

ARTICLE

Spatiotemporal overlap with invasive wild pigs (*Sus scrofa*) varies by species and season in a temperate ecosystem

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Abstract

Wild pigs (*Sus scrofa*), which are invasive in many regions globally, can alter ecosystems and compete with native species through interference competition and resource exploitation. Wild pig impacts on other species may increase with greater niche overlap, which could vary over time based on environmental conditions, resource availability, or biological traits like diet, especially as seasonal variation in wild pig diet has been widely documented. A limited number of studies have assessed spatial or temporal overlap between native species and invasive wild pigs, with only a handful simultaneously assessing overlap in these niche dimensions. We investigated the potential for interspecific interactions involving invasive wild pigs in the Piedmont region of South Carolina, USA, by examining seasonal spatiotemporal overlap with other wildlife using N-mixture models and diel activity overlap analyses. Site use by white-tailed deer (*Odocoileus virginianus*) and coyote (*Canis latrans*) was negatively associated with wild pig activity in the fall, when the species had high diel activity overlap, indicating spatial partitioning could reduce interference competition with wild pigs in this season. Conversely, white-tailed deer site use was positively associated with wild pig activity in the winter, suggesting higher spatial overlap may be necessary if resources are limited. Site use by bobcat (*Lynx rufus*) and nine-banded armadillo (*Dasypus novemcinctus*) in the spring, along with raccoon (*Procyon lotor*) and wild turkey (*Meleagris gallopavo*) site use in the summer, was positively associated with wild pig activity. With the exception of diurnal wild turkey, diel activity overlap between these species and wild pigs was high, although temporal partitioning could have occurred at finer spatiotemporal scales than we examined. Our results collectively emphasize the importance of accounting for seasonal spatial and temporal responses by individual species to invasive wild pigs, with special consideration given to species in seasons where high niche overlap with wild pigs is anticipated.

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KEYWORDS

competition, diel activity, interspecific interactions, N-mixture, partitioning, resource exploitation, spatial, suiform, temporal, ungulate

INTRODUCTION

Wild pigs (*Sus scrofa*), which are ungulates capable of altering abiotic, biotic, and structural components of ecosystems, may impact other species through various means. Aided by the ability of a single female to produce up to 20 piglets in a year (Bevins et al., 2014) and their propensity to form territorial social groups (Gabor et al., 1999; Kilgo et al., 2021; Sparklin et al., 2009), wild pigs can reduce the abilities of other animals to obtain important resources through aggressive interference competition (Osugi et al., 2019; Taylor & Hellgren, 1997). Wild pigs can also indirectly compete with other species through resource exploitation, either by destroying habitat with their rooting behavior or consuming shared resources (Singer et al., 1984; Sweitzer & Van Vuren, 2002; Yarrow, 1987). While their diet is dominated by plant matter, wild pigs also scavenge carrion, consume invertebrates and small vertebrates while rooting (Ballari & Barrios-García, 2014), and depredate bird (Sanders et al., 2020) and reptile (Engeman et al., 2016) nests, all of which can reduce food resources or survival of other animals. This dietary plasticity likely aids the persistence of wild pigs outside of their native range in Eurasia and northern Africa (Ballari & Barrios-García, 2014). Present on every continent except Antarctica (Long, 2003) and predicted to further increase their range through population growth (Lewis et al., 2017), more research is needed on wild pig resource selection and native species responses to invasive wild pigs.

The potential for interspecific competition due to niche overlap can change across spatiotemporal scales based on the resource selection of the species involved (Crombie, 1947). Animals can be displaced by both direct and indirect competition with wild pigs (Barrios-García & Ballari, 2012; McDonough et al., 2022), or may actively reduce spatiotemporal overlap with wild pigs to avoid competition (Garabedian et al., 2023; Perez Carusi et al., 2017). Examining shared space use between invasive wild pigs and other wildlife is therefore a key step in identifying where competition may occur or what strategies animals adopt to reduce competition. Prior research found that species richness in the Mississippi Alluvial Valley, USA, was 26% lower in forest fragments with wild pigs than fragments without wild pigs (Ivey et al., 2019). Likewise, species richness in the Brazilian Atlantic Forest was lower at sites occupied by wild pigs than sites unoccupied by them (Hegel et al., 2019). Sites with wild pigs also had

lower species occurrence and occupancy probability decreased for several species, although it increased for others (Hegel et al., 2019). In coastal Argentina, endangered pampas deer (*Ozotoceros bezoarticus*) appeared to avoid wild pigs at the landscape scale. Where they did overlap spatially, pampas deer increased vigilance and displayed alarm reactions when in close proximity to wild pigs, but fed and rested more when farther away (Perez Carusi et al., 2017). Collared peccaries (*Pecari tajacu*) and wild pigs in Texas, USA, had higher spatial overlap at the home range scale than the microhabitat scale, suggesting habitat partitioning within shared home ranges can compensate for overlap in temporal activity and diet (Gabor et al., 2001). Collectively, it is evident that responses to wild pigs vary by species and context, so there is a need for more studies that simultaneously examine the resource selection of multiple sympatric species within ecosystems that could be impacted by wild pigs.

While spatial partitioning is important to examine, temporal partitioning can also reduce interference competition between species by affording nonsynchronous spatial overlap (Schoener, 1974). Species can adjust their temporal activity patterns across daily, seasonal, and annual scales, reflecting biological needs, environmental conditions, and changes in resource availability. In Japan, wild pig presence impacted the feeding behavior of badgers (*Meles meles*) and raccoon dogs (*Nyctereutes procyonoides*) under cherry trees: badgers partially shifted the time of day when they fed and reduced feeding time per visit, while raccoon dogs shifted both temporally and spatially, feeding at different times and at trees infrequently visited by wild pigs (Osugi et al., 2019). In the Brazilian Pantanal, white-lipped peccaries (*Tayassu pecari*) altered their daily foraging time to limit interactions with wild pigs, but collared peccaries shifted to overlapping with them more, likely in avoidance of white-lipped peccaries (Galetti et al., 2015). In Texas, collared peccaries and wild pigs partitioned resources across space, time, and diet, with higher seasonal overlap in one niche dimension balanced by lower overlap in another (Ilse & Hellgren, 1995). Few other studies have simultaneously examined spatial and temporal overlap with wild pigs outside of their native range.

