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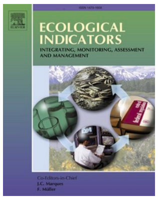

Original Articles

Disparate patterns of taxonomic and functional predator diversity under different forest management regimes

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ABSTRACT

Anthropogenic activities can alter natural disturbance regimes in ecosystems, and thereby affect the structure and function of biological diversity. As many of the world's ecosystems are degraded beyond natural recovery, well-defined restoration goals are necessary to maintain the ecological processes that provide valuable ecosystem services. Utilizing both taxonomic and functional approaches, we investigate the impacts of forest management practices in structuring predator communities in pine forest ecosystems under different forest management regimes. We focus on snakes as an indicator taxon, across pine forest systems in eastern Texas characterized by forest management practice frequency. Specifically, we investigate the responses of snake assemblages in the context of restoration efforts, comparing and contrasting these responses between high practice frequency (i.e., short burn intervals and thinning) and low practice frequency treatments (i.e., long burn intervals and no thinning). Taxonomic diversity was greater in the high-frequency treatment than in the low-frequency treatment, while functional diversity was similar between treatments. Functional redundancy was observed to increase with increasing forest management practice frequency, despite differences in taxonomic diversity and community-weighted means of traits between predator assemblages in each treatment. Consequently, increased frequency of prescribed fires and thinning operations may lead to greater stability and resilience in pine-forest ecosystems. Our study contributes to the understanding of how anthropogenic disturbances influence community organization in terrestrial ecosystems. Furthermore, this study reveals the importance of ecological restoration as a tool in disturbance prone ecosystems, and highlights importance of incorporating a multi-dimensional approach to meet desired restoration goals and ensure the health of forest ecosystems.

1. Introduction

Anthropogenic impacts are drastically modifying environments, affecting the structure and function of biological diversity in ecosystems across the globe (Hansen et al., 2012; Hautier et al., 2015; Newbold et al., 2015, 2016). Biodiversity is linked to the stability of ecosystems under the premise that functional complementarity among different species in an ecosystem can buffer the effects of environmental change (Hooper et al., 2012; Ives and Carpenter 2007). However, understanding the potential outcomes of diversity/stability relationships is still limited in natural systems under persistent human influences such as those influenced by forest management practices (Ives and Carpenter, 2007; Loreau et al., 2002; McCann, 2000).

Persistent anthropogenic impacts can have substantial effects on the resilience of ecological communities and the stability of ecosystems (Mori et al., 2013). As such, disturbance regimes play a crucial role in structuring ecosystems because variations in disturbance type(s), size, season, severity, frequency, intensity, and duration act on multiple spatial and temporal scales (Newman, 2019; Pickett and White, 2013). Many fire-climax ecosystems have adapted dependence on natural fire regimes, as successional stages are maintained through these disturbance-mediated processes (Vale 2013). Alterations to fire regimes can have a substantial impact on vegetative heterogeneity and resource availability, and habitats and associated ecological communities are expected to respond in different ways across disturbance gradients (Miller et al., 2011). For example, many studies have described significant species loss and subsequent community disassembly of vegetative communities following anthropic promotion or interruption of fire regimes (Buisson et al., 2019; Brudvig and Damschen 2011; Diaz-Toribio et al., 2020). These modifications to the composition and structure of

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vegetative habitats may alter habitat quality for associated consumers, leading to the loss of ecosystem function and decreased secondary productivity (Bihn et al., 2010; Micheli and Halpern, 2005; Petchey and Gaston, 2002, 2006).

In pine forest ecosystems of the southern United States, high demands for timber production, in addition to fluctuations in land ownership and increased urbanization, have resulted in substantial alterations to disturbance regimes, mainly through the suppression of natural and anthropogenic fires (Fox et al., 2007; Frost, 1993; Vale, 2013). Such dramatic changes from historic conditions has been shown to have had adverse effects on regional biodiversity and the provision of a broad range of valuable ecosystem services (e.g., primary production, wildlife habitat, timber provisions, carbon sequestration, and recreation) (Miller et al., 2009; Sohngen and Brown, 2006). Given the widespread suppression of natural disturbances in these systems, restoration efforts that mimic natural disturbance regimes have garnered more interest in recent decades and are increasingly being implemented (Guldin, 2019; Jin et al., 2018; Ryan et al., 2013). Since applied forest management practices alter successional trajectories, differential management prescriptions can drive communities to alternative stable states with implications for stability and the resilience of ecological communities (Beckage and Ellingwood, 2009). Management strategies to restore these ecosystems to given desired conditions are largely dependent on disturbance type, frequency, and intensity. Therefore, restoration success will ultimately rely on the ability of land managers to develop and apply effective and ecologically sustainable forest management plans (Crouzeilles et al., 2016). Diversity-disturbance relationships are influenced simultaneously by disturbance frequency and intensity (Miller et al., 2011). Since such relationships define the persistence of given disturbance regimes, the relative frequency and effectiveness of restoration practices are important factors that can influence the underlying mechanisms of community assembly. Identifying the influence of disturbance (i.e., restoration practice frequency) on diversity-stability relationships in these managed pine systems is of great ecological and economic importance as the need for sustainable use of forest resources increases (Greene et al., 2016; Harrington et al., 2013; Higgs, 2017).

Most studies investigating the effects of forest management on animal communities in southern pine forests have largely examined changes in species richness, relative abundance, and demographic vital rates to forest structural components (e.g., Demarais et al., 2017; Earl et al., 2016, 2017; Miller and Miller, 2004). Despite this abundance of knowledge, evaluating species loss or gain alone in these systems, through observed changes in species richness or abundance, is a limited approach. Functional diversity, which reflects the diversity and distribution of functional traits in species assemblages, is an important component of biodiversity and is a powerful tool for understanding the nature of species interactions in complex ecosystems (Buchmann and Roy 2002; McGill et al., 2006). Diversity is maintained through predator–prey relationships, in which both direct (i.e., predation) and indirect effects (i.e., prey behavior) can affect resource use and productivity at lower trophic levels (Carpenter et al., 2001; Schmitz, 2009). Strong predator–prey interactions, in which there are increased linkages between predators and prey, stabilize systems as the additive effects of species and their interactions support the complexity of ecosystems (Allesina and Tang, 2012). Weak predator–prey interactions, in which the linkages between predator and prey species decrease, can destabilize systems by altering the nature of species interactions through both indirect and direct effects such as apparent competition, exploitative competition, or predator–prey relationships (McCann, 2000). As a result, ecosystem processes are less resilient to disturbance, thus, increasing the susceptibility for cascading species losses across trophic levels (Allesina and Tang, 2012; Estes et al., 2011). Despite the importance of predators in structuring ecosystems, there is little information on how predator guilds are organized in response to forest management in the context of both taxonomic and functional diversity (Gagic et al., 2015). Understanding these relationships are especially important for conservation strategies concerned with the question of whether forests with infrequent and low-intensity management regimes can preserve the functional diversity of higher trophic levels (Bihn et al., 2010).

As obligate predators, snakes are a model taxon to investigate responses of taxonomic and functional diversity because they are diverse in a number of ecological and life-history traits. Snakes may utilize different foraging strategies and species can vary in prey preference, prey size, and foraging mode (Shine and Bonnet, 2000; Weatherhead and Madsen, 2009). Most snake species utilize a number of habitat types within their home range, serving as suitable indicators of the quality of multiple habitats within an ecosystem and generally exhibit predictable patterns of seasonal activity from year to year (Beaupre and Douglas, 2009). Few studies have integrated both taxonomic and functional approaches to elucidate assembly mechanisms in these predator assemblages (but see de Fraga et al., 2018; França et al., 2008).

Here, we compare taxonomic (i.e., species richness, abundance, evenness) and functional (i.e., functional richness, dispersion, and evenness) snake diversity in response to frequency-level (i.e., high- and low-frequency treatments) of forest management practices (e.g., burning and thinning), across two east Texas pine ecosystems. First, we hypothesized that taxonomic diversity would be greater in the high-frequency treatment compared to the low-frequency treatment, supporting a greater number of snake species and increased species evenness. Second, we hypothesized that functional diversity would also be greater in the high-frequency treatment as active management conditions may increase microhabitat diversity and prey availability allowing for the persistence of functionally unique species. Alternatively, we predicted snake assemblages would exhibit lower functional diversity in the low-frequency treatment as infrequent management practices may lead to biotic homogenization with dominant snake species that possess traits better suited for persisting in such environmental conditions.

2. Methods

2.1. Study area

This study was conducted in the Pineywoods ecoregion of Texas, in the pine-dominated uplands of the northwestern Gulf Coastal Plain (Fig. 1). This area is characterized in the northern extent by dry, deep sandy uplands that transition to well-drained, loamy soils on broad, gently sloping uplands consisting of mixed-pine and hardwood associations (Griffith et al., 2004; Marks and Harcombe, 1975). The climate in the region is warm temperate with average annual temperatures ranging from 12.3 to 25.5 °C. Average annual rainfall is uniformly distributed throughout the year, ranging from 813 to 1270 mm (Griffith et al., 2004). Prior to European settlement, these upland sites were dominated by disturbance-adapted shortleaf pine (*Pinus echinata*) that occurred in both pure and mixed-pine (loblolly pine, *Pinus taeda* and longleaf pine, *Pinus palustris*) stands (Marks and Harcombe, 1975; Masters, 2007). Many of the historical shortleaf pine forests of the region are now either displaced by more commercially viable loblolly pine or hardwood tree species that have encroached and persisted in the absence of natural and anthropogenic fire (Elliott and Vose, 2005).

