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FOOD-WEB AND FUNCTIONAL TRAIT COMMUNITY STRUCTURE OF PREDATOR ASSEMBLAGES IN PINE FORESTS UNDER DIFFERENT MANAGEMENT REGIMES

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FOOD-WEB AND FUNCTIONAL TRAIT COMMUNITY STRUCTURE OF PREDATOR ASSEMBLAGES IN PINE FORESTS UNDER DIFFERENT MANAGEMENT REGIMES

By

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FOOD-WEB AND FUNCTIONAL TRAIT COMMUNITY STRUCTURE OF PREDATOR ASSEMBLAGES IN PINE FORESTS UNDER DIFFERENT MANAGEMENT REGIMES

By

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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 taxonomic, functional, and food-web approaches, I investigated the impacts of forest management practices in structuring predator communities in two pine forest systems of eastern Texas. The results of this study indicate that the increased frequency of forest management practices such as prescribed fires and thinning operations encourages predator diversity while increasing functional and trophic redundancy within predator assemblages. Consequently, increased frequency of such activities may lead to greater stability and resilience in pine-forest ecosystems. My research enhances the understanding of the influence of anthropogenic disturbances in terrestrial ecosystems, and highlights the importance of ecological restoration that incorporates a multi-dimensional approach to meet desired restoration goals and ensure the health of pine ecosystems.

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INTRODUCTION

Anthropogenic impacts are drastically modifying environments, affecting the structure and function of biological diversity in ecosystems across the globe (Bocherens 2018; Hansen et al. 2012; Hautier et al. 2015, Newbold et al. 2015, 2016, Vitousek et al 1997). 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). Many studies have found a positive correlation between diversity and stability (Campbell et al. 2011, McCann 2000). However, the extent of this relationship is still limited in natural systems under persistent human influences (Ives and Carpenter 2007, Loreau et al 2002, McCann 2000). Persistent anthropogenic pressures/impacts, both intentional (e.g., fire suppression and overharvesting) and inadvertent (e.g., eutrophication), can have substantial effects on the resilience of ecological communities and the stability of ecosystems (Mori et al. 2013). Yet, the inherent complexity of ecosystems presents challenges to understanding these relationships. Ecosystem stability is multi-faceted, with different ecosystem properties (e.g., biotic material production, nutrient cycles, biological diversity) leading to multiple diversity-stability relationships (Ives and Carpenter 2007).

Therefore, disentangling the mechanisms that define these processes is dependent on the nature of disturbances, and requires knowledge of how both species interactions and environments are subsequently altered in response (Hooper et al. 2012). An ecological disturbance is defined as any event that disrupts the structure of an ecosystem, community, or population that changes resource availability or the physical environment (Newman 2019, Pickett and White 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. For example, many fire-climax pine ecosystems have adapted dependence on natural fire regimes, as successional stages are maintained through these disturbance-mediated processes (Vale 2013). Therefore, alterations to fire regimes can have a substantial impact on vegetative heterogeneity and resource availability in these systems (Miller et al. 2011). Consequently, different habitats and their associated communities are expected to respond in different ways across disturbance gradients. For example, many studies have described significant species loss and subsequent community disassembly of vegetative communities following anthropic promotion or interruption of fire (Buisson et al. 2019, Brudvig and Damschen 2011, Diaz-Toribio et al. 2020, Miller et al. 2009). These modifications to the composition and structure of 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 2007).

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 as a form of land management (Ryan et al. 2013). Such practices have the potential to substantially alter successional trajectories and drive communities to alternative stable states (Beckage and Ellingwood 2008). As such, these practices have implications for the stability of ecosystems and the resilience of ecological communities. Subsequently, the relationship between species richness on ecosystem function and stability has become an increasingly studied and experimentally applied approach to understanding community assembly in a wide variety of systems prone to, or maintained by, disturbance (Ostfeld and LoGuidice 2003, Swartz et al. 2000).

Pine forest ecosystems of the southern United States are known to support high biodiversity and provide 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). However, these systems contribute greatly to global timber production, and as a result, these ecosystems have undergone dramatic changes over time (Walker and Oswald 1999). Large tracts of native pine forests that once covered much of the region were significantly reduced by the 1930s because of extensive logging and conversion to agricultural croplands (Frost 1993). In response to the large-scale deforestation of previous decades, management approaches have transitioned to support widespread intensive silviculture of more economically viable pine species to meet industry demands (Fox et al. 2007). This high demand for timber production, in addition to fluctuations in land ownership and increased urbanization, have resulted in substantial alterations to disturbance regimes, mainly the suppression of natural and anthropogenic fires (Fox et al. 2007, Frost 1993, Vale 2013). With these trends likely to continue, areas of fire-maintained natural pine forests are expected to decrease (Wear and Greis 2002). Restoration of these native pine forest habitats and the diversity they support is of critical ecological and economic importance. The continued interest in preserving these ecosystems has led to management efforts that reintroduce disturbance regimes that mimic natural conditions that have otherwise been suppressed (Guldin 2019, Jin et al. 2018). The success of such endeavors will ultimately rely on the ability of land managers to develop and apply robust and ecologically sustainable forest management plans (Crouzeilles et al. 2016). Thus, understanding the underlying mechanisms of community assembly in these pine systems and identifying diversity-stability relationships in forests affected by habitat degradation and alteration is of the utmost importance (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, DeMaynadier and Hunter 1995, 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 for predicting how the loss or addition of species affect the functional properties of an ecosystem. Taxonomic diversity approaches largely ignore the reality that communities are composed of species with different evolutionary histories as well as a diverse array of morphological, ecological, and physiological traits that influence how species interact among each other and with their environment (DeVictor et al. 2010, Graham and Fine 2008, Jarzyna and Jetz 2018, Petchey and Gaston 2002, 2006, Tillman 2001). Communities may exhibit drastic contrasts between different aspects of biodiversity, suggesting that species diversity (i.e., species richness and abundance) may not always be a reliable predictor of the diversity and strength of functional effects of species assemblages (De Bello et al. 2010, Fukami et al. 2005, Villéger et al. 2010). There is a growing body of research incorporating trait-based approaches to provide a more robust and integrated framework to understand why species persist or decline in response to natural or anthropogenic gradients (Campbell and Mandrak 2020, Leavitt and Schalk 2018, Schalk et al. 2015, Violle et al. 2007, Weiher et al. 2011).

Incorporating species functional traits is a powerful tool for understanding the nature of species interactions in complex ecosystems (Buchmann and Roy 2002, McGill et al. 2006). Apex predators, for example, can have cascading effects on the organization of biodiversity at lower trophic levels, and consequently, ecosystem function (Estes et al. 2011, Carpenter et al. 2001). 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). Therefore, the strength and persistence of predator-prey interactions can either stabilize or destabilize ecosystems. Strong predator-prey interactions stabilize systems as the additive effects of species and their interactions support the complexity of ecosystems (Allesina and Tang 2012). Weak predator-prey interactions 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). Despite the apparent 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 in the face of increasing environmental change brought forth by changing land-use practices (Bihn et al. 2010).

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 are obligate predators that range from generalized to specialized feeders, with prey preferences, prey size, and foraging modes that vary among species (Shine and Bonnet 2000, Weatherhead and Madsen 2009). Most species utilize a number of habitat types within their home range, serving as suitable indicators of the quality of multiple habitats within an ecosystem (Beaupre and Douglas 2009). Additionally, snakes generally exhibit predictable patterns of seasonal activity from year to year. For these reasons, snakes are useful indicators of ecosystem properties (e.g., habitat quality, regulation of prey populations, trophic-linkages), and an informative taxon for understanding these properties within ecosystems (Beaupre and Douglas 2009). Despite this, studies investigating how snake predators respond to disturbance in managed-pine systems are limited, and very few studies have integrated both taxonomic and functional approaches to elucidate assembly mechanisms in these predator assemblages (but see de Fraga et al. 2018, de França et al. 2008).

Here, I investigate the underlying patterns in which disturbance regimes organize predator assemblages in southern pine forests. I quantify both taxonomic and functional diversity to investigate how the frequency of forest management practices (i.e., prescribed fire, thinning) alters the structure and function of predator communities. Sites managed by a high-frequency of disturbance (hereafter high-frequency) encourage habitat heterogeneity by maintaining a multitude of environmental conditions. For example, prescribed fires and thinning operations alter the spatial complexity of vegetation and may provide a wider variety of microhabitats available to snake predators and prey, subsequently increasing prey availability to snake consumers (Litt et al. 2001). Utilizing snakes as model organisms to investigate these relationships, I hypothesized that taxonomic diversity would differ in response to different forest management regimes.

Specifically, I predicted that taxonomic diversity would be higher in high-frequency sites that experience disturbances that mimic natural disturbance regimes. Through these processes (e.g., frequent burning and thinning), I expected high-frequency sites to support a greater number of snake species and have higher taxonomic species evenness across these sites. Low-frequency management regimes lead to the homogenization of certain environmental conditions. For example, midstory development and increased buildup of detritus in closed-canopy forests may limit the diversity of microhabitats in these systems as well as the abundance and composition of prey resources important for maintaining high taxonomic diversity of snake predators. Therefore, I predicted that the pattern observed in low-frequency sites would exhibit a more uneven assemblage structure that is dominated by a few species. Additionally, I hypothesized that functional diversity would differ in response between forest management regimes. I predicted that functional diversity would increase at high-frequency sites, with functionally unique species persisting as an increasing diversity of microhabitats and prey resources are provided under active management conditions. In the low-frequency sites, I predicted that snake assemblages would exhibit lower functional diversity through the biotic homogenization of dominant snake species that possess traits better suited for persisting along the above predicted constraints.

METHODS

Study Area

This study was conducted in the Pineywoods ecoregion of Texas, in the pine-dominated mesic uplands of the northwestern Gulf Coastal Plain (Appendix, S1). 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 (Marks and Harcombe 1975). 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). However, widespread application of varied management strategies promoting commercial silviculture, along with the suppression of fire, has resulted in a multitude of structural and compositional responses within the vegetative communities that describe these upland sites today (Frost 1993, Vale 2013). Many of the historical shortleaf pine forests of the region are now either displaced by commercially favorable pine species or hardwood tree species that persisted in the absence of natural and anthropogenic fire (Elliot et al. 2005).

Surveys of snakes and representative prey assemblages were conducted at the Boggy Slough Conservation Area (SBSCA; hereafter high-frequency treatment) and the Stephen F. Austin Experimental Forest (SFAEF; hereafter low-frequency treatment) located in Trinity and Nacogdoches County of east Texas (Appendix, S1, S2). Average annual precipitation and average annual temperatures are similar between treatments (SBSCA: 1251 mm, 24.9°C, 12.3°C; SFAEF: 1243 mm, 25.5°C, 13.1°C) (Arguez et al. 2010). The high-frequency treatment, owned and operated by the T. L. L. Temple Foundation, is actively managed for a variety of conservation and production goals through the implementation of frequent prescribed burns on 1-3 year fire intervals, thinning, and regeneration harvests (R. Sanders, personal communication). The low-frequency treatment (SFAEF) is owned and operated by the U.S. Forest Service (USFS) as part of the Southern Research Station network. Until the early 1960s, the property was primarily used for silvicultural research, but has since supported wildlife research efforts conducted by the Wildlife Habitat and Silviculture Laboratory of the USFS, Southern Research Station (Russell et al. 2002). The low-frequency treatment sites experience burn intervals of 5-8 years, and has had limited forest harvesting within the last 50 years (D. Saenz, personal communication). Burn-intervals at these sites limit the effectiveness of prescribed fire practices that are carried out at sites within this treatment, and are not typically conducted at time when prescribed fire conditions are optimal. As such, these practices are less effective at altering the overall structure of vegetation that characterizes habitats within the low-frequency treatment.

Thus, determining how ecological processes will respond to forest management is a difficult endeavor because different forest management practices are dependent on the goals of land practitioners. For these reasons we define the nature of these anthropogenic practices in the context of our chosen treatments. The high-frequency treatment was characterized by having an increased practice frequency, meaning that intensive and frequent application of prescribed fires and thinning operations are associated with restoring open forest conditions; whereas, decreased practice frequency referred to closed forest conditions that have resulted from the lack of intensive and infrequent fires that are not efficient enough to drastically alter current stand conditions (see Van Lear et al. 2005).

Habitat composition and structure between the high-frequency and low-frequency treatments is substantially different despite a limited understanding of the effects of past disturbances on current stand conditions (Figure 1, see Chapter 2).

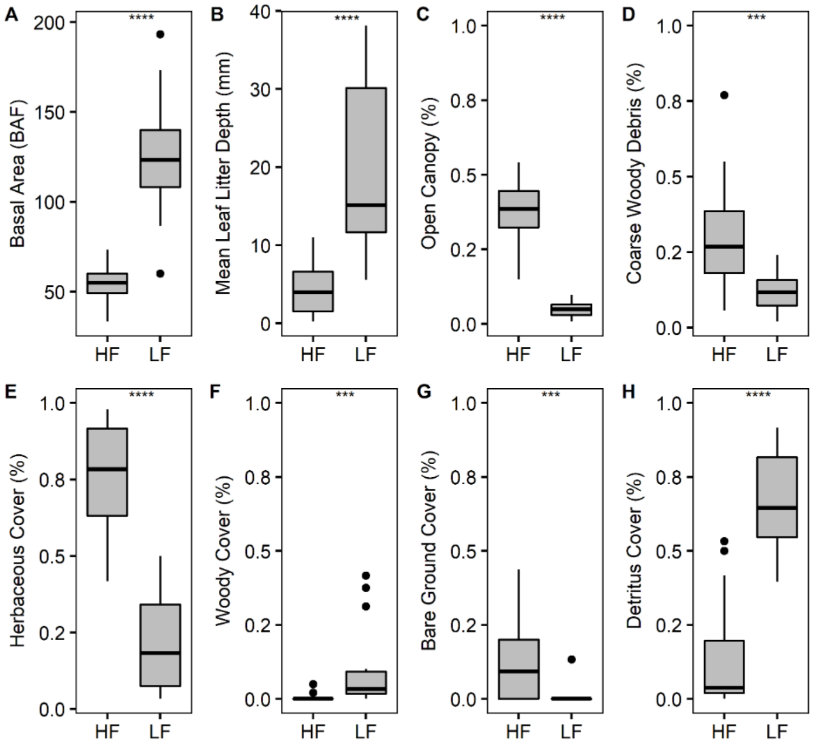

Figure 1. Comparisons of habitat variables under high-frequency (e.g., 1-3 year burn intervals, thinning; HF) and low-frequency (e.g., 5-8 year burn intervals, no thinning; LF) management regimes. A) Basal Area (BAF), a measure of stand density; B) Mean leaf litter depth; C) Percent open canopy; D) Percentage 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., *** = $P<0.001$, **** = $P<0.0001$).

The high-frequency sites are characterized by an open, park-like habitat structure in which abundant sunlight reaches the forest floor. The overstory is dominated by *P. echinata* with some stands containing a small hardwood component of primarily southern red oak (*Quercus falcata*). The well-developed herbaceous understory supports a diversity of grasses, sedges, and forbs including Florida paspalum (*Paspalum floridanum*), little bluestem (*Schizachyrium scoparium*), globe flatsedge (*Cyperus echinatus*), blackeyed susan (*Rudbeckia hirta*), catclaw sensitive briar (*Mimosa nutallii*), and southern dewberry (*Rubus trivialis*). Habitat structure in the low-frequency sites is characterized as a closed-canopy forest with an abundance of detritus collected on the forest floor (Figure 1). The overstory is dominated by dense stands of mixed *P. taeda* and *P. echinata*, featuring a prominent hardwood component of various oak species in the red oak group (*Quercus* sect. *Lobatae*). These sites also possess a dense midstory component dominated by sweetgum (*Liquidamber styraciflua*) and sassafrass (*Sassafras albidum*). Because of these differences in forest structure and habitat, these locations were considered appropriate respective units for comparing high-frequency vs. low-frequency management regimes.

Snake Sampling

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 per year (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. 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 at sites within the high-frequency treatment from 2018-2020 and at sites within the low-frequency treatment from 2019-2020, from May-July in accordance with seasonal peaks in activity observed from previous snake trapping efforts within the region (J. Pierce, unpublished data).

Captured snakes were processed in the lab and released within 48 hours. All venomous snakes were anesthetized with isoflurane to allow safe handling while obtaining morphological measurements (Beaupre et al. 2004, Heard 2001). 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). For each marked individual, snout-to-vent length (SVL), tail length (TL), and body mass were recorded in the laboratory using a meter stick and a digital scale. Other functional trait data for continuous traits were measured using digital calipers (±0.01 mm) and adjusted for body size using the residual scores of linear regressions with SVL as the independent variable (Appendix, S3). Functional trait data for categorical traits were obtained from the literature (Howze and Smith 2015, Pierce et al. 2008, Sanders and Jacob 1981, Shine 2003, Sutton et al. 2017, Tennant 2006, Werler and Dixon 2010) (Appendix, S3).

Taxonomic Diversity

I measured species richness and evenness for each management treatment as whole using the relative abundances of species by trapping effort. Additionally, to gain a general understanding of species composition patterns in each management treatment and determine which species were driving differences in overall community organization, I performed a similarity percentages analysis using the ‘vegan’ package in R to determine the contribution of species to the overall dissimilarity between high frequency and low frequency treatments (Oksanen et al. 2013).

Taxonomic β-diversity

Despite the limitations of taxonomy for understanding the structure of species assemblages and the subsequent consequences on ecosystem functioning, incorporating components of both taxonomic and functional beta-diversity provides a better framework for testing the ecological processes structuring communities (Villégar et al. 2008). Decomposing beta diversity and partitioning both taxonomic and functional beta-diversity into turnover and nestedness components allows for the direct comparison of patterns that indicate niche differentiation, the intensity of niche filtering intensity, or functional convergence between communities (Villégar et al. 2013).

Therefore, I performed a Principle Coordinates Analysis (PCoA) ordination to describe differences in taxonomic composition and dispersion. Taxonomic dispersion has been proposed as an alternative measure of taxonomic β-diversity that is useful for interpreting differences within and between allocated treatments as it allows the relative weight of species abundances placed on changes in composition versus abundance to be specified explicitly (Anderson et al. 2006). Using this methodology, pairwise compositional dissimilarity between independent sampling sites based on species abundances was quantified by creating a dissimilarity matrix based on the Bray-Curtis dissimilarity. I then tested if sites within high-frequency and low-frequency treatments 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 high-frequency and low-frequency treatments I used the average distance of species to the group centroid as a measure of multivariate dispersion and performed a PERMUTEST (Anderson 2006).

To describe differences in taxonomic β-diversity, I 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 sites. All statistical analyses were performed in the ‘vegan’ package in R (Oksanen et al. 2013, R Development Core Team 2015).

Functional β-diversity

Functional traits were analyzed on 406 individual adult snakes represented by 19 species (number of snakes per treatment: high-frequency: 219 individuals, low-frequency: 187 individuals). I constructed a trait matrix of 13 continuous and categorical traits ecologically relative to functions of feeding ecology, habitat use, and reproductive mode (Beaupre and Douglass 2009, Pierce et al. 2008, Rossman 1996, Todd et al. 2017; Appendix S3). For continuous traits, I calculated community-weighted means and used these average values per species (Petchey and Gaston 2006). I coded categorical traits into independent binary traits because the levels that described them were not mutually exclusive (Petchey and Gaston 2007).