Spatiotemporal overlap could be mediated by food availability, so given that wild pig diet varies seasonally, the potential for competition between wild pigs and other species could change throughout the year. Across their

range in the United States, invasive wild pigs have been documented consuming grasses, forbs, fruits, underground plant parts, invertebrates, and vertebrates in all seasons (Baber & Coblenz, 1987; Barrett, 1978; Taylor & Hellgren, 1997; Wilcox & Van Vuren, 2009; Wood & Roark, 1980). Although geographical variation exists, grasses and forbs tend to be the greatest component in spring and early summer (Barrett, 1978; Taylor & Hellgren, 1997; Wood & Roark, 1980), so indirect competition with small herbivores and their predators may be greatest then. When seasonally available, soft and hard mast tend to dominate the diet of wild pigs (Baber & Coblenz, 1987; Henry & Conley, 1972; Wood & Roark, 1980; Yarrow, 1987), so indirect and direct competition with herbivores and omnivores that consume soft or hard mast might peak during the summer through winter months. When aboveground food is scarcer during late fall through winter, underground plant parts and animal matter can play larger roles in wild pig diet (Ballari & Barrios-García, 2014; Barrett, 1978; Taylor & Hellgren, 1997), so competition with certain omnivores may be higher during this time. Examining spatial and temporal overlap between wild pigs and other species on a seasonal basis could more thoroughly identify where competition may occur or is already occurring.

Our objective was to examine whether spatial and temporal partitioning could mediate potential interactions between wild pigs and other species throughout the year in a forested temperate ecosystem. We hypothesized that spatial overlap between wild pigs and other species is influenced by wild pig activity (Gabor et al., 2001; Melberg, 2012), predicting that species site use increases as wild pig activity decreases. We further hypothesized that spatial overlap varies seasonally, reflecting changes in local environmental conditions and resource availability (Gabor et al., 2001; Ilse & Hellgren, 1995), and predicted that spatial overlap between a given species and wild pigs is greater in seasons with higher dietary overlap. Specifically, we predicted that in our study area (1) overlap with small herbivores (diet predominantly composed of plant material; Kissling et al., 2014) is greatest in the spring, reflecting the early growth of grasses and forbs (Kilburg et al., 2014), (2) overlap with large herbivores is greatest in the fall, reflecting hard mast availability (Scarlett, 2004; Schrecengost et al., 2008), (3) overlap with a hypercarnivore (diet almost entirely composed of vertebrates; Echarri et al., 2017; Van Valkenburgh, 1991) is greatest in the spring, reflecting vegetation consumption by small herbivores and wild pigs, (4) overlap with large mesocarnivores (diet substantially composed of vertebrates; Echarri et al., 2017) is greatest in the spring and summer, reflecting vegetation consumption by small herbivores and wild pigs in the spring and the regional availability of soft mast in summer

(Cherry et al., 2016; Schrecengost et al., 2008), (5) overlap with small mesocarnivores is greatest in the summer and fall, reflecting soft and hard mast availability, and (6) overlap with omnivores (diet composed of animal and plant material; Kissling et al., 2014) is greatest in the fall, reflecting hard mast availability. We also hypothesized that spatial overlap is mediated by temporal partitioning (Carothers & Jaksić, 1984; Galetti et al., 2015; Osugi et al., 2019; Schoener, 1974) and that temporal overlap varies with seasonal changes in environmental conditions and resource availability. We predicted that wild pigs and other animals partition diel activity where they spatially overlap and that temporal overlap is greater in seasons with lower spatial overlap than seasons with higher spatial overlap. By providing insight into the potential for competition between wild pigs and other species, results from this study can inform invasive wild pig management and guide future studies on interspecific interactions within invaded ecosystems.

METHODS

Study area

Our study occurred within approximately 6100 ha of nearly contiguous temperate forest in the Piedmont of South Carolina, USA. This physiographic region is characterized by gently rolling terrain between the Blue Ridge and Coastal Plain provinces. The study area ranges in elevation from approximately 120–180 m and average monthly temperature for the area ranges from 6.2 to 27.2°C, with an annual mean of 16.9°C. The climate is subtropical, with an average of 119.5 cm of precipitation annually. Red clay is the primary soil type, followed by sandy loam. Much of the landscape was historically savanna, which was grazed by American bison (*Bison bison*) and inhabited and likely managed by Native Americans, potentially including the Cherokee, Yuchi, Shawnee, Chickasaw, Apalachee, Yamasee, and Westo (Cobb & Depratter, 2012; Gallay, 2002; “Native Land Digital,” accessed April 3, 2022, <https://native-land.ca>). Savanna conversion to cotton (*Gossypium* spp.) and tobacco (*Nicotiana tabacum*) began in the late 1700s and these crops were grown and harvested by slaves (Edmonds, 1999). The area today mainly consists of planted loblolly pine (*Pinus taeda*) stands in various stages of ecological succession, with management practices including thinning, clear-cutting, and prescribed burning. Pines are interspersed in areas with hardwoods, especially hickory (*Carya* spp.), white oak (*Quercus alba*), and southern red oak (*Q. falcata*). Notable soft mast includes persimmon (*Diospyros virginiana*), blackberry (*Rubus alleghensis*), and muscadine (*Vitis rotundifolia*).

The occurrence of fields managed for small game species and food plots planted for white-tailed deer (*Odocoileus virginianus*, hereafter “deer”) is associated with hunting in the study area. Deer archery hunting season began mid-September and gun season began approximately mid-October, with both going through December. Wild turkey (*Meleagris gallopavo*, hereafter “turkey”) hunting also occurred from the beginning of April through mid-May. Wild pigs were recorded in McCormick County before 2005 and continue to spread to new areas, despite 10 years of population control in the county. Abundance is nonetheless lower in McCormick County than nearby counties and, based on wildlife camera surveys, density appears lower in our study area relative to other areas in South Carolina along the nearby Savannah River (Garabedian et al., 2023). Opportunistically shot on sight or captured in box traps, approximately 135 wild pigs were removed from our study area over three years. The coyote (*Canis latrans*) is also a relatively novel species in our study area, with the first record in South Carolina occurring in 1978 and the first record near our study area occurring in 1982. The nine-banded armadillo (*Dasypus novemcinctus*, hereafter “armadillo”) has also expanded from its native range into the area.

Data collection

We used a grid sampling design to survey for wild pigs and other species with wildlife cameras across our study area (Appendix S1: Figure S1). We first created a grid of 1-km² cells in ArcGIS 10.6 (ESRI, Redlands, CA, USA) with the Create Fishnet tool, then deployed a Bushnell Trophy Cam HD Aggressor No Glow camera (Bushnell Corporation, Overland Park, KS, USA) as close to the center of each cell as possible on an unpaved road. In total, we deployed 93 cameras approximately 50–80 cm off the ground, attached to a tree or t-post, and angled cameras approximately 45° down a single unpaved road or aimed them at an intersection. We set infrared sensors to the finest detection window possible, capturing one photo every 0.6 s until detection ceased. Our survey periods were two weeks in winter, spring, summer, and fall 2020 (the first 14 days of February, May, August, and November, respectively).

