

## The Influence of Management Practice on the Snakes in Forest Food Webs

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**ABSTRACT:** Anthropogenic activities in disturbance-mediated ecosystems might affect certain ecological processes that, in turn, can affect the stability and resilience of those ecosystems. In upland pine forests, land-use practices such as intensive silviculture and fire suppression have contributed to the loss of diversity-rich pine savannahs throughout the southeast. Whereas the application of management strategies has been shown to alter forest structure in pine ecosystems, less is known about how these efforts influence pathways of energy flow and the consumer–resource relationships therein. Here, we investigated the effects of frequency of forest management on the trophic structure and resource use of snake communities in two pine forests under high and low frequencies of management (i.e., shorter fire return intervals and thinning versus longer fire return intervals and limited thinning). We sampled snakes, prey, and dominant basal resources across each site for three summers from 2018 to 2020. Using stable isotope analysis, we compared community-wide metrics of trophic structure and generated isotopic mixing models to determine the relative contribution of resources to snake consumers. We found that the high-frequency site supported an increased diversity of snake species, and that species exhibited increased trophic redundancy. The low-frequency site supported fewer snake species that relied on a wider range of resources, and occupied a wider range of relative trophic positions. Mixing models of consumer–resource relationships, and prey relative abundance, indicated that snakes were more generalized in their resource use in the high-frequency site, and utilized a broader diversity of prey more evenly. In contrast, snakes in the low-frequency site were more specialized in their prey use. We suggest that anthropogenic activities mimicking natural disturbances can drive food-web structure in these forest ecosystems. Increased frequency of forest management practices such as prescribed fires and thinning operations might support snake species diversity while also increasing trophic redundancy. Consequently, such management applications can lead to greater stability and resilience in pine-forest ecosystems. Our research further highlights the importance of ecological restoration that incorporates food-web perspectives to ensure the health of pine ecosystems.

**Key words:** Energy flow; Forest management; Predator–prey relationships; Resource use; Squamata; Stable isotope analysis; Trophic redundancy; Trophic web

DISTURBANCES are important mechanisms underlying the structure and function of ecological communities within ecosystems (Turner 2010; Pickett and White 2013; Supp and Ernest 2014; Jentsch and White 2019). The influence of these disturbances can vary in type, size, season, frequency, severity, intensity, timing, and duration across multiple spatial and temporal scales (Sousa 1984; Dornelas 2010; Buma 2015). 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 (Thom and Seidl 2016; Moreno-Mateos et al. 2017). Consequently, identifying the dynamic processes in which disturbances shape the functional properties of ecological systems is of the utmost importance.

Food webs provide 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 1996; 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,

understanding how anthropogenic disturbances affect trophic structure in complex ecosystems is still limited, particularly in terrestrial systems (Shurin et al. 2006; Cameron et al. 2019). 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 (Strong and Frank 2010; Terborgh and Estes 2013; May 2019). 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 diversity, ecologists can test hypotheses investigating the mechanisms that stabilize or destabilize food webs to predict niche responses to shifts in community composition (McCann 2000; Hooper et al. 2005; Thébault and Loreau 2005).

According to food-web theory, ecosystem stability is predicted to increase as the number of connections in the food web increases (Montoya et al. 2006; LeCraw et al. 2014; Gellner and McCann 2016). 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. Therefore, these linkages are more susceptible to disturbances that could potentially result in trophic cascades (Finke and Denno 2004). Species that are dietary generalists tend to stabilize food webs because they typically have many weak interactions with different resource types, and 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

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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 (Rooney and McCann 2012; Calizza et al. 2017; Noto and Gouhier 2020). Decreased overlap (i.e., increased niche partitioning) among consumers reflects divergent patterns of resource use that destabilize food webs as overall trophic diversity increases (Hector and Hooper 2002; Finke and Snyder 2008). 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 (Sanders et al. 2013, 2018; Cirtwill et al. 2018). Trophic redundancy stabilizes food webs by decreasing the likelihood that species loss will lead to a trophic cascade, thereby increasing ecosystem resilience to disturbances (Borrvall et al. 2000; Brodie et al. 2014; Sanders et al. 2015, 2018; Price et al. 2019).

Disentangling the interactions that occur within food webs is a difficult endeavor in complex systems. This is 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 (Votier et al. 2003; Nielsen et al. 2018). These methods also rely on the ability to 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; Durso et al. 2022). 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 a complementary or alternative technique to 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 ( $^{13}\text{C}/^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) 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 ( $^{15}\text{N}$ ) 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 that can be used to examine aspects of a consumer's trophic ecology and, subsequently, the trophic diversity and redundancy within species assemblages (Newsome et al. 2007). 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 physiological rate, and can represent the diet of a given consumer, across a period of several weeks.

SIA techniques can be limited by overlap between isotopic signatures of prey groups, the lack of inclusion of important food sources, and the use of incorrect trophic enrichment values (Durso et al. 2022). SIA is less susceptible to temporal biases in sample collection than traditional methods, however, and better reflects the diets of consumers in a given space and time (West et al. 2006; Boecklen et al. 2011; Durso et al. 2022). The applications of SIA to food-web studies offer quantitative insight into factors influencing community dynamics and can reveal pathways of energy transfer (Semmens et al. 2009; Parnell et al. 2010). Comparing changes in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the presence and absence of disturbances can then reveal how food-web structure (e.g., trophic breadth, trophic position) might change following a disturbance (Jennings et al. 2001; Bearhop et al. 2004; di Lascio et al. 2013).

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 aboveground biomass (Veldman et al. 2013; Diaz-Toribio et al. 2020; Matula et al. 2020). Therefore, forest management has the potential to alter ecological gradients (e.g., habitat and resource availability) that structure species assemblages in these 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 (White and Harley 2016; Rother et al. 2020). However, these fire-subclimax 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; Sohngen and Brown 2006; Mori et al. 2017). Forest management practices can mimic natural disturbances with the goal of restoring these biologically diverse systems (Kirkman and Jack 2017; Guldin and Black 2018; Jin et al. 2018; Guldin 2019). 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 (Christensen 2014; Guldin and Black 2018). 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 understand how communities and ecosystems respond to management efforts (Bellmore et al. 2017; Layman and Rypel 2020; 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 informing

ecological restoration efforts (e.g., Vander Zanden et al. 2016). For example, excess nutrient loading (e.g., agricultural or industrial run-off) into lakes and reservoirs can lead to algal blooms that increase water turbidity and fish die-off, alter food webs, and result 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 such 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 piscivorous fish predators, or removing biomass of planktivorous 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 increase the resilience of lakes to future nutrient influxes (Mao et al. 2020; Rask et al. 2020).

Given the potential for forest management practices 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 solutions that protect forest resources (Layman et al. 2020; Loch et al. 2020). 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). The spatiotemporal heterogeneity that results from these practices, however, also regulates trophic dynamics and ecosystem structure because both bottom-up and top-down 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 alter predator–prey relationships, and food-web structure, will provide a better path to restoring resilient and functional pine forest systems (Bowman and Legge 2016; Vander Zanden et al. 2016; Layman et al. 2020; Loch et al. 2020).

The loss of predators because of anthropogenic activities can have detrimental impacts on ecosystems (Estes et al. 2011; Terborgh and Estes 2013; Ripple et al. 2014). In either aquatic or terrestrial environments, changes in the vertical structure of food webs have extensive cascading effects that influence the functionality and resilience of ecosystems (Terborgh et al. 2001; Heithaus et al. 2008; Estes et al. 2011). Top-down effects are now widely recognized as important processes that regulate biodiversity and ecosystem function (Terborgh and Estes 2013). Knowledge on these dynamics can provide further insights as to how systems respond to ecological restoration efforts. 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 but 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). Therefore, snakes can serve as useful taxa to understand how disturbances influence trophic interactions and ecosystem properties (Beaupre and Douglas 2009).

In this study, we examined how differences in forest management practice frequency (e.g., prescribed fire, thinning) affected the food-web structure and resource use of predator assemblages (i.e., snakes) in southern pine forests inferred from stable isotope patterns. Through these processes, we expected prevailing habitat conditions under different disturbance regimes (e.g., high versus low frequency) to be coupled with bottom-up processes that affect food-web structure, and in turn, alter top-down processes that influence the resiliency of predator assemblages. Specifically, we investigated (1) community-wide measures of food-web structure including trophic position, trophic range, and isotopic niche space within and between predator assemblages; and (2) resource use within predator assemblages at high- and low-frequency sites. Utilizing snakes as a model taxon to investigate food-web structure, we hypothesized that differences in practice frequency may shift the energetic pathways that support the food webs, subsequently leading to differences in trophic structure of predator assemblages between sites. We predicted that the high-frequency site would likely feature greater environmental heterogeneity that could provide additional energetic pathways and support a greater diversity of snakes. We also predicted that this diverse predator assemblage would consist of species occupying similar isotopic niches resulting in increased trophic redundancy. At the low-frequency site, we hypothesized that environmental conditions may reduce the number of energetic pathways that support the food web, limiting prey resources available to consumers at multiple trophic levels, and resulting in a lower diversity of snakes at the top of the food web. We predicted that snakes would partition their isotopic niches to limit niche overlap under these conditions, leading to increased trophic diversity at the low-frequency site. Taxonomic and functional diversity of both primary and secondary consumers might respond differently to disturbance and subsequent habitat changes between management regimes (i.e., practice frequency) affecting secondary productivity (see Adams et al. 2022). Because secondary production encapsulates underlying energy acquisition and trophic relationships, we hypothesized that resource use within predator assemblages would differ between high- and low-frequency sites. We expected generalist predators would alter their resource use in high-frequency and low-frequency sites, potentially exploiting different prey groups based on their availability under different management conditions. We predicted that snakes in the high-frequency assemblage would broaden their resource use as management conditions may support increased prey availability of functional prey groups that could be then be exploited by snakes. In contrast, we predicted snakes in the low-frequency site would shift their resource use to exploit fewer functional prey groups that persist in low-frequency conditions.