Our study was conducted across two pine forest ecosystems characterized by different disturbance regimes. Boggy Slough Conservation Area (hereafter, high-frequency treatment; 31.30544°N, −94.93916°W, WGS84) is owned and operated by the T.L.L. Temple Foundation, and is actively managed for conservation and timber production through the implementation of frequent prescribed burns (1–3-year intervals), thinning, and regeneration harvests (R. Sanders, personal communication). The Stephen F. Austin Experimental Forest (hereafter, low-frequency treatment; 31.50167°N, −94.76401°W, WGS84) is owned and operated by the U.S. Forest Service (USFS), Southern Research Station. Until the early 1960’s, the property was primarily used for silvicultural research, but has since supported wildlife research efforts

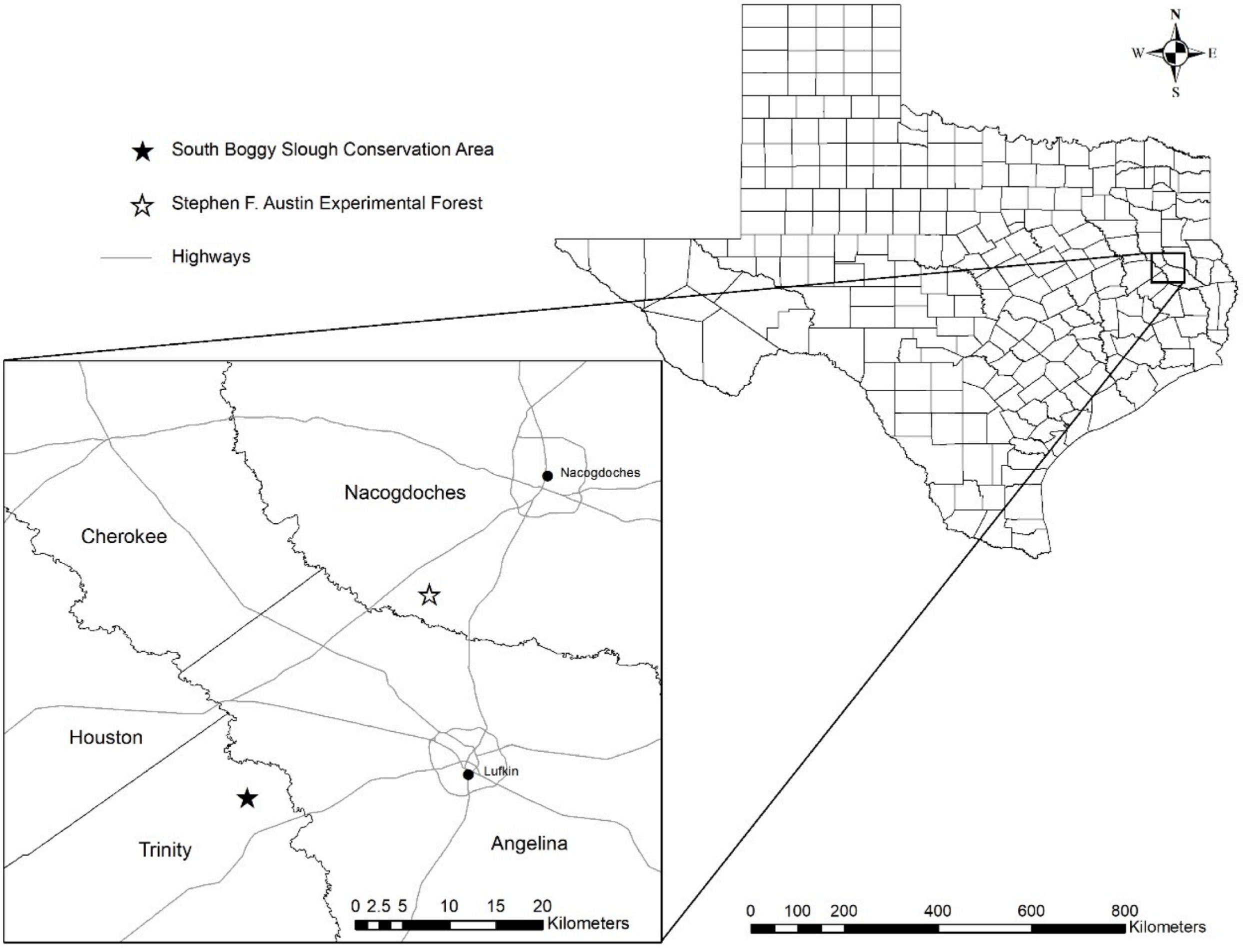

Fig. 1. The study area and the locations of study sites in east Texas, USA.

conducted by the Wildlife Habitat and Silviculture Laboratory of the USFS, Southern Research Station (Russell et al., 2002). The low-frequency treatment is characterized by burn intervals of 5–8 years, and has experienced limited forest harvesting within the last 50 years (D. Saenz, unpublished data).

To evaluate differences in habitat structure between high- and low-frequency treatments we measured eight vegetative habitat variables associated with overall forest structure. These variables were measured to indicate habitat features related to stand density, groundcover, and canopy cover in each sampled location and included measures of basal area, leaf litter depth, percent open canopy, percent coarse woody debris, percent herbaceous cover, percent woody cover, percent bare ground cover, and percent detritus cover (see Supplementary materials, Appendix S1 for more details). We then pooled and averaged these measurements by sampling locality and treatment to test for differences in habitat structure.

2.2. *Snake sampling and prey availability*

Box-traps equipped with four drift fences comprised of hardware cloth (length = 15 m; mesh size = 6.4 mm) and four pitfall traps (19 L) (Burgdorf et al., 2005) were used to sample snakes at ten trap locations per treatment for two years (N = 20 total). Sampling localities were selected based on criteria previously outlined for high-frequency and low-frequency treatments, and separated by a minimum distance of 450 m. This distance was considered appropriate to minimize recaptures and was based on previous trapping efforts and home range studies of large-bodied, active snakes in east Texas pine forests (Johnson et al., 2007; J. Pierce, unpublished data; Schalk et al., in press). Additionally, box traps were moved yearly a minimum distance of 100 m from previous independent sampling localities to reduce trap shyness and ensure adequate sample sizes of snakes could be obtained. Traps were checked daily within the high-frequency treatment from 2018 to 2020 and at sites within the low-frequency treatment from 2019 to 2020, from May-July in accordance with seasonal peaks in activity observed from previous trapping efforts within the region (J. Pierce, unpublished data). All captured snakes were uniquely marked using a combination of ventral scale clipping and heat-branding with Bovie© Deluxe High Temperature disposable medical cautery units (Winne et al., 2006).

To evaluate differences in prey availability between high- and low-frequency treatments we recorded captures of potential snake prey in box traps and pitfalls, and performed sweep netting for invertebrates twice a month at each independent sampling locality across high-frequency and low-frequency treatments. We then pooled the most abundant prey captured into groups based on taxonomic identity and aspects of life-history. These groups included Ensifera (crickets and their allies), Caelifera (grasshoppers), Coleoptera (terrestrial beetles), Araneae (large spiders), Decapoda (crayfish), Anura (frogs and toads), Caudata (salamanders), Lacertilia (lizards), Rodentia (small rodents), and Eulipotyphla (shrews and moles). Prey availability was measured as the number of individuals captured per trap day. To test for differences in prey availability between treatments, we performed Wilcoxon rank sum tests for each prey group since none of the distributions met the assumptions of parametric tests.

2.3. Taxonomic diversity

We measured species richness and evenness for each management treatment as a whole using the relative abundances of species by trapping effort. To interpret differences in taxonomic composition within and between treatments we also quantified taxonomic β-dispersion, incorporating the relative weight of species abundances (Anderson et al., 2006). Using this methodology, pairwise compositional dissimilarity between independent sampling locations based on species abundances was quantified by creating a dissimilarity matrix based on the Bray-Curtis dissimilarity. We then tested if high- and low-frequency trapping locations differed in snake guild composition using Permutational Multivariate Analysis of Variance (PERMANOVA) using 999 iterations in the model. To investigate differences in taxonomic β-dispersion between treatments we used the average distance of species to the group centroid as a measure of multivariate dispersion and performed a PERMUTEST (Anderson et al., 2006).

To describe differences in taxonomic β-diversity, we performed a Principle Coordinates Analysis (PCoA) ordination of a matrix of Bray-Curtis similarity index on species relative abundance data between treatments. Relative abundances were calculated from individual captures and by trapping effort (i.e., trap days) in each treatment. Bray-Curtis similarities were transformed into dissimilarities between treatment sampling locations. All statistical analyses were performed in the ‘vegan’ package in R (Oksanen et al., 2013; R Core Team, 2021).

2.4. Functional diversity

To quantify the functional richness (FRic; volume of functional space occupied), dispersion (FDis; mean distance of all species to the weighted centroid in trait space), and evenness (FEve; regularity of the distribution of species abundances and dissimilarities in functional space) of snake assemblages, we measured 13 continuous and categorical traits on 406 individual adult snakes represented by 19 species (number of snakes per treatment: high-frequency: 219 individuals, 123 males, 96 females; low-frequency: 187 individuals, 113 males, 74 females). Continuous traits included head length, head width, head depth, eye diameter, internarial distance, inter-ocular distance, and circumference at mid-body. These traits were measured using digital calipers (±0.01 mm) and adjusted for body size using the residual scores of linear regressions with snout-to-vent length as the independent variable. Categorical functional trait data included assessments on presence or absence of venom, foraging mode, habitat use, and reproductive mode and were obtained from the literature (Shine, 2003; Tennant, 2006; Werler and Dixon, 2010). Collectively, these selected traits reflected relative functions of feeding ecology, habitat use, and reproductive mode (Beaupre and Douglass, 2009; Rossman, 1996; Todd et al., 2017; Supplementary material, Appendix, S2). To visualize the functional trait space occupied by the snake communities in high-frequency versus low-frequency treatments, we performed a PCoA with species scores calculated from the dbFD analyses in the R package ‘FD’ using the ‘gower’ distance matrix (Laliberté and Legendre, 2010; Laliberté et al., 2014; Petchey and Gaston, 2007). To test for differences for each functional diversity metric between high-frequency and low frequency trapping locations, we grouped independent alpha diversities by management regime, testing for normality using the Shapiro-Wilk test. Since none of the indices met the assumptions for parametric *t*-test, differences in means were tested using Wilcoxon rank sum test for each functional diversity metric.

Linear models were used to compare each of these metrics across a species richness gradient by treatment, with functional richness (FRic) and weighted-functional diversity (FDis) as response variables. Since both metrics may be correlated with species richness, input values for indices were produced using a standardization method based on a null model framework (see Rader et al., 2014). To investigate whether or not prevailing environmental conditions resulting from management practice frequency promoted certain phenotypes within snake communities in each treatment, community-weighted means were calculated for continuous functional traits. Because these data met the assumptions of normality and homogeneity of variance, we tested for differences between treatment sites using paired *t*-tests. Additionally, we tested for differences in the frequency distribution of categorical traits using the proportion of traits present in each assemblage, grouping them accordingly to management treatment. Categorical data for traits did not meet the assumptions of parametric tests, so Wilcoxon rank sum tests were used to test for significant differences in each categorical trait between treatments.