Over the course of our study, we documented several seasonal vegetation characteristics at each camera site that we predicted would influence our ability to detect animal use of a site. We recorded the primary vegetation class (nonforested, pine forest, hardwood forest, or mixed vegetation) within 50 m. We estimated the average distance at which individual cameras could detect subjects without vegetative obstruction by placing a rangefinder

over each camera and recording the distance in meters at five designated angles that were later averaged and capped at a maximum distance based on camera model specifications. We estimated understory density with a vegetation profile board (Nudds, 1977), placing it in line with the camera 10 m from each road edge and viewing it from 10 m away at 1-m height along three bearings (0, 120, and 240°). We also took overstory density measurements at these locations with a concave densiometer. We averaged the six measurements for each vegetation index to achieve a single understory and overstory value for each site.

We also obtained several site-specific and sampling occasion characteristics remotely. We used the “rgee” package (Aybar et al., 2020) in R to calculate average enhanced vegetation index (EVI) within 150-, 250-, and 500-m buffers for each survey period (Didan, 2015). EVI is derived from the spectral bands reflected by leaves, with its formula correcting for atmospheric effects, radiant transfer through canopy, and soil reflectance (Huete et al., 2002). EVI can be sensitive to aspects of canopy structure (Huete et al., 2002) and can be linked to aspects of animal ecology (Bårdsen & Tveraa, 2012; Gigliotti et al., 2020; Pettorelli et al., 2011; Requena-Mullor et al., 2014). We used site-specific forestry records to account for recent prescribed burns, calculating the number of days since the last known timber stand burn within 150-, 250-, and 500-m buffers. When there were no records of a recent burn within the buffers, we assigned a conservative date approximating the start of our presence in the study area to ensure we did not overestimate the time since an area was burned. We used the breaklines data from the South Carolina Department of Natural Resources LiDAR Hydrolines database and the Statewide Highways data from the South Carolina Department of Transportation to calculate distance to nearest water feature (in meters) and distance to nearest paved road (in meters) with the Near tool in ArcGIS Pro 2.8.6 (ESRI, Redlands, CA, USA). We obtained daily precipitation (in millimeters) and daily high temperature (in degrees Celsius) records for the closest weather station (McCormick; GHCNd: USC00385660) from the National Centers for Environmental Information. We also used the “suncalc” package in R to calculate daily moon phase, where a value of 0 represents new moon, 0.5 represents full moon, and 1 represents waning crescent (Thieurmél & Elmarhraoui, 2019). All R analyses were conducted in version 4.1.1 (R Core Team, 2021).

Spatial analysis

We fit N-mixture models following the parameterization of Royle (2004) to examine seasonal spatial overlap between

wild pigs and other wildlife. We specifically used the Poisson latent abundance distribution to estimate the effects of wild pig activity and other factors on spatially replicated daily count data for a variety of vertebrates in our study area (Fiske & Chandler, 2011; Royle, 2004). Conditional two-species occupancy models (e.g., Richmond et al., 2010) or multispecies occupancy models (e.g., Rota et al., 2016) could also increase understanding of spatial associations between species, but preliminary analyses indicated that wild pig detections were too low in our study area for such models to perform well. We classified photographs according to vertebrate species with digiKam (digiKam Team, 2019) and Timelapse2 (Greenberg et al., 2019) and sampled daily count data from cameras that were active for at least three consecutive nights during a survey period. We compiled species detection histories with sampling occasions of daily intervals using the “camtrapR” package (Niedballa et al., 2016). We considered photographic detections of the same species separated by at least 30 min to be independent detection events, which we then tallied within each 24-h sampling occasion. We additionally compiled seasonal histories combining human and vehicle detections per sampling occasion to serve as a metric for daily human activity at each site. We calculated average coyote (the largest predator in our system) detections per sampling occasion to serve as a metric for predation risk and average wild pig detections per sampling occasion to serve as a metric for potential interspecific competition. We also calculated average deer detections per sampling occasion for inclusion in the coyote and wild pig analyses. We restricted our overlap analyses to species photographed at a minimum of three sites in all four seasons.

We developed a set of six a priori detection models containing a null model and five univariate models representing alternative hypotheses concerning the effects of environmental factors (moon phase, precipitation, and temperature) and site characteristics (human activity and camera detection distance) on detection probability. We then developed species-specific sets of 14 a priori abundance models containing a null model, a global model, and 12 models representing alternative hypotheses concerning the effects of local vegetation characteristics, landscape features, and interspecific interactions on expected abundance (Table 1). We screened covariates for collinearity using nonparametric Spearman’s rank correlation with a cutoff of $r = |0.7|$ (Dormann et al., 2013) and variance inflation factor (VIF) with a cutoff of $VIF = 3$ (Zuur et al., 2010). These tests produced values below the predetermined cutoffs, with one exception: moon phase and daily high temperature were positively correlated during our fall survey period. We retained both covariates in the first step of our fall analyses, but in following steps we only included the covariate with the best fit.

TABLE 1 A priori hypotheses and candidate N-mixture models for evaluating species site use (λ) during each season in 2020 near McCormick, South Carolina, USA.

A priori hypothesis	Model
Local vegetation characteristics	
1. Vegetation type	$\beta_0 + \beta_1(\text{veg}) + p$
2. Understory density and overstory density	$\beta_0 + \beta_1(\text{under}) + \beta_2(\text{over}) + p$
Landscape features	
3. Enhanced vegetation index (EVI)	$\beta_0 + \beta_1(\text{evi}) + p$
4. Days since last burn	$\beta_0 + \beta_1(\text{burn}) + p$
5. EVI and days since last burn	$\beta_0 + \beta_1(\text{evi}) + \beta_2(\text{burn}) + p$
6. Distance to nearest water feature	$\beta_0 + \beta_1(\text{water}) + p$
7. Distance to nearest paved road	$\beta_0 + \beta_1(\text{paved}) + p$
Interspecific interactions	
8. Wild pig activity	$\beta_0 + \beta_1(\text{pig}) + p$
9. Coyote activity	$\beta_0 + \beta_1(\text{coy}) + p$
Local vegetation characteristics, landscape features, and interspecific interactions	
10. Understory density, EVI, and wild pig activity	$\beta_0 + \beta_1(\text{under}) + \beta_2(\text{evi}) + \beta_3(\text{pig}) + p$
11. Overstory density, days since last burn, and coyote activity	$\beta_0 + \beta_1(\text{over}) + \beta_2(\text{burn}) + \beta_3(\text{coy}) + p$
12. Understory density, overstory density, distance to water, distance to paved road, wild pig activity, and coyote activity	$\beta_0 + \beta_1(\text{under}) + \beta_2(\text{over}) + \beta_3(\text{water}) + \beta_4(\text{paved}) + \beta_5(\text{pig}) + \beta_6(\text{coy}) + p$

Note: Wild pig activity was not included in wild pig analyses and coyote activity was not included in coyote analyses. Deer activity replaced all occurrences of wild pig activity in the wild pig models, replaced coyote activity in the 9th and 12th coyote models, and was added to the 10th coyote model. Detection covariates were determined from detection probability (p) model selection results. Null and global models are not shown.