## MATERIALS AND 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. In the northern extent, this ecoregion is characterized 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 single-species and mixed pine (loblolly pine, *Pinus taeda* and longleaf pine, *Pinus palustris*) stands (Marks and Harcombe 1975; Masters 2007). The widespread application of management strategies to promote 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 (Diaz-Toribio et al. 2020; Frost 1993). 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 (Elliott and Vose 2005).

Surveys of snakes and representative prey assemblages were conducted at the Boggy Slough Conservation Area (Trinity County, TX; 31.30544°N, -94.93916°W, datum = WGS84 in all cases; hereafter high-frequency site) and the Stephen F. Austin Experimental Forest (Nacogdoches County, TX; 31.50167°N, -94.76401°W, hereafter low-frequency site). The high-frequency site, overseen by the T.L.L. Temple Foundation, is actively managed for a variety of conservation goals (i.e., biodiversity, game management, restoration of native pine species) through the implementation of frequent forest management practices (i.e., 1 to 3-yr fire return intervals, thinning, and regeneration harvests; R. Sanders, personal communication). Although thinning operations are often conducted at this site, these operations are largely implemented to maintain stand compositions of native pines, and are not largely focused on timber production. The low-frequency site is overseen by the U.S. Forest Service (USFS) as part of the Southern Research Station network. Although historically managed for silvicultural research, specifically the development of commercially viable pine species, current implementation of management practices at this site is infrequent (i.e., 5 to 8-yr fire intervals, limited harvesting; Russell et al. 2002). The low-frequency site has been designated as a reference forest by the USFS, and as a result, thinning operations have not been conducted since the early 1990s.

#### Forest Habitat Structure

To identify any emerging patterns of biomass transfer at the base of food webs relative to forest structure, we measured eight habitat variables associated with stand density, ground cover, and canopy cover in each sampling location across sites. A standardized sampling design was implemented by establishing nested subplots within a larger circular plot in which the center of the plot was the approximate location of a trapping array (i.e.,  $n = 50$ ; see Adams et al. 2022). 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 (%). 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 to

identify the persistent environmental gradients occurring within and across sites (i.e., high and low frequency).

Differences in the frequency of forest management practices had significant effects on the overall structure and composition of forest habitats occurring in each site (Adams et al. 2022). We initially assumed these differences in the structural properties between sites would reflect differences in the number of energetic pathways at the base of respective food webs. For example, sampling localities in the low-frequency site were homogenous in terms of forest structure (e.g., closed-canopies, high amounts of leaf litter buildup) and dominant basal resources were consistent in terms of species richness and abundance across all sampling localities (Adams et al. 2022). In contrast, the high-frequency site 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 (Adams et al. 2022).

#### 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 following the design outlined in Burgdorf et al. (2005). We established 10 trap locations per site per year ( $n = 20$  total; cumulative totals, high-frequency site = 30 total, low-frequency site = 20 total; see Adams et al. 2022). Prescribed fires at both sites are typically conducted during the cool season (i.e., winter and spring). However, application of prescribed fire at the high-frequency site is typically rotated between stands year to year to ensure a 1 to 3-yr fire interval. Therefore, traps were installed at localities at least one growing season (i.e., more than a year) postburn to ensure dominant vegetation had recovered. To minimize recaptures and ensure adequate sample sizes of snakes, sampling localities were separated by a minimum distance of 450 m and were moved yearly a minimum distance of 100 m from previous sampling localities (see Adams et al. 2022). Our trapping effort only resulted in five recaptures of the five most common species, with only one recapture occurring in a different sampling locality from initial capture (Schalk et al. 2022; Appendix I). Traps were checked daily from May to July across three summers (2018 to 2020) at the high-frequency site and two summers at the low-frequency site (2019 to 2020). Captured snakes were uniquely marked using a combination of ventral scale clipping and heat-branding with a medical cautery unit (Winne et al. 2006). Venomous snakes were anesthetized with isoflurane to allow for safe handling during processing (Beaupre 2004; Kane et al. 2020). Scale clips obtained from ventral marking were placed into small sealable bags, labeled, and stored in a freezer at  $-23.3^{\circ}C$  for later isotopic analysis. Juvenile snakes were excluded from our analyses (Appendix I). We defined juveniles based on values for maximum snout-to-vent length (mm) obtained from the literature (Werler and Dixon 2010).

Relevant prey species were opportunistically sampled from box-trap and pitfall captures for SIA analyses. To assess dietary sources of snakes, we collected ~3 to 5 individuals of prevalent prey species based on capture totals observed in each site per year. Upon collection, vertebrates were euthanized either by

cervical dislocation or cranial concussion to prevent biases in isotopic ratios of carbon and nitrogen that can arise with chemical euthanasia. Collected invertebrate and vertebrate prey taxa were labeled and stored on ice until they could be transferred to a  $-80^{\circ}\text{C}$  freezer. We recorded species-level identity, capture per unit effort, and method of capture (e.g., box trap versus pit-fall) for all species encountered during sampling (Adams et al. 2022). This provided insight on resource availability and the composition of different trophic guilds occurring in each site. Because of limitations of our trap design for sampling small-bodied arthropods, we supplemented sampling efforts with monthly sweep netting at each sampling location.

To determine the extent to which management practice frequency influences primary producer baselines in high- and low-frequency sites, we harvested the aboveground mass of two to three specimens for the five most dominant plant basal resources found at each sampling location. Plants were identified to the species level, whenever possible. Multiple studies have attempted to synthesize and define carbon isotope compositions of terrestrial C3 and C4 plants in several different ecosystems (e.g., Buchmann et al. 1996; Murphy and Bowman 2009; Diefendorf et al. 2010). We used these sources, along with other public databases, to define photosynthetic pathways for dominant species and classify  $\delta^{13}\text{C}$  carbon ranges (Kohn 2010; Kattge et al. 2020). Plants chosen as indicators of site-level isotopic basal resource values either occurred at all sampling locations (e.g., living and dead vegetative material from dominant overstory tree species) or occurred in relatively high abundances in several sampling locations (e.g., herbaceous grasses, forbs, and vines). To account for temporal variation in the turnover of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the tissues of snake and prey consumers, basal resources were collected in May, June, and July of each year. This was also done 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

To minimize the risk of their contamination, samples selected for stable isotope analysis were cleaned with deionized water to remove any inorganic or organic material. Stomach contents and digestive tracts were removed from vertebrate prey items to limit bias in isotopic analyses, whereas individual 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  $60^{\circ}\text{C}$  for 48 h, or until reaching 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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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 ( $\sim 1$  to 3 mg) and packaged into  $9 \times 10$ -mm Ultra-Pure tin capsules. All weighed samples were then sent to the Stable Isotope Ecology Laboratory at the University of Georgia to be analyzed for stable isotopes ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) using an isotope mass spectrometer. Measurements are reported in delta notation ( $\delta$ ), where

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left( R_{\text{sample}}/R_{\text{standard}} \right) - 1 \times 1,000$$

and  $R$  is the ratio of the heavy/light isotope content (e.g.,  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ). 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 forest management regimes, samples were pooled across sampling localities and years into high-frequency and low-frequency sites. Within this framework, we tested for differences in the isotopic signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  within different levels of each food web. Distributions of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in each test were first tested for normality using a Shapiro–Wilks test. When these data did not meet the assumptions for parametric analyses, we performed Wilcoxon tests to determine differences between groups. Snake consumers were separated by species within each site. Isotopic baselines for each site were grouped by photosynthetic pathway (C4 vs. C3). However, a C4 pathway was not detected in any of the dominant basal resources sampled within the low-frequency site. For this reason, we pooled resources into independent categories based on life form (e.g., herbaceous, woody, and detritus) for further analyses. Depending on the analyses performed, prey samples from each site were grouped either into primary or secondary consumers, or into eight prey groups based on taxonomic and functional roles of species. The functional grouping of prey taxa was based on both taxonomy and the trophic ecology of prey species, as defined in previous studies (Marshall 2006; Tipton 2012; Hibbitts and Hibbitts 2015; Schmidly and Bradley 2016; Ubick et al. 2017). To highlight taxonomic differences between high-frequency and low-frequency sites, we performed similarity percentage (SIMPER) analyses based on the Bray–Curtis dissimilarity for snake consumers and prey groups using the ‘simper’ function in the package *vegan* in R (Oksanen et al. 2019).

