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ARTICLE

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Can a mesocarnivore fill the functional role of an apex predator?

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Abstract

As keystone species, apex predators play a role in structuring most ecosystems through competition and facilitation, thereby affecting community structure, prey abundance and behavior, vegetation, and abiotic processes. Apex predators are also highly threatened and have been extirpated from much of North America, leading to mesocarnivores, such as coyotes (*Canis latrans*), becoming de facto apex predators in many ecosystems. However, it is unknown if these mesocarnivores can fill the same functional keystone role as true apex predators. We compared the spatial and temporal habitat use of mesocarnivores in two similar study systems, one with pumas (*Puma concolor*) and one without, to determine how the role of coyotes in structuring the carnivore community changes in the absence of pumas. We used multispecies occupancy and relative abundance models to examine the spatial avoidance of pumas and coyotes by the smaller mesocarnivores, and temporal overlap and avoidance-attraction ratios to examine temporal avoidance. We found that coyotes partially fill the functional role of apex predators, but with weaker effects than pumas. Where pumas were absent, site use intensity and relative abundance increased for coyotes (180% and 1250%) and raccoons (*Procyon lotor*, 308% and 3273%) and decreased for bobcats (*Lynx rufus*, 36% and 55%), gray foxes (*Urocyon cinereoargenteus*, 13% and 32%), and striped skunks (*Mephitis mephitis*, 3% and 12%). Coyotes and raccoons shifted their temporal activity away from pumas, while gray foxes shifted their activity closer to pumas. Detection likelihood decreased for all species after detection of a puma (67%–93%) or coyote (46%–94%) in both sites, but small mesocarnivores avoided pumas more than coyotes in the study area with both. Interactions between carnivores are complex and best understood with multiple measures and in the context of the full community. While coyotes appear to suppress smaller mesocarnivores by some measures (e.g., temporal avoidance), they do not by others (e.g., spatial avoidance) and have overall weaker effects than pumas. Our results suggest that coyotes are not a substitute for apex predators, and conserving true apex predators is likely important for maintaining ecosystem health.

KEYWORDS
carnivore, community ecology, competition, interspecific interactions, keystone species, mesopredator, predation, trophic cascade

INTRODUCTION

Large carnivores play an integral role in structuring most ecosystems (Estes et al., 2011) and are critical to conservation, both in their use as an umbrella species to conserve biodiversity (Carroll et al., 2001) and as charismatic flagship species to promote conservation (Sibarani et al., 2019). Paradoxically, they are also one of the most threatened guilds on the planet (Estes et al., 2011; Ripple et al., 2014), as many of the same attributes that make them effective umbrella species also put them in conflict with humans (Ripple et al., 2014; Weaver et al., 1996) and their slow reproductive rates lead to slow recovery from persecution (Prugh et al., 2009). Large carnivores have vast home ranges and rely on abundant prey populations to sustain them (Estes et al., 2011; Ripple et al., 2014). This makes them vulnerable to habitat loss and fragmentation (Ripple et al., 2014; Treves & Karanth, 2003), but also makes them valuable species to monitor for overall ecosystem health as they are likely to be affected before other species (Carroll et al., 2001). Large carnivores are usually at the top of the food chain (e.g., apex predators) and often act as keystone species (a species having a dominating influence on community composition), making them crucial to ecosystem health.

The functional (i.e., keystone) role of apex predators is a complex balance between suppression and facilitation based on predation and competition with other carnivores (Prugh & Sivy, 2020; Ripple & Beschta, 2004; Sivy et al., 2017). Through predation, apex predators affect both the abundance and the behavior of prey (Donadio & Buskirk, 2016; Ripple & Beschta, 2004), benefiting the vegetative community (Beschta & Ripple, 2009; Brook et al., 2012; Schmitz et al., 2000), and affecting ecosystem dynamics such as disease, wildfire, and biogeochemical cycles (Beschta & Ripple, 2009; Estes et al., 2011). Predation by apex predators further provides a consistent food source to scavengers of all taxa (Barry et al., 2019; Wilmers et al., 2013), especially mesocarnivores that could not otherwise regularly feed on large prey (Allen et al., 2015; Prugh & Sivy, 2020).

Apex predators also shape the behavior and populations of mesocarnivores through competition due to shared prey (Prugh & Sivy, 2020; Wang et al., 2015). This competition includes direct killing of mesocarnivores (Palomares & Caro, 1999), mediating behavior through fear (e.g., avoidance; Brook et al., 2012; Hayward & Slotow, 2009), and a combination of provisioning food as carrion while also reducing access to other resources (Hall et al., 2021; Prugh & Sivy, 2020; Wilmers et al., 2003). As a result of this competition, mesocarnivores may have reduced abundance (Brook et al., 2012), avoid apex predators spatially and/or temporally (de Satgé et al., 2017; Hall et al., 2021; Hayward & Slotow, 2009), and can be pushed into less desirable habitat, such as high human-use areas (Di Bitetti et al., 2010; Thinley et al., 2018). Smaller carnivores may also benefit from apex predator suppression of larger mesocarnivores (Allen et al., 2015; Levi & Wilmers, 2012; Newsome & Ripple, 2015; Wang et al., 2015), as this releases them from similar suppression by the mesocarnivore (a form of mesopredator release; Crooks & Soule, 1999; Levi & Wilmers, 2012; Prugh et al., 2009). Due to the complexity of these relationships, it can be difficult to fully understand the impact of the apex predator until they are lost. Apex predators have been extirpated or suffered significant range reductions throughout most of North America due to habitat loss and the use of lethal controls (Brook et al., 2012; Prugh et al., 2009). Conversely, many mesocarnivores are more tolerant of fragmented habitat and may live in close proximity to humans (Prugh et al., 2009). While mesocarnivores are also frequently persecuted, they recover more quickly than apex predators due to higher reproductive rates and densities (Prugh et al., 2009).

In the absence of true apex predators, large mesocarnivores, such as coyotes (*Canis latrans*), become the de facto apex predator and often increase in abundance after being released from the pressures of competition (Prugh et al., 2009), as has been seen in southern California and Yellowstone National Park following the extirpation of wolves (*Canis lupus*; Ripple et al., 2013; Roemer et al., 2009). Their release from competition with large carnivores can result in cascading trophic effects that restructure the carnivore guild and entire ecosystem—for example, smaller carnivores may be suppressed by the increased competition (Levi & Wilmers, 2012; Palomares & Caro, 1999; Wang et al., 2015) and the main prey of the mesocarnivore may be suppressed by increased predation (Crooks & Soule, 1999; Miller et al., 2012). At the same time, other herbivorous prey, too large for the mesocarnivore, may be released from predation pressures which in turn suppress vegetation leading to large-scale changes within the ecosystem (Beschta & Ripple, 2009; Ripple et al., 2014). While a great deal of research exists on linear trophic cascades consisting of only three species (e.g., apex predator–mesopredator–prey or apex predator–prey–vegetation; Beschta & Ripple, 2009; Miller et al., 2012; Schmitz et al., 2000), little is known about the effects of mesopredator release on the carnivore community as a whole. It is expected that the largest mesocarnivore will become dominant in the absence of a true apex predator, but little research has addressed whether a dominant mesocarnivore can fill the functional keystone role of an apex predator, although this likely depends on the species and complexity of specific ecosystems (Prugh & Sivy, 2020).