3. Results

3.1. Forest habitat structure and management practice frequency

Forest habitat structure was markedly different between high-frequency and low-frequency treatments (Fig. 2). We found significant differences in basal area (m^2), mean leaf litter depth (mm), percent open canopy (%), percent coarse woody debris (%), and percent groundcover (%) between high-frequency and low-frequency treatments (Fig. 2).

3.2. Prey availability

There were noted differences in the availability of certain prey groups found in high-frequency and low-frequency treatments (Fig. 3). We found significant differences in the availability of Anura, Coleoptera, Ensifera, Lacertilia, and Rodentia prey groups (Fig. 3). Caelifera (grasshoppers) were not captured in the low-frequency treatment, while Caudata (salamanders) were not found in the high-frequency treatment (Fig. 3). These observed differences in prey availability suggests that differences in management practice frequency may also lead shifts in prey availability between treatments as environmental conditions change.

3.3. Taxonomic diversity

Overall, mean species richness was greater in the high- (n = 19 spp.) than the low-frequency treatment (n = 12 spp.). All species captured in the low-frequency treatment were represented in the high-frequency treatment samples. Species’ capture per unit effort (CPUE) differed across management regimes as well (Fig. 4). Specifically, *Agkistrodon contortrix*, *Coluber constrictor*, and *Agkistrodon piscivorus* contributed the most to the dissimilarity observed between treatments (Fig. 4). This dissimilarity was due to high captures of *A. contortrix* at the low-frequency treatment, high captures of *C. constrictor* at the high-frequency treatment, and having only a single capture of *A. piscivorus* in the low-frequency treatment (Fig. 4). The high-frequency treatment was more even in terms of species CPUE, as captures in the low-frequency treatment were dominated by three species, *A. contortrix*, *Thamnophis proximus*, and *Pantherophis obsoletus* (Fig. 3).

Taxonomic β-diversity was significantly greater in high-frequency sampling localities than low-frequency sampling localities (PERMANOVA, n = 999, F = 7.5129, Pr(>F) = 0.008; Fig. 5). Further analyses of taxonomic β-dispersion revealed that assemblages in the high-frequency localities also showed a higher degree of taxonomic diversity (β-dispersion = 0.4103) in terms of species richness and CPUE than assemblages in the low-frequency localities (β-dispersion = 0.2796) (PERMUTEST, n = 999, F = 9.724, Pr(>F) = 0.001).

3.4. Functional diversity

Partitioning assemblages in regards to their functional diversities

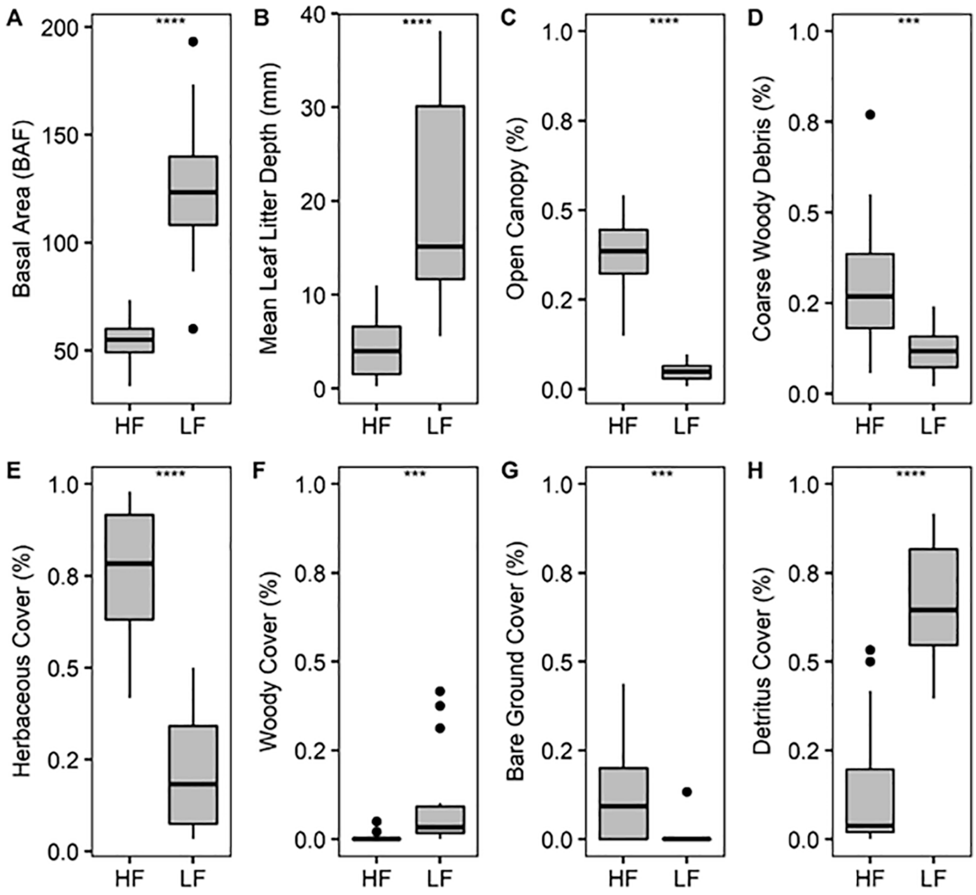

Fig. 2. Comparisons of habitat variables under high-frequency (i.e, 1–3 year burn intervals, thinning; HF) and low-frequency (i.e, 5–8 year burn intervals, no thinning; LF) management regimes. A) Basal Area (BAF), a measure of stand density; B) Mean leaf litter depth; C) Percent open canopy; D) Percentage of coarse woody debris (e.g., snags and logs); E) Percent herbaceous ground cover (e.g., grasses, sedges, forbs); F) Percent woody ground cover (e.g., vines, shrubs, seedlings); G) Percent bare ground cover (e.g., exposed soil); H) Percent detritus cover (e.g., non-living plant material). A significant difference in habitat variables is indicated by an asterisk (*). The number of asterisks correspond to significance level (i.e., *** = $P < 0.001$, **** = $P < 0.0001$).

and according to management regime, we found no difference in snake FRic between high- and low-frequency treatments (Wilcoxon rank sum, $p = 0.845$; Fig. 6A-B).

A high degree of overlap was observed between snake assemblages in functional trait space, in which the addition of new species in the high frequency treatment had little effect on functional richness (Fig. 7).

We also observed no differences in overall FDis between high- and low-frequency treatments (Wilcoxon rank sum test, $p = 0.14$; Fig. 6C). However, FEve was significantly greater in the high-frequency treatment than in the low-frequency treatment (Wilcoxon, $p < 0.001$; Fig. 6D). This suggests a pattern of functional redundancy across both management treatments, with increased regularity of functional traits observed in the high-frequency snake assemblage. When examined across a species richness gradient, the high-frequency snake assemblages exhibited a greater degree of functional redundancy compared to the low-frequency snake assemblage (Supplementary materials, Appendix, S4A-B).

Analyzing community-weighted means for continuous traits between high frequency and low frequency treatments resulted in a general pattern towards larger-bodied snakes in the high frequency treatment (Fig. 8). Of the eleven continuous traits measured, only jaw length was not significantly different between high- and low-frequency treatments (Fig. 8). Additional analyses of the distributions of categorical traits between high frequency and low frequency treatments revealed ambush foraging mode, the possession and use of venom to subdue prey, and viviparity (traits possessed by viperid snakes) were more frequently observed in the low frequency treatment (Wilcoxon, $p < 0.05$; Fig. 9).

4. Discussion

Overall, we observed contrasting patterns of taxonomic and functional diversity within snake assemblages in regards to the relative frequency (i.e., high- versus low-frequency treatments) of applied forest management practices. We found that the high-frequency treatment supported a greater number of species than the low-frequency treatment, supporting our first hypothesis that there would be greater taxonomic diversity under active management conditions. Despite this finding, functional diversity was comparatively similar across management regimes, therefore, we failed to support the hypothesis that functional diversity would be greater in the high-frequency treatment.

Previous studies have shown that restoration of open-pine forests with intensive management can benefit species diversity by increasing the structural complexity of habitats (Davis et al., 2010; Litt et al., 2001; Pastro et al., 2011). Conner et al. (2002) found that bird species diversity in longleaf and loblolly pine forests was lower in the absence of disturbance, in which the alteration of understory microhabitats resulted in the biotic homogenization of avian assemblages. Similarly, management activities that mimic natural disturbances may alter the taxonomic composition of snake communities through the provisioning of microhabitats. For example, the loss or lower CPUE of active, diurnal snake species was apparent in the low-frequency treatment in this study. The development of dense understory and midstory vegetation that persists when management is infrequent or ineffective likely limits those species ability to find suitable microhabitats for refuge and foraging in infrequently managed sites.