The trophic structure of the snake community in each site was quantified using stable isotope-derived metrics that described 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. 2007). 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 sites in  $\delta^{15}\text{N}$  (Post 2002). Ignoring baseline values and using unadjusted values of  $\delta^{15}\text{N}$  to infer trophic position can lead to erroneous results and limit the interpretation of where species are located within food webs (Post 2002). The average  $\delta^{15}\text{N}$  of invertebrate primary consumers was used as the baseline to estimate trophic range and relative trophic positions for each treatment (Table 1). Invertebrate primary consumers were utilized instead of plant resources because they have been shown to integrate temporal and spatial variation in producers’ isotopic composition accurately (Vander Zanden and Rasmussen 1999). The trophic positions of snakes might be underestimated based on the  $\delta^{15}\text{N}$  of primary producers collected in this study, which varied within sampling localities in each site. This could have been

TABLE 1.—Isotopic values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of functional groups for basal resources and prey in high- and low-disturbance frequency sites in east Texas. Values represent means ( $\pm 1$  SD) across functional groups and sites.

Functional group	Taxa	High frequency			Low frequency		
		<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
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)	22	-30.38 (0.87)	-3.33 (1.27)
	C3 (canopy effects)	18	-32.10 (0.44)	-1.29 (2.54)	21	-32.45 (0.92)	-2.81 (2.04)
Primary consumers	Primary consumers	64	-24.80 (4.66)	0.78 (1.73)	63	-25.60 (1.85)	1.62 (1.24)
Secondary consumers	Secondary consumers	102	-25.24 (2.13)	4.79 (1.32)	66	-26.57 (2.50)	4.41 (1.59)
Anurans	Frogs and toads	41	-25.92 (2.43)	4.64 (1.35)	23	-26.31 (2.86)	4.47 (1.47)
Caudates	Salamanders	—	—	—	10	-29.36 (2.11)	6.03 (0.75)
Decapods	Crayfish	6	-22.82 (1.90)	1.93 (0.69)	5	-26.93 (0.33)	2.60 (0.36)
Herbivorous arthropods	Caelifierans (grasshoppers)	34	-24.39 (5.97)	0.01 (1.72)	—	—	—
	Coleopterans (terrestrial beetles)	12	-25.52 (1.08)	1.12 (1.63)	22	-23.83 (0.54)	0.19 (0.69)
	Ensiferans (crickets)	12	-26.24 (2.82)	2.02 (1.08)	41	-25.89 (2.33)	1.57 (0.88)
Predatory arthropods	Arachnids (spiders and scorpions)	21	-24.69 (0.98)	4.75 (0.96)	24	-25.82 (0.59)	4.36 (0.65)
	Carabids (predatory beetles)	8	-25.20 (1.03)	4.34 (1.09)	6	-27.94 (0.96)	3.67 (1.31)
Small mammals	Eulipotyphlans (shrews)	10	-23.93 (2.12)	6.37 (0.83)	13	-21.84 (4.96)	7.55 (1.01)
	Rodents (omnivores)	17	-25.27 (2.37)	4.54 (1.55)	6	-25.96 (0.93)	4.12 (1.07)
Squamates	Lizards	5	-24.58 (2.14)	4.55 (0.68)	10	-26.29 (0.70)	2.55 (0.29)

attributable to local factors that influenced higher enrichment or depletion of the nitrogen found in soils between sampling localities (Vanderklift and Ponsard 2003). The trophic position (TP) of a given snake species was calculated as

$$\text{TP} = \lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base}}) / 1.63\text{‰}$$

where  $\lambda$  is the trophic position of the baseline organisms (e.g.,  $\lambda = 2$  for primary consumers),  $\delta^{15}\text{N}_{\text{consumer}}$  is the measured  $\delta^{15}\text{N}$  of each snake individual at each treatment,  $\delta^{15}\text{N}_{\text{base}}$  is the mean  $\delta^{15}\text{N}$  for the baseline in each treatment, and  $\Delta_n$  is the trophic fractionation for  $\delta^{15}\text{N}$  (Vander Zanden and Rasmussen 1999; Post 2002). Fractionation can be influenced by a variety of factors (e.g., diet of prey, predator physiology, disturbance) that might be hard to predict (Pilgrim 2005; Murray and Wolf 2012; Saiz et al. 2015). However, knowledge of trophic enrichment in snakes is limited and most enrichment factors are obtained from previous studies (Stellati et al. 2019; Durso et al. 2020, 2022; Rebelato et al. 2020). We used a simulated fractionation value of 1.63‰ based on the means and standard deviations of isotopic ratios from our sampling (Quezada-Romegialli et al. 2018). Once the TP for each snake sample was calculated, TP values were averaged for each snake species across high- and low-frequency sites. We also examined how the range in trophic position per species (hereafter, trophic range; TR = maximum TP – minimum TP) might vary between high- and low-frequency sites. 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. 2007). Trophic range was calculated for those species captured >3 times in each site, and only after potential outliers were assessed (Jackson et al. 2011).

To determine whether isotopic niche space of snake communities differed between sites, we performed a permutational analysis of variance (PERMANOVA) at 999 iterations (Anderson 2017). 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 site. The predictor variables in the PERMANOVA were species and site (and interactions), and a Euclidean distance dissimilarity matrix based on the isotopic values (i.e.,  $\delta^{13}\text{C} - \delta^{15}\text{N}$ ) of snake consumers was the response variable.

The PERMANOVA was performed using the ‘adonis’ function in the package vegan in R (Oksanen et al. 2019).

We investigated the trophic structure of snake communities within and between sites using the community-wide metrics proposed by Layman et al. (2007). These metrics use the stable isotope composition of different food-web components to describe trophic structure by measuring the relationships of species in isotopic space (Layman et al. 2007, 2012). Carbon ( $\delta^{13}\text{C}$ ) range (CR), nitrogen ( $\delta^{15}\text{N}$ ) 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 and 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. 2007). Total area was not used in our 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 ‰<sup>2</sup>; Batschelet 1981). SEAs 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 (Jackson et al. 2011). We also calculated the SEA corrected for small sample sizes (SEA<sub>C</sub>), the overlap in SEA<sub>C</sub>, and the difference in SEA sizes between high- and low-frequency sites. 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. 2007). 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. 2007).

The metrics developed by Layman et al. (2007) might be difficult to interpret when comparing between sites because the values can vary with sample size. A Bayesian approach allows for the incorporation of sampling error estimates representing different community components, however, returning posterior distributions of the estimated metrics (Jackson et al. 2011). The posterior distributions provide a measure of uncertainty that allows for statistical comparisons to be made. Additionally, this approach is less sensitive to variations in the number of species, and can be applied to make comparisons between different communities (Jackson et al. 2011). Therefore, we calculated Bayesian estimates for all aforementioned metrics of isotopic niche diversity for each snake community (e.g., high- vs low-frequency disturbance). 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- and low-frequency sites 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 (dis)similarities between sites (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. 2010; Jackson et al. 2011). All Bayesian analyses used to produce comparable posterior distributions of community-wide trophic structure included only those species with  $\geq 3$  individuals represented in a given community. Data were tested for normality before these analyses using a Kolmogorov–Smirnov test in the base ‘stats’ package of R (R Core Team 2023).

To investigate shifts in resource use between high- and low-frequency sites, we determined the proportion of prey groups contributing to sampled snake assemblages. We used Bayesian stable-isotope mixing models in the MixSIAR package in R to estimate the proportion of potential prey contributing to the diet of snakes in each site (Moore and Semmens 2008; Semmens et al. 2009; Stock and Semmens 2013). Individual models were also produced for the five most common shared snake species between sites with respect to the functional prey groups sampled within those sites. 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 taxonomic and functional similarity that reflected species’ roles in the food webs. We 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 combine prey resources of similar isotopic signatures and limit biases in the models (Table 1). To examine the proportions of potential prey items for each community, the models included all snake consumers in each site, with species as a random effect. A Markov Chain Monte Carlo 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 and Carlin 1996). Fractionation values for each source were obtained from the literature (DeMots et al. 2010; Cloyd et al. 2015; Hyodo 2015;

Lattanzio and Miles 2016). 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

### Isotopic Analyses of Basal Resources

Isotopic analyses showed significant differences in the isotopic signatures (i.e.,  $\delta^{13}C - \delta^{15}N$ ) of basal resources between sites (PERMANOVA,  $F = 17.51$ ,  $Pr[>F] = 0.001$ ; Appendix II). The  $\delta^{15}N$  values of basal resources were variable within sampling localities, but differences between sites were not detected (Table 1). In both treatments,  $\delta^{15}N$  values were generally depleted in primary consumers (Table 1). Most herbaceous plants in the open understories of sampling locations represented the C3 photosynthetic pathway and, while present in the high-frequency site, C4 grasses were dominant only at a few sites (Table 1; Appendix II).