We compared two ecosystems with similar carnivore guilds, one with pumas (*Puma concolor*) in the Santa Cruz Mountains of central California, and the other without in Fort Hood, Texas, to determine how carnivore community structure changed in the absence of an apex predator and whether a large mesocarnivore (coyotes) filled the functional role of the extirpated apex predator. While bobcats are a similar size to coyotes, we did not expect them to become the dominant species in the absence of pumas, as coyotes have been known to kill or exclude bobcats (Dyck et al., 2021) and coyotes are able to kill larger prey than bobcats (Gese & Grothe, 1995), making them the more likely apex predator. Pumas historically existed throughout Texas but were extirpated from all but the southwestern edge of the state in the mid-1900s due to habitat loss and intensive predator control (Schmidly & Bradley, 2004). Our first objective was to determine the effects of pumas on mesocarnivores to understand their functional role within the carnivore community. To do this, we compared the spatial and temporal habitat use of four mesocarnivores: bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*) to that of coyotes and pumas. We hypothesized that we would observe a cascade among carnivores in Santa Cruz where pumas negatively affected their closest competitors (coyotes, whose diet most closely overlaps with pumas; Gese & Grothe, 1995), releasing smaller mesocarnivores (the other four species) from the competition with coyotes (Wang et al., 2015). Specifically, we expected coyotes to avoid pumas spatially and temporally (Hayward & Slotow, 2009; Wang et al., 2015) and have low relative abundance (Newsome & Ripple, 2015) in Santa Cruz (Table 1). We further expected the smaller mesocarnivores to show no spatial avoidance of pumas as they may provide a food source via carrion (Allen et al., 2015; Wang et al., 2015), but we expected temporal avoidance as pumas are still a potential predator. We expected the smaller mesocarnivores to show spatial and temporal avoidance of coyotes as a direct competitor and potential predator (Wang et al., 2015) and have a higher relative abundance in Santa Cruz due to reduced effects from the suppressed coyote population (Newsome & Ripple, 2015).

Our second objective was to determine if coyotes fill the functional role of an apex predator in the absence of pumas. To do this, we compared the spatial and temporal habitat use of six mesocarnivores—the same species as Santa Cruz plus eastern spotted skunk (*Spilogale putorius*) and ringtail (*Bassariscus astutus*)—to coyotes at Fort Hood in central Texas and then compared our results in Fort Hood to those of Santa Cruz. We hypothesized that if coyotes filled the functional role of an apex predator, we would observe coyotes suppressing their closest competitors (bobcats, whose diet most closely overlaps with coyotes; Lesmeister et al., 2015) and releasing the other five smaller mesocarnivores, but if they were undergoing mesopredator release and only partially filling the full functional role, they would suppress all six smaller mesocarnivores in Fort Hood (Crooks & Soule, 1999). Specifically, we expected coyotes to have higher relative abundance in Fort Hood than in Santa Cruz (Newsome & Ripple, 2015), bobcats to have lower relative abundance, and the other mesocarnivores to have increased or stable relative abundance between Fort Hood and Santa Cruz if coyotes fill the full functional role, and all of the smaller mesocarnivores to have lower relative abundance if coyotes only partially fill it (Newsome & Ripple, 2015). Additionally, smaller mesocarnivores should show spatial and temporal avoidance of coyotes in Fort Hood (Hall et al., 2021), as coyotes are a potential predator and less likely to provide carrion than pumas (Table 1). However, if coyotes do not fill any part of the functional role of an apex predator, we would not expect to see suppression of the smaller mesocarnivores. Specifically, there should be no difference in relative abundance of the smaller mesocarnivores between Santa Cruz and Fort Hood, and the smaller mesocarnivores should not show more spatial or temporal avoidance of coyotes in Fort Hood than they did in Santa Cruz (Table 1).

METHODS

Study area

The Fort Hood study area took place on the 87,890-ha military installation in Bell and Coryell Counties, Texas (Figure 1a). Fort Hood is surrounded primarily by agricultural land with larger urban areas to the south.

TABLE 1 Expected effects, positive (+), negative (−), or no effect (0) of the dominant carnivore on the smaller carnivore for each measure of suppression (spatial or temporal avoidance) based on our hypotheses.

Hypothesis	Site	Dominant carnivore	Smaller carnivore	Spatial			Temporal	
				RA	ψ	SUI	DTA	AAR
Pumas suppress coyotes releasing smaller mesocarnivores	Santa Cruz	Puma	Coyote	**−**	**−**	**−**	**−**	**−**
			Bobcat	**+**	**+**	**+**	**−**	**−**
			Gray fox	**+**	**+**	**+**	**−**	**−**
			Raccoon	**+**	**+**	**+**	**−**	**−**
			Striped skunk	**+**	**+**	**+**	**−**	**−**
	Santa Cruz	Coyote	Bobcat	0	0	0	−	−
			Gray fox	0	0	0	−	−
			Raccoon	0	0	0	−	−
			Striped skunk	0	0	0	−	−
Coyotes fill apex functional role by suppressing closest competitor and releasing other small carnivores	Fort Hood	Coyote	Bobcat	**−**	**−**	**−**	**−**	**−**
			Gray fox	**+**	**+**	**+**	−	−
			Raccoon	**+**	**+**	**+**	−	−
			Striped skunk	**+**	**+**	**+**	−	−
Coyotes undergo mesopredator release and suppress all smaller carnivores. Filling some of functional roles	Fort Hood	Coyote	Bobcat	**−**	**−**	**−**	**−**	**−**
			Gray fox	**−**	**−**	**−**	**−**	**−**
			Raccoon	**−**	**−**	**−**	**−**	**−**
			Striped skunk	**−**	**−**	**−**	**−**	**−**
Coyotes do not fill functional role and have no effect on smaller carnivores	Fort Hood	Coyote	Bobcat	0	0	0	0	0
			Gray fox	0	0	0	0	0
			Raccoon	0	0	0	0	0
			Striped skunk	0	0	0	0	0

Note: Boldface indicates strong effect and regular text indicates weak effect.
Abbreviations: AAR, avoidance-attraction ratios; DTA, daily temporal activity; RA, relative abundance; SUI, site use intensity; ψ, occupancy.

For landscape, climate, and vegetation descriptions, see Avrin et al. (2021). The land is primarily used for military training, including live weapons, aviation, and mechanized maneuvers, but recreation activities, such as hiking, hunting, and fishing, are also allowed as well as some cattle grazing (Hayden et al., 2000).

The Santa Cruz study area took place in roughly 140,000 ha of the southern Santa Cruz Mountains, California, in Santa Cruz, San Mateo, and Santa Clara counties (Figure 1b), bounded by the Pacific Ocean to the west and mixed urban and agricultural areas to the north, south, and east. For landscape, climate, and vegetation descriptions, see Wilmers et al. (2013). There are large tracts of intact native vegetation throughout the study area with state and county parks that allow recreational activities, such as hiking, biking, and dog walking (Wang et al., 2015). Private lands vary in degree of use with some agricultural activity (small farms and cattle ranches) dispersed throughout the area (Wilmers et al., 2013).

Camera trapping design

In Fort Hood we deployed camera traps in three time periods, (1) March–June 2011, September 2011–June 2012, October–November 2012, (2) November 2018–April 2019, and (3) December 2019–May 2020. We arranged camera traps in seven systematic grids (although one grid could not be deployed in 2018–2019) of 20 cameras each spaced 500 m apart in forests (Figure 1a) for a total of 400 camera trap deployments over all 3 years. We left each grid in place for 6–56 trap nights (mean = 42 trap nights) before moving the camera traps to the next grid. Grid order was different each year. For specifics on camera trap setup, see Avrin et al. (2021). In 2018–2019 and 2019–2020, we deployed scent lures of sardines or fatty acid tablets at 93 camera traps (two-thirds of the cameras) as part of a study on the efficacy of scent lures (Avrin et al., 2021).