If we consider species foraging behaviors, *Coluber contrictor* and *C. flagellum*, are visual hunters with high resource demands, that must search for food throughout the day often utilizing multiple microhabitats (Howey et al., 2016; Howze and Smith, 2015). However, environmental conditions in the low-frequency treatment could be advantageous to only a few species that possess similar ecological characteristics. As such, these species can tolerate the environmental

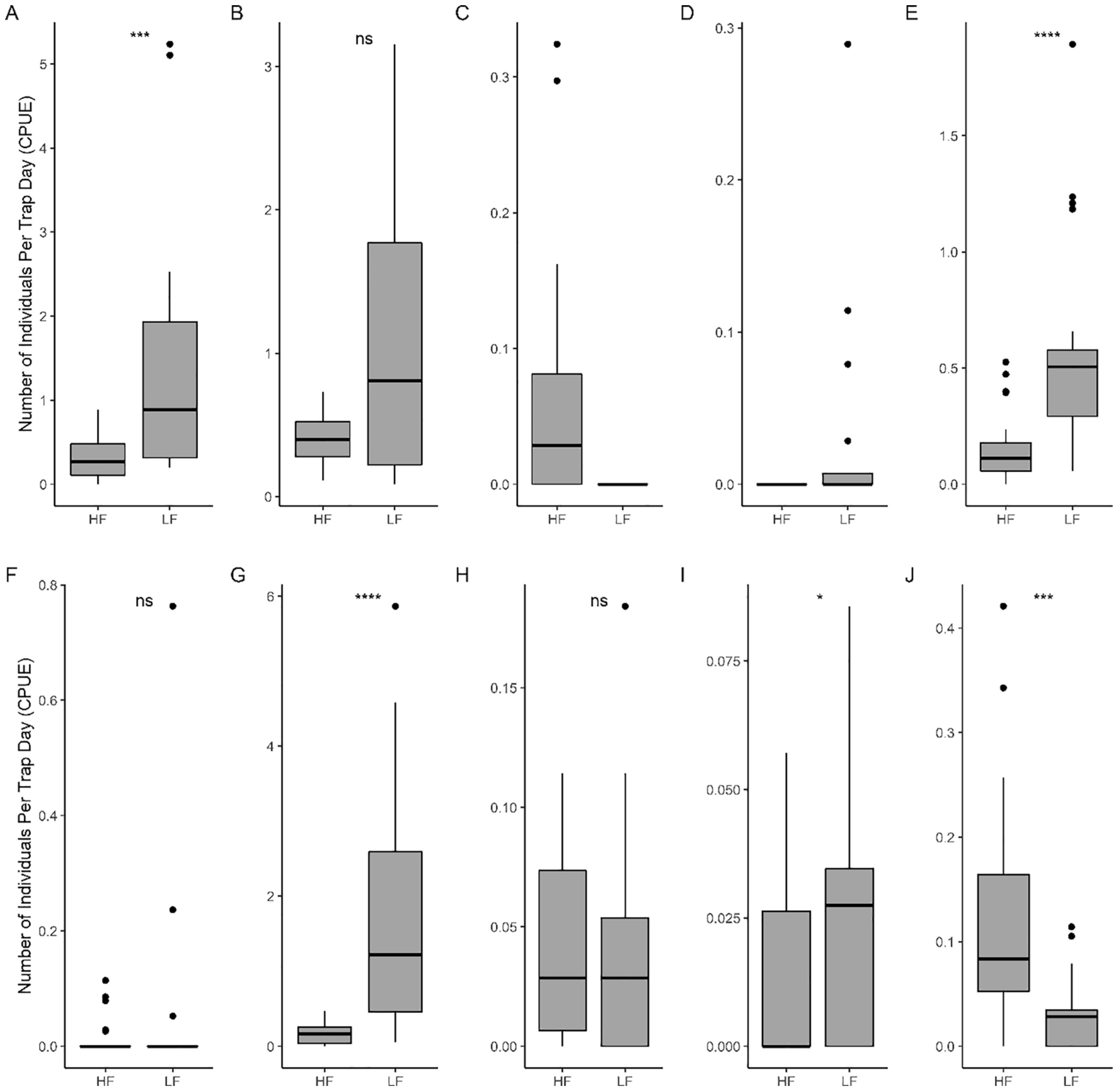

Fig. 3. Number of individuals per trap day based on capture per unit effort (CPUE) of A) Anura (frogs and toads), B) Araneae (spiders), C) Caelifera (grasshoppers), D) Caudata (salamanders), E) Coleoptera (terrestrial beetles), F) Decapoda (crayfish), G) Ensifera (crickets), H) Eulipotyphla (shrews and moles), I) Lacertilia (lizards), and J) Rodentia (small rodents) prey groups in high-frequency (HF; e.g., subjected to thinning and burning) and low-frequency (LF) treatments. Note the difference in the scale of the y-axis in each figure. A significant difference in CPUE across sites is indicated by an asterisk (*). Asterisks correspond to significance level (e.g., * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

filters imposed under low-frequency management as forest canopies close and other species are lost. The dominance of *A. contortrix* at low-frequency sites may be due to their ability to forage and survive within small home ranges and find abundant ambush microhabitats in forests with abundant shade and leaf litter buildup (Steen et al., 2014; Sutton et al., 2017).

Increased habitat heterogeneity in the high-frequency treatment under both frequent thinning and prescribed burning practices resulted in snake assemblages more even in CPUE and likely provided additional habitats for taxonomically unique species that were not found in the low-frequency treatment. Steen et al. (2013) reported that efforts (i.e., long-term applications of both prescribed fires and thinning) applied to restore basal resource conditions to a more natural state, were beneficial to maintaining snake microhabitats in degraded pine ecosystems. In this study, frequent thinning operations and prescribed fires collectively resulted in complex understories at most sites in the high-frequency treatment. First, thinning operations in the high-frequency treatment created an abundance of coarse woody debris and large piles of tree bark that may have supported the persistence of transient or fossorial species within the predominantly herbaceous understory developed from previous fires (Davis et al., 2010). Fossorial species such as *Micrurus tener, Haldea striatula,* and *Lampropeltis triangulum* were captured at least twice in this treatment, with *H. striatula* and *L. triangulum* never captured in the low-frequency treatment. Second, skidder trails from mechanical thinning operations would often hold water for long periods allowing for the establishment of herbaceous plants characteristic of many ephemeral wetland habitats. Such environments may have provided temporary habitats for semi-aquatic (i.e., *Nerodia* spp.) and fully aquatic snakes (i.

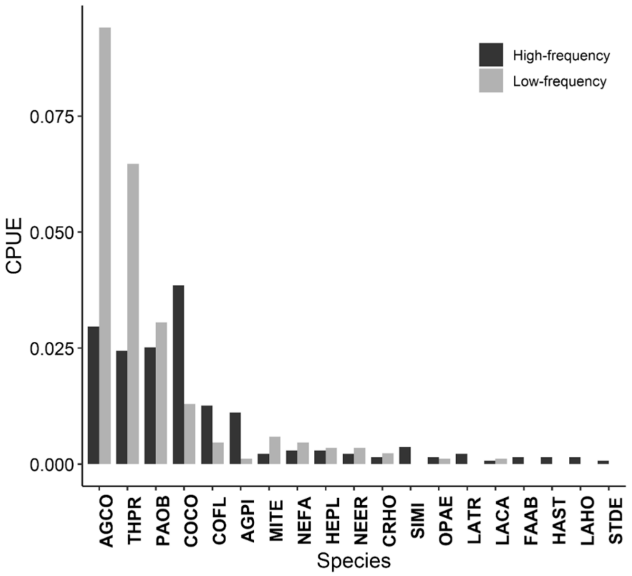

Fig. 4. Species capture per unit effort (CPUE) of snake captures in high frequency forest management (e.g., thinning, burning) and low frequency forest management regimes. Abundance values were calculated relative to total trap effort across high-frequency (1350 trap days) and low-frequency (850 trap days) sites. Species codes are listed in Appendix, S3.

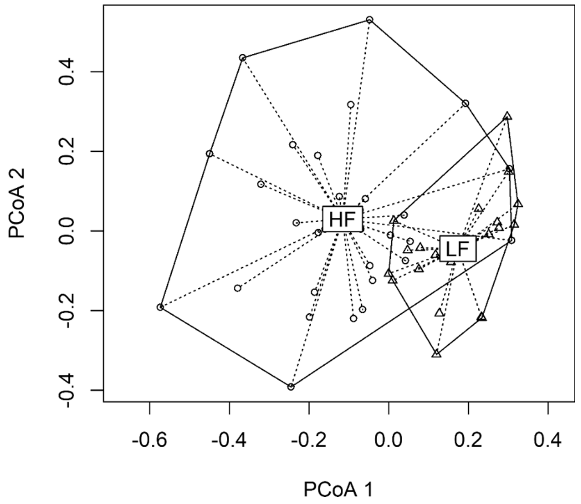

Fig. 5. Principle Coordinates Analysis (PCoA) of taxonomic β-dispersion observed in high-frequency (HF; open circles) and low-frequency (LF; open triangles) sites. Pairwise compositional dissimilarity between independent sites based on species occurrences was quantified by creating a dissimilarity matrix based on the Bray-Curtis dissimilarity.

e., *Farancia abacura*) dispersing from other environments in search of higher quality habitat or mates. Thus, structurally complex understories associated with high-frequency management in this study appear to provide microhabitats for a number of snake species exhibiting a wide range of feeding ecologies, foraging strategies, and habitat uses.

Taxonomic shifts in predator communities due to changes in prey availability have also been recognized as a potential mechanism of community organization (Estes et al., 1978; Kurzava and Morin, 1998; Stier et al., 2014). For example, manipulations of habitat complexity (i.e., woody debris) in degraded Neotropical streams revealed that aquatic taxa abundance and diversity increased in response to increasing habitat complexity, consequently increasing the number of trophic links, predators, and prey in treatments from prior degraded conditions (Ceneviva-Bastos et al., 2017). Therefore, the availability and abundance of prey resources in disturbed or perturbed systems can directly affect the taxonomic diversity of predator guilds through species interactions.

Recognizable shifts in prey capture per unit effort were observed between treatments, as CPUE of functional prey groups were more even in their relative contribution to the overall prey diversity in the high-frequency treatment (Adams, 2021). The high-frequency treatment contained a wider diversity of prey available to snake consumers in terms of prey taxa, trophic guild, and body size. Conversely, only a few dominant prey groups contributed to the majority of prey diversity found in the low-frequency treatment (e.g., crickets, anurans, and spiders).

Given that prey may be responding to increased habitat heterogeneity resulting from frequent forest management practices, prey availability may be a potential mechanism linked to the observed patterns of taxonomic snake diversity. Small mammals are well-documented prey items for many snake species, and small mammal diversity and abundance has been shown to increase in pine-grassland forest under frequent management regimes (Masters et al., 1998, Russel et al., 2004; Werler and Dixon, 2010). This is likely because forest management practices, such as prescribed fires, can encourage structural complexity of vegetative communities in these forests and provide multiple sources of productivity these herbivores can exploit to avoid competition (Russel et al., 2004; Versuchuyl et al., 2011).

The creation of temporary aquatic habitats from thinning operations could have also contributed to increased prey availability and, consequently, increases in snake taxonomic diversity in high-frequency sites. *Agkistrodon piscivorus* contributed prominently to differences in taxonomic composition between high and low-frequency treatments. This semi-aquatic species is unique from other viperids captured in this study, in that they will utilize a more generalized (i.e., ontogenetic shift to more active than ambush) foraging strategy as adults (Eskew et al., 2009). Since many of these novel microhabitats are facilitated through greater frequency or intensity of management practices, they may also increase the number of habitats suitable for breeding populations of anurans, providing resources for semi-aquatic snakes not typically found in upland habitats (Cromer et al., 2002; DiMauro and Hunter, 2002).