To compare and make inferences on functional diversity patterns across management regimes, I used the distance-based functional diversity (dbFD) function in the ‘FD’ package in R (Laliberté et al. 2014). When executed, the dbFD function performs an initial test to determine whether trait data require a reduction in dimensionality. This is advantageous as this reduces redundant trait axes that could overly weight the estimation of FD using multiple covarying traits (Laliberté et al. 2014). In addition, dbFD calculates Gower distances between species, an index that is better suited for analyzing mixed continuous and discrete traits. The Gower distance matrix is then transformed by calculating square roots of the produced dissimilarities to avoid negative eigenvalues in the PCoA calculated from the distance metric (Laliberté and

Legendre 2010). Principle Coordinates Analysis was used to obtain scores representing four different functional indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis). In which FRic measures the volume of trait space occupied by an assemblage, whereas FEve and FDiv characterize how regular or dissimilar, respectively, the species are distributed in functional trait space (Villégar 2008). We used the FDis index to represent an alternative measure of functional β-diversity as this index estimates functional diversity based on average distances to the centroid of multivariate dispersion (Anderson 2006, Legendre and Legendre 2010). In addition, FDis is not affected by species richness, is more flexible when considering the numbers and types of traits used, and is not as strongly influenced by the presence of outliers (Anderson et al. 2006). To test for differences for each functional diversity metric between high-frequency and low frequency sites I grouped independent alpha diversities by management regime, testing for normality using the Shapiro-Wilk test. Since none of the indices met the assumptions of parametric t-test, I tested for differences in means using Wilcoxon rank sum test for each metric.

To visualize the functional trait space occupied by the snake communities in high-frequency versus low-frequency treatments, I performed a PCoA with species scores calculated from the dbFD analyses in the R package ‘FD’ (Laliberté and Legendre 2010). 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). I used linear models to compare each of these metrics between treatment sites, 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, I calculated the community-weighted means for continuous functional traits. Because these data met the assumptions of normality and homogeneity of variance, I tested for differences between treatment sites using paired t-tests. Additionally, I 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 I used Wilcoxon rank sum tests to test for significant differences in each categorical trait between high-frequency and low-frequency sites.

RESULTS

Taxonomic Diversity

Overall, mean species richness was higher in the high-frequency treatment (n = 19 spp.) than the low-frequency treatment (n = 12 spp.). In addition, there was complete nestedness of species richness as all species captured at the low-frequency treatment were also captured at the high-frequency treatment. Species' abundances shifted across management regimes as well (Table 1).

Table 1. Similarity percentages analysis (SIMPER) analysis identifying the contribution (%) of each snake species (n = 19 spp.) to the Bray-Curtis dissimilarity metric between high-frequency (HF) and low-frequency (LF) management regimes. Abundance values used in the dissimilarity matrix were calculated relative to total trap effort across high-frequency (1350 trap days) and low-frequency (850 trap days) sites. Species are listed in order of their contribution to differences between management regimes and common names are provided in Appendix S6.

Snake species	Average dissimilarity	Mean contribution (HF)	Mean contribution (LF)	Cumulative contribution
Agkistrodon contortrix (AGCO)	0.2037	0.0296	0.0918	0.4741
Coluber constrictor (COCO)	0.0839	0.0385	0.0129	0.6692
Agkistrodon piscivorus (AGPI)	0.0326	0.0111	0.0012	0.7450
Coluber flagellum (COFL)	0.0259	0.0126	0.0047	0.8052
Pantherophis obsoletus (PAOB)	0.0177	0.0252	0.0306	0.8464
Sistrurus miliarius (SIMI)	0.0121	0.0037	0.0000	0.8747
Micrurus tener (MITE)	0.0120	0.0022	0.0059	0.9026
Lampropeltis triangulum (LATR)	0.0073	0.0022	0.0000	0.9195
Nerodia fasciata (NEFA)	0.0057	0.0030	0.0047	0.9328

Table 1. Continued

Snake species	Average dissimilarity	Mean contribution (HF)	Mean contribution (LF)	Cumulative contribution
Farancia abacura (FAAB)	0.0049	0.0015	0.0000	0.9441
Haldea striatula (HAST)	0.0049	0.0015	0.0000	0.9555
Lampropeltis holbrookii (LAHO)	0.0049	0.0015	0.0000	0.9668
Nerodia erythrogaster (NEER)	0.0043	0.0022	0.0035	0.9767
Crotalus horridus (CRHO)	0.0029	0.0015	0.0024	0.9834
Storeria dekayi (STDE)	0.0024	0.0007	0.0000	0.9890
Heterodon platirhinos (HEPL)	0.0019	0.0030	0.0035	0.9934
Lampropeltis calligaster (LACA)	0.0014	0.0007	0.0012	0.9967
Opheodrys aestivus (OPAE)	0.0014	0.0007	0.0012	1.0000

Specifically, *Agkistrodon contortrix*, *Coluber constrictor*, and *Agkistrodon piscivorus* contributed the most to the dissimilarity observed between treatments (Table 1). This dissimilarity was due to high captures of *A. contortrix* at the low-frequency sites, high captures of *C. constrictor* at the high-frequency sites, and having only a single capture of *A. piscivorus* at one low-frequency site (Appendix, S4). The high frequency treatment was more even in terms of species abundances, as captures in the low frequency sites were dominated by three species, *A. contortrix*, *Thamnophis proximus*, and *Pantherophis obsoletus* (Appendix, S4).

Taxonomic β-diversity, in terms of species composition, was significantly greater in high-frequency sites than low-frequency sites (PERMANOVA, n = 999, F = 7.5129, Pr(>F) = 0.008; Figure 2). Further analyses of taxonomic β-dispersion revealed that assemblages in the high frequency sites also showed a higher degree of taxonomic diversity (β-dispersion = 0.4103) in terms of species richness and abundance than assemblages in the low frequency sites (β-dispersion = 0.2796) (PERMUTEST, n = 999, F = 9.724, Pr(>F) = 0.001).

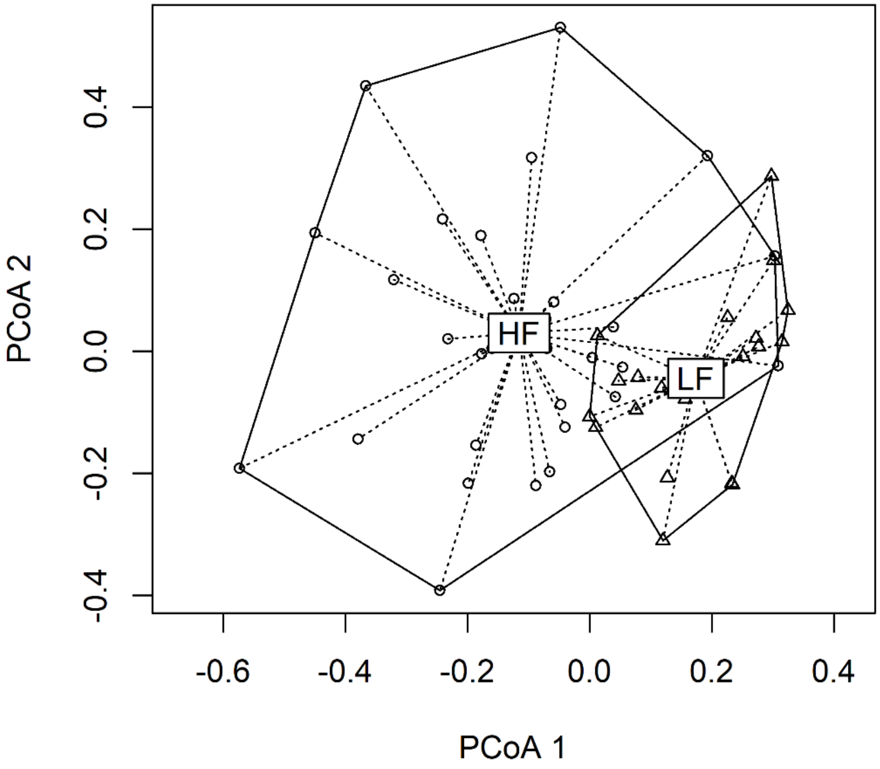

Figure 2. Principle Coordinates Analysis (PCoA) of taxonomic β-dispersion observed inhigh-frequency (HF; open circles) and low-frequency (LF; open triangles) sites. Pairwise compositional dissimilarity between independent sites based on species occurrences was quantified by creating a dissimilarity matrix based on the Bray-Curtis dissimilarity.

Functional Diversity

Partitioning assemblages in regards to their functional diversities and according to management regime, I found no difference in snake FRic between high-frequency and low frequency sites despite differences in taxonomic species richness (Wilcoxon rank sum, $p = 0.845$; Figure 3A, 3B). I observed a high amount of overlap 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 (Figure 4). Instead, I observed that the subtle differences in overall functional richness between high frequency and low frequency treatments were most likely due to differences in intraspecific variation of shared species within treatment sites (Figure 4).

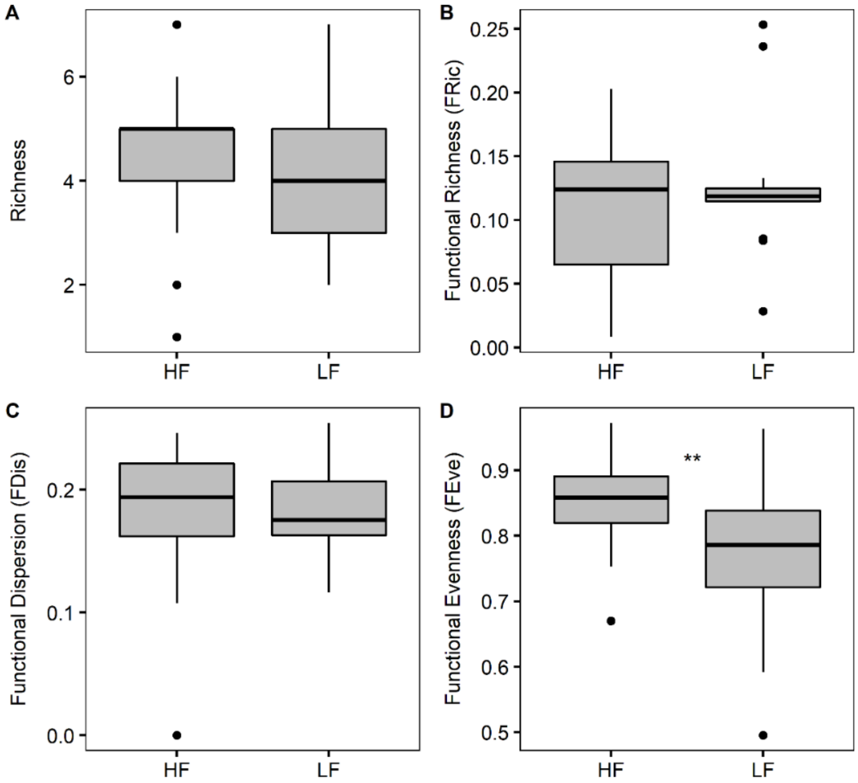

Figure 3. Functional α-diversity indices of snake communities located in high-frequency management (e.g., thinning, burning) and low-frequency management forests. A) Species richness of assemblages (sampling sites) within each treatment, B) Functional richness (FRic); minimum convex hull volume C) Functional 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).

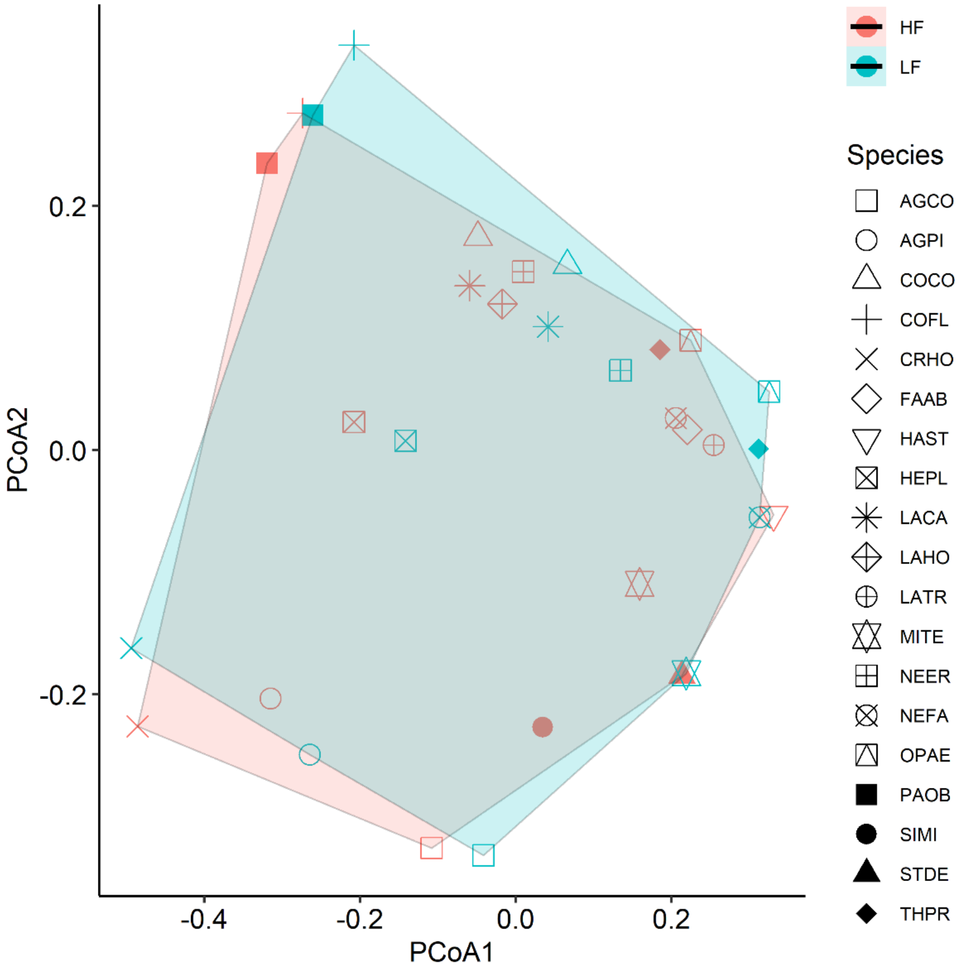

Figure 4. Principle coordinates analysis of snake communities in functional trait space. Convex hulls represent the functional richness (FRic) of snake communities at high frequency (red) and low frequency (blue) sites. Species codes are listed in Table 1.

I also observed no differences in overall FDis between high frequency and low frequency treatments (Wilcoxon rank sum test, $p = 0.14$; Figure 3C). However, I found that FEve in the high frequency treatment was significantly greater than in the low frequency treatment (Wilcoxon rank sum test, $p < 0.001$; Figure 3D). These results suggest 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 (Figure 5A, 5B).

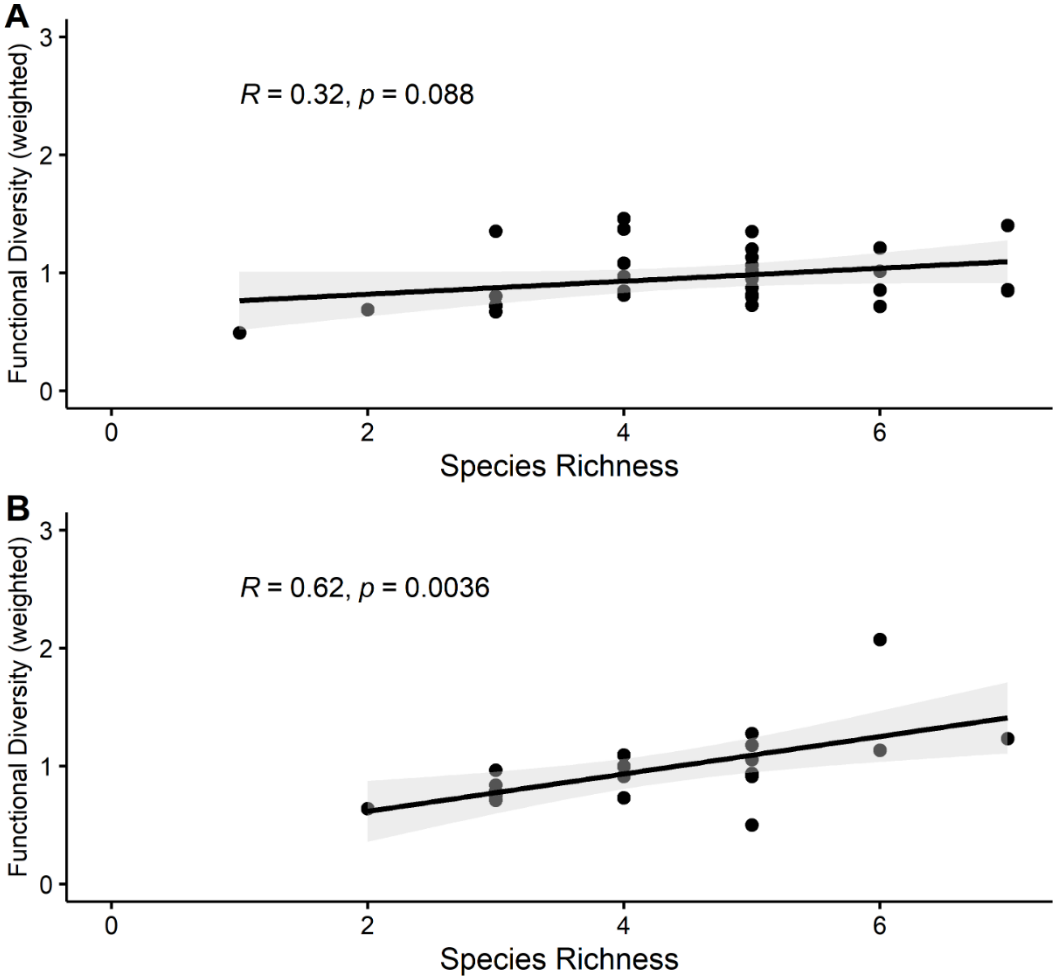

Figure 5. Linear regressions of the relationship between functional diversity and species richness. The functional diversity index was produced from UPGMA trees with A) representing high-frequency sampling sites and B) representing low-frequency sites.

Analyzing community-weighted means of continuous traits between high frequency and low frequency treatments resulted in a general pattern towards larger-bodied snakes in the high frequency treatment (Figure 6). Of the eleven continuous traits measured, only jaw length was not significantly different between high frequency and low frequency treatments (Figure 6). 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 (Mann-Whitney, $p < 0.05$; Figure 7). The high abundances of *A. contortrix* (a viperid snake) occurring in the low frequency treatment are the most likely explanation of those traits prevalence across that snake assemblage.