All continuous covariates were centered and scaled to mean = 0 and standard error = 1 to facilitate comparison of their effects.

Our N-mixture analyses were conducted in the “unmarked” package (Fiske & Chandler, 2011) in three steps following an information theoretic approach. We first evaluated the effects of our detection covariates on detection probability (p) while holding expected abundance (λ) constant across all camera sites. We used the “MuMIn” package (Bartoń, 2020) for model selection based on the Akaike information criterion (Akaike, 1974) adjusted for small sample sizes

(AIC_c; Hurvich & Tsai, 1989) to examine the relative importance of the six models and considered those with $\Delta\text{AIC}_c < 2$ and more weight than the null model to be competitive (Burnham & Anderson, 2002). When the null model was the top model, we held detection probability constant across all camera sites in subsequent analyses. In the second modeling step, we included all covariates from the top detection models in N-mixture models to determine the most suitable buffer size (150, 250, and 500 m) at which to examine the effects of EVI and days since last burn on expected abundance. We once again ranked models according to ΔAIC_c and the buffer size with the most weight was included in the final step, along with the most suitable detection covariates from the first step. In the third step, we ran the N-mixture models from our candidate sets of 14 models (Table 1) and ranked them according to ΔAIC_c , once again considering models with $\Delta\text{AIC}_c < 2$ and more weight than the null model to be competitive. In each of the three steps we omitted models from model selection that produced errors or failed to converge. We conducted all analyses in R version 4.1.1 (R Core Team, 2021).

We relaxed the assumption that sampling units were closed to changes in abundance during the survey period because the home ranges of wild pigs, deer, and some carnivores most likely encompassed several camera sites. We interpreted detection probability (hereafter “detection”) as the probability a species was both present and detected (MacKenzie et al., 2004) and interpreted expected abundance as predicted intensity of site use (Gigliotti et al., 2022; hereafter “site use”). We assessed the significance of covariate effects with 95% confidence intervals (CIs) and considered intervals not overlapping zero an indication of statistical significance. If a covariate occurred in multiple top models, we assessed its significance with the highest ranked model it occurred in. To evaluate support for our prediction that spatial overlap between a species and wild pigs is greater in seasons with high dietary overlap, we assigned each species to a general diet category: rabbits (*Sylvilagus floridanus* and possibly *S. aquaticus*) as small herbivore (Carter et al., 2023; Kissling et al., 2014), deer as large herbivore (Johnson et al., 1995; Kissling et al., 2014; McShea & Schwede, 1993), bobcat (*Lynx rufus*) as hypercarnivore (Neale & Sacks, 2001; Thornton et al., 2004), coyote as large mesocarnivore (Jensen et al., 2022), gray fox (*Urocyon cinereoargenteus*; Neale & Sacks, 2001; Wood et al., 1958) and raccoon (*Procyon lotor*; Melville et al., 2015; Rulison et al., 2012) as small mesocarnivore, and gray squirrel (*Sciurus carolinensis*; McShea & Schwede, 1993; Shealer et al., 1999; Steele et al., 1996), armadillo (Sikes et al., 1990; Whitaker et al., 2012), turkey (Dalke et al., 1942; Glover & Bailey, 1949), and wild pig (Kissling et al., 2014)

as omnivore. We were unable to examine overlap between wild pigs and red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginiana*), and fox squirrel (*S. niger*) due to our sample size criteria.

Temporal analysis

We investigated temporal partitioning between wild pigs and other species by examining overlap in their diel activity patterns during each seasonal survey period. Using the kernel density estimation developed by Ridout and Linkie (2009), we first described the diel activity distribution of each species that was included in spatial analyses. We considered photographic detections of the same species separated by at least 30 min to be independent samples of the underlying continuous activity of that species. We converted the vector of detection times into radians and estimated activity over 24 h as a probability density function (Ridout & Linkie, 2009) with the “overlap” package (Meredith & Ridout, 2018) in R version 4.1.1 (R Core Team, 2021). We then examined temporal overlap between wild pigs and each species by overlaying their estimated activity patterns. This yielded the coefficient of overlap (Δ), which ranges from 0 (no overlap in activity) to 1 (complete overlap in activity). We used the $\hat{\Delta}_1$ estimator in all pairings because wild pigs had less than 50 detections each season. We obtained CIs with 10,000 smoothed bootstrap samples (Meredith & Ridout, 2018) and considered a lack of overlap between season CIs an indication of statistical significance.

RESULTS

Spatial overlap

We used data from 79 cameras active in winter, 78 cameras in spring, 88 cameras in summer, and 81 cameras in fall. We had a total of 1106 trap nights in winter, 1040 in spring, 1198 in summer, and 1132 in fall. Wild pigs were detected at 12.66% of active camera sites in winter, 15.38% in spring, 25.00% in summer, and 24.69% in fall (Appendix S1: Table S1). Deer and coyotes were the species most frequently detected at camera sites: deer were detected at 94.32%–96.30% of sites across seasons and coyotes were detected at 71.60%–77.22% of sites across seasons (Appendix S1: Table S1). Species site detection was less than 70% across seasons for rabbit (42.05%–59.49%), bobcat (39.77%–43.21%), red fox (0%–2.47%), gray fox (2.27%–30.86%), raccoon (30.77%–48.15%), striped skunk (0%–6.33%), Virginia opossum (2.56%–3.80%), fox squirrel

(1.14%–8.97%), gray squirrel (17.72%–26.92%), armadillo (12.66%–32.95%), and turkey (31.82%–65.38%; Appendix S1: Table S1).

The top covariates affecting detection (Table 2) and site use (Figure 1; Appendix S1: Table S2) varied by season for each species, with only some covariates having statistically significant effects. Rabbit detection was negatively affected by precipitation, average camera detection distance, and daily high temperature (Table 2). Deer detection was positively affected by camera detection distance and moon phase, but negatively affected by precipitation and temperature (Table 2). Bobcat detection increased with increasing moon phase and human activity but was negatively affected by camera detection distance (Table 2). Coyote detection was positively associated with moon phase and precipitation (Table 2). Daily high temperature negatively affected both gray fox and gray squirrel detection in the fall, whereas it positively affected armadillo detection in this season (Table 2). Precipitation had a negative effect on squirrel detection in the winter, but a positive effect in the spring (Table 2). Raccoon detection increased with moon phase and decreased with precipitation (Table 2). Turkey detection increased with camera detection distance in the winter (Table 2). Wild pig detection was positively affected by moon phase, camera detection distance, and human activity (Table 2).