Furthermore, increased practice frequency can affect the taxonomic diversity of snake predators by altering the abundance or biomass of other prey taxa that may not be prominently featured in most diets of species captured in this study. A previous study in the low-frequency treatment found that arthropod densities were higher in pine stands devoid of midstories than those in which infrequent practice frequency led to the development of dense midstory structure (Collins et al., 2002). This has drastic implications for higher-order consumers, such as snake predators, because high arthropod abundances support both insectivorous snakes as well as many lower-level consumers that could be consumed by snakes (e.g., anurans, salamanders, lizards, and small mammals).

Despite substantial differences in patterns of taxonomic diversity, we observed patterns of functional redundancy across management treatments, in which increased practice frequency resulted in increased functional redundancy in snake predators. Previous studies of migratory bird communities have demonstrated that often losing or gaining species from an assemblage reveals little about the loss or gain of functional diversity (Almeida et al., 2018; Edie et al., 2018; Prescott et al., 2016). Baiser and Lockwood (2011) found that functional dominance of certain traits shared among birds may dampen the extent to which functional diversity is predicted to increase with the addition of functionally distinct species. Despite differences in other morphological traits related to performance and the observed shift in taxonomic diversity, high degrees of trait overlap of a few dominant traits present in each bird assemblage subsequently decreased functional diversity (Baiser and Lockwood, 2011). Similarly, in their examination of the spatio-temporal dynamics of desert lizard assemblages, Leavitt and Schalk (2018) found that despite the addition or loss of taxonomically distinct species,

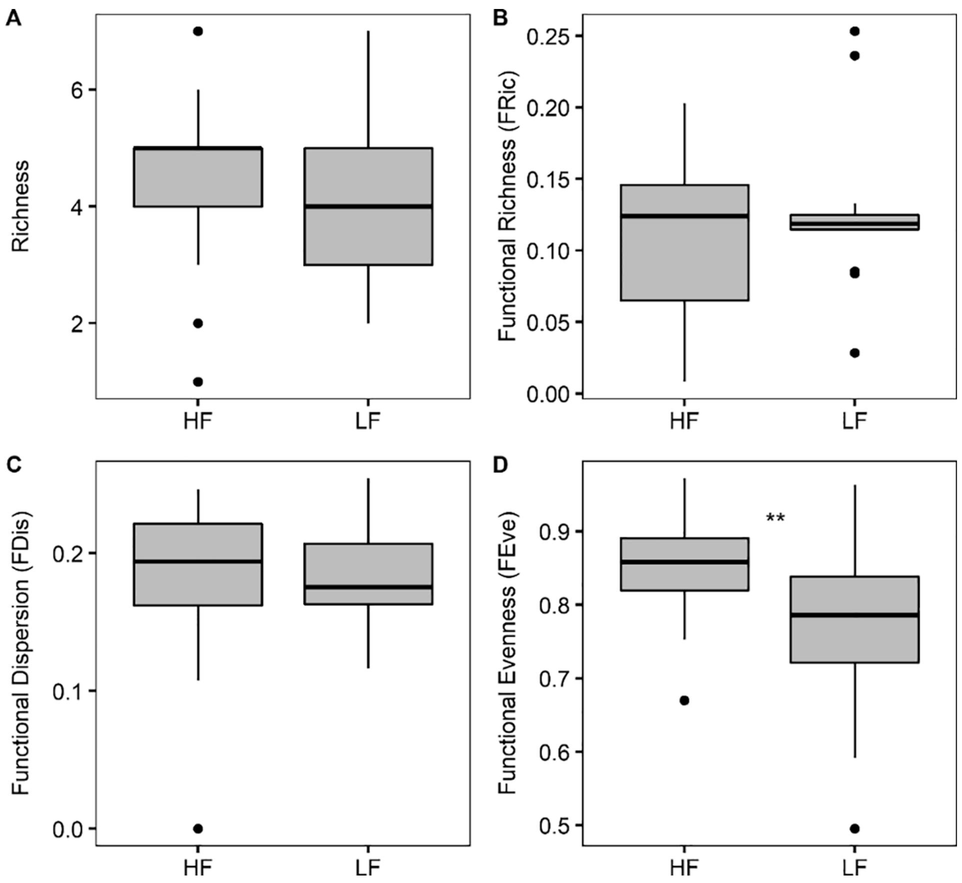

Fig. 6. Functional α-diversity indices of snake communities located in high-frequency management and low-frequency management forests. A) Species richness of assemblages (sampling sites) within each treatment, B) Functional richness (FRic); minimum convex hull volume C) Functional dispersion (FDis); mean distance of all species to the weighted centroid of the community in trait space. D) Functional evenness (FEve); evenness of abundance distribution in filled trait space. A significant difference functional diversity index is indicated by an asterisk (*). Asterisks correspond to significance level (** = P < 0.01).

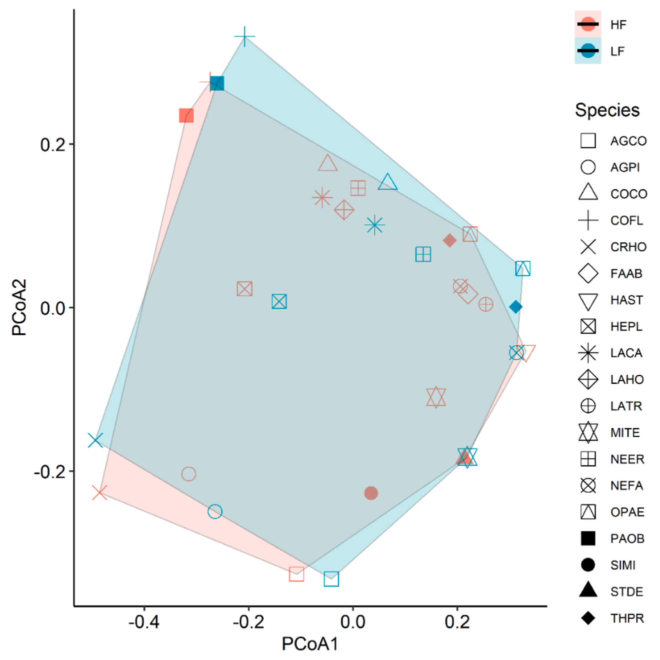

Fig. 7. Principle coordinates analysis of snake communities in functional trait space. Convex hulls represent the functional richness (FRic) of snake communities at high frequency (red) and low frequency (blue) sites. Species codes are listed in Appendix, S3.

functional diversity did not exhibit substantial changes. Instead, the functional similarity of traits due to the composition of the regional species pool may prevent the addition or loss of species in local assemblages from diverging in functional diversity (Leavitt and Schalk, 2018). We observed an inverse relationship between forest practice frequency, species diversity, and functional diversity, suggesting that trait filtering mechanisms may lead to greater functional redundancy of snakes inhabiting frequently managed sites. Functional richness and dispersion are important to understand the effects of forest management on functional diversity because they indicate whether species within a given habitat are performing similar (i.e., redundancy) or different (i.e., complementary) roles for a given ecosystem service (Laliberté et al., 2010). While species diversity increased in the high-frequency treatment, FRic and FDis did not. Functional evenness, while generally expected to decline in disturbed ecosystems as taxonomic diversity is lost and a few stress-tolerant species become dominant, did not decline with increased practice frequency (Mouillot et al., 2013).

One potential explanation is that species in ecosystems with increased practice frequency are more tolerant to disturbance (Drapeau et al., 2016). Since restoration efforts are meant to mimic natural disturbance regimes, similar traits could become convergent among species in frequently disturbed environments and more snake species may coexistence with similar functional roles. On the contrary, not all disturbance is equal. In low-frequency management regimes, redundancy among species may be solely explained by biotic homogenization resulting from some other process, such as the limitation of resources (Pulsford et al., 2016).

In this context, the persistence of individual traits across assemblages or communities may serve as complementary metric to help disentangle the relationship between taxonomic and functional diversity (Muscarella and Uriarte, 2016). Although functional dispersion and community-weighted means of traits are strongly related to environmental factors and disturbance, these metrics respond differently because assemblages can differ greatly in species composition but not in trait variability (Grime, 2006). Analysis of individual continuous traits in this study