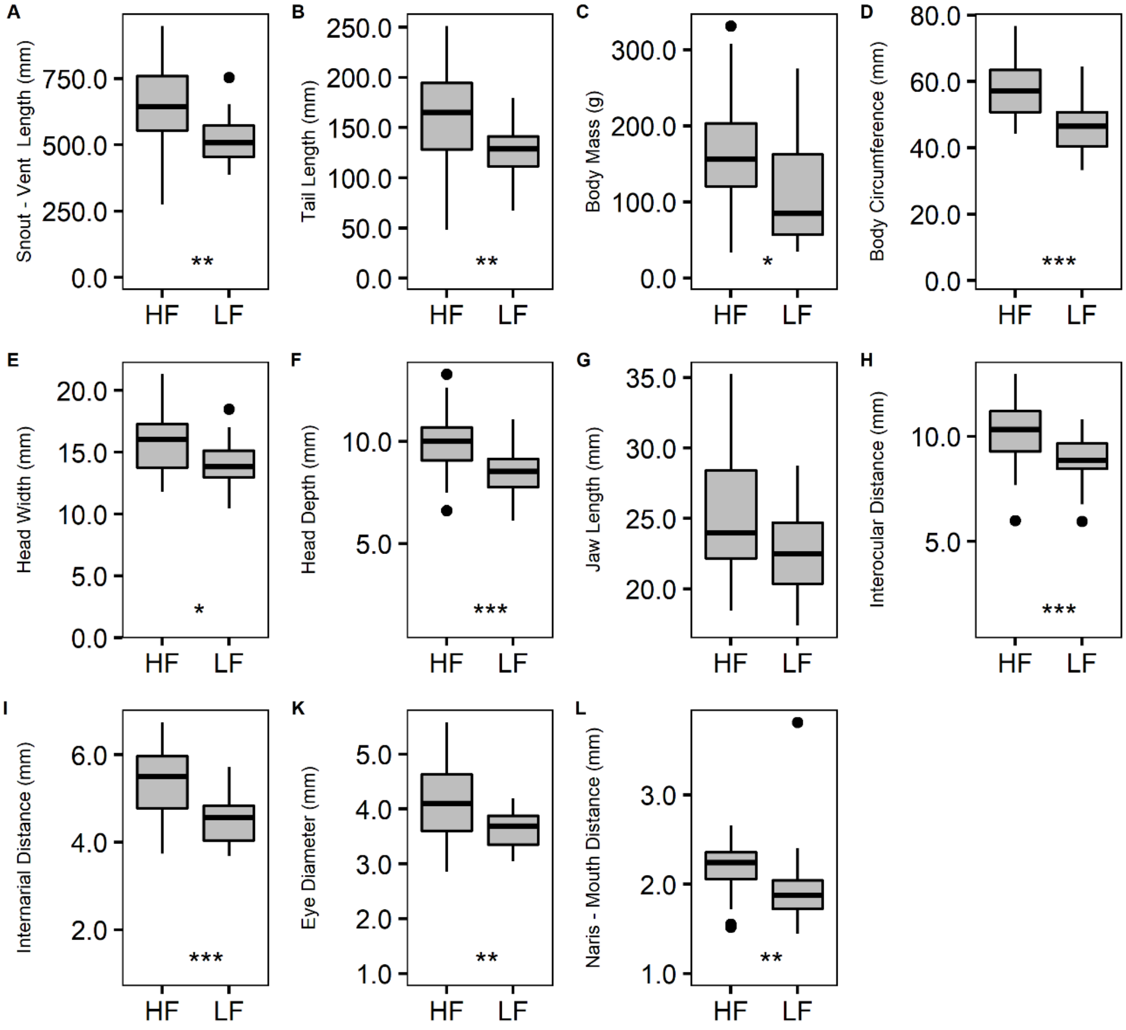

Figure 6. Community weighted means of the eleven continuous functional traits of snakes located in high-frequency management (e.g., subjected to thinning and burning) and low-frequency management forests. A significant difference in trait is indicated by an asterisk (∗). Asterisks correspond to significance level (e.g., * = P<0.05, ** = P<0.01, *** = P<0.001).

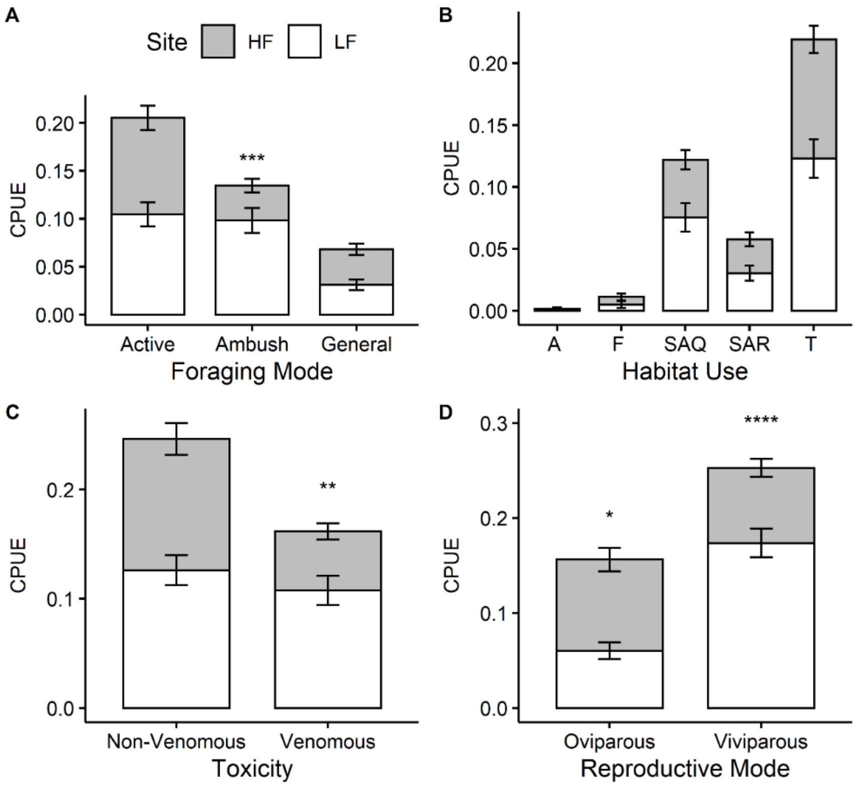

Figure 7. Trait distributions of categorical traits in high frequency and low frequency sites calculated the capture per unit effort values (CPUE's) of sampled assemblages. Abbreviations for habitat use categories in (B) are as follows: A, mostly aquatic; F, semi-fossorial; SAQ, semi-aquatic; SAR, semi-arboreal; 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).

DISCUSSION

Overall, I observed contrasting patterns of taxonomic and functional diversity within snake assemblages in regards to the frequency of applied forest management practices between treatments. I found that the high-frequency treatment supported a greater number of species than the low-frequency treatment, supporting my first hypothesis. Despite greater taxonomic diversity in high-frequency sites, functional diversity was comparatively similar across management regimes, therefore, I failed to support the hypothesis that functional diversity would be higher in the high-frequency treatment.

The observed differences in taxonomic diversity between management treatments in this study is consistent with studies of other taxa in similarly managed systems. 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, Greene et al. 2016, Pastro et al. 2011, Masters et al 1998, Singleton et al. 2013). 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, practice frequency may alter the taxonomic composition of snake communities through the provisioning of microhabitats. For example, the loss or lower abundances 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 these species ability to find suitable microhabitats for refuge and foraging in infrequently managed sites. *Coluber contrictor* and *C. flagellum*, both visual hunters with high resource demands, must search for food throughout the day often utilizing cover in multiple microhabitats to thermoregulate efficiently (Howey et al. 2016, Howze and Smith 2015). However, environmental conditions in low-frequency sites could be advantageous to only a few species that possess similar ecological characteristics. As such, these species can tolerate the environmental filters imposed under low-frequency management as forest canopies close and other species are lost. For example, 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).

Additionally, increased habitat heterogeneity in high-frequency sites under both frequent thinning and prescribed burning practices resulted in snake assemblages more even in abundance and likely provided additional habitats for taxonomically unique species that were not found in low-frequency sites. Other studies of reptile assemblages in fire-disturbed systems have demonstrated the importance of management practice frequency and type in maintaining snake diversity (Litt et al. 2001, Steen et al. 2013). 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. Thinning operations can create multiple types of microhabitats utilized by snakes through a variety of mechanisms associated with the forest management efforts. First, thinning operations in the high-frequency treatment create 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 sedges and rushes 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.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.

Alternatively, 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). Habitat complexity (i.e., heterogeneity) affects food-web structure and, subsequently, affects the stability of predator-prey dynamics (Grabowski 2004, Livernois et al. 2019, Morris et al. 2017). Therefore, the availability and abundance of prey resources in disturbed or perturbed systems may directly affect the taxonomic diversity of predator guilds through species interactions (Steen et al. 2013). There was variation in the abundance of prey between treatments that suggested potential shifts in resource availability may result from changes in habitat structure. For example, the abundances of functional prey groups were more even in their relative contribution to the overall prey diversity in high-frequency sites. The high-frequency sites 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. For example, small mammals are well-documented prey items for many snake species captured, and small mammal diversity and abundance has been shown to increase in pine-grassland forest under frequent management regimes (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 (Masters et al. 1998, 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. For instance, *Agkistrodon piscivorus* contributed prominently to differences in taxonomic composition between high and low-frequency treatments. *Agkistrodon piscivorus* are generally associated with aquatic environments and are 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 increase the number of habitats suitable for breeding populations of anurans (C. Adams, personal communication). Therefore, these temporary aquatic environments that arise with increased management practice frequency may provide resources that allow for the persistence of semi-aquatic snakes not typically associated with upland habitats, contributing to increased taxonomic diversity of snake predators in the high-frequency treatment. 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 lead 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 shrews).

Despite substantial differences in patterns of taxonomic diversity, I 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, 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). I 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. 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 a limitation of resources (Pulsford and Lindenmayer 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 Uriate 2016). Although functional dispersion and community-weighted means of traits are strongly related environmental factors and disturbance, these metrics respond differently because assemblages can differ greatly in species composition but not in trait variability (Grime 2006). For example, analysis of individual continuous traits in this study 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). One potential mechanism could be that snakes in high-frequency treatments have higher resources 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. 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 functionally redundancy changes as species' roles shift under different environmental conditions may 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 this 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 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). I used functional dispersion alongside metrics of richness and evenness. This was chosen 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 and contrasting 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). 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 my 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 one can begin to understand the organization of ecological communities within pine-forest ecosystems and the resilience of these ecosystems to anthropogenic disturbance regimes.

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Management Practice Frequency Increases Predator Trophic Redundancy in Forest Ecosystems

INTRODUCTION

Disturbances are important mechanisms underlying the structure and function of ecological communities within ecosystems (Jentsch and White 2019, Pickett and White 2013, Supp and Ernest 2014, Turner 2010). The influence of these disturbances can vary in type, size, season, frequency, severity, intensity, timing, and duration across multiple spatial and temporal scales (Buma 2015, Dornelas 2010, Sousa 1984). The nature of such disruptive events leads to differential responses in species and functional diversity that, in turn, affect ecosystem properties (e.g., biotic production, nutrient cycling, biological diversity; Cardinale et al 2002, Hooper et al. 2005, Tilman et al. 2014). Furthermore, anthropogenic activities that mediate disturbances can have either positive or negative impacts on ecological systems with implications for the health of ecosystems and the services they provide (Moreno-Mateos et al. 2017, Thom and Seidl 2016). Consequently, identifying the dynamic processes in which disturbances shape the functional properties of ecological systems is of the utmost importance.

Food webs are a useful framework to investigate the assembly and resilience of ecological communities in response to both natural and human-induced disturbance regimes (Polis and Winemiller 2013, Layman et al. 2015, Schalk et al. 2017). These networks of consumer-resource relationships describe trophic interactions and patterns of resource use among coexisting species as well as energy flow within ecosystems (Paine 1980, Pimm 1982). Despite the utility of food-web approaches, our understanding of how anthropogenic disturbances affect trophic structure in complex ecosystems is still limited, particularly in terrestrial systems (Cameron et al. 2019, Shurin et al. 2006). Nonetheless, studies incorporating food-web approaches have demonstrated that human impacts in food webs can have profound effects on bottom-up and top-down processes that regulate stability in food webs across natural systems (see May 2019, Terborgh and Estes 2010, Strong and Frank 2010). Because characterizing the trophic structure of a community can shed light on the ecological function and resource use of different species beyond traditional community metrics of species richness and abundance, ecologists can test hypotheses investigating the mechanisms that stabilize or destabilize food webs to predict niche responses to shifts in community composition (Hooper et al. 2005).

According to food-web theory, ecosystem stability is predicted to increase as the number of connections in the food web increases (Gellner and McCann 2016, LeCraw et al. 2014, Montoya et al. 2006). Thus, fluctuations in the populations of well-connected species are less likely to impact the rest of the community than those with limited, strong connections (Dunne et al. 2002). Simple food chains comprised of species with specialized diets have strong interactions, and are therefore more susceptible to disturbances that could potentially result in trophic cascades (Finke and Denno 2004). However, species that are trophic generalists tend to stabilize food webs, as they typically have many weak interactions with resources, and because their populations are more likely to exhibit resilience to fluctuations in resource availability (Purvis et al. 2000). Thus, the additive effects of weaker interactions in food webs are predicted to dampen fluctuations induced by strong interactions between consumers and resources (Gellner and McCann 2016). Additionally, the degree of (dis)similarity in resource use within and among species in a community might also affect stability (Calizza et al. 2017, Noto and Gouhier 2020, Rooney and McCann 2012). Decreased overlap (i.e., increased niche partitioning) among consumers reflects divergent patterns of resource use that destabilize food webs as overall trophic diversity increases (Finke and Snyder 2008, Hector and Hooper 2002). In contrast, increased niche overlap (i.e., decreased partitioning) results in multiple consumers being functionally equivalent in the context of their trophic ecology, also known as trophic redundancy (Cirtwill et al. 2018, Sanders et al. 2013, 2018). Trophic redundancy stabilizes food webs by decreasing the likelihood that species loss will lead to a trophic cascade, thereby increasing ecosystem resilience and stability to disturbances (Borrvall et al. 2000, Brodie et al. 2014, Sanders et al. 2015, 2018).

Disentangling the interactions that occur within food webs is a difficult endeavor in complex systems. This is primarily attributable to the logistical challenges associated with determining consumer-resource relationships and tracking the flow of nutrients within food webs (Horswill et al. 2018). Traditional methods of dietary analysis are often limited and subject to bias, as gut and fecal contents range over short temporal scales, and often do not accurately reflect proportional contributions of prey items (Nielson et al.

2018, Votier et al. 2013). These methods also rely on the ability to accurately identify prey items that have been subjected to digestive processes and assume that all ingested prey items are equally assimilated by the consumer (Bearhop et al. 2004). Additionally, reliance on these traditional methods requires large samples from consumers that might not be easily encountered or feed irregularly (Nagelkerken et al. 2009, Owen et al. 2011, Roeder and Kaspari 2017). Stable isotope analysis (SIA) has been increasingly utilized in food web studies as this technique is not limited by the same constraints as traditional methods of dietary analysis (Bearhop et al. 2004, Layman et al. 2012). This technique offers insight into the food-web structure of communities by comparing the relative abundance of naturally occurring carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotopes in consumer tissues. Because the ratios of these isotopes are predictably altered as they move up through the food chain, they can be used to estimate the position of consumers in a food web relative to other organisms (Post 2002). Carbon isotope ratios are influenced by the photosynthetic pathways of primary producers and, because they are largely conserved throughout food webs, provide information about the source of dietary carbon (Peterson and Fry 1987). Nitrogen isotope ratios can be used to identify the trophic level of a consumer because the heavier isotope (^{15}N) is preferentially incorporated each time nutrients from ingested tissues are assimilated (Peterson and Fry 1987, Post 2002). Collectively, this information characterizes the isotopic niche an organism occupies (Newsome et al. 2007), that can be used to examine aspects of a consumer’s trophic ecology and subsequently the trophic diversity and redundancy within species assemblages. Unlike stomach content analysis, which only provides a snapshot of a consumer's diet, SIA provides dietary information across a longer temporal scale because the rate at which isotopic information is incorporated varies among types of tissues (Phillips and Eldridge 2006, Newsome et al. 2007). For example, skin, feather, or scale tissues incorporate carbon and nitrogen from consumed prey items at a slower physiological rate, and can represent the diet of a given consumer across a time period of several weeks. Therefore, SIA is less susceptible to temporal biases in sample collection than traditional methods, and better reflects the diets of consumers in a given space and time (Boecklen et al. 2011, West et al. 2006). The applications of SIA to food-web studies offer quantitative insight into factors influencing community dynamics and can reveal pathways of energy transfer (Parnell et al. 2010, Semmens et al. 2009). Furthermore, comparing changes in $\delta^{13}C$ and $\delta^{15}N$ in the presence and absence of disturbances can reveal how food-web structure (e.g., trophic breadth, trophic position) might change following a disturbance (di Lascio et al. 2013, Jenning et al. 2001).

Characterizing the complex interactions that structure ecological communities is a critical step towards understanding the mechanisms that help stabilize ecosystems against disturbances (Vander Zanden et al. 2016). In ecosystems under heavy anthropogenic pressure, such as forests, management actions such as the application or suppression of fire, plantation forestry, and mechanical thinning operations create disturbances by altering the diversity of vegetative communities and shifting above ground biomass (e.g., functional responses of plant diversity to fire, gap-dynamics in temperate forests) (Diaz-

Toribio et al. 2020, Matula et al. 2020, Veldman et al. 2013). Therefore, forest management has the potential to alter ecological gradients (e.g., habitat and resource availability) that can have cascading effects on the mechanisms that structure species' assemblages in these forest systems (Bowman and Legge 2016, Diaz-Toribio et al. 2020). Pine-dominated forests of the southeastern United States are biologically diverse systems maintained and organized by disturbances, particularly fire events (Rother et al. 2020, White and Harley 2016). However, these fire-climax forests have been greatly reduced or degraded because of changes in land-use practices that alter disturbance regimes (Diaz-Toribio et al. 2020). Investigating how disturbance regimes drive the mechanistic processes that affect ecosystem health in these disturbance-maintained systems is both ecologically and economically important because forests provide a wide range of ecosystem services (e.g., timber production, carbon sequestration, supporting biodiversity) (Mori et al. 2017, Sohngen and Brown 2006). There is interest in restoring these biologically diverse systems using forest management as a tool to reintroduce disturbance regimes that mimic natural conditions (Guldin and Black 2018, Guldin 2019, Jin et al. 2018, Kirkman and Jack 2017). Current development and application of this type of ecosystem management has largely been based on conventional wisdom, insights from single-species studies, pressure to conserve specialist species, and adaptive management (Dobson 2009). Moreover, most applications of forest management to restore southern pine forests have focused on restoring structural properties of systems along stages of succession, and have largely ignored the importance of functional properties (Palmer et al. 2016, Vander Zanden et al. 2016).

Incorporating food-web approaches into restoration management plans can link these processes to better understand how communities and ecosystems respond to management efforts (Layman et al. 2020). In recent decades, theoretical and empirical evidence accumulated across a variety of study systems has strengthened the notion that food-webs are fundamental to inform ecological restoration efforts (e.g., Vander Zanden et al. 2016). For example, excess nutrient loading (e.g., from agricultural or industrial run-off) into lakes and reservoirs can lead to severe algal blooms that increase water turbidity and fish-die off, altering food-webs and resulting in the loss of ecosystem services (e.g., recreational fishing, potable water; Havens 2014). Food-chain models studying the effects of biomanipulation have shown promise for restoring these eutrophic lakes via the facilitation of trophic cascades (McCrackin et al. 2017, Mao et al. 2020, Zhang et al. 2020). Management practices that manipulate food-web structure by increasing picivorous fish predators, or removing biomass of planktivourous fish, reduce predation on zooplankton and increase grazing pressure of zooplankton on phytoplankton (Havens 2014). Long-term monitoring efforts suggest that the control of phytoplankton with food-web based management strategies can not only improve water quality, but also increases the resilience of lakes to future nutrient influxes by suppressing the severity of algal blooms (Mao et al. 2020, Rask et al. 2020).

Given the potential for forest management to alter the taxonomic and functional diversity of predator assemblages in southern pine forests, incorporation of food-web perspectives could further elucidate the mechanisms underlying ecosystem functioning and lead to modern solutions that protect vital forest resources (Layman et al. 2020, Loch et al. 2020; see Chapter 1). Current applications of restoration management in southern pine forests oversimplify the impacts of forest management practices (e.g., prescribed fire, thinning), under the perception that restoring mosaic landscapes alone will lead to the assembly of natural, biodiverse communities and inherent stability (Bowman and Legge 2016). However, spatiotemporal heterogeneity that results from these practices also regulates trophic dynamics and ecosystem structure, because both bottom-up (e.g., resource-driven) and top-down (predator-controlled) ecological processes can be reinforced by different expressions of the disturbance mosaic (Bowman et al. 2016, Ponisio 2020). Therefore, strengthening our understanding of how forest management regimes alters predator-prey relationships, and food-web structure, will provide a better path to restoring resilient and functional pine forest systems (Bowman and Legge 2016, Layman et al. 2020, Loch et al. 2020, Vander Zanden et al. 2016).