Rabbit site use increased with understory density in both the winter and spring, along with EVI within 150 m

in the winter and coyote activity in the spring (Figure 1). Rabbit site use increased with time since last burn within 250 m in the summer, while site use in the fall increased with overstory density, time since last burn within 500 m, and coyote activity (Figure 1). As a large herbivore, deer site use was positively associated with wild pig activity in the winter, along with EVI within 500 m, but was negatively associated with wild pig activity in the fall (Figures 1 and 2). Deer site use decreased with increased distance to water in both the spring and fall and decreased with increased distance to paved road in all seasons except winter (Figure 1). Deer site use in the fall was also predicted to be higher in both nonforested areas and areas with less understory density and greater overstory density (Figure 1).

Bobcat site use increased with understory density in all seasons except the fall, when there were no significant predictors of site use for this hypercarnivore (Figure 1). Bobcat site use also increased with EVI within 150 m in the winter, whereas in the spring, it increased with EVI within 500 m and wild pig activity (Figures 1 and 2). Coyotes, which we classified as large mesocarnivore, were predicted to have higher site use in nonforested areas in both the winter and summer; site use was negatively associated with all other vegetation classes in the winter and negatively associated with hardwood forest in the summer (Figure 1). Coyote site use in the summer was also positively associated with time since last burn within 500 m and distance to paved road, but negatively

TABLE 2 The best predictors of detection probability (p), as determined from N-mixture models with delta corrected Akaike information criterion (ΔAIC_c) < 2 and more weight than the null model, for 10 species during each season in 2020 near McCormick, South Carolina, USA.

Species	Winter	Spring	Summer	Fall
Rabbit	precip (–)	dist (–)	dist (–)	temp (–)
Deer	dist (+)	precip (–)	moon (+) temp (–)	temp (–)
Bobcat	human (–)	moon (+) precip (+)	human (+) dist (–)	dist (–)
Coyote	dist (–) temp (–)	moon (+)	moon (+)	precip (+)
Gray fox	dist (–)	none	none	temp (–)
Raccoon	moon (+)	moon (+) temp (–)	precip (–)	human (–)
Gray squirrel	precip (–)	precip (+)	moon (+)	temp (–)
Armadillo	none	dist (–)	none	temp (+)
Turkey	dist (+)	none	none	human (–)
Wild pig	moon (+)	dist (+)	dist (–)	human (+)

Note: Estimate signs are shown in parentheses and covariates with significant effects (95% confidence intervals did not overlap zero) are shown in bold.

Expected abundance (λ) was held constant across all camera sites. None of the covariates were carried forward if the null model was the top model.

Abbreviations: dist, average camera detection distance; human, daily human activity; moon, daily moon phase; precip, daily precipitation; temp, daily high temperature.

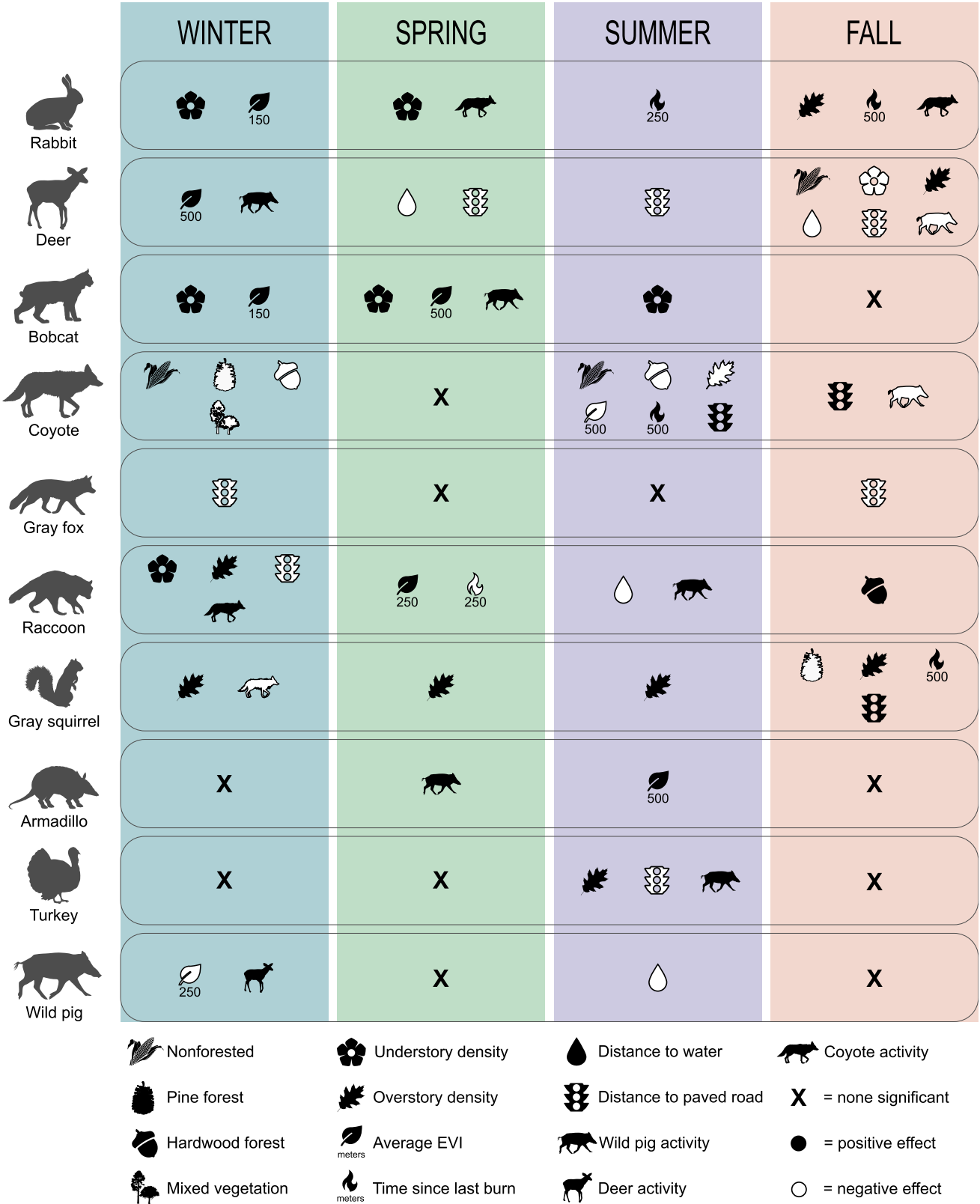


FIGURE 1 Statistically significant predictors of expected abundance (λ), as determined from N-mixture models with delta corrected Akaike information criterion (ΔAIC_c) < 2 and more weight than the null model, for 10 species during each season in 2020 near McCormick, South Carolina, USA. Positive effects are in black, negative effects are in white, and “X” denotes no statistically significant predictors. Numbers below the average enhanced vegetation index (EVI) and time since last burn icons denote the buffer size (in meters) used in models.