### Isotopic Signatures of Snakes and Prey Resources

Snake consumers varied between sites in species’ richness and relative abundance (see Adams et al. 2022 for detailed descriptions of snake relative abundance and species composition between high- and low-frequency sites; Tables 2, 3). Isotopic values of  $\delta^{13}C$  and  $\delta^{15}N$  for snake consumers were significantly different between sites as a function of site, species, and their interaction (PERMANOVA,  $F \geq 7.90$ ,  $Pr[>F] \leq 0.01$ ; Table 3; Appendix II). Species diversity and relative abundance of potential prey supporting snake consumers also varied between sites (Table 4; and see Adams et al. 2022). For example, 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 (Table 1). Further grouping of prey taxa based on taxonomic similarity and trophic roles showed differences in the isotopic signatures within functional prey groups (Table 1). 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 were significantly different between site in terms of site and taxa (PERMANOVA,  $F \geq 7.90$ ,  $Pr[>F] \leq 0.001$ ), but not in interaction between site and taxa (Appendix II). Primary consumers exhibited similar isotopic values of  $\delta^{13}C$  and  $\delta^{15}N$  as a function of site, species, and their interaction (Table 1; Appendix III). Within the high-frequency site, 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 sites, which indicates that snakes occupied similar trophic positions in both high- and low-frequency sites. In the high-frequency site, the difference in  $\delta^{15}N$  between the primary consumer baseline and the species of highest  $\delta^{15}N$  (Texas Coralsnakes, *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 Snakes, *Heterodon platirhinos*) in the low-frequency site (Table 3). The lowest relative trophic positions recorded in the high-frequency and low-frequency

TABLE 2.—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-(1,350 trap days) and low-(850 trap days) disturbance frequency sites in east Texas. Species are listed in order of their contribution to differences between management regimes; common names are provided in Appendix 1.

Snake species	Average dissimilarity	Mean contribution (HF)	Mean contribution (LF)	Cumulative contribution
<i>Agkistrodon contortrix</i>	0.2037	0.0296	0.0918	0.4741
<i>Coluber constrictor</i>	0.0839	0.0385	0.0129	0.6692
<i>Agkistrodon piscivorus</i>	0.0326	0.0111	0.0012	0.7450
<i>Masticophis flagellum</i>	0.0259	0.0126	0.0047	0.8052
<i>Pantherophis obsoletus</i>	0.0177	0.0252	0.0306	0.8464
<i>Sistrurus miliarius</i>	0.0121	0.0037	0.0000	0.8747
<i>Micrurus tener</i>	0.0120	0.0022	0.0059	0.9026
<i>Lampropeltis triangulum</i>	0.0073	0.0022	0.0000	0.9195
<i>Nerodia fasciata</i>	0.0057	0.0030	0.0047	0.9328
<i>Farancia abacura</i>	0.0049	0.0015	0.0000	0.9441
<i>Haldea striatula</i>	0.0049	0.0015	0.0000	0.9555
<i>Lampropeltis holbrookii</i>	0.0049	0.0015	0.0000	0.9668
<i>Nerodia erythrogaster</i>	0.0043	0.0022	0.0035	0.9767
<i>Crotalus horridus</i>	0.0029	0.0015	0.0024	0.9834
<i>Storeria dekayi</i>	0.0024	0.0007	0.0000	0.9890
<i>Heterodon platirhinos</i>	0.0019	0.0030	0.0035	0.9934
<i>Lampropeltis calligaster</i>	0.0014	0.0007	0.0012	0.9967
<i>Ophedrys aestivus</i>	0.0014	0.0007	0.0012	1.0000

sites were attributed to Rough Greensnakes (*Ophedrys aestivus*). Overall, pairwise species comparisons of the relative trophic positions of shared species between sites were similar; however, the range of trophic positions varied slightly among these species (Table 3).

Community-Wide Food-Web Structure

The food-web structure of snake assemblages differed between high-frequency and low-frequency sites (Fig. 1). We found evidence for increased niche diversification at the base of the low-frequency food web (CR; Fig. 2). The CR was significantly wider in the low-frequency site than in the high-frequency site. With no overlap in 95% credibility intervals (CIs), this indicates that snake consumers were supported by a greater diversity of basal resources in the low-frequency site (Fig. 2a). Trophic diversity was similar

between assemblages, indicating snake consumers occupied a similar trophic level across high- and low-frequency sites (NR; Fig. 2b). Although there was some overlap in the 95% CIs, NR was slightly greater in the low-frequency site (Fig. 2b). However, the extent of trophic diversity was much smaller in the high-frequency site (Fig. 1). 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 5; Fig. 2c).

Overlap in SEA between sites was relatively high (31.5%, corresponding to 36.46% and 49.19% of the total SEA for the high- and low-frequency sites, respectively); however, there was a large proportion of nonoverlap in SEA between sites (58%; Table 5). The average degree of trophic diversity was also greater in the low-frequency site, with no overlap in 95% CIs (CD; Fig. 2d). Additionally, there was a strong

TABLE 3.—Isotopic values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of snake species in high- and low-disturbance frequency sites. Trophic position (i.e., TP high-frequency/TP low-frequency) represents the average number of steps involved in biomass transfer, whereas trophic range (i.e., TR high-frequency/TR low-frequency) describes the variability in trophic position responses. Values represent means ( $\pm 1$  SD) across sites. Species with three or fewer captures ( $n$ ) from sampling efforts at either type of site are denoted with an asterisk. Note we were unable to obtain isotopic signatures from *Haldea striatula* tissues.

Snake species	$n$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TP	TR
<i>Agkistrodon contortrix</i>	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
<i>Agkistrodon piscivorus</i> *	15/1	-24.27 (0.76)/-25.07	7.19 (1.13)/8.66	5.11 (0.69)/5.69	2.77/NA
<i>Coluber constrictor</i>	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
<i>Crotalus horridus</i> *	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
<i>Farancia abacura</i> *	2/0	-31.35 (0.91)/NA	7.36 (0.99)/NA	5.26 (0.61)/NA	0.86/NA
<i>Heterodon platirhinos</i> *	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
<i>Lampropeltis calligaster</i> *	1/1	-23.34/-24.15	7.02/8.04	5.06/5.31	NA/NA
<i>Lampropeltis holbrookii</i> *	2/0	-23.31 (0.59)/NA	7.61 (0.30)/NA	5.41 (0.19)/NA	0.26/NA
<i>Lampropeltis triangulum</i> *	3/0	-24.14 (0.49)/NA	7.29 (1.53)/NA	5.22 (0.94)/NA	1.75/NA
<i>Masticophis flagellum</i>	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
<i>Micrurus tener</i> *	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
<i>Nerodia erythrogaster</i> *	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
<i>Nerodia fasciata</i>	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
<i>Ophedrys aestivus</i> *	2/1	-25.43 (0.47)/-28.22	3.43 (5.04)/-0.27	2.84 (3.09)/0.21	4.37/NA
<i>Pantherophis obsoletus</i>	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
<i>Sistrurus miliarius</i> *	4/0	-23.88 (0.63)/NA	6.48 (1.04)/NA	4.72 (0.64)/NA	1.5/NA
<i>Storeria dekayi</i> *	1/0	-24.33/NA	3.62/NA	2.97/NA	NA/NA
<i>Thamnophis proximus</i>	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



TABLE 4.—The 10 most abundant prey taxa found across sampled sites. Average dissimilarity between high- and low-disturbance frequency (HF and LF) 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
Squamata (lizards)	0.00217	0.003	0.006	0.997
Eulipotyphla (shrews and moles)	0.00217	0.006	0.009	1.000

pattern of trophic redundancy observed in the high-frequency snake assemblage, indicating snakes at this site had similar trophic roles (MNND, SDNND; Fig. 2). The MNND and SDNND values were lower in the high-frequency site when compared to the low-frequency site, with the distributions of Bayesian results showing no overlap in 95% CIs in both metrics (Fig. 2e,f). 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 sites (Fig. 3a,b). Both high- and low-frequency snake assemblages utilized mostly vertebrate prey (Fig. 4a,b). The snake assemblage at the high-frequency site utilized vertebrate prey groups in more equal proportions, however, with 68.7% of the estimated contribution of prey sources to snake diets explained by anuran (20.6%), eulipotyphla (i.e., shrews; 18.8% contribution), squamate (16.3%), and rodent (13.0%) prey (Fig. 4a). Invertebrate prey (i.e., arthropods) accounted for 31.3% of the estimated contribution to snake diets in the high-frequency site model (Fig. 4a). In contrast, snakes in the low-frequency site were less even in their utilization of vertebrate prey, with 78.1% of the estimated contribution of prey sources to snake diets

explained by caudate (24.1%), rodent (23.8%), anuran (11.5%), eulipotyphla (13.7%), and squamate (5.5%) prey (Fig. 4b). Similar to the high-frequency site, invertebrate prey (i.e., arthropods) contributed only an estimated 21.5% contribution to snakes at the low-frequency site (Fig. 4b).