The loss of predators because of anthropogenic activities can have detrimental impacts on ecosystems (Estes et al. 2011, Ripple et al. 2014, Terbough and Estes 2013). Many studies, in both aquatic and terrestrial environments, have demonstrated how changes in the vertical structure of food webs have extensive cascading effects that influence the functionality and resilience of ecosystems (Estes et al. 2011, Heithaus et al.

2008, Terbough et al. 2001). Top-down effects are now widely recognized as important processes that regulate and maintain biodiversity and ecosystem function (Terbough and Estes 2013). As such, there should be increased attention given to maintaining or restoring predation regimes as a component of ecological restoration. Snakes are model predators to investigate how forest management might affect food-web dynamics in southern pine forests. Snake species in these systems have diverse life-histories and exhibit predictable patterns of seasonal activity from year to year. In addition, snakes can range from generalized to specialized feeders, with prey preferences, prey size, and foraging modes that vary among species (Arnold 1993, Shine and Bonnet 2000, Weatherhead and Madsen 2009). Snakes also exhibit habitat-specific shifts in their diet, allowing for comparisons of resource use within and among species (Durso et al. 2013). As predators, snakes play important roles in food webs, as both predators and prey, regulating populations of herbivores and secondary consumers while also contributing to the overall connectivity of food-webs (i.e., trophic linkages) (Beaupre and Douglas 2009). Therefore, snake predators can serve as useful taxa to understand how disturbances influence trophic interactions and ecosystem properties (Beaupre and Douglas 2009).

In this study, I examined how differences in forest management practice frequency (e.g., prescribed fire, thinning) affect the food-web structure and resource use of predator assemblages in southern pine forests inferred from stable isotope patterns. Through these processes, habitat conditions that prevail under different frequency management regimes might be coupled within food-web structure resulting in bottom-up processes that affect food-web structure, and in turn, alter top-down processes that influence the resiliency of predator assemblages. Specifically, I investigated how management practice frequency (a) influenced community-wide measures of food-web structure including trophic position, trophic range, and isotopic niche space within and between predator assemblages, and (b) altered resource use within predator assemblages under different forest management regimes. Utilizing snakes as a model taxon to investigate food-web structure, I hypothesized that practice frequency will shift the energetic pathways that support food webs, subsequently affecting the trophic structure of predator assemblages between sites. Specifically, I predicted that greater practice frequency increases environmental heterogeneity and provided additional energetic pathways that would support a greater diversity of snakes. I further hypothesized that the more diverse predator assemblage at the high-frequency treatment would consist of species occupying similar isotopic niches resulting in increased trophic redundancy. At the low-frequency treatment, I hypothesized that environmental conditions would reduce the number of energetic pathways that support the food-web, limiting prey resources to consumers at multiple trophic levels, and resulting in a lower diversity of snakes at the top of the food-web. Because of the reduced energetic pathways at the low-frequency treatment, I further hypothesized that snakes would partition their isotopic niches to limit niche overlap, leading to increased trophic diversity. Taxonomic and functional diversity of both primary and secondary consumers might respond differently to disturbance and subsequent habitat changes between management regimes affecting secondary productivity. Because secondary production encapsulates underlying energy acquisition and trophic relationships, I hypothesized that resource use within predator assemblages to respond to changes in resource availability. I predicted that shifts in prey diversity between treatments would lead to an increase in the number of functional prey groups utilized by low-frequency predator assemblage, as generalist predators would expand their resource use to exploit a wider variety of resources in suboptimal conditions. In contrast, I predicted that snakes in the high-frequency assemblage would specialize on more valuable functional prey groups which, in turn, would be reflected in trophic redundancy within the food web.

METHODS

Study Areas

This study was conducted in the Pineywoods ecoregion of Texas, in the pine-dominated mesic uplands of the northwestern Gulf Coastal Plain (for additional information on historical and current land-use within the region, or landscape and climate characteristics see Chapter 1). Surveys of snake predators and representative prey assemblages were conducted at the Boggy Slough Conservation Area (Trinity County; hereafter high-frequency treatment) and the Stephen F. Austin Experimental Forest (Nacogdoches County; hereafter low-frequency treatment; Appendix, S1). The high-frequency treatment, owned and operated by the T. L. L. Temple Foundation, is actively managed for a variety of conservation and production goals through the implementation of frequent forest management (e.g., 1-3 year fire intervals, thinning, and regeneration harvests; R. Sanders, personal communication). The low-frequency treatment is an Experimental Forest owned and operated by the U.S. Forest Service as part of the Southern Research Station network. Although historically managed for silvicultural research, current management at this location is infrequent (e.g., 5-8 year fire intervals, limited harvesting). For additional information on differences between the high-frequency and low-frequency treatments see *Study Area* in Chapter 1.

Forest Habitat Structure

In an effort to identify any emerging patterns of biomass transfer at the base of food webs relative to these structural alterations, I measured eight habitat variables associated with stand density, groundcover, and canopy cover in each sampling location across treatments. I implemented a standardized sampling design by establishing nested subplots within a larger circular plot in which the center of the plot was the approximate location of a box trap array. Habitat variables included basal area (m^2/ha), mean leaf litter depth (mm), relative proportion of canopy openness (%), and the cumulative proportion of coarse woody debris (m^2). Additional measurements of understory ground cover composition were also measured to estimate the percent cover of herbaceous grasses and forbs, woody shrubs, bare ground, and detritus (Daubenmire 1959). These data were averaged for each sampling location and pooled according to site-specific management to identify the persistent environmental gradients occurring within and across treatments (i.e., high-frequency and low-frequency).

Sampling of Snakes, Prey, and Basal Resources

Snakes and prey species were collected using 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) at the end of each fence (Burgdorf et al. 2005) at 10 trap locations per treatment per year (N=20 total; cumulative totals: HF = 30 total, LF = 20 total; see Chapter 1). Traps were checked daily at the high-frequency sites from 2018-2020 and at the low-frequency sites from 2019-2020, from May-July. Captured snakes were placed in bags and 19 L buckets and brought into the lab for processing. In the lab, 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). Venomous snakes were anesthetized with the chemical inhalant isoflurane to allow for safe handling during this process (Beaupre et al. 2004, Kane et al. 2020). Scale clips obtained from ventral marking were placed into small sealable bags, labelled, and stored in a freezer at -23.3°C for later isotopic analysis.

Relevant prey species were opportunistically sampled from box-trap and pitfall captures for SIA analyses. To assess that dietary sources of snakes were adequately sampled for SIA, I collected ~3-5 specimens of each dominant prey species based on capture totals observed in each treatment per year. Upon collection, ectothermic vertebrates were euthanized by a process of cooling then freezing, while endothermic vertebrates were euthanized either by cervical dislocation or cranial concussion to prevent biases in isotopic ratios of carbon and nitrogen that may arise with chemical euthanasia (M. Pilgrim, pers. comm., Shine et al. 2015). Both invertebrate and vertebrate prey taxa that were collected were labeled and stored on ice until they could be later stored at -80°C. I recorded species-level identity, capture per unit effort, and method of capture (e.g., box-trap versus pitfall) for all species encountered during sampling. This was done to gain insight on resource availability and the composition of different trophic guilds occurring in each treatment. Limitations of trap design for sampling small-bodied arthropods led me to supplement my sampling efforts with monthly sweep netting within the pre-established habitat plots.

To determine the extent in which frequency of forest management influences primary producer baselines in each treatment, I harvested the above ground mass of 2-3 specimens for the five most dominant basal resources found at each sampling site. Plants were identified to the species level, when possible. Plants chosen as indicators of site-level isotopic basal resource values either occurred at all sites (e.g., living and dead vegetative material from dominant overstory tree species) or occurred in relatively high abundances in several sites (e.g., herbaceous grasses, forbs, and vines). In order to account for temporal variation in the turnover of $\delta^{13}C$ and $\delta^{15}N$ in the tissues of snake and prey consumers, basal resources were collected at the beginning, midpoint, and end of each sampling period. Collecting basal resources in this way also allowed me to account for any shifts in basal resource biomass that might have occurred across the growing season in each year of sampling.

Stable Isotope Sample Preparation and Analysis

Samples selected for stable isotope analysis were thoroughly cleaned with deionized water to remove any inorganic or organic material to prevent biological contamination. Stomach contents and digestive tracts were removed from vertebrate samples to limit bias in isotopic analyses, and plant samples contained leaf, stem, and flowering bodies (if present) (Mateo et al. 2008). Snake scales, plant samples, and invertebrate and vertebrate prey were then dried in an oven at 60°C for 48 h or until reaching a stable dry mass. Once all samples reached a stable dry mass, dried samples were homogenized using a mortar and pestle and stored in glass vials. Homogenization of whole-body samples was necessary to predict average isotopic signatures of $\delta^{13}C$ and $\delta^{15}N$ in each sample. Snake scales, however, could not be homogenized without substantial loss of material, and were instead cut into smaller clippings. Snake scale clippings and subsamples of each homogenized sample were then weighed (~1-3 mg) and packaged into 9 x 10 mm Ultra-Pure tin capsules. Packaged samples were sent to the Stable Isotope Ecology Laboratory at the University of Georgia to be analyzed for stable isotopes (^{13}C and ^{15}N) using an isotope mass spectrometer. Measurements are reported in delta notation (δ) where

$$\delta^{13}\mathrm{C} \text{ and } \delta^{15}\mathrm{N} = [R_{\mathrm{sample}}/R_{\mathrm{standard}}]) - 1 \times 1{,}000$$

and *R* is the ratio of the heavy/light isotope content (e.g., $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Isotope ratios are expressed in per mil (‰) relative to international reference standards V-PDB (Vienna PeeDee Belemnite) for carbon and atmospheric nitrogen for nitrogen (Gröning 2004).

Statistical Analyses

In order to compare differences in trophic structure in snake communities occurring in sites under different management regimes, samples were pooled across sampling sites and years into high-frequency and low-frequency treatments. Within this framework, I tested for differences in $\delta^{13}C$ and $\delta^{15}N$ within different levels of each food web. Distributions of $\delta^{13}C$ and $\delta^{15}N$ in each test were first tested for normality using the Shapiro-Wilks test. When these data did not meet the assumptions of ANOVA, I used Kruskal-Wallis to determine differences between groups. Snake consumers were separated by species within each treatment. Isotopic baselines for each treatment were grouped by photosynthetic pathway (C4 versus C3). However, I did not detect a C4 pathway in any of the dominant basal resources sampled within the low-frequency treatment. For this reason, I pooled resources into independent categories based on life form (e.g., herbaceous, woody, and detritus) for additional analyses. Prey samples from each treatment were grouped into either primary or secondary consumers or into 8 prey groups based on taxonomic and functional roles of species, depending on further analyses. This functional grouping of prey taxa was based on the trophic ecologies of prey species and were determined from the literature (Hibbitts and Hibbitts 2015, Marshall 2006, Schmidley and Bradley 2016, Tipton 2012, Ubick and Cushing 2005).

I quantified the trophic structure of snake communities using stable isotope-derived metrics that describe relative trophic position and trophic range, along with multiple community-wide metrics of isotopic niche space. Each of these metrics describes different aspects of trophic structure (Layman et al. 2007a). In addition, I also determined the proportion of functional prey groups contributing to sampled snake assemblages to investigate shifts in resource use between high-frequency and low-frequency treatments. Trophic position describes the average number of steps involved in biomass transfer within a given food-web, and was estimated relative to a resource baseline to account for inherent differences among treatments in $\delta^{15}N$ (Post 2002). Ignoring baseline values and using unadjusted values of $\delta^{15}N$ to infer trophic position can lead erroneous results and limit the interpretation of where species are located within food webs (Post 2002). The average $\delta^{15}N$ of invertebrate primary consumers was used as the baseline to estimate trophic range and relative trophic positions for each treatment. I used invertebrate primary consumers instead of plants resources because they have been shown to accurately integrate temporal and spatial variation in producers' isotopic composition (Vander Zanden & Rasmussen 1999). The values for trophic positions of snakes might be underestimates based on the $\delta^{15}N$ of primary producers collected in this study, which were highly varied within sampling sites in each treatment attributable to local factors that influenced higher enrichment or depletion of the nitrogen found in soils

(Vanderklift & Ponsard 2003). Species considered in the calculation of the baseline are reported in Appendix S5. The calculation for the trophic position of a given snake species was $TP = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{base})/\Delta_n$, where λ was the trophic position of the baseline organisms (e.g., $\lambda = 2$ for primary consumers), $\delta^{15}N_{consumer}$ was the measured $\delta^{15}N$ of each snake individual at each treatment, $\delta^{15}N_{base}$ was the mean $\delta^{15}N$ for the baseline in each treatment, and Δ_n was the trophic fractionation for $\delta^{15}N$ (Post 2002, Vander Zanden and Rasmussen 1999). I assumed a fractionation value of 1.63‰ for all snake consumers based on the literature (Seminoff et al. 2006, Vander Zanden and Rasmussen 1999). Once the TP for each snake sample was calculated, I averaged TP values for each snake species across high-frequency and low-frequency treatments. I also examined how the range in trophic position per species (hereafter, trophic range; TR = maximum TP – minimum TP) might vary between high frequency and low-frequency treatments. Trophic range describes the variability of snake feeding responses and is a measure that can be useful in describing the vertical structure of food webs (Layman et al 2007a). Trophic range was calculated for only those species captured >3 times in each treatment, and only after potential outliers were assessed (Jackson et al 2011).

To determine whether isotopic niche space of snake communities might change with forest management treatment, I first tested for differences in overall trophic structure between high-frequency and low-frequency treatments using $\delta^{15}N$ and $\delta^{13}C$ biplots and performed a permutational analysis of variance (PERMANOVA) at 999 iterations (Anderson 2005). A two-dimensional isotopic niche space was defined using the average isotopic signatures of snake species present in each community standardized by the average baseline values at each treatment. The predictor variables in the PERMANOVA were species and treatment (and interactions), and a Euclidean distance dissimilarity matrix based on the isotopic values of snake consumers was the response variable. The PERMANOVA was performed using the adonis function in the package ‘vegan’ in R (Oksanen et al. 2013).

I investigated the trophic structure of snake communities within and between treatments using the community-wide metrics proposed in Layman et al (2007a). These metrics use the stable isotope composition of the different food web components to describe trophic structure by measuring the spatial relationships of species in isotopic space (Layman et al. 2007a). Carbon ($\delta^{13}C$) range (CR), nitrogen ($\delta^{15}N$) range (NR), total area (TA), and mean distance to centroid (CD) are metrics that provide information on the trophic diversity within a food web. Specifically, CR indicates isotopic niche diversification at the base of the food web, NR describes trophic isotopic length, TA is the area of the convex hull that encompasses all groups within the food web as is a measure of the total isotopic diversity, and CD is the average Euclidean distance of each community component to the centroid and is a measure of the average isotopic diversity (Layman et al. 2007a). TA was not used in my final analyses of community-wide comparisons of trophic structure because this metric relies on extreme values and thus increases with sample size (Jackson et al. 2011). In place of this metric, the isotopic niches of snake communities within and across each treatment were calculated based on standard ellipse areas (SEA, expressed in ‰^{2}) (Batschelet 1981). SEA's are better indices of the isotopic niche of a community because they are comparable to univariate standard deviation and contain approximately 40% of the data. This measure is also not affected by biases associated with the number of groups included in analyses, allowing comparisons between communities with different numbers of species to be made (Jackson et al. 2011). I also calculated the SEA corrected for small sample sizes (SEA$_C$), along with the overlap in SEA$_C$ and difference in SEA sizes between high-frequency and low-frequency treatments. Two additional metrics, mean nearest neighbor distance (MNND) and the standard deviation of nearest neighbor distance (SDNND) are metrics related to trophic redundancy. Specifically, MNND measures the density of species packing in isotopic niche space and SDNND measures the evenness of species packing in isotopic niche space (Layman et al. 2007a). Therefore, smaller MNND values represent increased trophic redundancy attributable to many species having similar trophic niches, and smaller SDNND values indicate increased trophic redundancy because assemblage members have more overlap in their trophic niches (Layman et al. 2007a).

The metrics originally proposed and developed in Layman et al. (2007a) might be difficult to interpret when comparing between sites or certain treatments as they can vary with sample size. However, a Bayesian approach to these metrics allows for the incorporation of sampling error of estimates of the means of the different community components, and returns posterior distributions of the estimated metrics (Jackson et al. 2011). This provides a measure of uncertainty that allows for statistical comparisons to be made. In addition, this approach is less sensitive to variations in the number of species, and can applied to make comparisons between different communities (Jackson et al. 2011). Therefore, I calculated Bayesian estimates for all aforementioned metrics of isotopic niche diversity for each snake community (e.g., high-frequency and low-frequency). Bayesian estimates of CR, NR, CD, MNND, and SDNND were calculated using the 'SIAR' package in R (Parnell et al. 2010). The results obtained were compared between high-frequency and low-frequency treatments based on the visual analysis of the confidence intervals, in which the degree of overlap between the Bayesian distributions was used as an indication of similarities/dissimilarities between treatments (Layman et al. 2012). Bayesian standard ellipse areas (SEA_B) were calculated using the 'SIBER' extension of the 'SIAR' package in R (Parnell et al. 2008; 2010, Jackson et al. 2011). All Bayesian analyses used to produce comparable posterior distributions of community-wide trophic structure included only those species with ≥ 3 individuals represented in a given community. Data were tested for normality before these analyses using the Kolmogorov-Smirnov Test in the base 'stats' package of R (R Core Team 2020).

To estimate the proportion of potential prey sources to the diet of snakes in each treatment, I performed Bayesian stable-isotope mixing models in the 'MixSIAR' package in R (Moore and Semmens 2008, Semmens et al. 2009, Stock and Semmens 2013). Separate models were built for the five most common shared snake species between treatments with respect to the functional prey groups sampled with those treatments. MixSIAR estimates the probability distributions of each source to a consumer's stable isotope values while accounting for variability among consumer and source isotopic values, and uncertainty associated with tissue-diet discrimination factors (Phillips et al. 2014). Before running the models, potential prey sources were grouped based on ecological similarity that reflected species' roles in the food-webs (e.g., anurans; secondary consumers). I then analyzed each snake assemblage with prey sources in isotopic space with $\delta^{13}C$ and $\delta^{15}N$ biplots corrected with trophic discrimination factors to further combine prey resources of similar isotopic signatures and limit biases in the models (Appendix, S5). To examine the proportions of potential prey items for each community, the first models included all snake consumers in each treatment, with species as a random effect. A Markov Chain Monte Carlo (MCMC) analysis with three replicate chains was run for 300,000 iterations, discarding the first 200,000 samples and thinning by 100 (Phillips et al. 2014). Model convergence was confirmed using the Gelman-Rubin and Geweke diagnostic tests (Cowles et al. 1996). Fractionation values for each source were obtained from the literature (Appendix S5). MixSIAR results for sources were reported as posterior density distributions of proportional contributions to consumer mixture data as mean dietary proportions with associated credibility intervals.