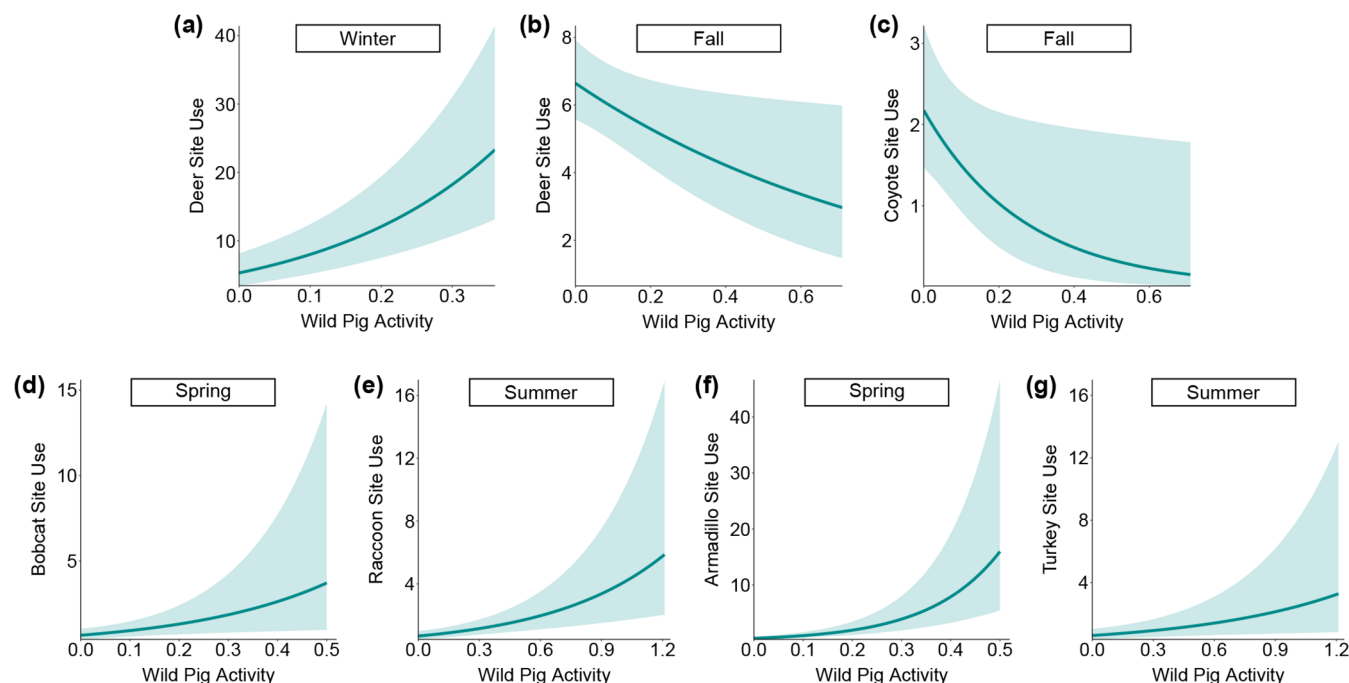


FIGURE 2 Statistically significant relationships between wild pig activity (average wild pig detections per 24-h sampling occasion) and (a) white-tailed deer site use in winter, (b) white-tailed deer site use in fall, (c) coyote site use in fall, (d) bobcat site use in spring, (e) raccoon site use in summer, (f) nine-banded armadillo site use in spring, and (g) wild turkey site use in summer near McCormick, South Carolina, USA. Shaded areas show 95% confidence intervals.

associated with overstory density and EVI within 500 m (Figure 1). In the fall, coyote site use was positively associated with distance to paved road and negatively associated with wild pig activity (Figures 1 and 2). Gray foxes, which we classified as small mesocarnivore, were predicted to decrease site use with increasing distance to paved road in the winter and fall (Figure 1). Also classified by us as a small mesocarnivore, raccoons were negatively associated with distance to paved road and positively associated with understory density, overstory density, and coyote activity in the winter (Figure 1). In the spring, raccoon site use increased with EVI within 250 m and decreased with time since last burn within 250 m (Figure 1). Raccoon site use in the summer increased with wild pig activity (Figure 2) and decreased with distance to water (Figure 1). In the fall, raccoon site use was greatest in hardwood forest (Figure 1).

Gray squirrels, which we included in the omnivore category, were associated with denser overstory in all seasons (Figure 1). Gray squirrel site use in the winter was also negatively associated with coyote activity (Figure 1). In the fall, gray squirrel site use was negatively associated with pine forest and positively associated with time since last burn within 500 m and distance to paved road (Figure 1). Armadillo site use was positively associated with wild pig activity in the spring (Figure 2), while in the summer it was positively associated with EVI within 500 m (Figure 1).

Turkey site use in the summer increased with wild pig activity (Figure 2) and overstory density but decreased with distance to paved road (Figure 1). There were no significant predictors of turkey site use in other seasons. Wild pigs decreased site use with increasing EVI within 250 m in the winter and were positively associated with deer activity, while their summer site use was negatively associated with distance to water (Figure 1). There were no significant predictors of wild pig site use in spring and fall.

Temporal overlap

Wild pigs showed a crepuscular diel activity pattern in spring and mostly nocturnal patterns in all other seasons (Figure 3). Rabbits showed a mostly nocturnal pattern in spring and nocturnal patterns in all other seasons. Deer activity was mostly crepuscular in all seasons. Bobcat activity was nocturnal in winter and summer and mostly nocturnal in spring (Figure 3) and fall. Coyotes, gray foxes, raccoons, and armadillos were nocturnal in all seasons. Gray squirrels and turkeys were diurnal in all seasons, resulting in consistently low temporal overlap between these species and wild pigs (Table 3). The coefficient of overlap was similar across seasons for many species, with wild pigs having consistently high temporal overlap ($\Delta \geq 0.60$ when taking bootstrapped CIs into