In Santa Cruz, we deployed camera traps over four time periods: (1) February–May 2015, (2) February–July

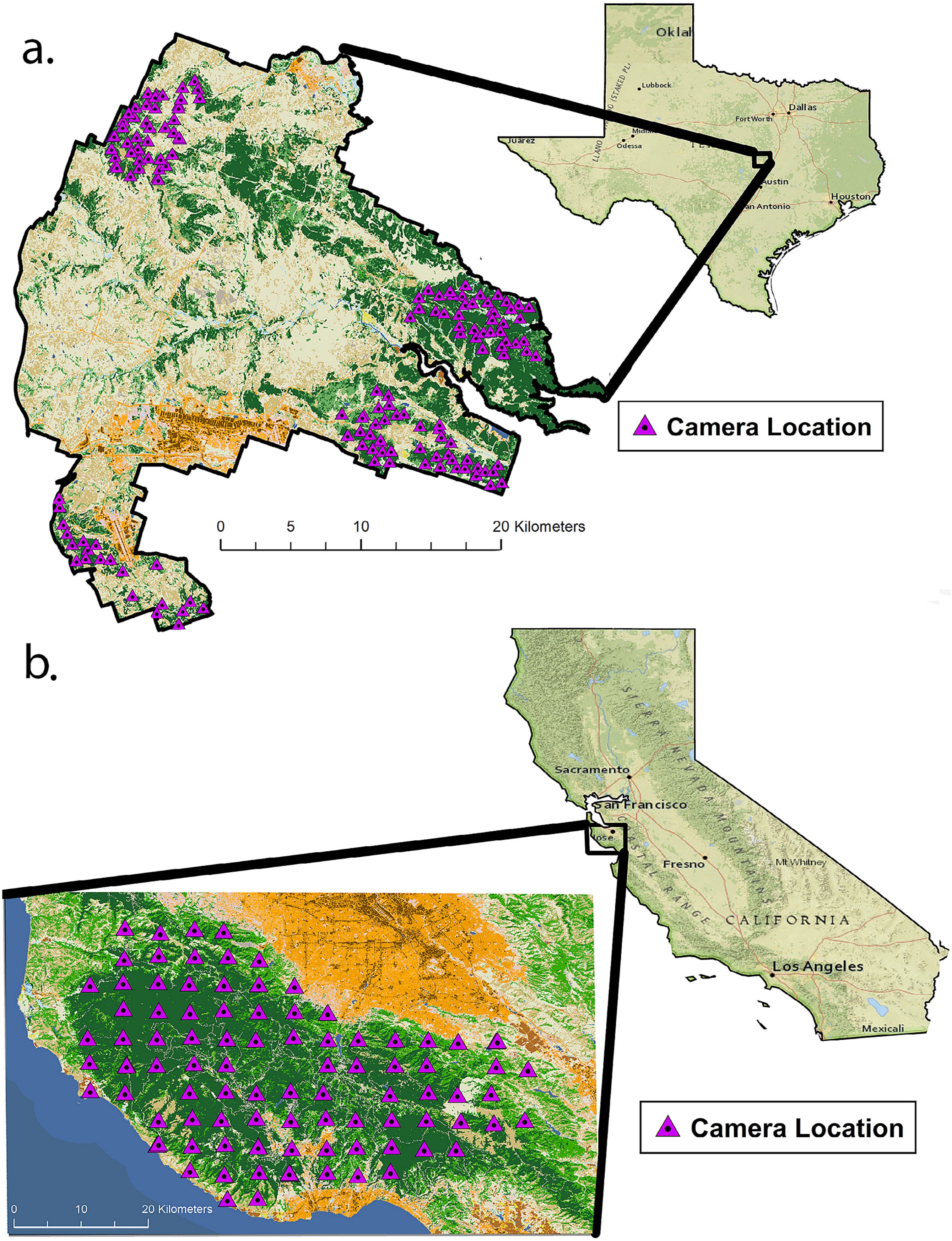

FIGURE 1 Map of study areas in Fort Hood, Texas (a) and Santa Cruz, California (b) with camera trap locations in purple. Landcover from 2016 National Land Cover Database data (green, forest; tan, grassland; orange, urban).

2016, (3) February 2017–January 2018, and (4) January–September 2018. We arranged camera traps in one grid, spaced 4 km apart and distributed evenly across the landscape (Figure 1b) for a total of 305 camera deployments over all 4 years (annual average = 76 cameras). We left camera traps in place for 30–365 trap nights (mean = 111 trap nights) and did not move them between locations. For specifics on camera trap setup, see Nickel et al. (2020). No lures were used with the cameras in Santa Cruz. It is possible that these differences in methods affected our data; however, we accounted for what differences we could in our models (see description under *Statistical Analysis*) and compared data over one-week intervals to reduce the effect of different deployment lengths. All cameras were out long enough to detect the eight focal species if present (Gompper et al., 2006; Kays et al., 2020).

Statistical analysis

We considered all photographs taken during one trigger as one detection. To reduce pseudoreplication, we combined all detections of each species at a camera that was <30 min apart into one event (Brook et al., 2012). To ensure enough data to run our analyses, we only included species with >100 events: puma, coyote, bobcat, gray fox, raccoon, striped skunk, eastern spotted skunk, and ringtail (Table 2). Only coyotes, bobcats, gray foxes, raccoons, and striped skunks were present in both study

TABLE 2 Carnivore detections by species and site.

	Cameras detected		Events		RA ± SE		ψ ± SE		*p* ± SE	
Species	**SC**	**FH**	**SC**	**FH**	**SC**	**FH**	**SC**	**FH**	**SC**	**FH**
Puma (*Puma concolor*)	194	…	788	…	2.32 ± 0.11	…	0.76 ± 0.04	…	0.18 ± 0.01	…
Coyote (*Canis latrans*)	74	359	606	3547	1.79 ± 0.09	21.14 ± 0.95	0.21 ± 0.05	0.92 ± 0.04	0.20 ± 0.01	0.56 ± 0.01
Bobcat (*Lynx rufus*)	252	280	3096	927	9.11 ± 0.31	5.43 ± 0.29	0.84 ± 0.03	0.95 ± 0.05	0.38 ± 0.01	0.28 ± 0.01
Gray fox (*Urocyon cinereoargenteus*)	186	280	5767	1981	16.88 ± 0.54	11.86 ± 0.56	0.68 ± 0.07	0.76 ± 0.04	0.53 ± 0.01	0.47 ± 0.01
Northern raccoon (*Procyon lotor*)	52	321	205	3094	0.58 ± 0.05	18.56 ± 0.84	0.19 ± 0.03	0.86 ± 0.03	0.12 ± 0.01	0.49 ± 0.01
Striped skunk (*Mephitis mephitis*)	217	176	2224	924	6.53 ± 0.23	5.66 ± 0.30	0.76 ± 0.03	0.62 ± 0.04	0.30 ± 0.01	0.31 ± 0.02
Eastern spotted skunk (*Spilogale putorius*)	…	64	…	242	…	1.49 ± 0.11	…	0.98 ± 0.09	…	0.04 ± 0.01
Ringtail (*Bassariscus astutus*)	…	51	…	262	…	1.59 ± 0.12	…	0.16 ± 0.04	…	0.20 ± 0.03
Western spotted skunk (*Spilogale gracilis*)	3	…	6	…	…	…	…	…	…	…
Hog-nosed skunk (*Conepatus leuconotus*)	…	6	…	8	…	…	…	…	…	…
Red fox (*Vulpes vulpes*)	2	2	6	3	…	…	…	…	…	…
North American river otter (*Lontra canadensis*)	…	2	…	2	…	…	…	…	…	…
American badger (*Taxidea taxus*)	7	3	11	3	…	…	…	…	…	…
Total	987	1544	12,709	10,993	…	…	…	…	…	…

Note: Events are ≥30 min apart, relative abundance (RA) is shown as detections per 100 trap nights based on General Linear Model, and detection (*p*) and occupancy (ψ) are unconditional estimates from a multispecies occupancy model with standard error (SE). All covariates held at *z*-scored mean (0), lure as none, and year as 2018 for both sites in occupancy estimates. Fort Hood (FH) cameras = 398 over 3 years, total trap nights = 16,698. Santa Cruz (SC) cameras = 305 over 4 years, total trap nights = 34,021.

areas. We performed all statistics in the program R (v. 4.0.2, R Core Team, 2020).