RESULTS

Forest Habitat Structure and Basal Resource Composition

Differences in forest management practice frequency had significant effects on the overall structure and composition of forest habitats occurring in each respective treatment (see Chapter 1). Initially, I assumed these differences in the structural properties between treatments would reflect differences in the number of energetic pathways at the base of respective food webs. For example, sampling sites in the low-frequency treatment were homogenized in terms of forest structure (e.g., closed-canopies, high amounts of leaf litter buildup) and dominant basal resources collected for isotopic analyses were consistent in terms of species richness and abundance across all sampling sites (Figure 1). In contrast, the high-frequency treatment featured increased heterogeneity of habitats, with extremely diverse plant communities in the understory (e.g., grasses, forbs, sedges, and rushes) along with increased proportions of coarse woody debris left behind from thinning operations (Figure 1). Isotopic analyses of basal resources showed significant differences in $\delta^{13}C$, but not in $\delta^{15}N$, between treatments (ANOVA; $F = 11.073$, $Pr(>F) = 0.001$). The $\delta^{15}N$ values of basal resources were highly variable within treatments, but did not differ significantly between treatments (Appendix, S5). In both treatments, $\delta^{15}N$ values were generally depleted in primary consumers (Appendix, S5). Despite the presence of C4 grasses represented in my sampling within the high-frequency treatment, most herbaceous plants in the open understories of sampling sites represented the C3 photosynthetic pathways and, while present at most sites, C4 grasses were only dominant in a few sites.

Isotopic Signatures of Snakes and Prey Resources

Snake consumers varied between treatments in both species richness and abundance (see Chapter 1, Table 1). Isotopic values of $\delta^{13}C$ and $\delta^{15}N$ for snake consumers were significantly different between sites in terms of treatment, species, and their interaction (PERMANOVA, F = 73.27, Pr(>F) = 0.001, PERMANOVA, F = 21.82, Pr(>F) = 0.001, PERMANOVA, F = 1.98, Pr(>F) = 0.01) (Table 2). Species diversity of potential prey resources supporting snake consumers also varied between sites (see Chapter 1; Appendix, S2). For example, caudates (i.e., salamanders) were a representative prey taxon in the low-frequency site that was not found in the high-frequency site, and caeliferans (i.e., grasshoppers) were represented in the high-frequency site but not found in the low-frequency site (Appendix S5). Further grouping of prey taxa based on taxonomic similarity and trophic roles showed differences in the isotopic signatures within functional prey groups (Appendix S5). Secondary consumers in the high-frequency site had a narrower range in $\delta^{13}C$ and in $\delta^{15}N$ values than in the low-frequency site, and average values for each isotope ratio were significantly different between site in terms of site and taxa, but not in interaction between treatment and species (PERMANOVA, F = 12.93, Pr(>F) = 0.001; PERMANOVA, F = 7.90, Pr(>F) = 0.001). Primary consumers did not differ in their isotopic values of $\delta^{13}C$ and $\delta^{15}N$ in site, taxa, or interaction of site and species (Appendix, S5). Within the high-frequency treatment only caeliferans had isotopic signatures that reflected herbivory on C4 resources.

Length of Trophic Structure and Relative Trophic Positions

There were no differences in average trophic position of snakes across treatments, which suggests that snake predators are occupying similar trophic position in both high frequency and low frequency treatments. In the high-frequency treatment, the difference in $\delta^{15}N$ between the primary consumer baseline and the species of highest $\delta^{15}N$ (Texas coral snake, *Micrurus tener*) was only slightly smaller than the difference in $\delta^{15}N$ between the primary consumer baseline and the species of the highest $\delta^{15}N$ (eastern hog-nosed snake, *Heterodon platirhinos*) in the low-frequency treatment (Table 2). The lowest relative trophic positions recorded in the high-frequency and low-frequency treatments were attributed to the rough green snake (*Opheodrys aestivus*). Overall, pairwise species comparisons of the relative trophic positions of shared species between treatments were similar; however, the range of trophic positions of varied slightly among these species (Table 2).

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Table 2. Isotopic values of δ13C and δ15N of snake species in high-frequency and low-frequency treatments. Trophic position (i.e., TP high-frequency / TP low-frequency) represents the average number of steps involved in biomass transfer while trophic range (i.e., TR high-frequency / TR low-frequency) describes the variability in trophic position responses. Values represent averages across treatments (±1 SD). Species with three captures or less from sampling efforts are denoted with an asterisk.

Snake species	**N**	**δ13C**	**δ15N**	**TP**	**TR**
Agkistrodon contortrix (AGCO)	42 / 77	-25.37 (0.73) / -26.00 (0.83)	5.78 (1.30) / 5.08 (1.16)	4.29 (0.80) / 3.50 (0.71)	3.04 / 3.41
*Agkistrodon piscivorus (AGPI)**	15 / 1	-24.27 (0.76) / -25.07	7.19 (1.13) / 8.66	5.11 (0.69) / 5.69	2.77 / NA
Coluber constrictor (COCO)	51 / 10	-23.23 (1.01) / -24.45 (0.74)	5.48 (0.95) / 4.98 (1.32)	4.11 (0.58) / 3.44 (0.81)	2.33 / 1.39
Coluber flagellum (COFL)	16 / 4	-24.00 (0.48) / -24.54 (1.15)	6.12 (0.55) / 5.91 (0.99)	4.50 (0.34) / 4.00 (0.61)	1.36 / 1.31
*Crotalus horridus (CRHO)**	2 / 2	-24.82 (0.30) / -23.36 (0.01)	5.61 (0.88) / 6.15 (0.66)	4.19 (0.53) / 4.15 (0.40)	0.76 / 0.57
*Farancia abacura (FAAB)**	2 / 0	-31.35 (0.91) / NA	7.36 (0.99) / NA	5.26 (0.61) / NA	0.86 / NA
*Heterodon platirhinos (HEPL)**	5 / 3	-24.12 (0.21) / 9.21 (1.47)	7.54 (0.88) / 9.21 (1.47)	5.37 (0.54) / 6.03 (0.91)	1.35 / 1.58
*Lampropeltis calligaster (LACA)**	1 / 1	-23.34 / -24.15	7.02 / 8.04	5.06 / 5.31	NA / NA

Table 2. Continued

Snake species	**N**	**δ13C**	**δ15N**	**TP**	**TR**
*Lampropeltis holbrookii (LAHO)**	2 / 0	-23.31 (0.59) / NA	7.61 (0.30) / NA	5.41 (0.19) / 5.34 (0.44)	0.26 / NA
*Micrurus tener (MITE)**	3 / 5	-23.43 (0.68) / -23.50 (0.30)	7.68 (0.25) / 8.01 (0.72)	5.46 (0.15) / 5.34 (0.44)	0.28 / 1.11
*Nerodia erythrogaster (NEER)**	3 / 3	-27.01 (0.93) / 6.20 (3.41)	5.09 (0.23) / 6.20 (3.41)	3.87 (0.14) / 4.18 (2.10)	0.25 / 4.02
Nerodia fasciata (NEFA)	4 / 4	-28.37 (2.17) / -29.20 (0.74)	6.12 (0.81) / 6.36 (1.28)	4.30 (0.37) / 4.28 (0.78)	1.18 / 1.68
*Opheodrys aestivus (OPAE)**	2 / 1	-25.43 (0.47) / -28.22	3.43 (5.04) / -0.27	2.84 (3.09) / 0.21	4.37 / NA
Pantherophis obsoletus (PAOB)	34 / 26	-24.31 (0.65) /-24.93 (0.64)	7.07 (0.89) / 6.84 (1.25)	5.08 (0.55) / 4.57 (0.77)	2.53 / 3.01
*Sistrurus miliarius (SIMI)**	4 / 0	-23.88 (0.63) / NA	6.48 (1.04) / NA	4.72 (0.64) / NA	1.5 / NA
*Storeria dekayi (STDE)**	1 / 0	-24.33 / NA	3.62 / NA	2.97 / NA	NA / NA
Thamnophis proximus (THPR)	34 / 51	-25.79 (1.25) / -26.88 (1.87)	6.48 (0.79) / 6.92 (1.11)	4.72 (0.48) / 4.63 (0.68)	1.52 / 2.61

Community-wide food-web structure

Food-web structure of snake assemblages differed between high-frequency and low-frequency treatments. I found evidence for increased niche diversification at the base of the low-frequency food web (CR, Figure 8). The CR was significantly wider in the low-frequency treatment than in the high-frequency treatment. With no overlap in 95% credibility intervals (CIs), this indicates snake consumers were supported by a greater diversity of basal resources in the low-frequency treatment (Figure 8a). Trophic diversity was similar between assemblages indicating snake consumers are occupying a similar trophic level across high- and low-frequency sites (NR; Figure 8). Although there was some overlap in the 95% CIs, NR was slightly greater in the low-frequency site (Figure 8b). However, the extent of trophic diversity was much smaller in the high-frequency site (Figure 9. The SEA distributions from Bayesian results showed an 88% probability that the snake assemblage in the high-frequency site occupied a smaller isotopic niche area than the snake assemblage in the low-frequency site (Table 3, Figure 9).

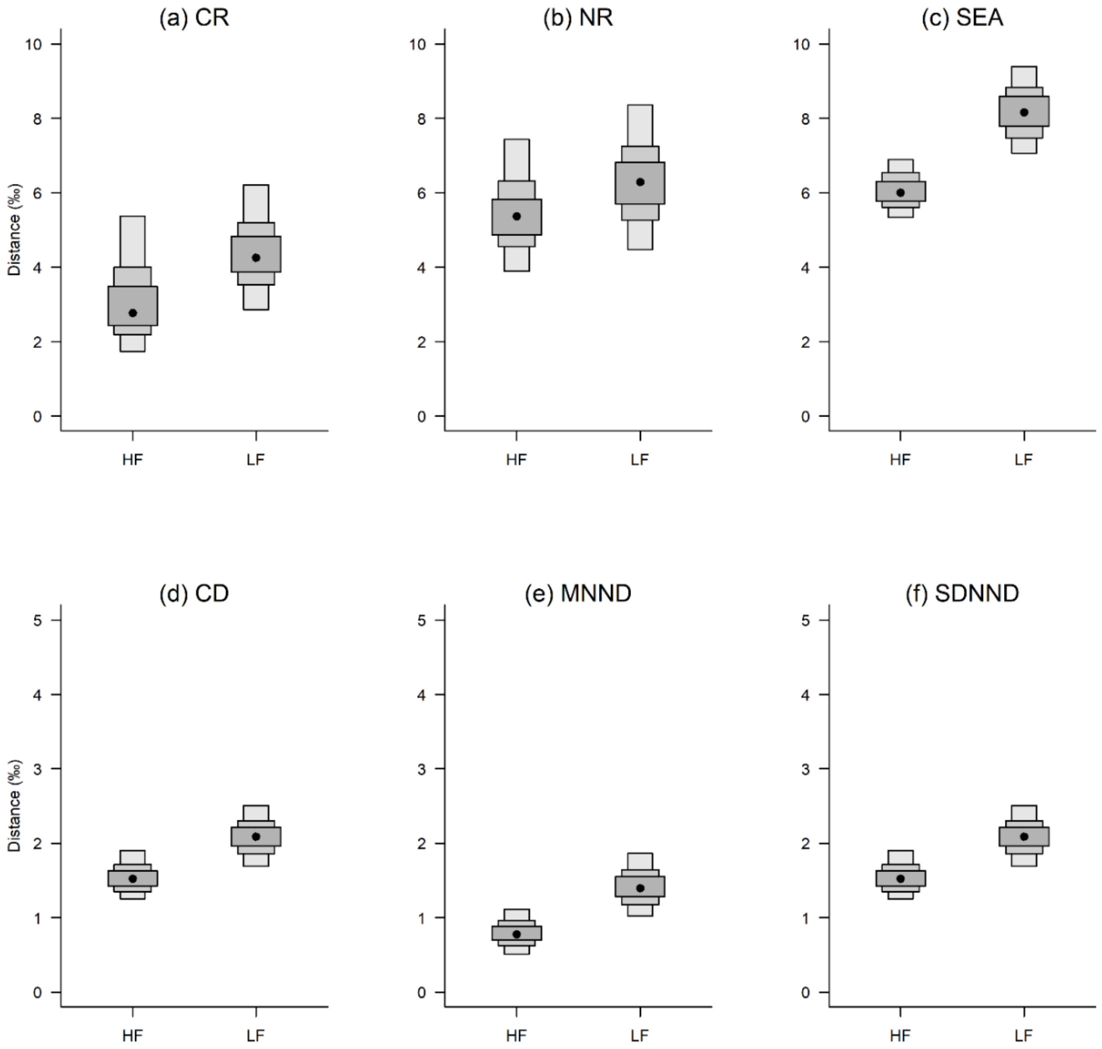

Figure 8. Bayesian results for the six community-wide metrics providing information on trophic diversity and trophic redundancy within high-frequency (HF) and low-frequency (LF) food webs — δ^{13}C range (CR), δ^{15}N range (NR), standard ellipses area (SEA), mean distance to centroid (CD), mean nearest neighbor distance (MNND), and standard deviation of the nearest neighbor distance (SDNND). Black dots are the mode (‰) and boxes indicate the 50%, 75%, and 95% credibility intervals for high-frequency (HF) and low-frequency (LF) treatments.

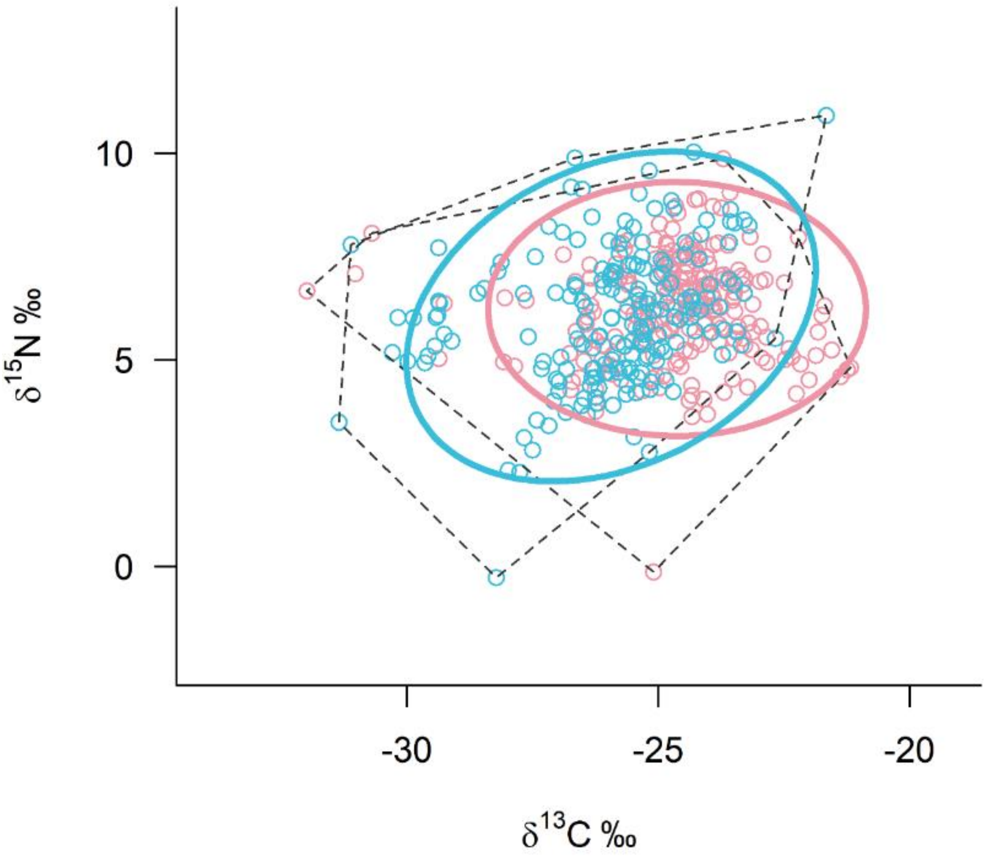

Figure 9. Biplot of δ^{13}C and δ^{15}N of snake assemblages from high-frequency (blue) and low-frequency (pink) treatments. Dotted lines are the total convex hull areas (TA) of snake communities in each treatment that correspond to the area encompassing all snake species and individuals. Solid lines represent standard ellipses areas (SEA_C) depicting isotopic niche space of snake assemblages in each treatment.

Table 3. Results of standard ellipses area analyses for snake communities in high-frequency and low-frequency treatments. Metrics listed are standard ellipse area (SEA) containing *c.* 40% of the bivariate isotopic signatures observed in a given snake assemblage, standard ellipse area corrected for small sample size (SEA_C), and standard ellipse area containing *c.* 95% of the bivariate isotopic signatures observed in a given snake assemblage.

	High-frequency	Low-frequency	SEA overlap	SEA 95% overlap	Proportion of non-overlap
SEA	6.06	8.17	3.42	31.49	0.58
SEA_C	6.09	8.22	NA	NA	NA
SEA 95%	36.46	49.19	NA	NA	NA

Overlap in SEA between treatments was relatively high (31.5%, corresponding to 36.46% and 49.19% of the total SEA for the high and low-frequency treatments, respectively); however, the proportion of non-overlap in SEA for treatments was much greater (58%) (Table 3). The average degree of trophic diversity was also significantly greater in the low-frequency treatment, with no overlap in 95% CIs (CD; Figure 8d). Additionally, there was a strong pattern of trophic redundancy observed in the high-frequency snake assemblage indicating snakes in this treatment had similar trophic roles (MNND, SDNND; Figure 8). The MNND and SDNND values were significantly lower in the high-frequency treatment when compared to the low-frequency treatment with the distributions of Bayesian results showing no overlap in 95% CIs in both metrics (Figure 8e, 8f). This reveals that snakes in the high-frequency site were more tightly packed in isotopic niche space and were more even in terms of species packing.

Resource Use of Snake Communities

Isotopic mixing models revealed that overall resource use of entire snake communities varied between treatments (Figure 10a, 10b). The high-frequency snake assemblage model showed that snake consumers heavily utilized anuran and mammalian prey groups with 68.6 % of the estimated contribution of prey sources to snake diets explained by anuran, insectivores (i.e., shrews), and rodent prey groups (Figure 11a). In contrast, overall resource use by snakes in the low-frequency treatment was more generalized, as most prey groups contributed equally in the model (Figure 11b). Arachnid, caudate, rodent, and squamate prey groups contributed the most to snake diets within this treatment with an estimated 65.2% contribution collectively (Figure 11b).