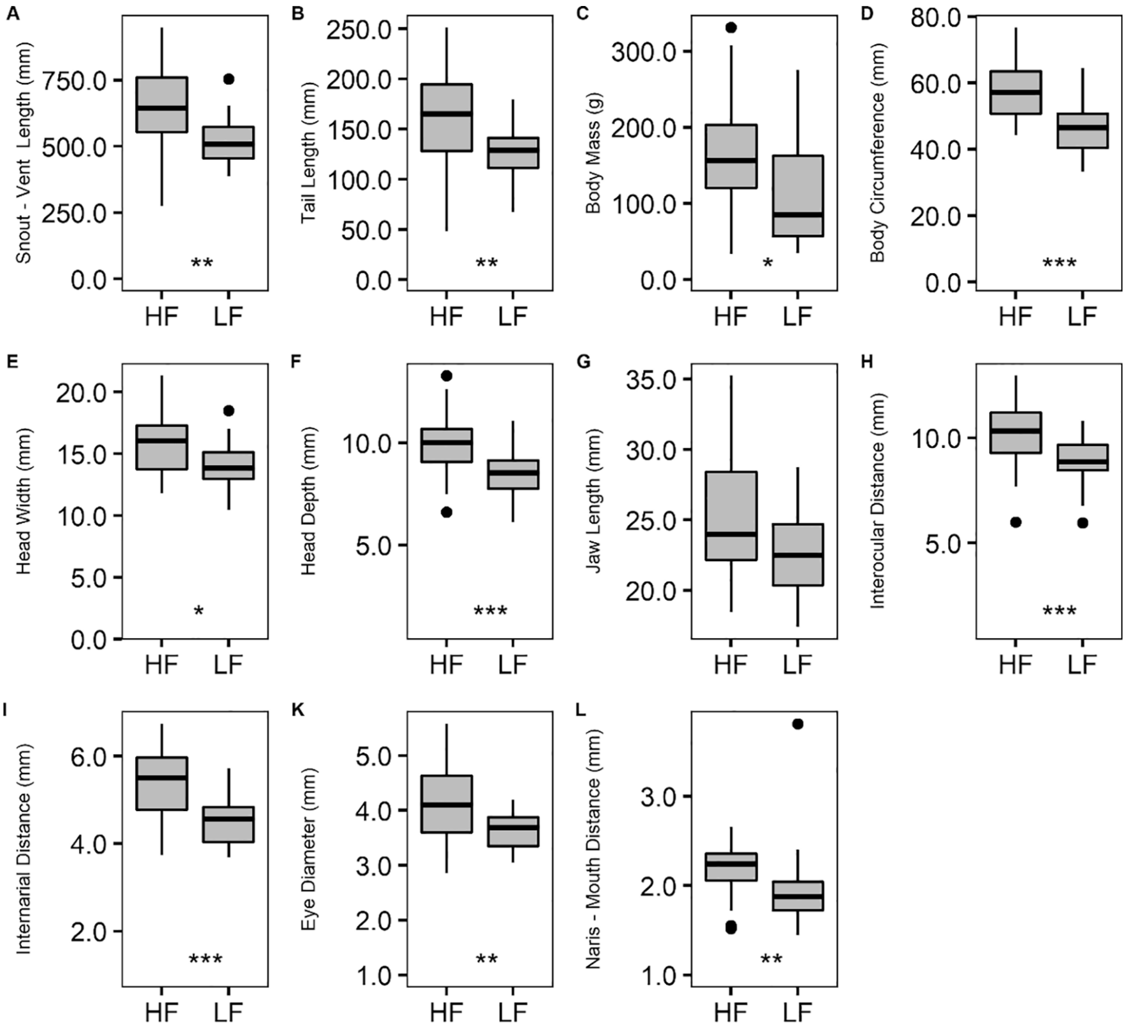

Fig. 8. Community weighted means of the eleven continuous functional traits of snakes located in high-frequency management and low-frequency management forests. A significant difference in trait is indicated by an asterisk (*). Asterisks correspond to significance level (e.g., * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

showed that, community-wide, there was a pattern of functional composition related to snakes having larger overall body size in the high-frequency treatment. Other studies have reported larger body sizes in snake communities inhabiting restored pine-grasslands systems compared to degraded control sites but the mechanism for this phenotypic trait selection was not well understood (Verschuyl et al., 2011). Snakes in high-frequency treatments may have higher resource demands and, therefore, may have greater impacts on prey communities in these environments with an abundance of resources. Large-bodied snakes with active foraging strategies tend to have higher resource demands, and must feed frequently while also managing thermoregulatory constraints (Todd et al., 2021). Alternatively, given the environmental constraints in low-frequency sites that may hinder the persistence of larger-bodied active snakes, smaller-bodied snakes (*A. contortrix* and *Thamnophis proximus*) may persist in large densities at smaller body sizes (Novak et al., 2020).

Restoring a mosaic habitat complexity with the frequent use of prescribed fire and mechanical thinning can bolster the diversity of snake predators. Increasing functional redundancy with increased frequency and intensity of forest management practices has implications for the resilience of predator guilds that, while taxonomically unique, are similar in their overall traits. In such a case, the random loss of any species at either management treatment may not result in the loss of functional diversity. However, the extent to which functional redundancy changes as species' roles shift under different environmental conditions may be due to other processes important for maintaining ecosystem functioning (Fetzer et al., 2015). Snake assemblages, although similar in functional diversity between treatments, may respond differently to practice frequency in regards to their trophic structure. The resilience of predators in these managed ecosystems and their role in maintaining ecosystem stability through trophic interactions (i.e., trophic redundancy) may be an important aspect of maintaining ecosystem complexity. The consequences of such variation in local communities may be hard to distinguish if assuming species occupying similar trophic positions are also functionally similar (Leibold et al., 1997). Chalcraft and Resetarits (2003) found differences among predators in the selection of prey and the ability to suppress prey numbers that led to continuous variation in larval amphibian community assembly, thus, preventing shifts to alternative stable states. Nonetheless, the maintenance of functional redundancy in predator assemblages is important for ensuring species losses are less likely to lead to cascading events in lower trophic levels or loss of ecosystem function. For example, low functional diversity among predators in highly-diverse reef ecosystems increased vulnerability to the removal of few keystone species and can lead to ecosystem collapse (Guillemot et al., 2011).

Even though our study provides novel value for understanding the ecological processes that organize communities in managed pine ecosystems, there are limitations that prevent a robust assessment of predator–prey relationships and their inherent effects on ecosystem

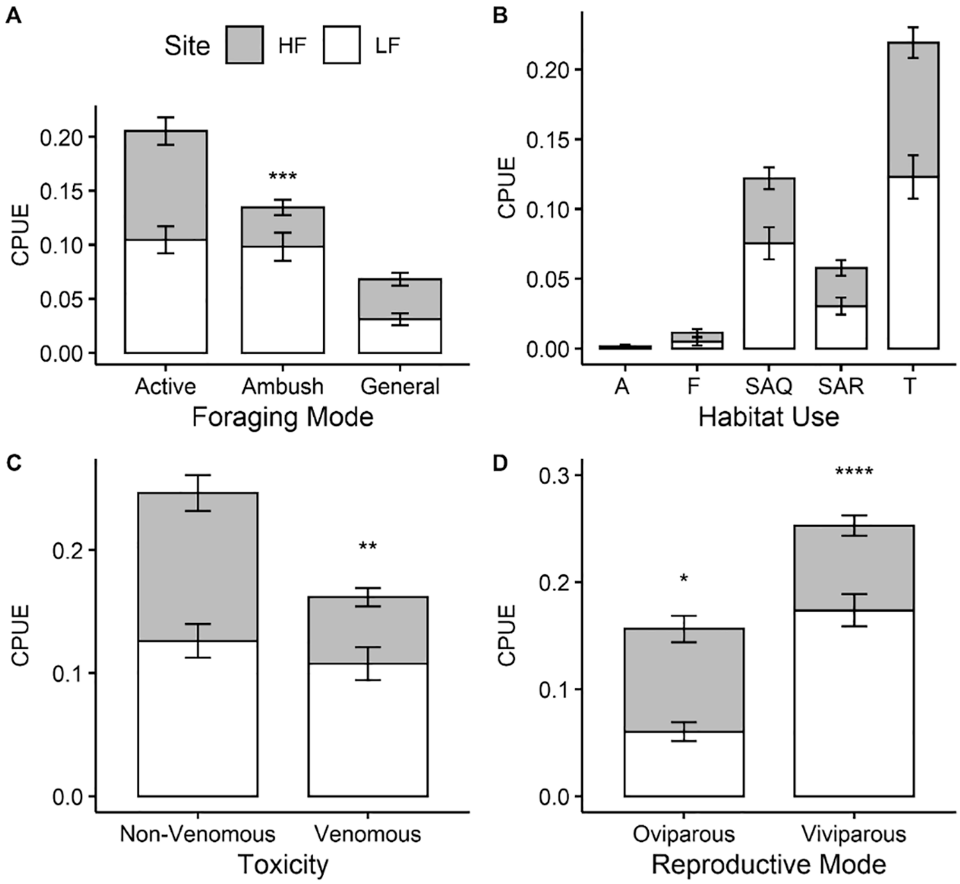

Fig. 9. Trait distributions of categorical traits in high frequency and low frequency sites calculated the capture per unit effort values (CPUE's) of sampled snake assemblages. Abbreviations for habitat use categories in (B) are as follows: A, mostly aquatic; F, semi-fossorial; SAQ, semi-aquatic; SAR, semi-arboreal; T, terrestrial. A significant difference trait is indicated by an asterisk (*). Asterisks correspond to significance level (e.g., * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ****= $P < 0.0001$).

stability. Other taxa, specifically higher-order consumers, may have greater impacts on the regulation of prey communities in these systems than tertiary snake consumers (Schalk and Cove, 2018; Jobe et al., 2019). Raptors, for example, can have strong interactions across multiple trophic levels, and have been shown as an important guild that features functional redundancy in several ecosystems (Jaksic, 2003). Additionally, there are many diversity indices that may be applied in trait-based frameworks, and many of these indices are either interrelated or have differential abilities in efficiently describing patterns of functional diversity depending on the roles of species in certain systems (Mason et al., 2013; Mouchet et al., 2010; Schleuter et al., 2010). We used functional dispersion, alongside metrics of richness and evenness, in place of functional divergence because it is a more independent measure complementary to the other conventional metrics used to determine patterns of functional diversity across the sampled assemblages (Cooke et al., 2019; Schleuter et al., 2010).

Comparing patterns of taxonomic and functional diversity within predator assemblages in disturbed ecosystems has important implications for the stability and resilience of ecosystems, because it provides a more robust framework for maintaining ecological processes and services (Cadotte et al., 2011; Villéger et al., 2010, 2013). As restoration efforts that mimic natural conditions are more widely applied, land managers can incorporate both structural and functional approaches to identify the complex interactions and important taxa that contribute to the health and resilience of ecosystems to disturbance (Aerts and Honnay, 2011; Laughlin et al., 2018). Thus, understanding the effects of restoration practices on the structure and function of ecological communities is vital to the implementation of sustainable land-use. Given the continued threats of land-use change, climate change, and biodiversity loss, increasing functional redundancy alongside overall biodiversity is a valuable outcome to such efforts.

Given our findings showing significantly greater taxonomic dispersion of snake assemblages within high-frequency sites compared to snake assemblages in low-frequency sites, the frequency and intensity of forest management practices likely play a key role in maintaining snake diversity by increasing both microhabitat and prey availability. This is important considering the potential for snakes to serve as valuable model organisms in such environments (e.g., obligate predators, low dispersal, varied life-histories, energetic constraints). Ultimately, by comparing and contrasting patterns of taxonomic and functional diversity within these predator assemblages we can begin to understand the organization of ecological communities within pine-forest ecosystems and the resilience of these ecosystems to anthropogenic disturbance regimes.

5. Ethics approval

The handling and use of animals in this study were approved by SFASU's IACUC, reference number 2018–006 and Scientific Research Permit No. SPR-0519-087.