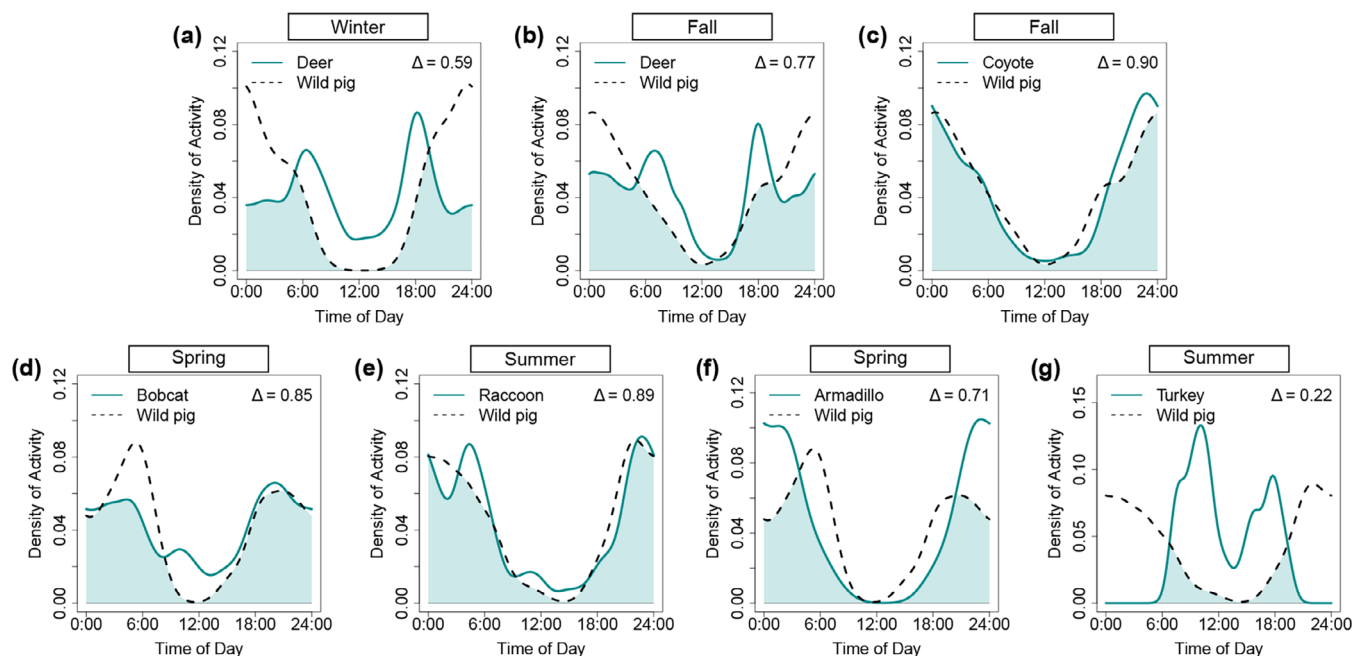


FIGURE 3 Diel activity overlap between wild pig and species showing a statistically significant spatial relationship with wild pig relative activity near McCormick, South Carolina, USA: (a) white-tailed deer in winter, (b) white-tailed deer in fall, (c) coyote in fall, (d) bobcat in spring, (e) raccoon in summer, (f) nine-banded armadillo in spring, and (g) wild turkey in summer. Density of activity is an estimate of the proportion of total daily activity that occurs at a specific time of day. Shaded areas show the density of overlap and Δ is the coefficient of overlap.

TABLE 3 Diel activity coefficient of overlap between wild pigs and nine species near McCormick, South Carolina, USA, during each season in 2020 and averaged across the year, with seasonal bootstrapped 95% confidence intervals shown in parentheses.

Species	Winter	Spring	Summer	Fall	Annual
Coyote	0.91 (0.77–1.00)	0.75 (0.60–0.88)	0.89 (0.80–0.96)	0.90 (0.80–0.98)	0.86
Rabbit	0.81 (0.66–0.93)	0.84 (0.70–0.95)	0.80 (0.69–0.90)	0.89 (0.78–0.97)	0.84
Bobcat	0.71 (0.55–0.86)	0.85 (0.70–0.97)	0.91 (0.81–0.99)	0.81 (0.67–0.92)	0.82
Raccoon	0.76 (0.60–0.89)	0.71 (0.55–0.85)	0.89 (0.80–0.96)	0.73 (0.60–0.84)	0.77
Deer	0.59 (0.45–0.73)	0.81 (0.68–0.91)	0.80 (0.71–0.88)	0.77 (0.67–0.87)	0.74
Armadillo	0.77 (0.54–0.94)	0.71 (0.54–0.86)	0.76 (0.64–0.87)	0.68 (0.52–0.82)	0.73
Gray fox	0.73 (0.54–0.90)	0.51 (0.26–0.74)	0.79 (0.54–0.97)	0.61 (0.46–0.74)	0.66
Gray squirrel	0.14 (0.04–0.26)	0.33 (0.20–0.46)	0.25 (0.15–0.36)	0.22 (0.12–0.31)	0.24
Turkey	0.10 (0.01–0.21)	0.30 (0.17–0.43)	0.22 (0.13–0.31)	0.21 (0.11–0.31)	0.21

consideration) with rabbits and coyotes (Table 3). Gray fox coefficients of overlap varied the most, with CI bounds ranging from $\Delta = 0.26$ to $\Delta = 0.97$ (Table 3). We did not consider seasonal differences statistically significant since all CIs overlapped for each species (Table 3).

DISCUSSION

Our findings build on previous studies to suggest that the potential impacts of invasive wild pigs on other

vertebrates are highly variable among species and across seasons. Similar to investigations at the northern extent of their introduced range (O'Brien et al., 2019), spatial overlap with wild pigs varied by species and season, with species associations being neutral in certain seasons but negative or positive in others. However, seasonal species associations that we observed contrasted with those observed by O'Brien et al. (2019), suggesting spatial overlap between invasive wild pigs and a given species could vary by region or land cover type. Temporal avoidance of wild pigs has been documented in the Brazilian Pantanal

(Galetti et al., 2015), but we did not find strong evidence for this. Most species in our study area had moderate to high diel activity overlap with wild pigs across all seasons, similar to consistently high temporal overlap between collared peccaries and wild pigs in Texas (Ilse & Hellgren, 1995). Collectively, our results suggest that spatial partitioning is a more likely mechanism than diel activity partitioning for avoiding competition with wild pigs in our study area.

Our results support previous research on native ungulates and invasive wild pigs that documented spatial avoidance (Gabor et al., 2001; Perez Carusi et al., 2017) and previous research that found temporal overlap to be lowest when spatial overlap was highest (Ilse & Hellgren, 1995). Deer elsewhere in South Carolina have shown negative spatial responses to wild pig density in the fall (Garabedian et al., 2023), and we similarly observed a negative relationship between deer site use and wild pig activity in this season, suggesting deer might avoid areas where wild pigs are most active in the fall. It could be that wild pigs in our study area outcompeted deer for limited hard mast, excluding them through interference competition or resource exploitation (Elston & Hewitt, 2010; Yarrow, 1987); conversely, hard mast may have been more broadly distributed than we expected, enabling wild pigs and deer to maintain their diel activity patterns and coexist through spatial partitioning in the fall (Ilse & Hellgren, 1995). By contrast, deer site use and wild pig activity were positively associated in the winter, when resources such as food and vegetative cover were likely more limited and patchily distributed, necessitating higher spatial overlap. Interference competition in this season may have been minimized by nonsynchronous spatial overlap (Carothers & Jaksic, 1984; Crombie, 1947; MacArthur & Levins, 1967; Schoener, 1974), as other ungulates have been shown to adjust their temporal activity to avoid competition with sympatric wild pigs (Galetti et al., 2015; Ilse & Hellgren, 1995). Deer and wild pigs in our study appeared to have more moderate diel activity overlap in the winter relative to other seasons, and while the difference was not statistically significant, this could signal lower temporal overlap on a finer scale than diel activity.