To determine if pumas and coyotes changed the spatial habitat use of smaller mesocarnivores (bobcats, gray foxes, raccoons, striped skunks, eastern spotted skunks, and ringtails), we used single-season, multispecies occupancy models (Rota et al., 2016) in package unmarked (v. 1.1.1; Fiske & Chandler, 2021). We created capture histories for each species at each camera with a capture occasion of one week. We ran one model for all species in Fort Hood and one model for all species in Santa Cruz, allowing for only second-order interactions among species. To account for variation within the occupancy data unrelated to the species interactions, we included habitat covariates including year, short and long-term climate variables, camera-level habitat variables, prey availability, and lure for independent species occupancy and detection (see Table 3 for detailed descriptions), but not for the interaction between species as our data were too sparse. We were unable to include large-scale habitat variables in our models to account for broad differences between study areas as our data were not set up for a multiscale approach, which would allow for a range of values at each site. All covariates had an $R < 0.70$, and we *z*-score standardized all continuous variables for ease of comparison. We included all covariates for each species and then used a backward stepwise process to remove the covariate with the highest *p* value until only significant covariates remained (Appendix S1: Tables S1 and S2), allowing us to account for variation among camera trap sites and study areas. We used these optimized models to determine the significance of interactions between pumas, coyotes, and the smaller carnivores. We are unaware of a goodness-of-fit test suitable for a multispecies occupancy model and so were unable to perform one. As our study was conducted during spring and summer—when many species reproduce—it is possible the assumption of population closure was violated in our models. However, if this was true, it was true at both sites, so it likely did not affect our comparison much. Further, some species, such as pumas, reproduce year-round, making it impossible to be sure of closure at any time of year. We considered the detection probabilities from our occupancy models as "intensity of site use" since the probability of a species being detected is influenced by their abundance and behavior, such as avoiding areas with a perceived risk, so more intense use leads to more detections (Suraci et al., 2021). We then used this to compare the space use of each species between our two study areas. We estimated the intensity of use and 95% CIs using the predict function in unmarked and determined if site use intensity was significantly different between study areas for each species based on the CI.

To further explore the spatial effects of pumas and coyotes on smaller mesocarnivores, we compared the relative abundance of each smaller mesocarnivore between study areas using a generalized linear model with a negative binomial distribution (we were unable to use a zero-inflated or mixed model due to the sparsity of our data). While other factors could affect species' relative abundance, a correlation between puma presence/absence and the relative abundance of smaller species would suggest an effect of pumas on their populations. We modeled the number of detection events per week by an interaction between species and study area to allow for comparisons of relative abundance between study areas for each species. We also included climate and habitat covariates (Table 3), which we *z*-score standardized, to account for seasonal and landscape variation in detections, and a lure covariate to account for the use of lures in Fort Hood. We tested model fit with the poisgof function in package epiDisplay (v. 3.5.0.2; Chongsuvivatwong, 2022). We used the package emmeans (v. 1.5.2-1; Russel et al., 2020) to directly compare mean weekly detections between study areas for each species and predicted detections per 100 trap nights from the model for each species in each study area using the predict function. Lure was held constant (no lure), and all other variables were held at *z*-score mean (0) for all predictions.

To determine if pumas and coyotes changed the temporal activity of mesocarnivores, we used a kernel density estimation procedure (Ridout & Linkie, 2009). We converted the time stamp of each detection to radians and fit a kernel density to this for each study area to create a distribution of activity over a 24-h period for each species. We then compared the activity distributions of mesocarnivores to those of coyotes in Fort Hood and pumas and coyotes in Santa Cruz using the compareAct function in package activity (v. 1.3.1; Rowcliffe, 2021). We further compared the activity of each species between study areas (e.g., coyotes in Fort Hood to coyotes in Santa Cruz) for those species that were present in both sites (coyote, bobcat, gray fox, raccoon, and striped skunk) to determine if their temporal activity changed in the presence of pumas. While this is correlational data and other factors may affect it, changes in temporal activity would suggest avoidance of pumas.

We further explored temporal avoidance of pumas and coyotes by the smaller mesocarnivores using avoidance-attraction ratios (Parsons et al., 2016). We measured the time between subsequent detections of each mesocarnivore when no larger carnivore (puma or coyote) passed between (T1) and when a larger carnivore passed between detections of the mesocarnivore (T2). We only considered occasions when either a puma or a coyote passed between mesocarnivore detections, never when both passed between to avoid complicating the

TABLE 3 Covariates included in multispecies occupancy models with description of what we measured, where and when data were accessed, which analysis they were included in, reason for inclusion, and their range of values for each site in our data.

				Value range	
Covariate	**Description and source**	**Analysis**	**Reason**	**Fort Hood**	**Santa Cruz**
Year	Year data were collected.	Occupancy	Included to account for possible variation between years.	2011, 2018, 2019	2015–2018
Distance to roads	Meters from camera trap to nearest paved road—2011, 2015, and 2018 US Census Bureau TIGER/Line database, accessed 22 April 2021, www.census.gov.	Occupancy	Roads represent a measure of human activity, and carnivores may avoid them (Lesmeister et al., 2015).	0.3–2105 m	0.05–1472 m
Distance to water	Meters from camera trap to nearest water body based on "open water" polygon in 2011 and 2016 NLCD Landcover Data, accessed 20 April 2021, www.mrlc.gov.	Occupancy	As water is a vital resource and required more frequently than food, carnivores are unlikely to be far from it (Lesmeister et al., 2015).	250–4060 m	91–6090 m
Terrain ruggedness index	Average percent difference in elevation between pixels: USGS 10 m Digital Elevation Model, accessed 24 April 2021, www.nationalmap.gov.	Occupancy	Increased ruggedness increases energetic costs, carnivores may select habitat with a lower cost.	0.6%–5.1%	0.9%–15%
Proportion forest	Proportion of area within a 250-m radius circle around camera that is forest—2011 and 2018 NLCD Landcover Data, accessed 20 April 2021, www.mrlc.gov.	Occupancy and relative abundance	Most of these species prefer forest habitat and may select areas with higher forest cover (Lesmeister et al., 2015).	0.2–1	0–1
Forest edge	Total length of forest edge within a 250-m radius circle around camera; 2011 and 2018 NLCD Landcover Data, accessed 20 April 2021, www.mrlc.gov.	Occupancy	Some species, such as coyotes, prefer edge habitat and may select for areas with more edge while others who prefer contiguous forest (bobcat) may select against (Lesmeister et al., 2015).	1575–4642 m	0–4292 m
Prey availability	Combined detections of deer (*Odocoileus* spp.), lagomorphs, and rodents for puma and coyote or just lagomorphs and rodents all other carnivores based on natural history per 100 trap nights (Appendix S2).	Occupancy	Relative abundance suggests an intensity of use by prey species at each camera that relates to intensity of use by carnivores in response (Parsons et al., 2019).	0–1677 det/100 tn	0–280 det/100 tn
Annual precip	Average centimeter of precipitation for entire study area each year (based on date of first to date of last camera each year). From nearest NOAA weather station accessed 27 April 2021, www.noaa.gov.	Occupancy	Large climatic differences between years, such as El Nino or La Nina could affect species occupancy.	30.25–59.16 cm	0.84–7.32 cm