Mixing-model outputs of the most common snake species occurring in both high- and low-frequency sites revealed shifts in resource use indicating site-specific differences in resource use (Copperheads, *Agkistrodon contortrix*; North American Racers, *Coluber constrictor*; Western Ratsnakes, *Pantherophis obsoletus*; Western Ribbonsnakes, *Thamnophis proximus*; Figs. 5, 6). In the high-frequency site, *A. contortrix* were specialized in their diets, as arachnids (29.2%), anurans (29.2%), and squamates (19.1%) were estimated to contribute the most to *A. contortrix* resource use (Fig. 5a). In the low-frequency site, *A. contortrix* exhibited a broader, generalized strategy as coleopterans (23.8%), caudates (15.2%), squamates (15.1%), rodents (12.7%), and ensiferans (10.2%) contributed more evenly to their diets (Fig. 6a). Additionally, we documented multiple regurgitations of detritus-feeding coleopterans and ensiferans from *A. contortrix* captured at the low-frequency site (C.S. Adams, personal observation). At both sites, small mammals (i.e., rodent and eulipotyphla prey groups) were estimated to have the greatest contribution to *C. constrictor* diets (i.e., high frequency = 42.7%; low frequency = 35.5%). However, *C. constrictor* utilized multiple invertebrate and vertebrate prey groups at the high-frequency site, whereas *C. constrictor* at the low-frequency site were more specialized (Figs. 5b, 6b). Decapods, which were estimated to contribute 11.3% to *C. constrictor* diets at the high-frequency site, were also observed in regurgitations during snake processing (C.S. Adams, personal observation). *Pantherophis obsoletus* exhibited similarities in resource use to *C. constrictor*, as they were more generalized in the high-frequency site and specialized in the low-frequency site. Eulipotyphlans (31.1%), squamates (30.3%), and rodents (10.9%) were the largest contributors to *P. obsoletus* diet in the high-frequency site (Fig. 5c). Conversely, rodents (70.3%) were the primary prey group observed in *P. obsoletus* diets at the low-frequency site (Fig. 6c). At both sites, *T. proximus* showed patterns of specialization in their resource use. Anurans (44.5%) and squamates (26.2%) were estimated to contribute the most to *T. proximus* diets in the high-frequency site, while caudates (43.6%) and anurans (25.6%) were estimated as the largest contributors to *T. proximus* diets in the low-frequency site (Figs. 5d, 6d).

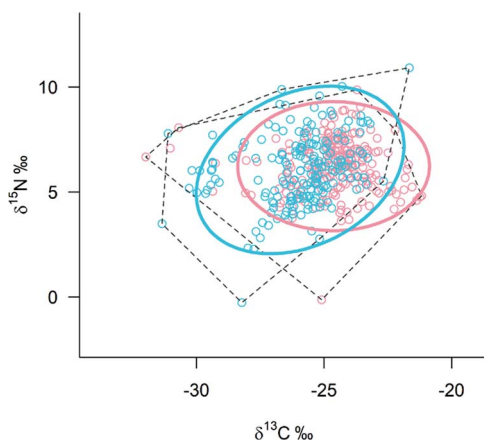


FIG. 1.—Biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in snake assemblages from high- (blue) and low- (pink) disturbance frequency sites. Dotted lines are the total convex hull areas (TA) of snake communities in each site that correspond to the area encompassing all snake species and individuals. Solid lines represent standard ellipse areas ( $\text{SEA}_C$ ) depicting isotopic niche space of snake assemblages in each site.

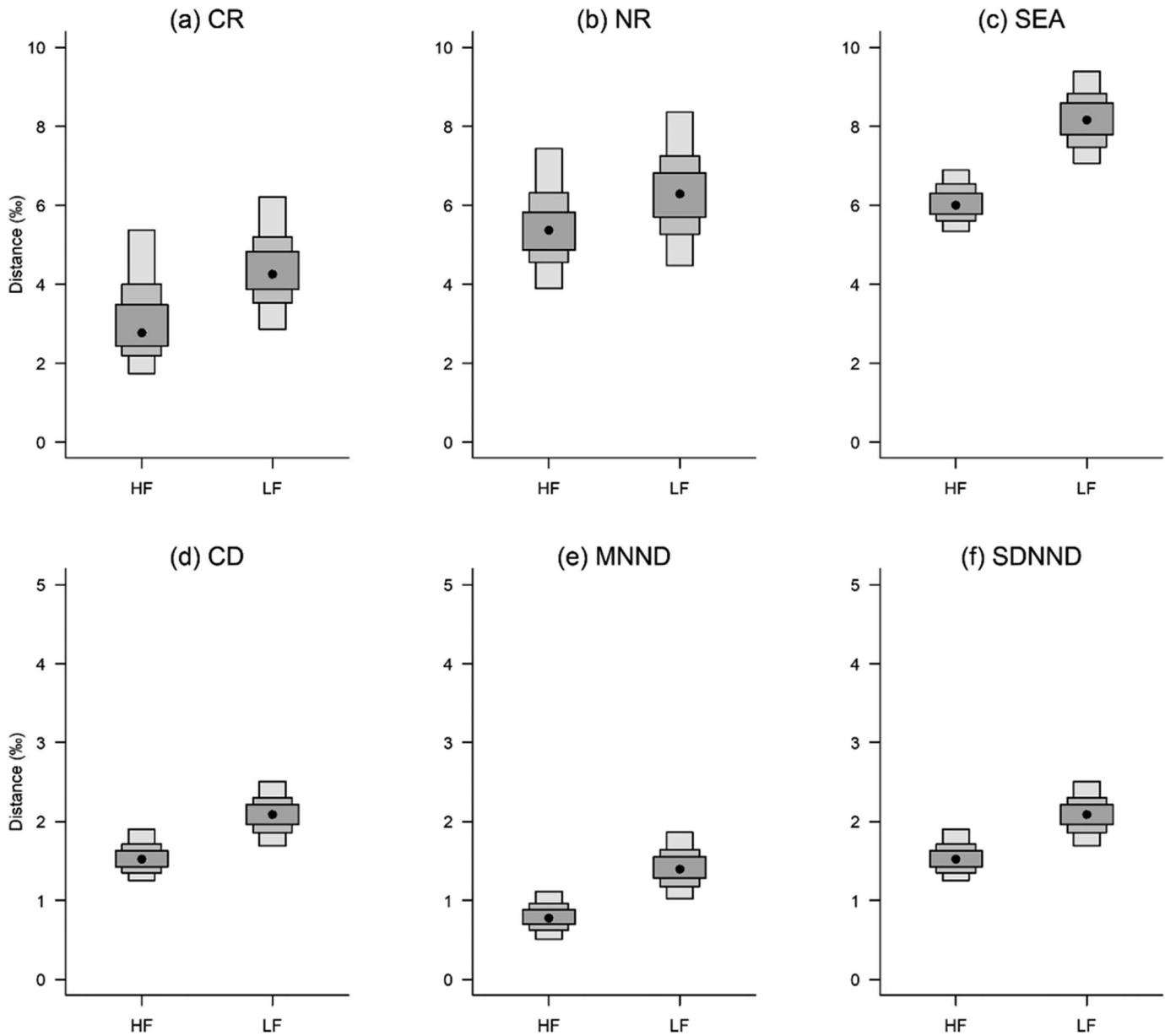


FIG. 2.—Bayesian results for the six community-wide metrics providing information on trophic diversity and trophic redundancy within food webs of high-(HF) and low-(LF) disturbance frequency sites:  $\delta^{13}\text{C}$  range (CR),  $\delta^{15}\text{N}$  range (NR), standard ellipses area (SEA), mean 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) sites.