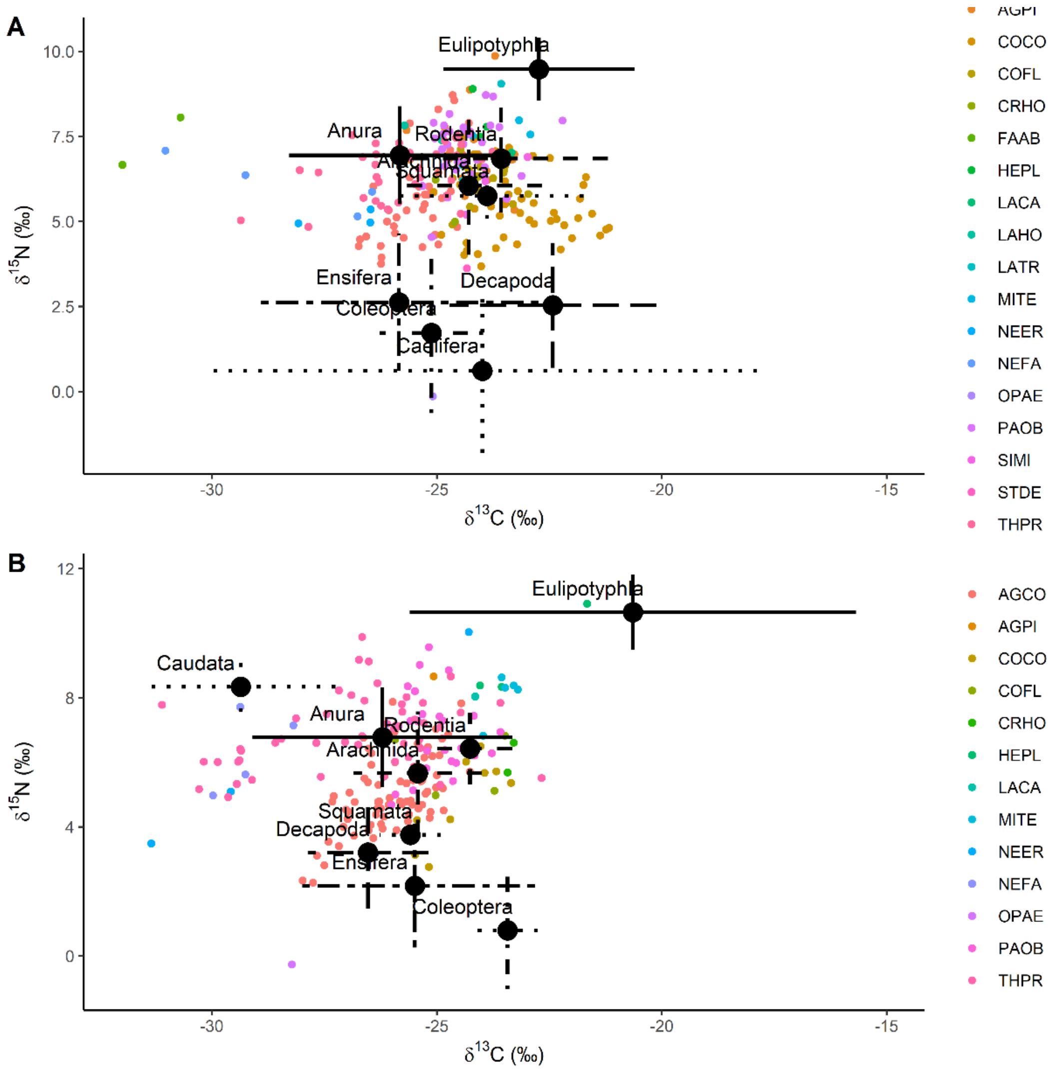

Figure 10. $\delta^{13}C - \delta^{15}N$ isotopic biplots of snake assemblages (colored circles) and prey resources (mean values of $\delta^{13}C - \delta^{15}N$ ± SD; black circles) incorporating corrected trophic discrimination factors in (A) high-frequency and (B) low-frequency treatments. Species codes for snake species are listed in Table 2.

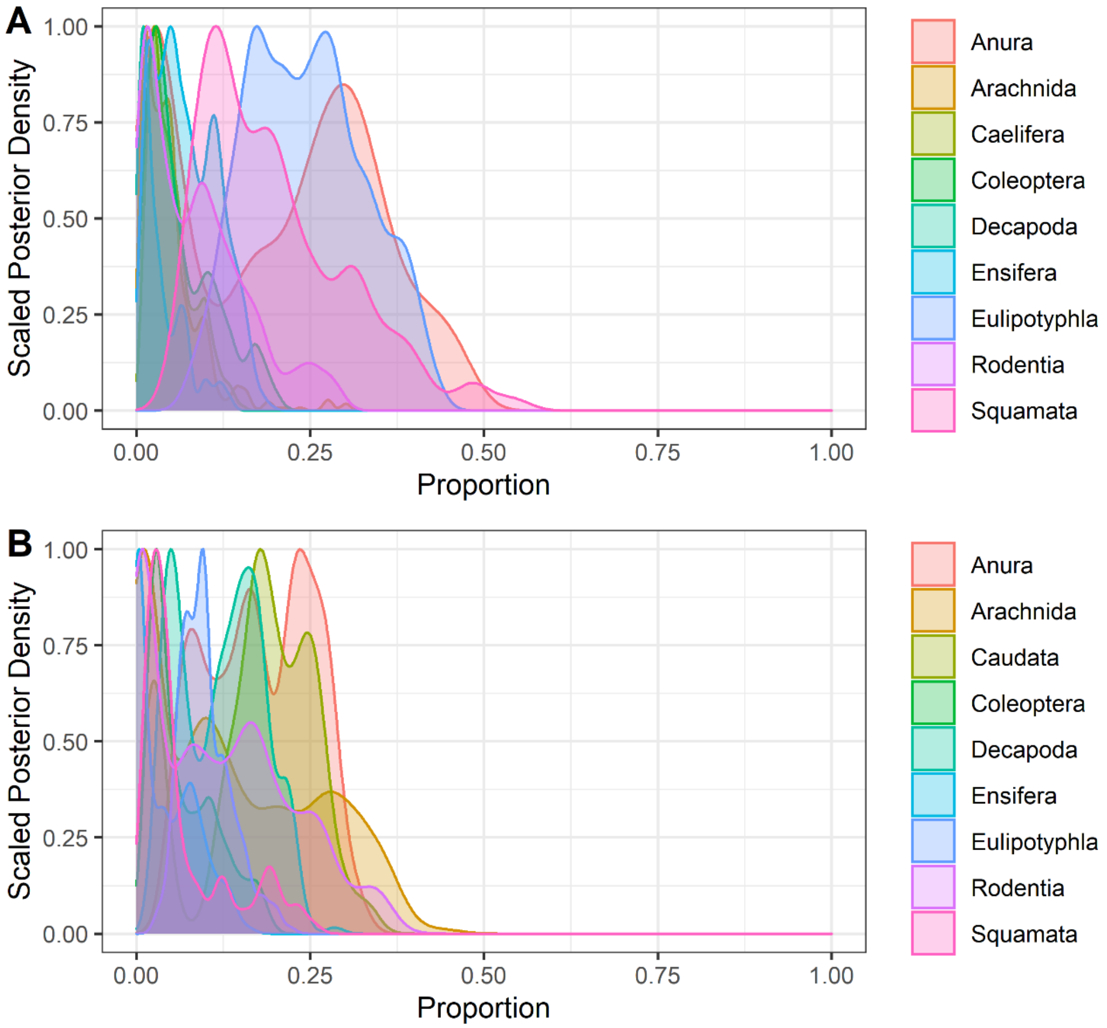

Figure 11. Results from isotopic mixing models depicting the contribution of prey sources for all snake species captured in the (A) high-frequency and (B) low-frequency treatments. Results are reported as posterior density distributions of proportional contributions to snake consumer mixture data as mean dietary proportions with associated credibility intervals (i.e., 25%, 50%, 75%, 100%).

Mixing models of the most common snake species occurring in both high-frequency and low-frequency food webs revealed shifts in resource use indicating site-specific specialization in resource use (AGCO, copperhead, *Agkistrodon contortrix*; COCO, racer, *Coluber constrictor*; PAOB, western ratsnake *Pantherophis obsoletus*; THPR, western ribbonsnake, *Thamnophis proximus*; Figure 12A, 12B). For example, predatory arthropods (i.e., spiders and carabid beetles) were estimated to contribute 21.4% to the diets of these snake species in the low-frequency treatment, while they were not well represented in the high-frequency treatment (9.9 %). Analyses of pairwise resource use between species showed that species utilized prey resources differently between treatments. In the high-frequency treatment, *A. contortrix* exhibited a broader, generalized strategy as anurans (34.1%), herbivorous arthropods (33.0%), and squamates (13.5%) were estimated to contribute the most to their diets (Figure 13A). In the low-frequency treatment, *A. contortrix* were specialized in their diets, with squamates (66.9%) the largest estimated contributor and herbivorous arthropods (17.8%) the second largest contributor (Figure 13E). In both treatments, *C. constrictor* were specialized, but exhibited shifts in their primary prey between treatments, with decapods estimated as the largest contributor in the high-frequency treatment and herbivorous arthropods the largest contributor in the low-frequency treatment (74.2 and 73.3 % respectively) (Figure 13B, 13F). *Pantherophis obsoletus* exhibited similarities in resource use to *A. contortrix* as they were generalized in the high-frequency treatment and specialized in the low-frequency treatment. Decapods (22.4%), predatory arthropods (24.0%), and small mammals (30.6%) were the largest contributors to *P. obsoletus* in the high-frequency site (Figure 13C). Conversely, small mammals (67.6%) were the primary prey group observed in *P. obsoletus* diets at the low-frequency treatment (Figure 13G). *Thamnophis proximus* in both treatments showed patterns of specialization in their resource use. Squamates were estimated to contribute 72.6% to *T. proximus* diets in the high-frequency treatment, and predatory arthropods (71.8%) and amphibians (20.8%) were estimated as the largest contributors to *T. proximus* diets in the low-frequency treatment.

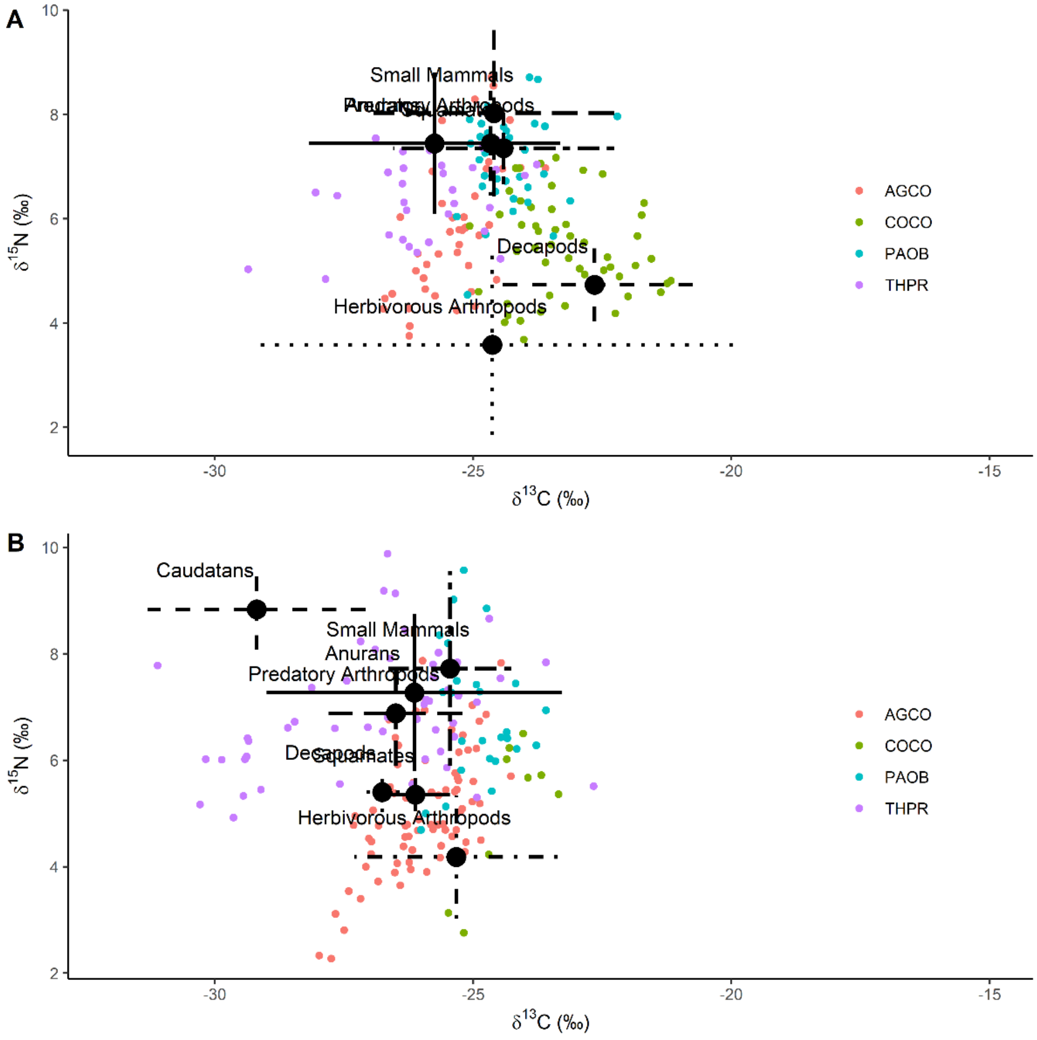

Figure 12. $\delta^{13}C - \delta^{15}N$ isotopic biplots of most common species shared between snake assemblages (colored circles) and prey resources (mean values of $\delta^{13}C - \delta^{15}N \pm SD$; black circles) incorporating corrected trophic discrimination factors in A) high-frequency and B) low-frequency treatments. Species codes for snake species are listed in Table 1.

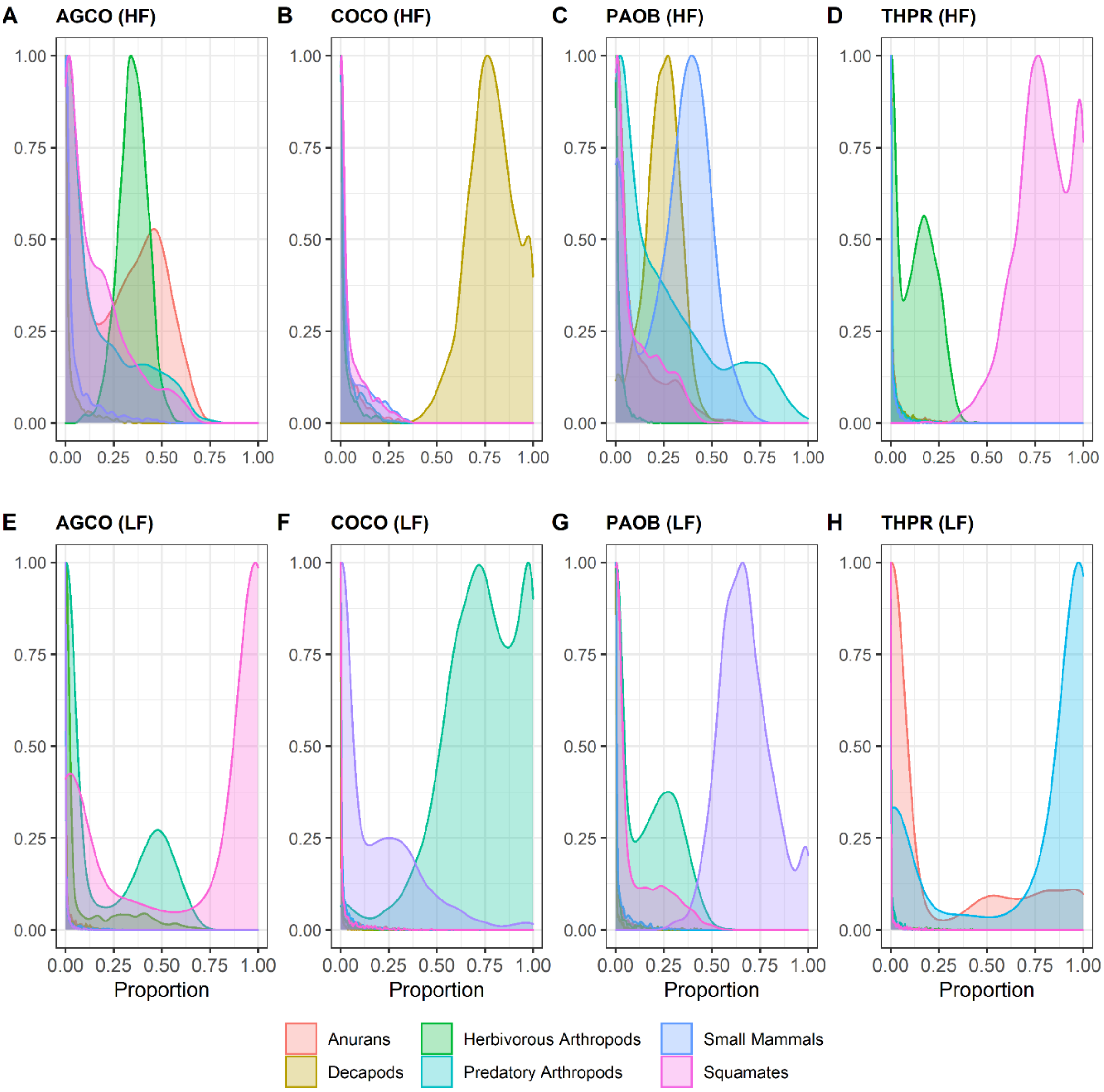

Figure 13. Results from isotopic mixing models depicting the contribution of prey sources to snake species across the four most common shared species captured in the A) high-frequency and B) low-frequency treatments. Results are reported as posterior density distributions of proportional contributions to snake consumer mixture data as mean dietary proportions with associated credibility intervals (i.e., 25%, 50%, 75%, 100%). Species codes are listed in Table 2.

DISCUSSION

Differences in the frequency and intensity of applied forest management practices substantially impacted food-web structure in pine forest systems by modifying environmental conditions that structure habitats, shift energetic pathways, and ultimately resource use of consumers in these systems. Stable isotope analyses of dominant basal resources, primary and secondary consumers, and snake predators revealed contrasting patterns of food-web organization in response to forest management frequency. I found that the trophic structure of predator assemblages differed between treatments. I observed greater trophic diversity at the low-frequency management treatment and lower trophic diversity with increased trophic redundancy at the high-frequency management treatment, supporting my first hypothesis. Overall, resource use and niche breadth of snake predators varied in response to practice frequency. I found that that predator assemblages differed in their resource use between high-frequency and low-frequency treatments as snake consumers utilized different functional prey groups, supporting my second hypothesis.

Effects of Forest Management on Food-web Structure

Greater trophic redundancy was observed at the high-frequency snake assemblage compared to the low-frequency snake assemblage. This observed difference in trophic diversity was not attributed to these predators shifting their trophic positions (*sensu* Schalk et al. 2017) as species from both assemblages exhibited consistency in their trophic positions across both treatments. Rather, the observed increase in trophic redundancy was caused by a contraction in the diversity of basal resources (i.e., $\delta^{13}C$ range) supporting these predators at the high-frequency treatment. These results are surprising as the high-frequency treatment contained an additional energetic pathway (i.e., C4 plants) not found in the low-frequency treatment.

Forest management strategies at the high-frequency treatment are implemented to mimic natural disturbance regimes and maintain forest stands at an early stage of succession (Hanberry et al. 2018). Frequent fire disturbance has been well documented as a driver of increased productivity and overall biodiversity in similar forest ecosystems as the increased sunlight on the forest floor creates diverse herbaceous understories (DellaSala et al. 2014, Freeman et al. 2019). As such, these disturbance-influenced ecosystems can have a broader spatial extent of production providing resource-rich environments allowing many consumers to exploit similar resources. For example, despite the addition of seed-producing C4 grasses, fruit producing C3 forbs were the most dominant understory cover in high-frequency sites. The dominance of C3 forbs was attributable to relatively few species (i.e, black raspberry, *Rubus occidentalis* and blueberry, *Vaccinium* spp.) known for their high-productivity in early-seral forests and their nutritional benefits to a wide variety of wildlife (McWethy et al. 2010). C4 grasses adapted to higher-temperature environments possess anatomical and biochemical features that impact nutritional quality and might not be as palatable to consumers (Barbehenn et al. 2004, Silva Pedro and Rammer 2017). Given the similarity in carbon signatures of prey resources (e.g., secondary consumers) at multiple trophic levels in the high-frequency treatment, the trophic redundancy observed in the high-frequency snake assemblage likely results from both predators and prey maximizing energetic uptake at each trophic level. Furthermore, this pattern prevails along a narrow and highly productive C3 pathway fostered by frequent forest management practices that preserve conditions for fruit-producing C3 plants to dominate. Experimental studies in which one or more energetic pathways were manipulated have shown that consumers at multiple trophic levels can shift their resource exploitation to take advantage of highly productive pathways (Klemmer and Richardson 2013, Nowlin et al. 2007). For example, productivity was altered with increased decomposition of salmon carcasses within experimental mesocosms replicating benthic food webs (Kiffney et al. 2018). As a result, primary consumers shifted their resource use and had a strong dependence on the energetic pathway associated with carcass loading, which led to increased trophic redundancy in both secondary and tertiary consumers (Kiffney et al. 2018).