(Continues)

TABLE 3 (Continued)

Covariate	Description and source	Analysis	Reason	Value range	
				Fort Hood	Santa Cruz
Max temp	Average maximum temperature (in degrees Celsius) for each 1-week capture occasion based on nearest NOAA weather station, accessed 27 April 2021, www.noaa.gov.	Occupancy (detection) and relative abundance	Maximum temperature can affect how active animals are (less active when it is hot) and thus how likely to be detected.	−3.30 to 37°C	13–37°C
Precip	Average centimeter of precipitation for each 1-week capture occasion based on the nearest NOAA weather station, accessed 27 April 2021, www.noaa.gov.	Occupancy (detection) and relative abundance	Carnivores may be less active while it is raining.	0–36 cm	0–8 cm
Lure	Attractants used at camera in Fort Hood for 2 of 3 years as part of separate study. Attractants not used in Santa Cruz.	Occupancy (detection) and relative abundance	Lures may attract carnivores and thus increase detections.	Sardines, fatty acid tablet, or no lure	N/A

Abbreviations: det/100tn, detections per 100 trap nights; N/A, not available; NLCD, National Land Cover Database.

model. We compared T1 and T2 for each mesocarnivore with pumas and with coyotes using Cox proportional hazard models to determine if the time between detections of a mesocarnivore was significantly increased by the passage of a larger carnivore in the middle (Parsons et al., 2016). This model predicts the likelihood of an event (the second passage of the mesocarnivore) based on the presence of a hazard (the passage of a larger carnivore in between). An increase in time between detections of a mesocarnivore with the passage of a larger carnivore between indicates an avoidance of the larger carnivore by the mesocarnivore.

RESULTS

In Fort Hood, we collected a total of 519,410 photographs over 16,698 trap nights (annual average = 5566 trap nights), resulting in 10,993 carnivore events (Table 2). Bobcats had the highest occupancy (0.93 ± 0.09), despite having the third lowest detections, followed closely by coyotes (0.91 ± 0.06) and raccoons (0.87 ± 0.09; Table 2). In Santa Cruz, we collected a total of 560,865 photographs over 34,021 trap nights (annual average = 8505 trap nights), resulting in 12,709 carnivore events. Bobcats had the highest occupancy (0.84 ± 0.03), followed by pumas (0.77 ± 0.04) and striped skunks (0.77 ± 0.03; Table 2).

Effects of pumas in Santa Cruz

In Santa Cruz, puma occupancy significantly increased with prey relative abundance and proportion of forest around cameras (Appendix S1: Table S1 and Appendix S2: Table S1). Puma's intensity of use of the Santa Cruz study areas was moderate (detection probability = 0.18 ± 0.01 SE). Both bobcats and gray foxes were significantly more likely to co-occur with pumas ($\beta = 1.09 \pm 0.42$ SE, $p = 0.01$ and $\beta = 0.90 \pm 0.34$ SE, $p = 0.01$, respectively), but no other species responded significantly to puma occupancy (Figure 2a).

All species had significantly different temporal activity from pumas in Santa Cruz based on our kernel density analysis ($p < 0.01$ for all; Figure 3). Coyotes had the largest difference in activity compared to pumas (0.23 ± 0.05) and showed more diurnal activity than pumas. Bobcats had the next largest difference in activity from pumas (0.18 ± 0.03) and were similarly more diurnal. In our avoidance-attraction ratio analyses, pumas significantly decreased the likelihood of a second detection of all mesocarnivores (i.e., the time between detections of a mesocarnivore significantly increased when a puma was detected between). Raccoons had the largest reduction in likelihood of a second detection (93%, $\beta = -2.69 \pm 1.12$ SE, $p = 0.02$) followed by striped skunks (71%, $\beta = -1.23 \pm 0.09$, $p < 0.01$), coyotes (69%, $\beta = -1.18 \pm 0.21$, $p < 0.01$), bobcats

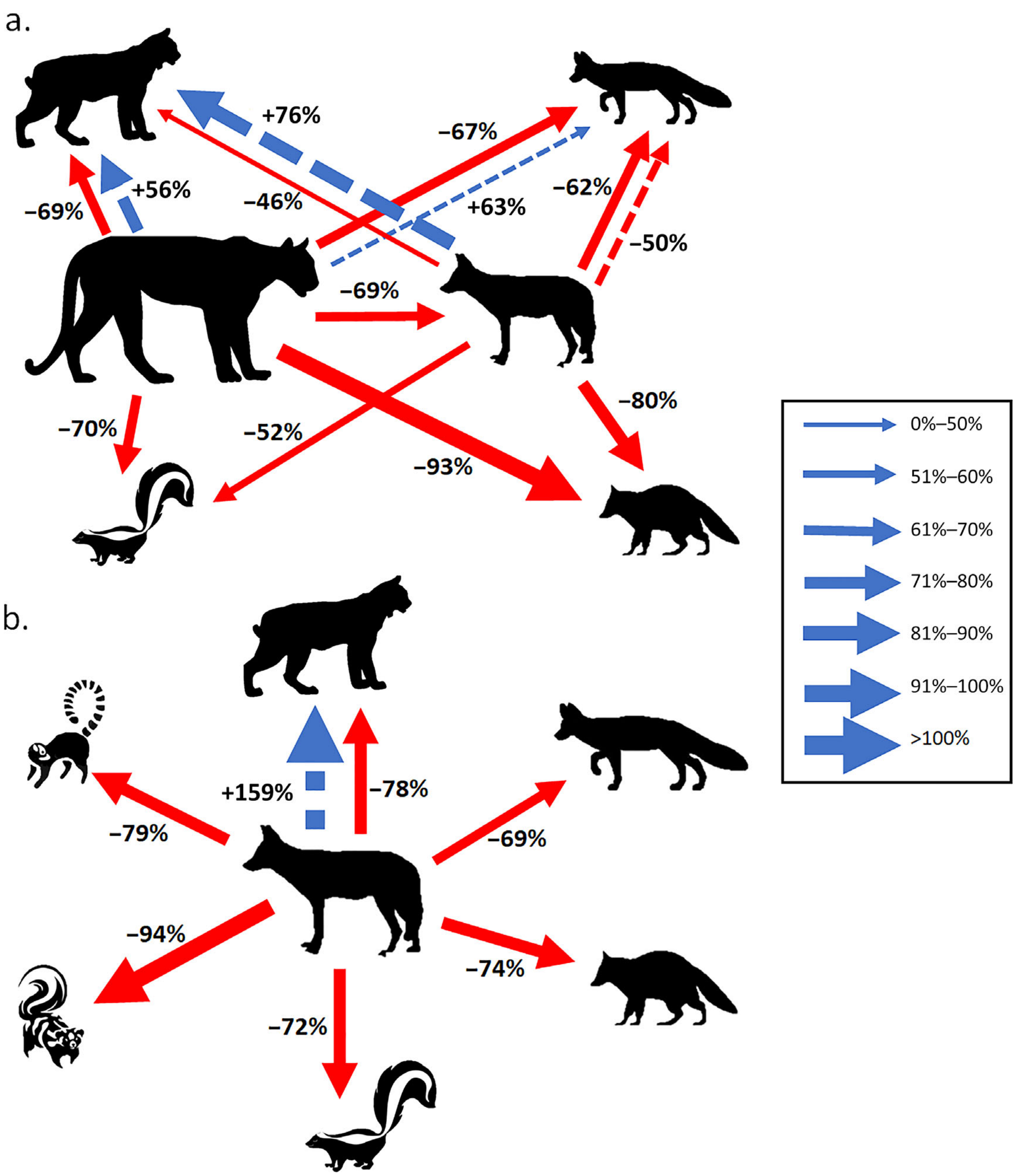

FIGURE 2 Significant spatial (dashed line) and fine-scale temporal (solid line) effects of pumas and coyotes on small mesocarnivores; bobcats, gray foxes, raccoons, and striped skunks in Santa Cruz (a) and the effects of coyotes on the same plus eastern spotted skunk and ringtail in Fort Hood (b). For the temporal effects, the number denotes the percent change in the likelihood of detecting the small mesocarnivore after a puma or coyote is detected. For the spatial effects, the number denotes the percent change in occupancy of the small mesocarnivore given the presence of a puma or coyote. Red represents a negative effect, blue a positive effect, and no arrow represents no significant effect, while the width of the arrow is associated with the strength of the effect.

