results varying from short-term (<3 years) depressions in herbaceous richness (Blake et al., 1987; Guynn et al., 2004) to short-term increases in species richness (Iglay et al., 2014b; Jones and Chamberlain, 2004; Woodall, 2005). Herbicide type and application rates play key roles in plant community response sometimes favoring community dominance of herbicide-tolerant species (Iglay et al., 2010). However, well-established hardwood competition may resist prescribed fire, eliciting the need for a one-time herbicide application targeting woody vegetation (e.g., imazapyric active ingredient; Edwards et al., 2004; Iglay et al., 2014b; Mixon et al., 2009; Welch et al., 2004).

Prescribed fire and selective herbicide can improve habitat quality in intensively managed pine stands for many wildlife species (Sladek et al., 2008; Thompson, 2002; Wigley et al., 2000; Woodall, 2005), including conditions for pine–grassland birds in decline such as Bachman's sparrow (*Aimophila aestivalis*), brown-headed nuthatch, and northern bobwhite (*Colinus virginianus*; Burger et al., 1998; Masters et al., 2001; Singleton et al., 2013), as represented by greater bird diversity and abundance of ground nesting birds. However, prescribed fire's effects on soil moisture and temperature, vegetation structure, leaf-litter depth, wetland hydroperiod, and refugia can have short-term negative effects on some herpetofaunal species (Grant et al., 1994; Schurbon and Fauth, 2003), as seen by variable responses between reptiles and amphibians in our meta-analysis. Many invertebrates included in this meta-analysis (e.g., Iglay et al., 2012a) were forest-associated species that preferred moist to wet soil typical of closed-canopy forests (Laroche and Larvière, 2003). Hence, drier soils immediately following fire and resultant open conditions may not provide suitable habitat conditions for current inhabitants, potentially leading to hydrophilic invertebrates' avoiding treated stands (Iglay et al., 2012a). However, open forest and pyrophilic herpetofauna and invertebrate species could be attracted to open pine conditions as area of open pine conditions increases across a landscape and long-range migrants begin to colonize an area (for invertebrates: Holliday 1991a, 1991b; Spence and Niemela, 1994). Ultimately, direct and indirect effects of specific burn regimes on less studied taxa such as herpetofauna and invertebrates require more research considering our current lack of understanding and mixed responses in the literature documented (e.g., positive, deleterious, and neutral herpetofaunal responses to burning with and without herbicide; Jones et al., 2000; Langford et al., 2007; Perry et al., 2012, 2009; Sutton et al., 2013).

5. Management implications

Using one-time banded herbicide applications for herbaceous weed control subsequent to chemical and/or mechanical site preparation can enhance conditions for some plant and animal species associated with open pine forests, at least for the short-term. Negative relationships between short-term effects of stand establishment intensity and avian biodiversity are well documented (Hanberry et al., 2012; Iglay et al., 2012b, Lane et al., 2011a,b), and our results suggest that open pine focal birds may decline more rapidly than closed-canopy forest interior and forest edge species as stand establishment intensity increases. However, selection of management intensity is influenced by many factors such as site-specific edaphic and vegetation conditions, and economic objectives of landowners (Jones et al., 2010).

Prescribed fire is a cost-effective conservation tool for managers interested in promoting an herbaceous understory that supports myriad wildlife from multiple taxa. Coupled applications of prescribed fire and herbicide appear most effective at increasing overall avian biodiversity and promoting open pine focal species. However, application of prescribed fire can be difficult or infeasible in many locations due to smoke management and proximity to urban/suburban areas, necessitating herbicide use to suppress hardwood encroachment and maintain biodiversity similarly to fire (Iglay et al., 2014b; Liechty and Fristoe, 2013; Oswald et al., 2009). While fire and herbicide applications promote open pine avian species, there may be unknown trade-offs with other guilds and taxa, emphasizing the need for long-term monitoring to ascertain impacts to various taxa and the supporting stand structure. If maintaining herpetofaunal diversity is the goal of management, a matrix of thinned, burned and thinned, and burned stands with riparian zones, wetland buffers, and unharvested pine stands

(e.g., Baughman, 2000) would create a variety of conditions suitable to reptiles of differing thermal requirements and pool-breeding amphibians (Perry et al., 2012, 2009; Sutton et al., 2013). Intense stand establishment practices can temporarily reduce habitat quality for some species, but several studies note increased habitat suitability and a return of many species within the first three years after management. Managers can meet conservation goals by using a range of stand establishment practices across landscapes and creating refugia in buffered riparian zones and adjacent stands that are not concurrently undergoing manipulation (e.g., fire, herbicide, thinning).

6. Summary and conclusions

Investigating biodiversity responses to common stand-establishment and mid-rotation management using meta-analysis supported past research observations of variable effects but raised numerous questions. Less intensive stand establishment practices (e.g., chemical or mechanical site preparation compared to their combination with or without subsequent broadcast herbicide release) had short-term benefits for many species associated with open-pine forests. Mid-rotation applications of fire, herbicide, fire + herbicide, and thinning elicit species-specific responses from positive to negative. However, a literature library saturated by bird and plant responses inevitably introduces bias when attempting to illuminate causal relationships between forest management techniques and biodiversity responses. Additionally, few studies examined effects of the actual thinning process as most were conducted after thinning had taken place. Others have documented value of thinning for a number of taxa including bats (Elmore et al., 2005; Humes et al., 1999), birds (Verschuyl et al., 2011; Wilson and Watts 1999), and small mammals (Verschuyl et al., 2011).

Additional research on taxa such as herpetofauna, small mammals, and invertebrates will expand understanding of biodiversity responses to forest management. Managed pine forests have demonstrable conservation potential but realizing their full potential requires coordinated efforts to establish relationships between forest conditions and species assemblages and to maintain suitable conditions across the landscape. Meanwhile, long-term studies executed at an operational scale are needed to understand persistent effects of repeated disturbances and biodiversity fluctuations over entire rotations among multiple taxa.

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