DISCUSSION

We found differences in food-web structure between high-frequency and low-frequency sites, indicating that forest management practices in these pine forests could modify environmental conditions that structure habitats, shift energetic pathways, and ultimately affect resource use of

consumers in these systems. Stable isotope analyses of dominant basal resources, primary and secondary consumers, and snakes revealed contrasting patterns of food-web organization in response to management practice frequency. We found support for our first hypothesis that trophic structure of predator assemblages differs between sites. We observed greater trophic

TABLE 5.—Standard ellipses area analyses for snake communities in high- and low-disturbance frequency sites. 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 ( $\text{SEA}_C$ ), 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 nonoverlap
SEA	6.06	8.17	3.42	31.49	0.58
$\text{SEA}_C$	6.09	8.22	NA	NA	NA
SEA 95%	36.46	49.19	NA	NA	NA

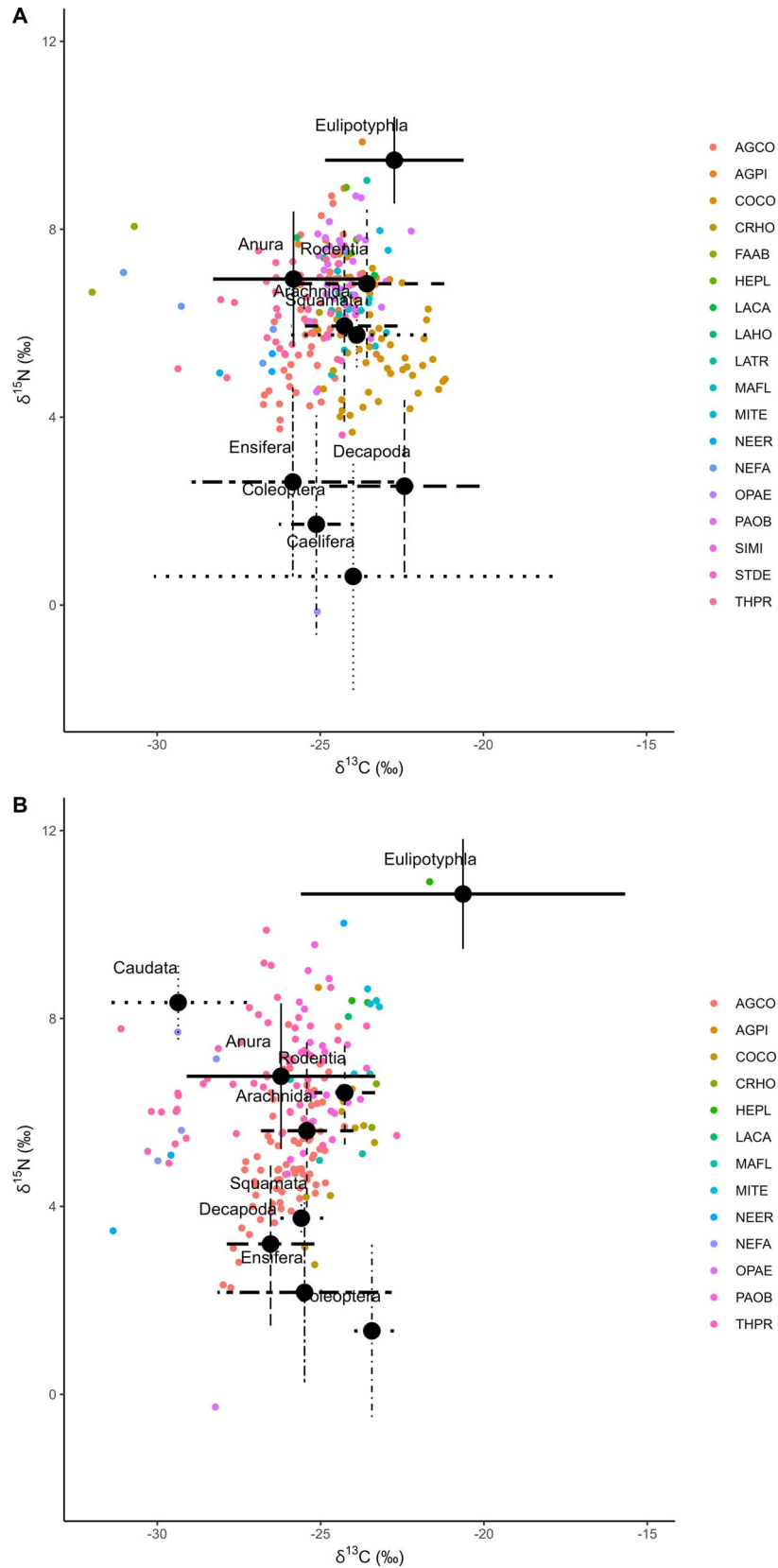


FIG. 3.—Biplots of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in snake assemblages (colored circles) and Arachnidae, Anura, Caelifera, Caudata, Coleoptera, Decapoda, Ensifera, Eulipotyphla, Rodentia, and Squamata prey resources (mean values of  $\delta^{13}\text{C} - \delta^{15}\text{N} \pm 1$  SD; black circles) incorporating corrected trophic discrimination factors in (A) high- and (B) low-disturbance frequency sites. Species codes for snake species are listed in Appendix 1.



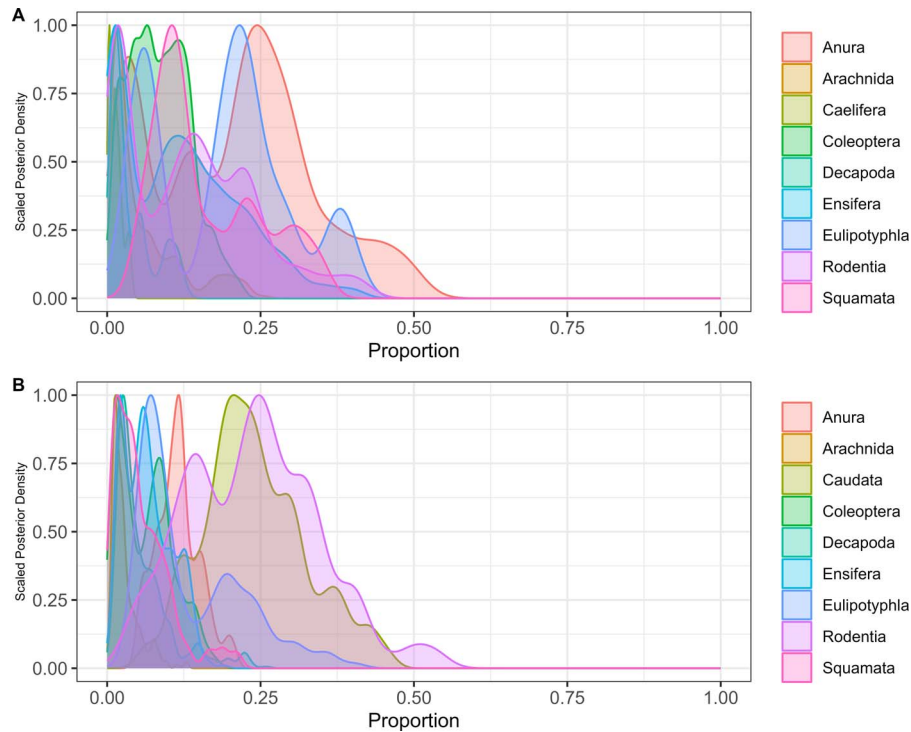


FIG. 4.—Isotopic mixing models depicting the contribution of prey sources for all snake species captured in the (A) high- and (B) low-disturbance frequency sites. Results are reported as posterior density distributions of proportional contributions to snake consumer mixture data as mean dietary proportions with associated credibility intervals (i.e., 25%, 50%, 75%, 100%).

diversity in the low-frequency site and lower trophic diversity with increased trophic redundancy in the high-frequency site. We expected resource use and niche breadth of snakes to vary between high- and low-frequency sites, and found evidence supporting our second hypothesis that predator assemblages differed in their resource use between high- and low-frequency sites as snake consumers utilized different functional prey groups.

#### Forest Management Frequency and Food-Web Structure

Greater trophic redundancy was observed in 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 sites. Rather, the observed increase in trophic redundancy was caused by a contraction in the diversity of basal resources (i.e.,  $\delta^{13}\text{C}$  range) that support these predators at the high-frequency site. These results are surprising, as C3 and C4 plants were both dominant basal resources at the high-frequency site as compared to the low-frequency site in which C3 plants were the dominant basal resources.

Forest management regimes characterized by high-frequency treatments are implemented to maintain forest as subclimax communities (Hanberry et al. 2018). Frequent fire disturbance is 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 effect of providing resource-rich environments allowing many consumers

to exploit similar resources. Despite the presence of seed-producing C4 grasses, fruit-producing C3 forbs were the most dominant understory cover at the high-frequency site. The dominance of C3 forbs was attributable to relatively few species (i.e., black raspberry, *Rubus occidentalis*, and blueberry, *Vaccinium* spp.) known for both their high productivity in early seral forests and their nutritional benefits to a variety of wildlife (McWethy et al. 2010). These C3 forbs are particularly reliant on sunlight reaching the forest floor, and their establishment following prescribed fire and logging operations in open-pine systems is well known (Arthur et al. 1998; Clendenin and Ross 2001). 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 et al. 2017). Given the similarity in carbon signatures of prey resources (e.g., secondary consumers) at multiple trophic levels in the high-frequency site, the trophic redundancy observed in the snake assemblage occupying the high-frequency site likely results from both predators and prey maximizing energetic uptake at each trophic level. Furthermore, this isotopic pattern prevails along a narrow and productive C3 pathway fostered by frequent forest management practices that preserve conditions for fruit-producing C3 plants to dominate.