(69%, $\beta = -1.18 \pm 0.07$, $p < 0.01$), and gray foxes (67%, $\beta = -1.11 \pm 0.06$, $p < 0.01$; Figure 2a).

Effects of coyotes in Santa Cruz

In Santa Cruz, coyotes were less likely to occur in forests, farther from water, and their occupancy varied with year (Appendix S1: Table S1). Bobcats were significantly more likely to co-occur with coyotes ($\beta = 1.60 \pm 0.61$ SE, $p = 0.01$), while gray foxes were significantly less likely to co-occur with coyotes ($\beta = -0.94 \pm 0.32$ SE, $p < 0.01$). No other mesocarnivores responded significantly to coyote occupancy (Figure 2a).

Based on our kernel density analysis, all species except bobcats ($p = 0.28$) had significantly different

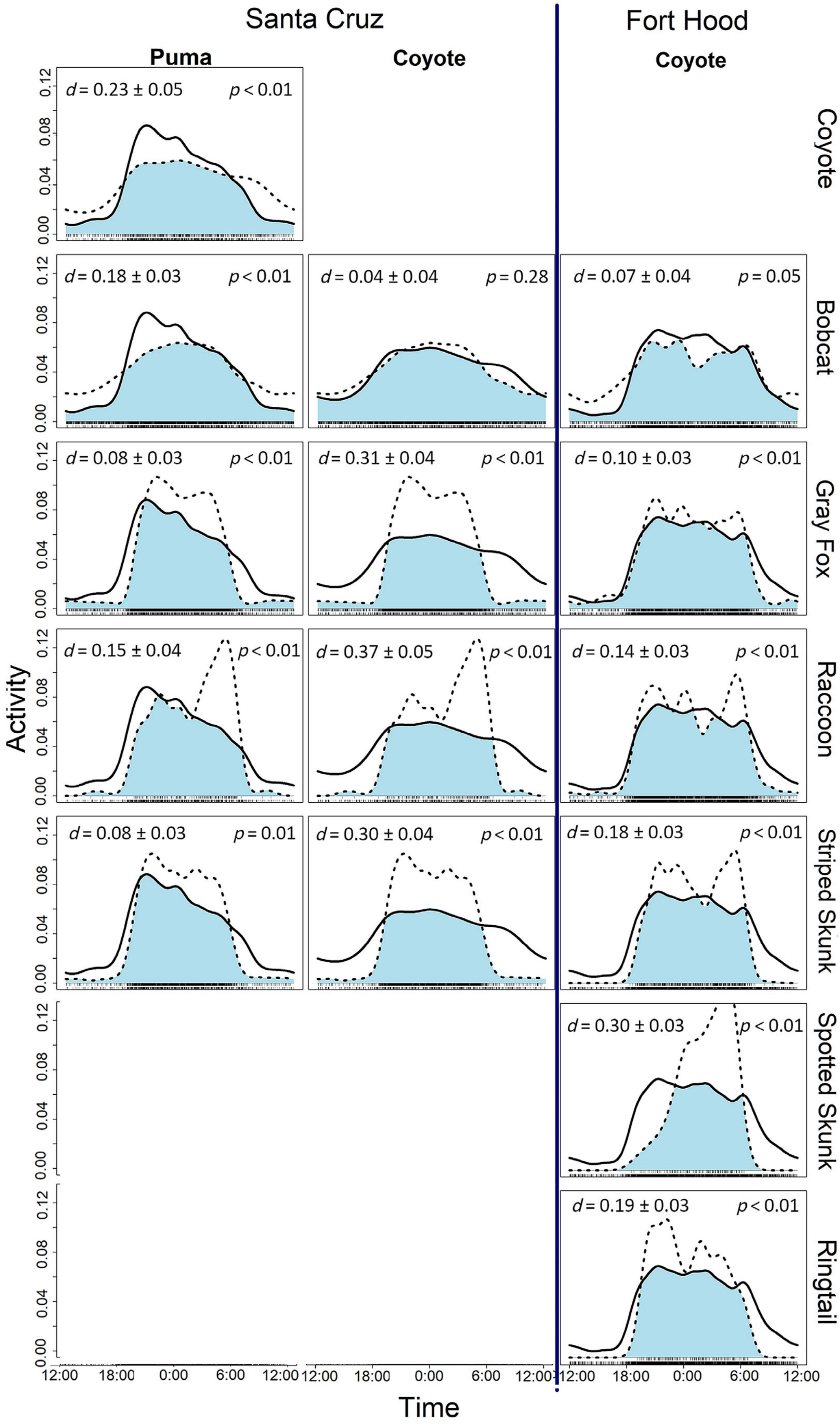

FIGURE 3 Legend on next page.

temporal activity than coyotes in Santa Cruz ($p < 0.01$ for all). Raccoons had the largest difference in activity (0.37 ± 0.05), followed by gray foxes (0.31 ± 0.04), and striped skunks (0.30 ± 0.10; Figure 3), and all showed more nocturnal activity than coyotes whose activity spread more evenly across nocturnal and diurnal periods. In our avoidance-attraction ratio analysis, coyotes had smaller effects on mesocarnivores than pumas but still significantly reduced the likelihood of a second mesocarnivore detection ($p < 0.01$ for all). Raccoons had the largest reduction (80%, $\beta = -1.62 \pm 0.54$) followed by gray foxes (62%, $\beta = -0.98 \pm 0.16$), striped skunks (52%, $\beta = -0.74 \pm 0.13$), and bobcats (46%, $\beta = -0.62 \pm 0.08$; Figure 2a).

Effects of coyotes in Fort Hood

In Fort Hood, coyote occupancy was only significantly affected by year (Appendix S1: Table S2). Bobcats were significantly more likely to co-occur with coyotes ($\beta = 1.83 \pm 0.71$ SE, $p = 0.01$), but no other mesocarnivore responded significantly to coyote occupancy (Figure 2b).

In Fort Hood, all species had significantly different daily temporal activity from coyotes based on our kernel density analysis ($p < 0.01$ for all except bobcat $p = 0.05$). Eastern spotted skunks had the largest difference (0.30 ± 0.03), followed by ringtails (0.19 ± 0.03) and striped skunks (0.18 ± 0.03), and all were primarily nocturnal, although peak activity varied (Figure 3). Based on the avoidance-attraction ratios, the probability of the second detection of all mesocarnivore species significantly decreased when a coyote was detected between ($p < 0.01$ for all), and by a larger degree than in Santa Cruz (Figure 2). Eastern spotted skunks had the largest reduction in likelihood of a second detection (94%, $\beta = -2.80 \pm 0.77$) followed by ringtails (79%, $\beta = -1.58 \pm 0.32$), bobcats (78%, $\beta = -1.54 \pm 0.12$), raccoons (74%, $\beta = -1.35 \pm 0.06$), striped skunks (72%, $\beta = -1.28 \pm 0.10$), and gray foxes (69%, $\beta = -1.18 \pm 0.07$; Figure 2b).