Decreased forest management practice frequency might have created conditions in which basal resource diversity increased, despite an apparent homogenization of structural habitats. As such, partitioning of basal resources by functional prey groups might be a potential mechanism that resulted in increased trophic diversity in the low-frequency snake assemblage. Studies of simple food chains in pristine and degraded shallow Caribbean coral reefs have reported similar patterns of trophic structure suggesting that these patterns are consistent across aquatic and terrestrial ecosystems (e.g., Le Bourg et al. 2018). Morillo-Velarde et al. (2018) found that habitat degradation (i.e., acroporid coral die-off from white band disease) altered trophic pathways, but food chain length remained unchanged (i.e., δ^{15}N range). Specifically, the δ^{13}C range was broader and originated from more sources in the degraded food chain because of macroalgal consumption by a variety of mesograzers and omnivores that were then consumed by herbivorous fishes (Morillo-Velarde et al. 2018). The δ^{13}C range was broader, originated from more sources in the degraded food chain, and was associated with multiple energetic pathways that introduced added variation in isotopic δ^{13}C of consumers (Morillo-Velarde et al. 2018). Similarly, lack of consistent and effective forest management at the low-frequency sites resulted in basal area and closed-canopy conditions that lead to homogenized understories and detritus buildup on forest floors. Reviews of food-web studies in ecosystems in which detritus is a major energy source has emphasized that such resources are not homogenous in terms of energy flow, energy quality, composition, and carbon value, and are instead highly variable in form and distribution across multiple spatial and temporal scales (Moore et al. 2004). Food webs vary in the extent to which detritus derives from allochthonous or autochthonous sources, which then results in multiple and dynamic consumer-resource pathways (Polis and Hurd 1996, Azam 1998). Ecosystems in which anthropogenic alterations result in detritus sources becoming the dominant inputs into food webs can alter the trajectories of both ground-level habitat and energy flow (Gessner et al. 2010, Moore et al. 2004). In the low-frequency treatment, this might have resulted in the variation in δ^{13}C pathways and consequently, the broader δ^{13}C range of snake consumers.

Effects of Forest Management on Resource Use

Differences in the structural complexity of habitats, and the number and type of energetic pathways, between high-frequency and low frequency treatments indicate the trophic structure of predator assemblages might be influenced by the responses of given functional prey groups to practice frequency (Gorini et al. 2012). Forest management that influences secondary production by changing environmental conditions would then be expected to shift the resource use of predators by directly or indirectly altering trophic linkages (Beckerman et al. 2006, Layman and Rypel 2020). Snakes are abundant predators in pine-forest ecosystems and are largely considered generalists because of commonalities between species (e.g., low-energetic demands and broad dietary niche breadths; Werler and Dixon 2010). Furthermore, prey availability is considered a major determinant of niche partitioning and coexistence within snake communities and, as such, the diversity of these predators in managed ecosystems is likely correlated with resource-use responses (Luiselli 2003, Luiselli 2006, Perkins et al. 2020, Toft 1985). Previous studies of terrestrial snake communities in temperate regions investigating patterns of resource use and coexistence dynamics are limited (Luiselli et al. 2006). However, given that the taxonomic diversity of predators was greater in the high-frequency treatment, and that predator diversity in the low-frequency treatment was dominated by only a few generalist species, predator assemblages could be exhibiting predictable responses to forest management by switching their overall resource use between treatments.

When all species were included (n =18 spp.), predators in the high-frequency treatment exhibited more specialization in resource use towards functional prey groups (e.g., anurans, small mammals, and squamates) consisting of larger-bodied, high quality prey. Vertebrate prey is well documented in diets of terrestrial generalist predators and, under a frequent forest management regime, increases in the number of microhabitats (e.g., coarse woody debris and herbaceous materials) can then be utilized by a wide variety of vertebrate taxa (Greene et al. 2016). Pine-grassland forests subjected to frequent applications of prescribed fire and thinning have been reported to increase the diversity and abundance of small mammals, and harbor comparable amphibian diversity to other forest types (Russel et al. 2004, Steen et al. 2010, Sutton et al. 2014). Under such conditions when certain vertebrate prey groups are abundant, coexistence may be facilitated as generalist predators take advantage of these high-quality resources. For example, Reynolds and Scott (1982) reported that the utilization of high-quality rodent prey was a major factor that influenced species coexistence between five snake species in a Chihuahuan desert ecosystem.

In contrast, predators in the low-frequency treatment (n = 12 spp.) utilized functional prey groups in equal proportions, which also included increased utilization of invertebrate prey groups. In this case, predators likely exploited more functional prey groups that included lower quality resources. Infrequent management leads to the homogenization of habitats and differences in productivity that inhibits the diversity of valuable prey resources to predators. Without the persistent influence of fire and thinning operations, closed-canopy forests lead to the development of dense understories and a build-up of leaf litter on the forest floor. Such conditions can have negative effects on small mammal abundance and might limit the diversity of other larger-bodied, high-quality prey taxa (Greene et al. 2016). Habitat generalists at the low-frequency treatment persist in a broad range of habitats, as such, generalized feeding strategies allow these species to take advantage of a wide variety of low-quality prey sources that are encountered more frequently (Parker and Hawkes 2018). For example, smaller-bodied, low-quality prey (e.g., poikilothermic prey; leaf litter dwelling arachnids and lizards) contributed as much as to overall resource use as high-quality prey (i.e., large-bodied anurans and small rodents) (Elser et al. 2000). Evidence from both museum-based and field studies of predator diets has revealed that sympatric species that share similar dietary preferences can partition resources in food-limited environments by altering the frequency of consumption of high-quality and low-quality prey (e.g., Jellyman and

McIntosh 2020, Luiselli 2006). Woo et al. (2008) found that the intraspecific resource use of generalist marine predators (guillemots [*Uria* and *Cepphus* spp.]) showed differential patterns of generalization and specialization that was attributed to the availability and exploitation of optimal foraging locations and behavioral adaptation to limited resources. Guillemots exhibited no difference in the overall fitness, which indicates that generalist predators employ different strategies of resource use in response to variation in prey allowing species to persist under a range of ecological contexts (Woo et al. 2008). This suggests that secondary production regulated by disturbance-mediated processes can drive differential resource use patterns in predator assemblages between high-frequency and low-frequency treatments.

The functional prey groups that were most important to predators at the high-frequency treatment occupied similar isotopic niches, suggesting that frequent forest management facilitates the conditions that allows generalist predators with varied feeding ecologies to exploit these resources while also occupying similar trophic roles. For example, despite their differences in feeding ecology and behavior, the resource use of the most common generalist predators corresponded with the differences in trophic structure observed between treatments. *Agkistrodon contortrix* are highly generalized in their dietary preferences, feeding on a diverse array of both invertebrate and vertebrate prey (Ernst and Ernst 2011, Schalk et al. 2018). At the high-frequency treatment, *A. contortrix* utilized anurans, small mammals, and squamates in greater proportions than other functional prey groups. At the low-frequency treatment, however, *A. contortrix* consumed primarily squamates (i.e., small-bodied lizards) and arthropods (i.e., herbivorous insects), increasing specialization towards frequently encountered, lower-quality prey. *Thamnophis proximus*, an active forager also known to consume a variety of invertebrate and vertebrate prey (Rossman 1996), were specialized in their resource use in both treatments. At the high-frequency treatment, *T. proximus* utilized mainly squamate prey, while utilizing predator invertebrates at the low-frequency treatment. In both of these two common predators, resource use has been reported to vary between populations because of differences in environmental conditions (Hampton et al. 2013, Schalk et al. 2018, Quevedo et al 2009), and in my study these patterns of resource use reflected the overall patterns of trophic structure I observed at high-frequency and low-frequency treatments. Predators exploited high-quality functional prey groups along a highly productive energetic pathway which contributed to increased trophic redundancy at the high-frequency treatment, whereas the utilization of lower quality functional prey groups by predators at the low-frequency treatment contributed to trophic niche-diversification at the base of the food web and greater overall trophic diversity.

Considering my findings, the relative frequency of forest management practices (e.g., burning and thinning) is an important determinant of food-web structure in pine forest ecosystems. Alterations to structural habitats brought on by different forest management practices can influence the diversity and abundance of resources that either directly or indirectly support predator assemblages (Howze and Smith 2021, Morris et al. 2013, Nelson et al. 2020). The importance of diverse predator assemblages, and the roles of predators within food webs is well known. Indeed, unravelling the interactions between predators and their prey is an informative approach for understanding how communities will respond to anthropogenic activities. However, understanding the cumulative effects of species interactions on trophic structure within real food webs is a difficult endeavor (Massoud et al 2018). Intraguild predation, omnivory, and multitrophic-level processes can influence trophic structure, and are not easily addressed when considering predator responses at only one trophic level (McLeod and Leroux 2020, Raffaelli et al. 2002, Wang et al. 2019). Nonetheless, with the substantial loss of apex predators from ecosystems across the globe, increased knowledge of the trophic roles of tertiary predators in ecosystems regulated by anthropogenic disturbance is important for understanding ecosystem functioning (Estes et al. 2011, Strong and Frank 2010).

Implications for Management of Forest Ecosystems

Increased intensity of forest management practices led to greater diversity of snakes and increased the trophic redundancy within the high-frequency assemblage. As tertiary predators, most snake species are fairly generalized in their resource use within terrestrial environments. As such, forest management that encourages the persistence of many generalist predators has important implications for the stability of pine forest ecosystems. Generalist predators represent key nodes in the structure of most food webs, as these predators can influence the number of trophic linkages within food webs because of their ability to exploit a broader array of prey resources than specialists (Closs et al. 1999). This results in many weak interactions with their prey that, that in turn, contribute to the complexity of food webs and the maintenance of ecosystem processes. Consequently, the loss of generalist species in food webs can reduce this complexity and alter the resource use relationships that influence ecosystem processes (Ings et al. 2009). Therefore, the resiliency of diverse assemblages of generalist predators performing similar trophic roles (i.e., increase trophic redundancy) can lead to greater stability in ecosystems prone to disturbance (Sanders et al. 2018). Increased forest management as a consistent disturbance in pine forests affects the horizontal and vertical diversity of food webs, acting as a driver of bottom-up processes that then reinforces top-down processes. Altering the trophic relationships between predator assemblages and their prey has consequences for the provision of ecosystem services, especially in ecosystems in which ecological succession is heavily influenced by anthropogenic activities (Zhao et al. 2019).

While many food-web studies reveal the negative impacts of anthropogenic activities on biodiversity and ecosystem function, food-web approaches are increasingly recognized as an important ecological tool to inform restoration practices (Layman et al 2020, Loch et al. 2020, Price et al. 2019). As many of the world’s ecosystems are degraded beyond natural recovery, ecological restoration is now imperative to restore damaged ecosystems and slow the loss of biodiversity (Hobbs et al. 2011). Ecosystem restoration has historically focused on maintaining key structural properties of habitats, however, and not considered the functional properties of ecosystems (Bellmore et al.

2017, Vander Zanden 2016). Considering trophic relationships can contribute to ecological restoration by encouraging a dynamic, interaction-driven view of ecosystems that alerts practitioners to those trophic interactions that have bearing on restoration outcomes (Naiman et al. 2012). Forest management practices that mimic or suppress natural disturbance regimes can drastically alter the ecological trajectory of ecosystem structure and pine forests are model systems for applying such multi-faceted approaches (Vander Zanden 2016).

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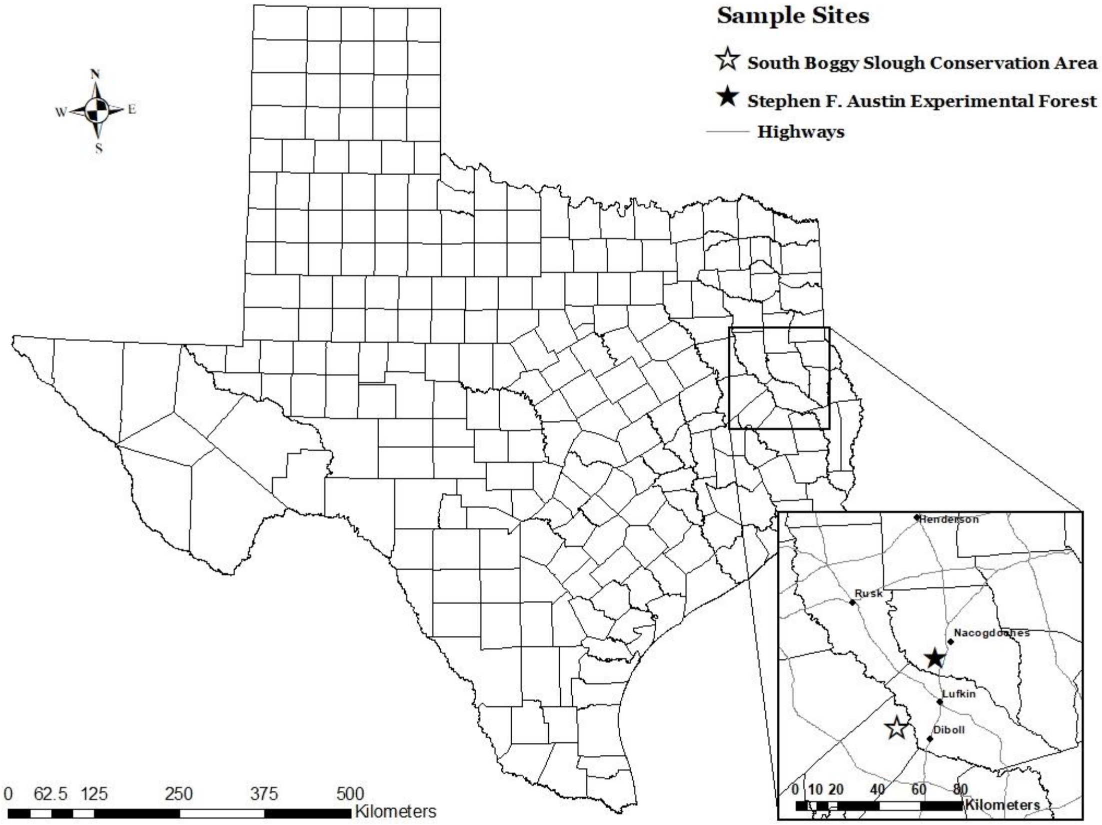
APPENDIX



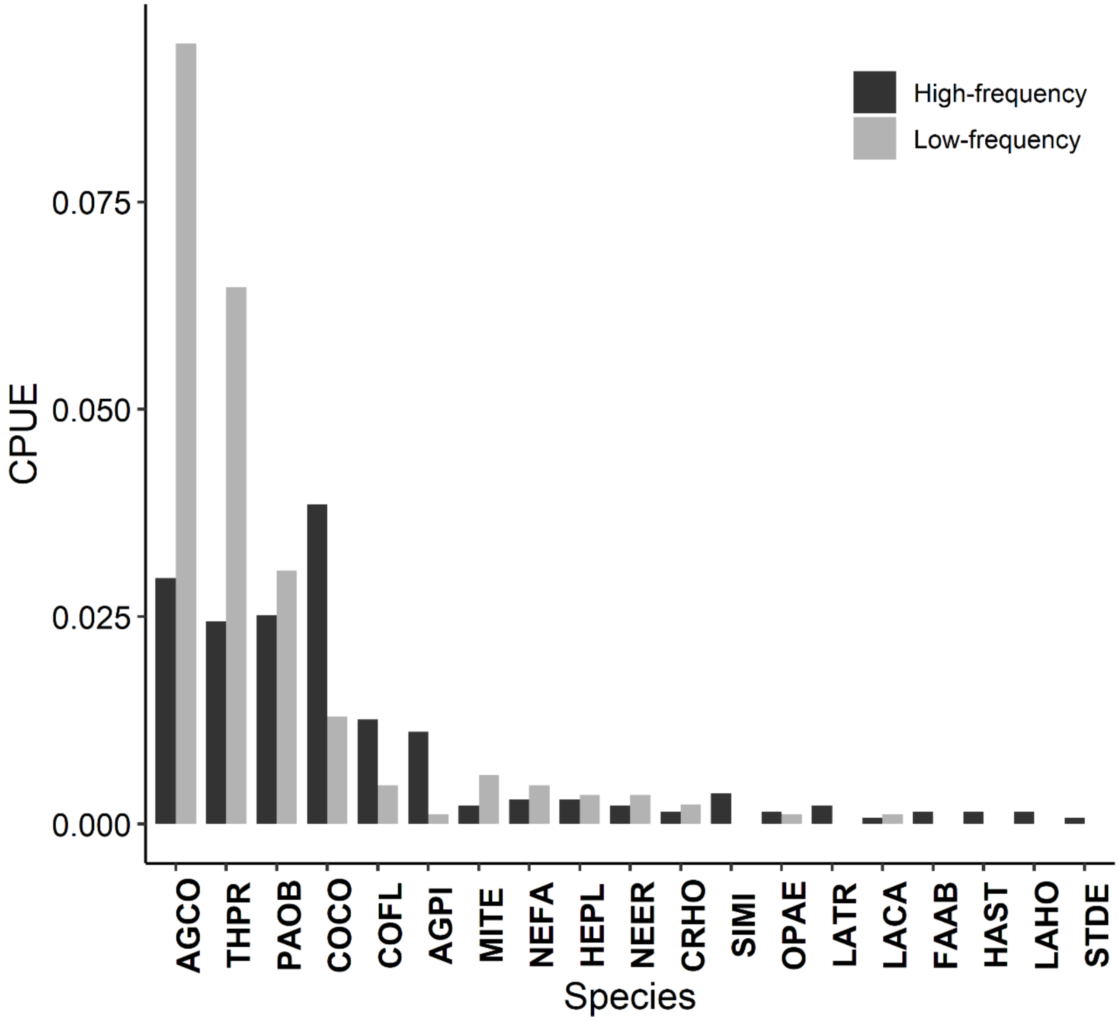
S1. Map of east Texas region (inset; Study area depicting locations of study sites)

S2. The 10 most abundant prey taxa found across sampled sites. Average dissimilarity between high-frequency and low-frequency sites for each taxon was calculated with SIMPER analysis. Contributions for each species were calculated from the Bray-Curtis dissimilarity matrix of species relative abundances to trapping effort. Taxa are listed in order of their contribution to the differences between sites.

Taxon	Average dissimilarity	Mean contribution (HF)	Mean contribution (LF)	Cumulative contribution
Ensifera (crickets)	0.2538	0.033	0.384	0.384
Anura (frogs and toads)	0.1764	0.065	0.309	0.652
Aranae (spiders)	0.12148	0.085	0.253	0.836
Coleoptera (terrestrial beetles)	0.07086	0.031	0.129	0.943
Rodentia (small rodents)	0.01374	0.026	0.007	0.964
Caelifera (grasshoppers)	0.00795	0.014	0.003	0.976
Decapoda (crayfish)	0.00723	0.002	0.012	0.987
Caudata (salamanders)	0.00434	0.000	0.006	0.993
Lacertilia (lizards)	0.00217	0.003	0.006	0.997
Eulipotyphla (shrews and moles)	0.00217	0.006	0.009	1.000

S3. Traits used to measure snake functional diversity with descriptions and variable coding (scale)

Trait type	Trait	Scale
Feeding ecology	head length (tip of snout to posterior edge of mandible) head width (at posterior edge of mandible) head depth (at highest point) eye diameter inter-narial distance inter-ocular distance circumference at mid-body	Continuous
Toxicity	venomous non-venomous	Binary
Foraging mode	active sit-and-wait generalized	Categorical
Habitat use	terrestrial fossorial semi-arboreal semi-aquatic	Categorical
Reproductive mode	oviparous viviparous	Binary



S4. Species abundances (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 Table 1.