Although fire maintains a well-developed herbaceous understory at the high-frequency site, we do not know the role that fire might play in shaping soil microbial community structure and the availability of soil nitrogen. For example, nitrogen-fixing microbes may decline as a direct response to fire severity (Wang et al. 2014). Also, elevated inorganic nitrogen has been observed in soils postfire (Gómez-Rey et al. 2013; Huber et al. 2013). Shifts in nitrogen caused by fire

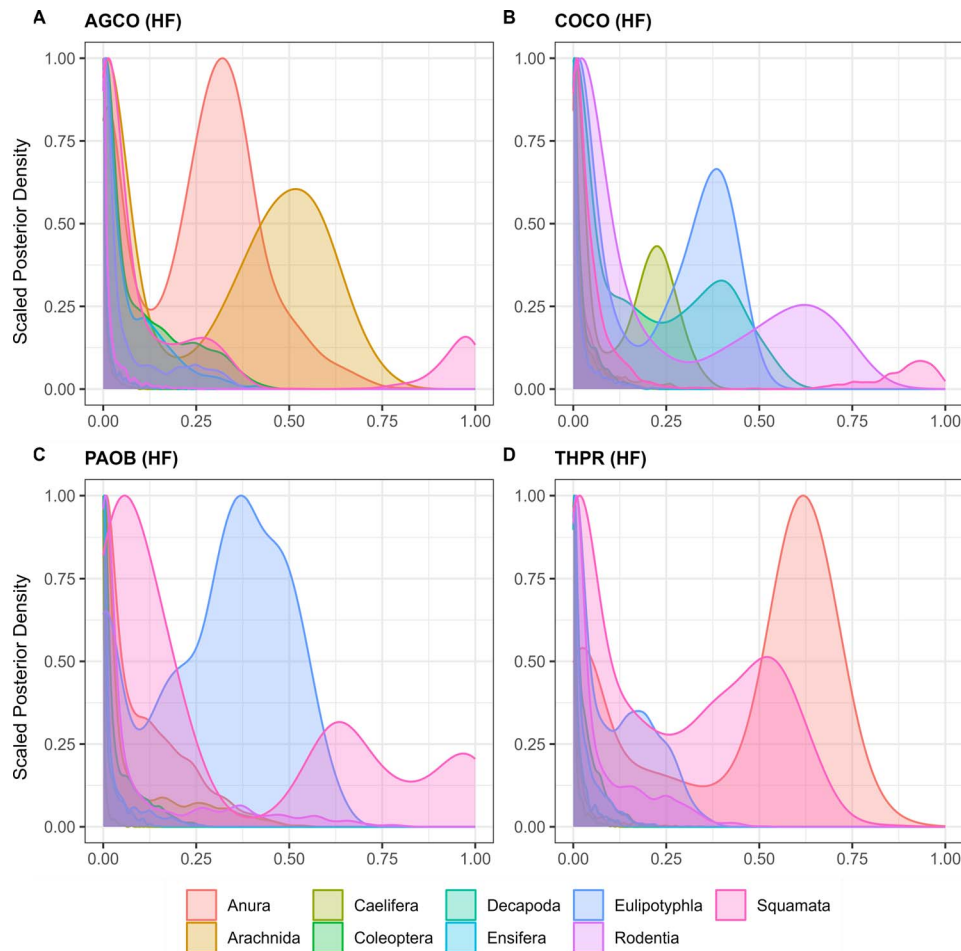


FIG. 5.—Isotopic mixing models depicting the contribution of prey sources to snake species across the four most common shared species captured in the high disturbance frequency site. Results are reported as posterior density distributions of proportional contributions to snake consumer mixture data as mean dietary proportions with associated credibility intervals (i.e., 25%, 50%, 75%, 100%). Species codes are listed in Appendix I.

may be short-term responses, but could still influence baseline  $\delta^{15}\text{N}$  values under high-frequency disturbance (i.e., frequent prescribed fire). We were unable to quantify these components of the soil food web because all of our sampling occurred at least one season postburn (Adams et al. 2022). How microbial communities recover or stabilize under different disturbance regimes may be an important determinant of food-web structure at higher trophic levels. Our study provides a perspective on the food-web structure within the growing season at these sites, which coincides with peak snake activity in this region (Fitch 1949; Schalk et al. 2022). The structure of these food webs may shift temporally, across seasons or across years, in response to variation in basal resources and prey availability. Still, 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 (Nowlin et al. 2007; Klemmer and Richardson 2013). 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 snake assemblage occupying the low-frequency site. 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., coral die-off from white band disease) altered trophic pathways, but food-chain length remained unchanged (i.e.,  $\delta^{15}\text{N}$  range). Specifically, the  $\delta^{13}\text{C}$  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). Similarly, lack of consistent and effective forest management in the low-frequency site resulted in basal areas and closed-canopy conditions that led to homogenized understories and detritus buildup on forest floors. Reviews of food-

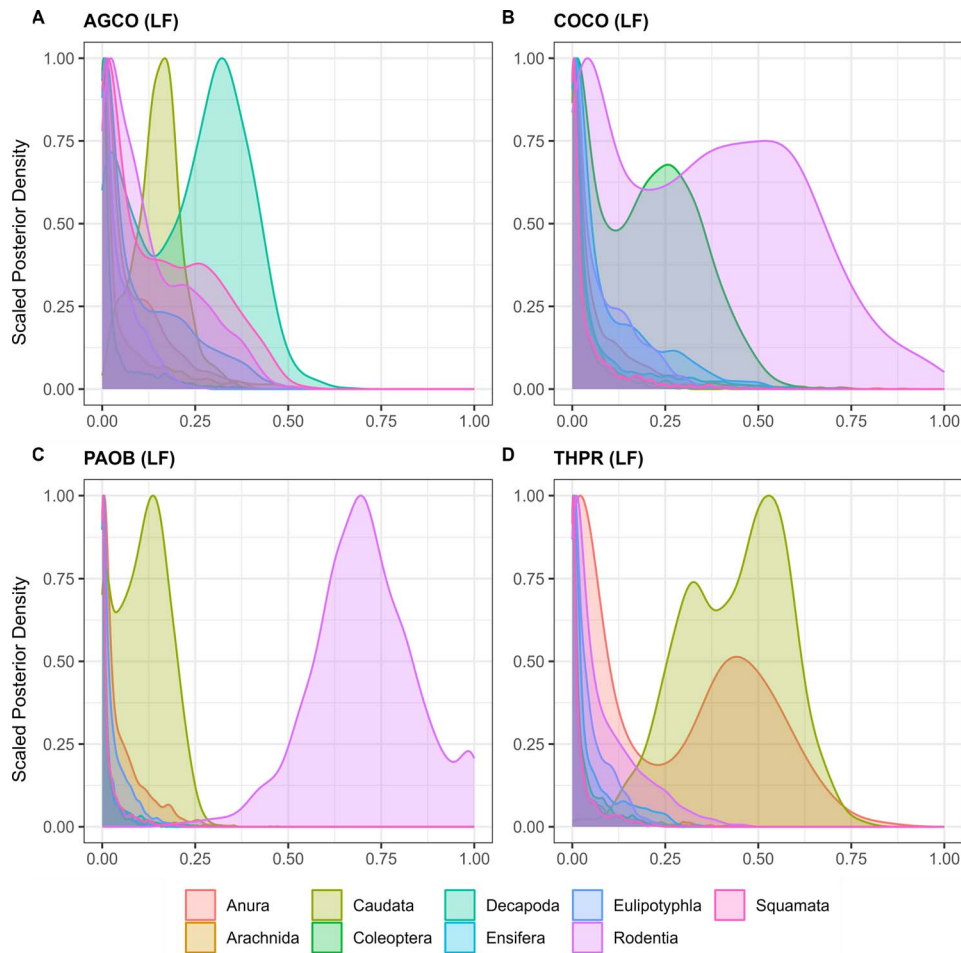


FIG. 6.—Isotopic mixing models depicting the contribution of prey sources to snake species across the four most common shared species captured in the low disturbance frequency site. Results are reported as posterior density distributions of proportional contributions to snake consumer mixture data as mean dietary proportions with associated credibility intervals (i.e., 25%, 50%, 75%, 100%). Species codes are listed in Appendix I.

web studies in ecosystems in which detritus is a major energy source have emphasized that such resources are not homogeneous 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 (e.g., Moore et al. 2004; Manlick et al. 2023). Food webs vary in the extent to which detritus is derived from decomposition rates and associated microbial communities, which then results in multiple and dynamic consumer-resource pathways (Polis and Hurd 1996; Moore et al. 2004; Mougi 2020). Previous studies have acknowledged how the biomass and community composition of microbes may influence trophic interactions in higher-order consumers (e.g., Sabo et al. 2005; Miyashita and Niwa 2006). 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 (Moore et al. 2004; Gessner et al. 2010; Mougi 2020). In the low-frequency site, this might have resulted in the variation in  $\delta^{13}\text{C}$  pathways and consequently, the broader  $\delta^{13}\text{C}$  range of snake consumers.