Comparison of Santa Cruz versus Fort Hood

Among species present in both study areas, intensity of use was significantly higher in Fort Hood than Santa Cruz for coyotes (detection probability in Fort Hood = 0.56, CI = 0.53–0.58 and in Santa Cruz = 0.20, CI = 0.18–0.23) and raccoons (Fort Hood = 0.49, CI = 0.47–0.51 and Santa Cruz = 0.12, CI = 0.10–0.15). Conversely, intensity of use was significantly higher in Santa Cruz than in Fort Hood for bobcats (detection probability in Santa Cruz = 0.38, CI = 0.37–0.40 and in Fort Hood = 0.28, CI = 0.25–0.31) and gray foxes (Santa Cruz = 0.53, CI = 0.51–0.55 and Fort Hood = 0.47, CI = 0.44–0.49; Figure 4). Coyote and raccoon relative abundance were also significantly higher in Fort Hood than in Santa Cruz (difference = 2.60 ± 0.08, $p < 0.01$; and difference = 3.52 ± 0.10, $p < 0.01$, respectively). Bobcat and gray fox relative abundance were significantly higher in Santa Cruz than in Fort Hood (difference = −0.44 ± 0.07, $p < 0.01$; and difference = −0.28 ± 0.06, $p < 0.01$, respectively; Figure 4). Our relative abundance model was a good fit for the data ($\chi^2 = 19{,}997$, df = 41,447, $p = 1$). Coyotes, gray foxes, and raccoons had significantly different daily temporal activity between Fort Hood and Santa Cruz. Coyotes exhibited the largest difference (0.14 ± 0.04, $p < 0.01$) with more nocturnal activity documented at Fort Hood, followed by raccoons (difference = 0.10 ± 0.04, $p = 0.01$) with more activity in early morning in Santa Cruz and gray foxes (difference = 0.07 ± 0.02, $p < 0.01$) who were more crepuscular in Fort Hood (Figure 3).

DISCUSSION

Apex predators have been extirpated throughout much of North America, leaving coyotes as the de facto apex predator in many ecosystems (Prugh et al., 2009). Although the effects of the losses of apex predators are well studied (Estes et al., 2011), it is still unclear if de facto apex predators, such as coyotes, fill the functional role of a true apex predator that has been extirpated. We compared two ecosystems with similar carnivore guilds, one with pumas and one without, to examine the role of pumas as an apex predator and coyotes in the absence of a true apex predator. While it is difficult to make direct comparisons in our study considering the large-scale differences between study areas, this inferential study is preferable to experimental removal studies where large numbers of carnivores are killed. Our analyses showed that puma occupancy was only affected by prey and habitat, as is expected of a carnivore at the top of the food chain, and

FIGURE 3 Graphs of daily temporal activity for large carnivores (figure top and solid line) and mesocarnivores (figure right and dashed line) with overlapping activity in blue. Activity is centered at midnight (0.00). Estimated difference in activity (*d*) is expressed with ± SE. Vertical blue line delineates break between Santa Cruz and Fort Hood.

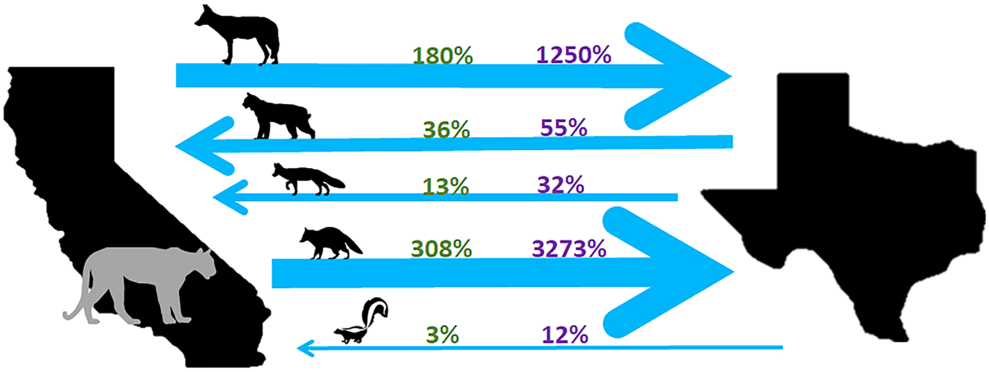

FIGURE 4 Percent difference in mesocarnivore site use intensity (green) and relative abundance (purple) between Santa Cruz, where pumas are present (left), and Fort Hood, where pumas are absent (right). Width of a line represents size of combined effects and direction of arrow indicates direction of effect. Mesocarnivores, from top to bottom: coyote, bobcat, gray fox, raccoon, and striped skunk. Values for striped skunk are not significant.

that pumas have structuring effects on the rest of the carnivore guild. We also found that coyotes seemed to partially fill the functional keystone role of an apex predator but showed more signs of mesopredator release and had weaker effects on mesocarnivores than pumas. Specifically, coyotes suppressed the populations of all but one other mesocarnivores and caused behavioral changes (e.g., temporal avoidance) in the absence of pumas, but they did not cause spatial avoidance and had smaller overall effects than pumas, highlighting the complexity of interactions within the carnivore community.

Our analyses confirmed our expectations and demonstrated, through correlation, the keystone role of pumas in Santa Cruz. Pumas appeared to suppress coyotes (their closest competitor) by reducing their relative abundance and intensity of site use (Figure 4), changing their daily temporal activity (Figure 3), and causing temporal avoidance (Figure 2a). Although other habitat or human factors between study areas may affect these as well, the stark difference suggests a direct effect of pumas on coyotes. As a result, smaller carnivores seem to have been released from competition with coyotes (Crooks & Soule, 1999; Levi & Wilmers, 2012; Prugh et al., 2009), as all of the smaller mesocarnivores (except raccoons, who also appeared to be negatively affected by pumas, likely due to direct predation; Allen et al., 2015) had increased relative abundance and intensity of site use in Santa Cruz, and either did not change their daily temporal activity or shifted it closer to that of pumas, demonstrating a potential trophic cascade (Levi & Wilmers, 2012; Newsome & Ripple, 2015; Wang et al., 2015). All species temporally avoided pumas at a finer scale (i.e., less likely to be detected at a camera after a puma was detected; Figure 2a), likely because pumas are a predation risk to most smaller species (Allen et al., 2015; Prugh & Sivy, 2020). Coyotes and raccoons, the only species suppressed by pumas in Santa Cruz, had a larger reduction in site use intensity and relative abundance between Santa Cruz and Fort Hood than any species suppressed by coyotes in Fort Hood, suggesting that pumas have a stronger suppressive effect than coyotes as apex predators. Although coyote avoidance of pumas did not show directly in our occupancy analysis, coyote occupancy was negatively associated with forests that pumas occupied. Coyotes frequently scavenge from puma kills (Allen et al., 2015; Prugh & Sivy, 2020), which can cause attraction at small scales (Sivy et al., 2017). Pumas are also known to suppress large prey populations (Ripple et al., 2014), change prey behavior (Donadio & Buskirk, 2016), and provide carrion to other species (Allen et al., 2015; Barry et al., 2019), completing their keystone role.