S5. Isotopic values of δ13C and δ15N of functional groups for basal resources and prey in high-frequency and low-frequency sites. Values represent averages across functional groups and treatments (±1 SD).

Functional Group (High-Frequency)	Taxa	N	δ13C	δ15N
(a) basal resources	C4 (grasses and sedges)	20	-12.97 (0.68)	-1.03 (2.89)
	C3 (other)	88	-29.36 (1.93)	-1.54 (2.43)
	C3 (canopy effects, low light)	18	-32.10 (0.44)	-1.29 (2.54)
(b) primary consumers	caeliferans (grasshoppers) coleopterans (terrestrial beetles) decapods (crayfish) ensiferans (crickets)	64	-24.80 (4.66)	0.78 (1.73)
(c) secondary consumers	anurans (frogs and toads) arachnids (spiders) carabids (predatory beetles) eulipotyphlans (shrews) rodents (omnivores) squamates (lizards)	102	-25.24 (2.13)	4.79 (1.32)

S5. Continued

Functional Group (Low-Frequency)	**Taxa**	**N**	**δ13C**	**δ15N**
(a) basal resources	C3 (other)	22	-30.38 (0.87)	-3.33 (1.27)
	C3 (canopy effects, low light)	21	-32.45 (0.92)	-2.81 (2.04)
(b) primary consumers	coleopterans (terrestrial beetles) decapods (crayfish) ensiferans (crickets)	63	-25.60 (1.85)	1.62 (1.24)
(c) secondary consumers	anurans (frogs and toads) arachnids (spiders) carabids (predatory beetles) caudates (salamanders) eulipotyphlans (shrews) rodents (omnivores) squamates (lizards)	66	-26.57 (2.50)	4.41 (1.59)

Continued

S5. Continued

Functional Group (High-Frequency)	Taxa	N	δ13C	δ15N
(a) anurans	frogs and toads	41	-25.92 (2.43)	4.64 (1.35)
(b) decapods	crayfish	6	-22.82 (1.90)	1.93 (0.69)

Functional Group (High-Frequency)	Taxa	N	δ13C	δ15N
(c) herbivorous arthropods	caeliferans (grasshoppers)	34	-24.39 (5.97)	0.01 (1.72)
	coleopterans (terrestrial beetles)	12	-25.52 (1.08)	1.12 (1.63)
	ensiferans (crickets)	12	-26.24 (2.82)	2.02 (1.08)
(d) predatory arthropods	arachnids (spiders and scorpions)	21	-24.69 (0.98)	4.75 (0.96)
	carabids (predatory beetles)	8	-25.20 (1.03)	4.34 (1.09)
(e) small mammals	eulipotyphlans (shrews)	10	-23.93 (2.12)	6.37 (0.83)
	rodents (omnivores)	17	-25.27 (2.37)	4.54 (1.55)

S5. Continued

Functional Group (High-Frequency)	**Taxa**	**N**	**δ13C**	**δ15N**
(f) squamates	lizards	5	-24.58 (2.14)	4.55 (0.68)

Functional Group (Low-frequency)	**Taxa**	**N**	**δ13C**	**δ15N**
(a) anurans	frogs and toads	23	-26.31 (2.86)	4.47 (1.47)
(b) caudates	salamanders	10	-29.36 (2.11)	6.03 (0.75)

S5. Continued

Functional Group (Low-frequency)	**Taxa**	**N**	**δ13C**	**δ15N**
(d) herbivorous arthropods	coleopterans (terrestrial beetles)	22	-23.83 (0.54)	0.19 (0.69)
	ensiferans (crickets)	41	-25.89 (2.33)	1.57 (0.88)
(e) predatory arthropods	arachnids (spiders and scorpions)	24	-25.82 (0.59)	4.36 (0.65)
	carabids (predatory beetles)	6	-27.94 (0.96)	3.67 (1.31)
(f) small mammals	eulipotyphlans (shrews)	13	-21.84 (4.96)	7.55 (1.01)
	rodents (omnivores)	6	-25.96 (0.93)	4.12 (1.07)
(g) squamates	lizards	10	-26.29 (0.70)	2.55 (0.29)

S6. Scientific and common names for allocated species codes of snakes captured during study**.**

Scientific name	**Common name**	**Species code**
Agkistrodon contortrix	Copperhead	AGCO
Agkistrodon piscivorus	Cottonmouth	AGPI
Coluber constrictor	Racer	COCO
Coluber flagellum	Coachwhip	COFL
Crotalus horridus	Timber rattlesnake	CRHO
Farancia abacura	Mudsnake	FAAB
Haldea striatula	Rough earthsnake	HAST
Heterodon platirhinos	Eastern hog-nosed snake	HEPL
Lampropeltis calligaster	Prairie kingsnake	LACA
Lampropeltis holbrooki	Speckled kingsnake	LAHO
Lampropeltis triangulum	Eastern milksnake	LATR
Micrurus tener	Texas coralsnake	MITE
Nerodia erythrogaster	Plain-bellied watersnake	NEER
Nerodia fasciata	Banded watersnake	NEFA
Opheodrys aestivus	Rough greensnake	OPAE
Pantherophis obsoletus	Western ratsnake	PAOB
Sistrurus miliarius	Pygmy rattlesnake	SIMI
Storeria dekayi	Dekay's brownsnake	STDE
Thamnophis proximus	Western ribbonsnake	THPR

VITA

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EDUCATION

M.S. Forestry — December 2020 — Stephen F. Austin State University, Nacogdoches, TX. Thesis Title: Food-web and functional trait community structure in east Texas Pine Forests with varied management regimes. Advisor: Dr. Christopher M. Schalk

B.S. Wildlife and Fisheries Sciences — December 2013 — Texas A&M University, College Station, TX.

PROFESSIONAL EXPERIENCE

Graduate Research Assistant — Aug 2018 – present — Arthur Temple College of Forestry & Agriculture, Stephen F. Austin State University, Nacogdoches, TX

Advisors(s): Christopher M. Schalk and Daniel Saenz.

Research Assistant — Jan 2014 – Jun 2018— Natural Resources Institute, Texas A&M University, College Station, TX.

Duties: Assisted in various studies investigating the distribution, movement patterns, and population status of threatened/endangered candidate species including Spot-tailed Earless Lizard (*Holbrookia lacerata*), Desert Massasauga (*Sistrurus catenatus edwardsii*), Reticulate Collared Lizard (*Crotaphytus reticulatus*), Louisiana Pinesnake (*Pituophis ruthveni*), and Western Chicken Turtle (*Deirochelys reticularia miaria*).

Supervisor(s): Wade A. Ryberg and Brian F. Pierce.

Research Assistant — May 2013 – Aug 2017—Natural Resources Institute, Texas A&M University, TX; East Foundation, San Antonio, TX.

Duties: Conducted biodiversity surveys of reptiles, amphibians, birds, and mammals on privately operated East Foundation ranchlands. Collected and prepared voucher specimens for deposition into natural history museums, and collected data for threatened/endangered species assessments.

Supervisor(s): Toby J. Hibbitts and Tyler A. Campbell.

Research Assistant — Jun 2013 —Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX.

Duties: Performed presence/absence surveys for endangered species candidate *Sceloporus arenicolus* in the mescelero sands of west Texas. Prepared voucher specimens for deposition in natural history museum.

Supervisor(s): Toby J. Hibbitts and Wade A. Ryberg.

Field Assistant — Jan 2013 – May 2013 — Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX.

Duties: Performed frog call surveys for endangered species candidate *Rana areolata* in Texas. Also prepared voucher specimens for deposition in natural history museum.

Supervisors(s): Toby J. Hibbitts

Curatorial Assistant — Sep 2012 – May 2013 — Biodiversity Research and Teaching Collections, Texas A&M University, College Station, Texas.

Duties: Enter museum records of amphibians and reptiles into a computer database. Also to help maintain the collection of amphibians and reptiles.

Supervisor: Toby J. Hibbitts

Field Technician — May 2012 – Aug 2012 — Field Technician, Andrews, Texas.

Duties: Operated pitfall traps and participated in mark/recapture study of lizards in the mescelero sands of west Texas.

Supervisors(s): Toby J. Hibbitts and Wade A. Ryberg

PUBLICATIONS

Anderson, A., Ryberg, W. A., Skow, K. L., Pierce, B. L., Frizzell, S., Neuharth, D. B., **Adams, C. S.**, Johnson T. E., Pierce, J. B., Rudolph, D. C., Lopez, R. R., Hibbitts, T. J. 2020. Modeling Louisiana Pinesnake Habitat to Guide the Search for Population Relicts. *Southeastern Naturalist*, *19*(4), 613-626.

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Hibbitts, T. J., D. K. Walkup, T. LaDuc, B. Wolaver, J. P. Pierre, M. Duran, D. Neuharth**,** S. Frizzell, **C. S. Adams**, T. E. Johnson, D. Yandell, W. A Ryberg. *In Review*. Natural History of the Enigmatic Earless Lizards (*Holbrookia lacerata* and *H. subcaudalis*). Journal of Natural History.

Garrett, T. B., Ryberg, W. A., **Adams, C. S.**, Campbell, T. A., & Hibbitts, T. J. 2019. Diurnal and nocturnal habitat use in reticulate collared lizards (Crotaphytus reticulatus). *The Southwestern Naturalist*, *63*(4), 209-215.

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Ryberg, W.A., B.D. Wolaver, H.L. Prestridge, B.J. Labay, J.P. Pierre, R.A. Costley, **C.S. Adams**, B.C. Bowers, and T.J. Hibbitts. 2017. Habitat modeling and conservation of the Western Chicken Turtle (*Deirochelys reticularia miaria*). *Herpetological Conservation and Biology* 12(2):307-320.

Adams, C.S., W.A. Ryberg, T.J. Hibbitts, B.L. Pierce, J.B. Pierce, and D.C. Rudolph. 2017. Evaluating effectiveness and cost of time-lapse triggered camera trapping techniques to detect terrestrial squamate diversity. Herpetological Review 48:44-48.

Hibbitts, T. J., Ryberg, W. A., **Adams, C. S.,** Fields, A. M. Lay, D., and Young, M. E. 2013. Microhabitat selection by a habitat specialist and a generalist in both fragmented and unfragmented landscapes. *Herpetology Conservation and Biology* 8:104-113.

NOTES AND SPECIES ACCOUNTS

Thompson, D.W., **C.S. Adams**, C.M. Schalk. 2020. *Farancia abacura* (Red-bellied Mudsnake) Overland Movement. Herpetological Review. 51:142-143.

Koenig, J.R, K.L. Jobe, S.E. Ebert, **C.S. Adams**, C.M. Schalk. 2019. *Liodytes rigida* (Glossy Swampsnake). Geographic Distribution. Herpetological Review. 50:530-531.

Walkup, D., C.S. Adams, W.A. Ryberg, T.J. Hibbitts. 2018. *Holbrookia lacerata* (Spot-tailed Earless Lizard). Predation. Herpetological Review. 49(4):742-743.

Neuharth, D.B., D. Walkup, S. Frizzell, J.Z. Kachel, C.S. Adams, T.J. Johnson, T.J. Hibbitts, W.A. Ryberg. 2018. Holbrookia lacerata (Spot-tailed Earless Lizard). Burying behavior. Herpetological Review. 49(4):536-537.

Adams, C.S., J.B. Pierce, D.C. Rudolph, W.A. Ryberg, and T.J. Hibbitts. 2017. *Pituophis ruthveni*. *Catalogue of American Amphibians and Reptiles (CAAR).*

Adams, C.S., T.J. Hibbitts, and T.A. Campbell. 2016. New amphibian and reptile county records from the lower Rio Grande Valley in Texas, USA. *Herpetological Review* 47:430-431.

TEACHING EXPERIENCE

Stephen F. Austin State University, Arthur Temple College of Forestry & Agriculture

Field Station (Summer 2019, Summer 2020).

Wildlife Techniques (Spring 2018, Spring 2019).

Introduction to Wildlife Management (Fall 2018).

CONFERENCE ACTIVITY/PARTICIPATION

Adams, C.S., C.M. Schalk, D. Saenz. 2020. Trophic and community structure of snake assemblages in shortleaf pine forests with different management regimes. Ecological Integration Symposium. College Station, TX. **Awarded Best Presentation – Fishes and Reptiles Section**.

Adams, C.S., C.M. Schalk, D. Saenz. 2020. Trophic and community structure of snake assemblages in shortleaf pine forests with different management regimes. Southeast Partners in Amphibian and Reptile Conservation. Nauvoo, AL.

Adams, C.S., C.M. Schalk, D. Saenz. 2020. Effects of forest management on snake functional diversity. Southeast Partners in Amphibian and Reptile Conservation. Nauvoo, AL.

Arnett, J.M., **C.S. Adams**, C.G. Montaña, C.M. Schalk. 2020. Mediterranean House Geckos exploit novel resources in a recipient lizard assemblage. Southeast Partners in Amphibian and Reptile Conservation. Nauvoo, AL.

Thompson, D.W., **C.S. Adams**, D. Saenz, C.M. Schalk. Increased management frequency decreases lizard abundance in forest ecosystems. Southeast Partners in Amphibian and Reptile Conservation. Nauvoo, AL.

Schalk, C.M., **C.S. Adams**, D.W. Thompson, K.L. Jobe, K.J. Ward, D. Saenz. 2020. Summer activity patterns of snakes in shortleaf pine forests. Southeast Partners in Amphibian and Reptile Conservation. Nauvoo, AL.

Thurmond, E.A., D. Saenz, J. Reid, K.A. Kidd, C. Adams, J. Childress, **C.S. Adams**. 2020. Avian Communities Respond to Restoration Treatments in East Texas Pine Forests. Texas Chapter of the Wildlife Society. Corpus Christi, TX. **Awarded first place in undergraduate poster presentations.**

Arnett, J.M., **C.S. Adams**, C.G. Montaña, C.M. Schalk. 2020. Mediterranean House Geckos exploit novel resources in a recipient lizard assemblage. SFASU’s Undergraduate Research Conference, Nacogdoches, TX

Thompson, D.W., **C.S. Adams**, D. Saenz, C.M. Schalk. 2020. Increased management frequency decreases lizard abundance in forest ecosystems. SFASU's Undergraduate Research Conference, Nacogdoches, TX.

Arnett, J.M., **C.S. Adams**, C.G. Montaña, C.M. Schalk. 2019. Mediterranean House Geckos exploit novel resources in a recipient lizard assemblage. Arthur Temple College of Forestry and Agriculture Undergraduate Research Showcase, Nacogdoches, TX. **Awarded Seventh Place Poster Presentation.**

Thompson, D.W., **C.S. Adams**, D. Saenz, C.M. Schalk. 2019. Increased management frequency decreases lizard abundance in forest ecosystems. Arthur Temple College of Forestry and Agriculture Undergraduate Research Showcase, Nacogdoches, TX. **Awarded Fifth Place Poster Presentation.**

Adams, C.S., C.M. Schalk, D. Saenz. 2019. Community organization of a snake guild in shortleaf pine forests. Texas Herpetological Society Meeting. Alpine, TX.

Adams, C.S., C.M. Schalk, D. Saenz. 2019. Community organization of a snake guild in shortleaf pine forests. Southwestern Partners in Amphibian and Reptile Conservation. Rodeo, NM.

Thompson, D.W., **C.S. Adams**, D. Saenz, C.M. Schalk. 2019. Assessing the functional role of skinks (Scincella lateralis) in forest food webs. Southwestern Partners in Amphibian and Reptile Conservation. Rodeo, NM.

Adams, C.S., D. Saenz, C.M. Schalk. 2019. Community organization of a snake guild in shortleaf pine forests. Ecological Integration Symposium. College Station, TX.

D.W. Thompson, **C.S. Adams**, D. Saenz, C.M. Schalk. 2019. Assessing the functional role of skinks (Scincella lateralis) in forest food webs. Ecological Integration Symposium. College Station, TX

Adams, C.S., D. Saenz, C.M. Schalk. 2019. Community organization of a snake guild in shortleaf pine forests. Texas Chapter of the Wildlife Society. Montgomery, TX.

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Adams, C.S., B. Wolaver, H.L. Prestridge, T.J. Hibbitts, W.A. Ryberg. 2017. Distribution and population status of the Western Chicken Turtle (*Deirochelys reticularia miaria*) in Texas. American Society of Ichthyologists and Herpetologists, Austin, TX.

Frizzell, S.L., D.B. Neuharth, **C.S. Adams**, T.E. Johnson, W.A. Ryberg, T.J. Hibbitts, B.D. Wolaver, J.P. Pierre, B.J. Labay, T.J. LaDuc, C.M. Duran. 2017. Comparative Analysis of Photo Identification for Mark-Recapture Data in the Spot-tailed Earless Lizard (*Holbrookia lacerata*). American Society of Ichthyologists and Herpetologists, Austin, TX.

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Pierce, J.B., A. Dube, K. Skow, **C.S. Adams**, B. Pierce, D.C. Rudolph, T.J. Hibbitts, W.A. Ryberg. 2016. Conservation of the Louisiana Pine Snake (*Pituophis ruthveni*) in Texas. Texas Chapter of the Wildlife Society, San Antonio, TX.

Hibbitts, T.J., W.A. Ryberg, D.B. Neuharth, **C.S. Adams**, D.E. Dittmer, J. Harvey, G.A. Voelker, B.J. Labay, J.P. Pierre, B. Wolaver, T.J. LaDuc. 2016. Current Distribution and Phylogenetic Relationships of *Holbrookia lacerata* in Texas. Texas Chapter of the Wildlife Society, San Antonio, TX.

Hibbitts, T.J., W.A. Ryberg, D.B. Neuharth, **C.S. Adams**, D.E. Dittmer, J. Harvey, G.A. Voelker, B.J. Labay, J.P. Pierre, B. Wolaver, T.J. LaDuc. 2016. Current Distribution and Phylogenetic Relationships of *Holbrookia lacerata* in Texas. American Society of Ichthyologists and Herpetologists. New Orleans LA.

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Adams, C.S., A. Galan, J.P. Pistone, J.P. Henningsen, T.J. Hibbitts, J. Light, G.A. Voelker. 2015. Assessment and Collection of Terrestrial Vertebrate Biodiversity on East Foundation Properties. East Foundation Research Partners Meeting, Kingsville, TX.

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Adams, C.S., T.J. Hibbitts, TA Campbell. 2014. Reptile and Amphibian Diversity on East Foundation Properties. Texas Chapter of the Wildlife Society, Corpus Christi, TX

GRANTS (Total Secured = $1,060)

2020. Adams, CS. Travel Grant, Southeastern Partners in Amphibian and Reptile Conservation. ($60). *Funded*.

2020. Adams, CS. Travel Grant, Arthur Temple College of Forestry & Agriculture. ($500). *Funded*.

2019. Adams, CS. Travel Grant, Arthur Temple College of Forestry & Agriculture. ($500). *Funded*.

MEDIA

2018. KTRE News, Lufkin, TX. "Citizens can help SFA scientists in Roadkill of Texas Project". Aired 1 March 2018. http://www.krte.com/story/37628171/citizens-can-help-sfa-scientists-in-roadkill-of-texas-project

SERVICE TO PROFESSION

Peer Reviewer: Journal of Herpetology (2017), Remote Sensing (2020), Herpetological Review (2021).

Board member: Texas Herpetological Society (2020-present).

RELEVANT SKILLS

- Experience with radiotelemetry and GPS monitoring devices
- Geographic Information Systems (GIS) certification
- Proficiency in R statistical programming language
- Handling of large datasets and maintenance of online databases.
- Identification and preservation of scientific specimens
- Leading public educational outreach programs
- Experience with towing and operating boats and other large equipment