#### Forest Management Frequency and Resource Use

Differences in the structural complexity of habitats, and the number and type of energetic pathways, between high- and

low-frequency sites, indicate the trophic structure of predator assemblages might be influenced by the responses of functional prey groups to disturbance 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; Colston et al. 2010; Lillywhite et al. 2014). Furthermore, coexistence is facilitated by dietary niche partitioning within snake communities and, as such, the diversity of these predators in managed ecosystems is likely correlated with resource-use responses (Toft 1985; Luiselli 2003, 2006a; Perkins et al. 2020). Previous studies investigating patterns of resource use and coexistence dynamics among terrestrial snake communities in temperate regions are limited (e.g., Luiselli 2006b). However, given that the taxonomic diversity of predators was greater in the high-frequency site, and that predator diversity in the low-frequency site 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 sites (Adams et al. 2022).



When all 18 species were included, snakes in the high-frequency site potentially exploited a wide variety of prey. In addition to exploiting vertebrate prey in more equal estimated proportions, overall resource use in the high-frequency snake assemblage also featured slightly higher contributions of invertebrate prey. Vertebrates are well documented in diets of generalist snake predators, whereas invertebrates are more likely to be consumed by small-bodied insectivorous snakes that are not well represented in our sampling efforts (e.g., *O. aestivus*; Trauth and McAllister 1995; Burgdorf et al. 2005; Schalk et al. 2018; Adams et al. 2022). Differences in lipid content, protein content, and water content between poikilothermic and homeothermic prey items can influence the physiological responses that contribute to growth in snakes (Dierenfeld et al. 2015). Although small mammals are typically high in lipid content, amphibians contain higher levels of chemical constituents that could also influence water loss and thermoregulation (Spencer et al. 2020). Under a forest management regime characterized by frequent disturbance, increases in microhabitat availability (e.g., coarse woody debris and herbaceous plant cover) may also increase prey availability to tertiary consumers (e.g., snakes; Greene et al. 2016). Diversity and abundance of small mammals and arthropods is higher in open pine forests subjected to frequent applications of prescribed fire and thinning and also support comparable amphibian diversity to other forest types (Steen et al. 2010; Sutton et al. 2014; Sheehan and Klepzig 2022). Under such conditions when multiple prey groups are abundant, coexistence might be facilitated when generalists utilize low- and high-quality prey (Reynolds and Scott 1982; Willson and Hopkins 2011; Durso et al. 2013). Although there could be some energetic trade-offs to consuming invertebrate prey, active-foraging snakes that rely on visual hunting may consume arthropods more readily in high-frequency conditions (Lourdais et al. 2014; Adams et al. 2022). For example, *C. constrictor* had a wider trophic range, and invertebrate prey groups were estimated as potentially important sources to their resource use at the high-frequency site. This species was also more common at the high-frequency site, and likely the largest-bodied active forager capable of subsisting on invertebrate prey (Lennon 2013; Adams et al. 2022).

In contrast, snakes in the low-frequency site ( $n = 13$  spp.) potentially exploited fewer vertebrate prey groups (i.e., caudates and rodents). Caudates, which were estimated to be an important component of diet in the low-frequency snake assemblage, were not sampled at the high-frequency site where the prevailing environmental conditions brought on by management practices may have limited their availability to snake consumers (Hocking et al. 2013). Similarly, other studies have documented how the shared use of resources may facilitate snake species coexistence when disturbances result in a temporally pulsed abundance of higher-quality prey (e.g., Luiselli et al. 2005; Hampton and Ford 2007; Willson et al. 2010). Despite having lower relative abundance in the low-frequency site (Adams et al. 2022), rodents were estimated to be an important component of diet for the snake assemblage at that site. In addition to prey availability, other factors (i.e., foraging mode, prey size, frequency of consumption,) may scale up to affect resource use in high- and low-frequency snake assemblages (Bolnick et al. 2003; Luiselli 2006a; Glaudas et al. 2019). The high-frequency assemblage consisted mostly of active-foraging snakes, whereas the low-frequency snake assemblage consisted mostly of snakes that exhibit sit-and-wait

foraging tactics (Adams et al. 2022). Snake species that employ sit-and-wait foraging strategies have been reported to often consume larger prey and feed less frequently than active foragers (Glaudas et al. 2019). Although we have evidence to suggest some potential prey differ in relative abundance between high- and low-frequency sites (Adams et al. 2022), we do not know the extent to which management practice frequency might affect prey encounter rates or the frequency of consumption of prey by snake consumers (sensu Tutterow et al. 2021). Sympatric predators that overlap in trophic niche space can partition resources by altering the frequency of consumption of high-quality and low-quality prey (e.g., Luiselli 2006a; Jellyman and McIntosh 2020). Patterns of generalization and specialization in the diets of generalist predators has been attributed to the availability and selection of optimal foraging locations and behavioral adaptation to limited resources. This strategy, used by generalist predators in response to variation in prey, enables 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 the snake assemblages between high- and low-frequency sites.

The prey most important to predators at the high-frequency site occupied similar isotopic niches, indicating that frequent management practices facilitate the conditions that allow 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 sites. *Agkistrodon contortrix* are highly generalized in their dietary preferences, feeding on an array of invertebrate and vertebrate prey (Trauth and McAllister 1995; McKnight et al. 2014; Schalk et al. 2018). In the high-frequency site, *A. contortrix* were supported by arachnids, anurans, and squamates in greater proportions than other prey. At the low-frequency site *A. contortrix* were even more generalized, consuming vertebrate and invertebrate prey in similar proportions. *Thamnophis proximus*, an active forager also known to consume a variety of vertebrate prey (Hampton 2008, 2013), specialized in their resource use at both sites. At the high-frequency site, *T. proximus* were supported by mainly anurans, as compared to being supported by both caudates and anurans at the low-frequency site. Salamanders typically exhibit strong responses to forest management (i.e., thinning), as shifts in abundance are well documented between open canopy (e.g., high-frequency) and closed canopy (e.g., low-frequency) forests (Chazal and Niewiarowski 1998; Hocking et al. 2013). Resource use of both *A. contortrix* and *T. proximus* varies between populations because of differences in environmental conditions (Quevedo et al. 2009; Hampton 2013; Schalk et al. 2018). Individual specialization in snake resource use that alters frequency-dependent interactions may influence ecological interactions that effect food-web structure in high-frequency and low-frequency sites (Bolnick et al. 2007; Layman et al. 2015).

The patterns of resource use we observed may also be a function of our approach (i.e., stable isotopes of scale tissues) to assess the trophic ecology of the snakes in these forest systems. In the absence of data obtained from stomach analyses, mixing-model estimations of snake diets may be

influenced by the inability to sample all potential prey items of snake consumers (Durso et al. 2022). For example, some snake species are known to consume avian prey, as well as avian eggs and chicks (DeGregorio et al. 2014, 2016). The inability to assess and sample isotopic signatures of avian prey, which feed upon forest arthropods, might have resulted in higher contributions of arthropods being predicted in resource use models. Management practice frequency may also influence the diversity and abundance of ground-nesting and shrub-nesting birds, thereby affecting prey availability to snakes that potentially feed on them (DeGregorio et al. 2014). In some cases, certain prey groups might serve as proxies for other prey groups because of sampling limitations and low isotopic variation within prey resources. Although we expected invertebrate groups to contribute to diets of *A. contortrix* in our mixing models, we were unable to sample some hemipterans (i.e., cicadas) that are known to be temporally exploited by *A. contortrix* (Lagesse and Ford 1996; Hendricks 2019). Furthermore, depredations at lower levels of food webs may result in overlap in isotopic signatures with minimal fractionation (Durso et al. 2022).

Management practice frequency, which results in differences in forest structure and basal resource availability, may lead to differences in the productivity of varying energetic pathways (i.e., carbon availability). Differences in resource use among snake assemblages then have implications for the number and strength of trophic linkages in these food webs. In our study, these patterns of resource use reflected the overall patterns of trophic structure that we observed in the high- and low-frequency sites. At the high-frequency site, snakes were more even in the diversity of prey that they utilized. These prey groups were supported by a narrow energetic pathway, which could have contributed to the increased trophic redundancy observed at the high-frequency site. At the low-frequency site, snakes utilized prey disproportionately to the available prey at that site. The prey that supported snakes were supported by a broader energetic pathway (i.e., carbon pool), which may underlie the observed trophic niche diversification at the base of the food web and greater overall trophic diversity at the low-frequency site.

Considering these 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 (Morris et al. 2013; Howze and Smith 2021). 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 processes spanning across multiple trophic levels can influence trophic structure, and are not easily addressed when considering predator responses at only one trophic level (Raffaelli et al. 2002; Wang et al. 2019; McLeod and Leroux 2020). 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 (Strong and Frank 2010; Estes et al. 2011).

## CONCLUSIONS

Disturbance-prone pine forests with increased frequency of forest management practices may support a greater diversity of snakes, and increase trophic redundancy within these consumers (Adams et al. 2022; Schalk et al. 2022). 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, and 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 produces many weak interactions with their prey 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., increased trophic redundancy) can lead to greater stability in ecosystems prone to disturbance (Sanders et al. 2018). Increased forest management practice frequency 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 reinforce 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).

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## SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/HERPMONOGRAPHS-D-23-00001.1.S1> and <https://doi.org/10.1655/HERPMONOGRAPHS-D-23-00001.1.S2>.

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