The role of coyotes in Fort Hood appeared to most closely match our hypothesis of mesopredator release and thus only partially fill the functional role of an apex predator in Fort Hood (Table 1), as they suppressed abundances of some mesocarnivores and caused immediate temporal avoidance; however, their effects were weaker than those of pumas. Three out of four mesocarnivores in Fort Hood had significantly lower relative abundance than in Santa Cruz (Figure 4), which may indicate suppression in Fort Hood where coyotes have been released and/or released in Santa Cruz where coyotes are suppressed by pumas, although other factors may affect this as well. This pattern of suppression is commonly observed with large canids in before-and-after studies when apex predators are lost (Brook et al., 2012; Kamler et al., 2003; Newsome & Ripple, 2015) and could be due to direct killing or reduced access to resources (Hall et al., 2021; Palomares & Caro, 1999). It is also possible that the higher number of mesocarnivore species in Fort Hood led to higher competition than in Santa Cruz, which could also affect species' relative abundance. All mesocarnivores were less likely to be detected after a coyote had passed a camera in both sites. In fact, three of the four showed higher avoidance in Fort Hood than in Santa Cruz, suggesting coyotes may have a stronger effect on all mesocarnivores in the absence of pumas, which is not what we would expect if they were filling the apex functional role. Conversely, raccoons had increased relative abundance and intensity of use in Fort Hood and exhibited less temporal avoidance of coyotes. Pumas and bobcats—which are more abundant in Santa Cruz—are known to kill raccoons (Allen et al., 2015), but coyotes do not seem to affect them (Chitwood et al., 2020), so raccoons may benefit from the release of coyotes, unlike the other small mesocarnivores. Some evidence suggests coyotes may also mediate prey behavior (Jones et al., 2016), but they are likely not as effective at this or suppressing populations as true apex predators (Prugh et al., 2009).

In contrast to pumas, the presence of coyotes was not associated with spatial avoidance in any mesocarnivore species and was related to a change in daily temporal activity of only one species. Only bobcats and gray foxes had a reduced intensity of site use in Fort Hood compared to Santa Cruz, partially supporting the hypothesis that coyotes fill the apex functional role; however, the difference between sites for these species was much smaller than the substantial change for coyotes between sites. Similarly, no mesocarnivores spatially avoided coyotes in Fort Hood, and bobcats were attracted to them in both sites, refuting this hypothesis. Coyotes and bobcats coexist across their range, although this can vary with habitat, and they may segregate diet where they overlap to avoid competition (Dyck et al., 2021), but if coyotes were a true apex predators, we would expect them to suppress their closest competitor. It is possible the other mesocarnivores use partitioning of habitat, diet, or temporal use to avoid competition (Lesmeister et al., 2015; Santos et al., 2019) with coyotes and thus do not need to avoid them spatially. In addition, all mesocarnivores, except bobcats in Santa Cruz, had significantly different temporal activity from coyotes at both sites, but only coyotes, raccoons, and gray foxes showed significantly different temporal activity between Fort Hood and Santa Cruz. Both raccoons and coyotes exhibited large differences in activity from pumas and may have changed their activity in Santa Cruz to avoid pumas (Figure 3). Gray fox activity differed more from that of coyotes than that of pumas, and so may have shifted their activity closer to that of pumas, possibly as protection from coyotes, who often kill foxes (Palomares & Caro, 1999). Gray foxes spatially avoided coyotes in Santa Cruz and were the only mesocarnivore to have offset temporal activity from coyotes in Fort Hood. Many studies have found such avoidance between canids (Hall et al., 2021; Kamler et al., 2003; Levi & Wilmers, 2012), and it is possible these effects are stronger within closely related species (i.e., taxonomic families; Prugh & Sivy, 2020) rather than being purely body size based. Taken together, these results partially support our hypotheses of what we would observe if coyotes acted as apex predators in Fort Hood, but they strongly support the mesopredator release hypothesis.

Other environmental or anthropogenic factors may affect the spatial and temporal habitat use and abundance of carnivores as well. Human disturbance and habitat fragmentation, which are more prevalent in Fort Hood, can force less tolerant species into remaining natural areas, thereby increasing interactions among carnivores (Parsons et al., 2019). Many carnivores also shift to more nocturnal activity in high human-use areas (Gaynor et al., 2018). Fort Hood is subject to short durations of intense human activity due to military training and Santa Cruz is subject to lower intensity but more frequent disturbance due to recreation, both of which could affect carnivore activity. Unfortunately, camera traps do not allow us to accurately measure human activity, especially on a military base where people are frequently off-trail, so we were not able to account for this in our models. Fort Hood also has smaller forest patches than Santa Cruz, but by focusing cameras in forests in both study areas and including camera-level habitat variables in our, we accounted for this difference in part. Larger-scale habitat variables may be required to fully account for the differences between our study areas, but we were unable to include these due to our initial camera setup. We were able to include annual precipitation in our models to account for large-scale climate variations such as El Niño, and it only affected the occupancy of striped skunks in Santa Cruz. Interactions among carnivores may also differ seasonally as resource (e.g., prey) availability changes (Petersen et al., 2019), and competition is generally higher when resources are scarcer (Dyck et al., 2021). Adding prey abundance, as we did in our occupancy analysis, or dietary analyses into a study can provide a fuller picture of competition between carnivores (Dyck et al., 2021).

It is also possible that differences in methods between our study areas, such as camera spacing and using lures in one area but not the other, could have biased our results. However, we accounted for the lure in our models, and it had no effect on relative abundance and only affected detections in our occupancy model of bobcats and eastern spotted skunks. We based all our predictions on no lure, so this should not have affected our results. Closer spacing of cameras in Fort Hood compared to Santa Cruz may have artificially inflated detections of carnivores with larger home ranges in Fort Hood as individuals could have been detected by multiple cameras. It is possible this partially accounts for the high detections of coyotes in Fort Hood; however, it is unlikely to cause as large of a difference as we observed. Further, coyotes are known to reduce their home range size in areas of high human density (Farmer & Allen, 2019), which may have reduced this effect. Three of the smaller mesocarnivores had higher detections in Santa Cruz, meaning if detections were artificially high in Fort Hood, it only strengthened our results showing the effects of apex predators. While large-scale before-and-after carnivore removal studies may provide more direct conclusions, they are often unrealistic due to ethical and logistical restraints. In the absence of such data, comparison studies such as ours can provide valuable insight into the role of large carnivores and possible effects of their absence.

Few studies have examined the loss of apex predators in the context of the full carnivore community, but interactions between carnivores and their functional roles in the ecosystem are complex (Dyck et al., 2021) and best understood in such a context (Prugh et al., 2009). Our results, while correlational, suggest that coyotes may fill some capacities as a de facto apex predator with some species, but their role more closely fits that of mesopredator release than a true apex predator. Coyotes have weak suppressive effects on their close competitors and prey, making them ineffective as keystone and umbrella species. Further, due to their tolerance of humans, opportunistic diet, and fast reproductive cycles, they may be more likely to cause conflict with humans and lead to higher economic costs (Prugh et al., 2009), meaning they are a poor flagship species and unlikely to garner strong support for conservation. Future before-and-after studies utilizing large carnivore reintroductions could provide further insight into the role of dominant mesocarnivores in structuring the carnivore community. It seems that coyotes and likely other top mesocarnivores cannot fully replace true apex predators, and the restructuring of the carnivore guild when an apex predator is lost may have important implications for biodiversity and human health (Levi & Wilmers, 2012).

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CONFLICT OF INTEREST

No authors have a conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data (Avrin et al., 2022) are available from the Illinois Data Bank: https://doi.org/10.13012/B2IDB-0980888_V1.

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SUPPORTING INFORMATION

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

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