6. Availability of data and material

The datasets analyzed during the current study are available from the corresponding author on reasonable request.

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CRediT authorship contribution statement

Connor S. Adams: Formal analysis, Methodology, Software, Investigation, Writing – original draft, Data curation, Visualization. **Daniel Saenz:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition. **Kathryn R. Kidd:** Methodology, Writing – review & editing, Supervision. **Christopher Schalk:** Conceptualization, Methodology, Investigation, Resources, Data Curation, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108591.

References

Adams, C., 2021. Food-web and functional trait community structure of predator assemblages in pine forests under different management regimes. MS dissertation, Arthur Temple College of Forestry and Agriculture. Stephen F. Austin State University, Nacogdoches, Texas, USA.

Aerts, R., Honnay, O., 2011. Forest restoration, biodiversity and ecosystem functioning. BMC Ecol. 11 (1), 29. https://doi.org/10.1186/1472-6785-11-29.

Allesina, S., Tang, S.i., 2012. Stability criteria for complex ecosystems. Nature 483 (7388), 205–208.

Almeida, S.M., Juen, L., Sobral, F.L., Santos, M.P.D., 2018. The influence of biogeographic history on the functional and phylogenetic diversity of passerine birds in savannas and forests of the Brazilian Amazon. Ecol. Evol. 8 (7), 3617–3627.

Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9 (6), 683–693.

Baiser, B., Lockwood, J.L., 2011. The relationship between functional and taxonomic homogenization. Glob. Ecol. Biogeogr. 20 (1), 134–144.

Beaupre, S.J., Douglas, L.E., 2009. Snakes as indicators and monitors of ecosystem properties. *Snakes: ecology and conservation*, 244-261.Beaupre, S. J., Jacobson, E. R., Lillywhite, H. B., & Zamudio, K. (2004). Guidelines for use of live amphibians and reptiles in field and laboratory research.

Beckage, B., Ellingwood, C., 2009. Fire feedbacks with vegetation and alternative stable states. Complex Syst. 18 (1), 159–173.

Bihn, J.H., Gebauer, G., Brandl, R., 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. Ecology 91 (3), 782–792.

Brudvig, L.A., Damschen, E.I., 2011. Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography 34 (2), 257–266.

Buchmann, N., Roy, J., 2002. Species diversity, functional diversity and ecosystem functioning. Biodiversity and ecosystem functioning: Syntheses and perspectives 17, 195–208.

Buisson, E., Le Stradic, S., Silveira, F.A.O., Durigan, G., Overbeck, G.E., Fidelis, A., Fernandes, G.W., Bond, W.J., Hermann, J.-M., Mahy, G., Alvarado, S.T., Zaloumis, N. P., Veldman, J.W., 2019. Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. Biol. Rev. 94 (2), 590–609.

Burgdorf, S.J., Rudolph, D.C., Conner, R.N., Saenz, D., Schaefer, R.R., 2005. A successful trap design for capturing large terrestrial snakes. Herpetol. Rev. 36 (4), 421–424.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48 (5), 1079–1087.

Carpenter, S.R., Cole, J.J., Hodgson, J.R., Kitchell, J.F., Pace, M.L., Bade, D., Cottingham, K.L., Essington, T.E., Houser, J.N., Schindler, D.E., 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecol. Monogr. 71 (2), 163–186.

Ceneviva-Bastos, M., Montaña, C.G., Schalk, C.M., Camargo, P.B., Casatti, L., 2017. Responses of aquatic food webs to the addition of structural complexity and basal resource diversity in degraded Neotropical streams. Austral Ecol. 42 (8), 908–919.

Chalcraft, D.R., Resetarits Jr., W.J., 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? Ecology 84 (9), 2407–2418.

Collins, C.S., Conner, R.N., Saenz, D., 2002. Influence of hardwood midstory and pine species on pine bole arthropods. For. Ecol. Manag. 164 (1-3), 211–220.

Conner, R.N., Shackelford, C.E., Schaefer, R.R., Saenz, D., Craig rudolph, D., 2002. Avian community response to southern pine ecosystem restoration for red-cockaded woodpeckers. Wilson J. Ornithol. 114 (3), 324–332.

Cooke, R.S.C., Bates, A.E., Eigenbrod, F., Schrodt, F., 2019. Global trade-offs of functional redundancy and functional dispersion for birds and mammals. Glob. Ecol. Biogeogr. 28 (4), 484–495.

Cromer, R.B., Lanham, J.D., Hanlin, H.H., 2002. Herpetofaunal response to gap and skidder-rut wetland creation in a southern bottomland hardwood forest. For. Sci. 48 (2), 407–413.

Crouzeilles, R., Curran, M., Ferreira, M.S., Lindenmayer, D.B., Grelle, C.E., Benayas, J.M. R., 2016. A global meta-analysis on the ecological drivers of forest restoration success. Nat. Commun. 7 (1), 1–8.

Davis, J.C., Castleberry, S.B., Kilgo, J.C., 2010. Influence of coarse woody debris on herpetofaunal communities in upland pine stands of the southeastern Coastal Plain. For. Ecol. Manag. 259 (6), 1111–1117.

Demarais, S., Verschuyl, J.P., Roloff, G.J., Miller, D.A., Wigley, T.B., 2017. Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the US. For. Ecol. Manag. 385, 308–330.

Diaz-Toribio, M.H., Carr, S., Putz, F.E., Roberts, D., 2020. Pine savanna plant community disassembly after fire suppression. J. Veg. Sci. 31 (2), 245–254.

DiMauro, D., Hunter Jr, M.L., 2002. Reproduction of amphibians in natural and anthropogenic temporary pools in managed forests. For. Sci. 48 (2), 397–406.

Drapeau, P., Villard, M.-A., Leduc, A., Hannon, S.J., Fischer, J., 2016. Natural disturbance regimes as templates for the response of bird species assemblages to contemporary forest management. Divers. Distrib. 22 (4), 385–399.

Earl, J.E., Harper, E., Hocking, D.J., Osbourn, M.S., Rittenhouse, T.G., Semlitsch, R.D., 2016. Effects of timber harvest on small mammal captures in experimental forestry plots. Anim. Biol. 66 (3-4), 347–362.

Earl, J.E., Harper, E.B., Hocking, D.J., Osbourn, M.S., Rittenhouse, T.A.G., Glennie, M., Semlitsch, R.D., 2017. Relative importance of timber harvest and habitat for reptiles in experimental forestry plots. For. Ecol. Manag. 402, 21–28.

Edie, S.M., Jablonski, D., Valentine, J.W., 2018. Contrasting responses of functional diversity to major losses in taxonomic diversity. Proc. Natl. Acad. Sci. U.S.A. 115 (4), 732–737.

Elliott, K.J., Vose, J.M., 2005. Effects of understory prescribed burning on shortleaf pine (Pinus echinata Mill.)/mixed-hardwood forests. J. Torrey Bot. 132 (2), 236–251.

Eskew, E.A., Willson, J.D., Winne, C.T., 2009. Ambush site selection and ontogenetic shifts in foraging strategy in a semi-aquatic pit viper, the Eastern cottonmouth. J. Zool. 277 (2), 179–186.

Estes, J.E., Smith, N.S., Palmisano, J.F., 1978. Sea otter predation and community organization in the western Aleutian Islands. Alaska. *Ecology* 59 (4), 822–833.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. Science 333 (6040), 301–306.

Fetzer, I., Johst, K., Schäwe, R., Banitz, T., Harms, H., Chatzinotas, A., 2015. The extent of functional redundancy changes as species' roles shift in different environments. Proc. Natl. Acad. Sci. U.S.A. 112 (48), 14888–14893.

Fox, T.R., Jokela, E.J., Allen, H.L., 2007. The development of pine plantation silviculture in the southern United States. J. For. 105 (7), 337–347.

de Fraga, R., Ferrão, M., Stow, A.J., Magnusson, W.E., Lima, A.P., 2018. Different environmental gradients affect different measures of snake β-diversity in the Amazon rainforests. PeerJ 6, e5628.

França, F.G.R., Mesquita, D.O., Nogueira, C.C., Araújo, A.F.B., 2008. Phylogeny and ecology determine morphological structure in a snake assemblage in the Central Brazilian Cerrado. Copeia 2008 (1), 23–38.

Frost, C.C., 1993, May. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In Proceedings of the Tall Timbers fire ecology conference (Vol. 18, pp. 17-43).

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W., Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proc. Royal Soc. B 282 (1801), 20142620. https://doi.org/10.1098/rspb.2014.2620.

Greene, R.E., Iglay, R.B., Evans, K.O., Miller, D.A., Wigley, T.B., Riffell, S.K., 2016. A meta-analysis of biodiversity responses to management of southeastern pine forests—opportunities for open pine conservation. For. Ecol Manag 360, 30–39.

Griffith, G.E., Bryce, S., Omernik, J., Rogers, A., 2004. Ecoregions of Texas. US Geological Survey, Reston, Virginia, USA.

Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. J. Veg. Sci. 17 (2), 255–260.

Guillemot, N., Kulbicki, M., Chabanet, P., Vigliola, L., Unsworth, R.K.F., 2011. Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. PloS one 6 (10), e26735.

Guldin, J.M., 2019. Restoration of native fire-adapted southern pine-dominated forest ecosystems: diversifying the tools in the silvicultural toolbox. For. Sci. 65 (4), 508–518.

Hansen, A.J., DeFries, R.S., Turner, W., 2012. Land Use Change and Biodiversity. In: Land Change Science. Springer, pp. 277–299.

Harrington, T.B., Miller, K.V., Park, N., 2013. Restoring a disappearing ecosystem: the Longleaf Pine Savanna (No. 13-04-R). USDA Forest Service-Savannah River, New Ellenton, SC.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T., Reich, P.B., 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348 (6232), 336–340.

Higgs, E., 2017. Novel and designed ecosystems. Restor. Ecol. 25 (1), 8–13.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486 (7401), 105–108.

Howey, C.A.F., Dickinson, M.B., Roosenburg, W.M., 2016. Effects of a landscape disturbance on the habitat use and behavior of the Black Racer. Copeia 104 (4), 853–863.

Howze, J.M., Smith, L.L., 2015. Spatial ecology and habitat use of the coachwhip in a Longleaf Pine forest. Southeast. Nat. 14 (2), 342–350.

Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. Science 317 (5834), 58–62.

Jaksic, F.M., 2003. How much functional redundancy is out there, or, are we willing to do away with potential backup species?. In: How landscapes change. Springer, Berlin, Heidelberg, pp. 255–262.

Jin, W., He, H.S., Shifley, S.R., Wang, W.J., Kabrick, J.M., Davidson, B.K., 2018. How can prescribed burning and harvesting restore shortleaf pine-oak woodland at the landscape scale in central United States? Modeling joint effects of harvest and fire regimes. For. Ecol. Manag. 410, 201–210.

Jobe, K.L., Montaña, C.G., Schalk, C.M., 2019. Emergent patterns between salamander prey and their predators. Food Webs 21, e00128. https://doi.org/10.1016/j.fooweb.2019.e00128.

Kurzava, L.M., Morin, P.J., 1998. Tests of functional equivalence: complementary roles of salamanders and fish in community organization. Ecology 79 (2), 477–489.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91 (1), 299–305.

Laliberté, E., Legendre, P., Shipley, B., Laliberté, M.E., 2014. Package 'FD'. Measuring functional diversity from multiple traits, and other tools for functional ecology.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A., Mayfield, M.M., 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecol. Lett. 13 (1), 76–86.

Laughlin, D.C., Chalmandrier, L., Joshi, C., Renton, M., Dwyer, J.M., Funk, J.L., Goslee, S., 2018. Generating species assemblages for restoration and experimentation: A new method that can simultaneously converge on average trait values and maximize functional diversity. Methods Ecol. Evol. 9 (7), 1764–1771.

Leavitt, D.J., Schalk, C.M., 2018. Functional perspectives on the dynamics of desert lizard assemblages. J. Arid Environ. 150, 34–41.

Leibold, M.A., Chase, J.M., Shurin, J.B., Downing, A.L., 1997. Species turnover and the regulation of trophic structure. Annu. Rev. Ecol. Evol. Syst. 28 (1), 467–494.

Litt, A.R., Provencher, L., Tanner, G.W., Franz, R., 2001. Herpetofaunal responses to restoration treatments of longleaf pine sandhills in Florida. Restor. Ecol. 9 (4), 462–474.

Loreau, M., Naeem, S., Inchausti, P., (Eds.). (2002). Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press on Demand.

Marks, P.L., Harcombe, P.A., 1975. Community diversity of coastal plain forests in southern east Texas. Ecology 56 (4), 1004–1008.

Mason, N.W.H., de Bello, F., Mouillot, D., Pavoine, S., Dray, S., Zobel, M., 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. J. Veg. Sci. 24 (5), 794–806.

Masters, R.E., Lochmiller, R.L., McMurry, S.T., Bukenhofer, G.A., 1998. Small mammal response to pine-grassland restoration for red-cockaded woodpeckers. Wildl. Soc. Bull. 148–158.

Masters, R.E., 2007. The importance of shortleaf pine for wildlife and diversity in mixed oak-pine forests and in pine-grassland woodlands. In Shortleaf pine restoration and ecology in the Ozarks: proceedings of a symposium (JM Kabrick, DC Dey, and D. Gwaze, eds.). United States Department of Agriculture, Forest Service, General Technical Report NRS-P-15 (pp. 35-46).

McCann, K.S., 2000. The diversity–stability debate. Nature 405 (6783), 228–233.

Mcgill, B., Enquist, B., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21 (4), 178–185.

Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8 (4), 391–400.

Miller, A.D., Roxburgh, S.H., Shea, K., 2011. How frequency and intensity shape diversity–disturbance relationships. Proc. Natl. Acad. Sci. U.S.A. 108 (14), 5643–5648.

Miller, D.A., Wigley, T.B., Miller, K.V., 2009. Managed forests and conservation of terrestrial biodiversity in the southern United States. J. For. 107 (4), 197–203.

Miller, K.V., Miller, J.H., 2004. Forestry herbicide influences on biodiversity and wildlife habitat in southern forests. Wildl. Soc. Bull. 32 (4), 1049–1060.

Mori, A.S., Furukawa, T., Sasaki, T., 2013. Response diversity determines the resilience of ecosystems to environmental change. Biol. 88 (2), 349–364.

Mouchet, M.A., Villéger, S., Mason, N.W., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24 (4), 867–876.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28 (3), 167–177.

Muscarella, R., Uriarte, M., 2016. Do community-weighted mean functional traits reflect optimal strategies? Proc. Royal Soc. B 283 (1827), 20152434. https://doi.org/10.1098/rspb.2015.2434.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D.i., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J.P.W., Purvis, A., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353 (6296), 288–291.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520 (7545), 45–50.

Newman, E.A., 2019. Disturbance ecology in the Anthropocene. Front Ecol. Evol. 7, 147.

Novak, M.V., Crane, D.P., Bell, L., Keiner, L., Gatto, C.R., McNabb, C.T., Parker, S.L., 2020. Spatial Ecology of Eastern Copperheads in Fragmented and Unfragmented Habitats. J. Herpetol. 54 (1), 97–106.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M.A.S.S., 2013. The vegan package. Community Ecology Package 10 (631–637), 719.

Pastro, L.A., Dickman, C.R., Letnic, M., 2011. Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. Ecol Appl 21 (8), 3238–3253.

Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5 (3), 402–411.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9 (6), 741–758.

Petchey, O.L., Gaston, K.J., 2007. Dendrograms and measuring functional diversity. Oikos 116 (8), 1422–1426.

Pickett, S.T., White, P.S., (Eds.). (2013). The ecology of natural disturbance and patch dynamics. Elsevier.

Prescott, G.W., Gilroy, J.J., Haugaasen, T., Medina Uribe, C.A., Foster, W.A., Edwards, D.P., 2016. Reducing the impacts of Neotropical oil palm development on functional diversity. Biol. Conserv. 197, 139–145.

Pulsford, S.A., Lindenmayer, D.B., Driscoll, D.A., 2016. A succession of theories: purging redundancy from disturbance theory. Biol. Rev. 91 (1), 148–167.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rader, R., Bartomeus, I., Tylianakis, J.M., Laliberté, E., van Kleunen, M., 2014. The winners and losers of land use intensification: Pollinator community disassembly is non-random and alters functional diversity. Divers. Distrib. 20 (8), 908–917.

Rossman, D.A., 1996. The garter Snakes: Evolution and Ecology. University of Oklahoma Press.

Russell, C.C., Thill, R.E., Kulhavy, D., 2002. The Stephen F. Austin Experimental Forest. East. Tex. Hist. J. 40 (2), 11.

Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Frontiers in Ecology and the Environment 11 (s1), e15–e24.

Schalk, C.M., Cove, M.V., 2018. Squamates as prey: Predator diversity patterns and predator-prey size relationships. Food Webs 17, e00103.

Schalk, C.M., Weng, Y.H., Adams, C.S., Saenz, D., in press. Spatiotemporal patterns of snake captures and activity in upland pine forests. Am. Midl. Nat.

Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity indices. Ecol. Monogr. 80 (3), 469–484.

Schmitz, O.J., 2009. Effects of predator functional diversity on grassland ecosystem function. Ecology 90 (9), 2339–2345.

Shine, R., 2003. Reproductive strategies in snakes. Proc. Royal Soc. B 270 (1519), 995–1004.

Shine, R., Bonnet, X., 2000. Snakes: a new 'model organism' in ecological research? Trends Ecol. Evol. 15 (6), 221–222.

Sohngen, B., Brown, S., 2006. The influence of conversion of forest types on carbon sequestration and other ecosystem services in the South Central United States. Ecol. Econ. 57 (4), 698–708.

Steen, D.A., Smith, L.L., Conner, L.M., Litt, A.R., Provencher, L., Hiers, J.K., Pokswinski, S., Guyer, C., 2013. Reptile assemblage response to restoration of fire-suppressed longleaf pine sandhills. Ecol. Appl. 23 (1), 148–158.

Steen, D.A., McClure, C.J.W., Brock, J.C., Craig Rudolph, D., Pierce, J.B., Lee, J.R., Jeffrey Humphries, W., Gregory, B.B., Sutton, W.B., Smith, L.L., Baxley, D.L., Stevenson, D.J., Guyer, C., Meiri, S., 2014. Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions. J. Anim. Ecol. 83 (1), 286–295.

Stier, A.C., Hanson, K.M., Holbrook, S.J., Schmitt, R.J., Brooks, A.J., 2014. Predation and landscape characteristics independently affect reef fish community organization. Ecology 95 (5), 1294–1307.

Sutton, W.B., Wang, Y., Schweitzer, C.J., McClure, C.J.W., 2017. Spatial ecology and multi-scale habitat selection of the Copperhead (Agkistrodon contortrix) in a managed forest landscape. For. Ecol. Manag. 391, 469–481.

Tennant, A., 2006. Lone Star Field Guide to Texas Snakes. Taylor Trade Publishing.

Todd, B.D., Nowakowski, A.J., Rose, J.P., Price, S.J., 2017. Species traits explaining sensitivity of snakes to human land use estimated from citizen science data. Biol. Conserv. 206, 31–36.

Todd, B.D., Nowakowski, A.J., Meiri, S., 2021. Ectothermy and the macroecology of home range scaling in snakes. Glob. Ecol. Biogeogr. 30 (1), 262–276.

Vale, T., (Ed.). (2013). Fire, native peoples, and the natural landscape. Island Press.

Verschuyl, J., Riffell, S., Miller, D., Wigley, T.B., 2011. Biodiversity response to intensive biomass production from forest thinning in North American forests–a meta-analysis. For. Ecol. Manag. 261 (2), 221–232.

Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. Glob. Ecol. Biogeogr. 22 (6), 671–681.

Villéger, S., Miranda, J.R., Hernández, D.F., Mouillot, D., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol Appl 20 (6), 1512–1522.

Weatherhead, P.J., Madsen, T., 2009. Linking behavioral ecology to conservation objectives. In: Snakes: Ecology and Conservation, pp. 149–171.

Werler, J.E., Dixon, J.R., 2010. Texas Snakes: Identification, Distribution, and Natural History. University of Texas Press.

Winne, C.T., Willson, J.D., Andrews, K.M., Reed, R.N., 2006. Efficacy of marking snakes with disposable medical cautery units. Herpetol. Rev. 37 (1), 52–54.