Prior research suggests the occurrence (O'Brien et al., 2019) and abundance (Stevens, 1996) of coyotes and wild pigs are positively correlated, but the only significant relationship we found between coyote site use and wild pig activity was a negative one in the fall. Although farrowing occurs throughout the year, most wild pigs in our study area were likely born in the winter and spring (VerCauteren et al., 2020), so we would expect wild pig activity to have a positive effect on coyote site use during these seasons if wild pigs benefit coyotes. However,

Keiter et al. (2017) and Chinn et al. (2021) documented fairly low coyote predation on juvenile wild pigs in South Carolina, and concurrent research in our study area found that wild pig was a minor component ($\leq 5\%$) of coyote diet across seasons (Jensen et al., *In review*). Our findings suggest that coyotes in our study area do not select areas maximizing access to juvenile wild pigs, but instead select areas with greater access to other foods shown to be important, such as fruit and fawns (Jensen et al., *In review*). Diel activity overlap between coyotes and wild pigs was high in all seasons, yet coyote activity was not a statistically significant predictor of wild pig site use in any season. This suggests that coyotes might avoid invasive wild pigs in the fall, rather than wild pigs avoiding coyotes, and mirrors the statistical relationship between deer site use and wild pig activity in this season.

Positive seasonal associations between wild pigs and smaller species in our study area could be driven by factors such as realized diet, thermal requirements, or landscape attributes. We predicted that bobcat spatial overlap with wild pigs would be greatest in the spring, based on the assumption that grasses and forbs would be readily available for wild pigs and small herbivores that bobcats prey on (Beasom & Moore, 1977). Although spatial overlap between bobcats and wild pigs was indeed highest in the spring, rabbits had a nonsignificant negative relationship with wild pig activity, so bobcat site use in this season may relate more to other prey (i.e., rodents; Godbois et al., 2003; Larson et al., 2015; Thornton et al., 2004). We predicted that raccoon spatial overlap with wild pigs would be driven by mast and thus would be greatest in the summer and fall (Byrne & Chamberlain, 2011; Chamberlain et al., 2002), but we only observed a significant positive relationship in the summer. Conversely, O'Brien et al. (2019) observed negative associations between raccoons and wild pigs during the summer and fall in Saskatchewan, Canada. However, Eckert et al. (2019) observed raccoons, along with armadillos, turkeys, and other species, using active wild pig wallows during the summer in South Carolina; it may be that animals in our study area also benefited from wild pig wallows. We predicted that armadillo and turkey spatial overlap with wild pigs would be greatest in the fall, but armadillos were instead positively associated with wild pigs in the spring and turkeys were positively associated with wild pigs in the summer. Spatial overlap with turkeys outside of nesting season may not be of great concern, but overlap should be monitored across years given the detrimental effects wild pigs could have when turkeys nest in the spring (Sanders et al., 2020). Wild pigs in our study area had low temporal overlap with turkeys, whereas higher spatial overlap between wild pigs and bobcats, raccoons, and armadillos did not appear mediated by

diel activity partitioning. Resource partitioning between these mammals and wild pigs likely occurred on more acute spatiotemporal scales (Zanni et al., 2021) or niche dimensions (Schoener, 1974), which could be influenced by landscape structure (Byrne & Chamberlain, 2011; Jones et al., 2022; Pollentier et al., 2017; Reed et al., 2017; Tucker et al., 2008) or the fine-scale distribution of food items. Thorough assessments of fine-scale resource availability and selection are challenging, but advancements in satellite imagery (Brown et al., 2022) and experimental studies involving food manipulation have great potential for elucidating wild pig effects on the spatiotemporal activity of other wildlife.

Failure to observe a relationship between wild pig activity and the site use of certain species in certain seasons could be due to partitioning occurring at finer spatiotemporal scales than we evaluated. New analytical techniques that simultaneously model spatial and temporal activities while accounting for imperfect detection could shed light on complex species interactions (Kellner et al., 2022). We calculated average wild pig activity over two weeks, but spatial activity patterns underlying our site use metric may be dynamic and determined over shorter time periods than our data reflect, even as brief as hours or minutes. “Relative” activity is influenced by abundance (Sollmann, 2018), but does not explicitly account for the number of individuals present, so effects may be underestimated when studying a social species like wild pig (Gabor et al., 1999; Kilgo et al., 2021; Sparklin et al., 2009). It is also plausible that the relatively low density of wild pigs in our study area compared with nearby areas, rather than shortcomings in our analytical techniques, obscured potential negative or positive impacts on species that could emerge if wild pig density were to increase. For instance, at the Savannah River Site in South Carolina, wild pig effects on deer space use increased with increasing wild pig density (Garabedian et al., 2023). It is also possible our results were influenced by wild pig harvest and removal efforts, as 40 were removed across the study area in 2019 and there was low detection in the first half of 2020, despite only a sow and boar being removed during that time. However, wild pig detections and the proportion of sites they occurred at were greater in the second half of 2020, even though removal efforts increased during that time. While this leads us to believe that wild pig removal had a negligible impact on their occurrence at wildlife camera sites across survey periods, further research is needed on the potential effects of wild pig distribution, density, and removal on animal resource selection and community dynamics.

Our research implies that responses to invasive wild pigs can vary across species and seasons, which has

important implications for the management of wild pigs and conservation of native wildlife. White-tailed deer are a prominent game species in the United States, and our results suggest that deer and wild pigs spatially partition in the fall, when hunters attempt to harvest deer. Whether hunting activity drives deer and wild pig activity where these ungulates spatially overlap, and whether this affects interactions between them, is an area of future research. Regardless of potential human impacts, resources may have been adequately abundant for deer and wild pigs to avoid each other in the fall, or aggressive wild pigs may have displaced deer from important forage in this season. Knowledge of the abundance and distribution of shared food items is necessary for determining whether competition occurs, especially as displacement could have a greater impact on deer in years with poor hard mast production (Wentworth et al., 1992). In contrast to the fall, deer and wild pigs had higher spatial overlap in winter, revealing a need for future research investigating if invasive wild pigs have behavioral and physiological impacts on deer when spatial overlap is high (Ferretti et al., 2011; Perez Carusi et al., 2017; Wentworth et al., 1992). Wild pigs do not appear to positively impact coyotes in our study area, and coyotes may even avoid them during the fall, suggesting wild pigs are not facilitating coyote range expansion or persistence. Wild pigs had relatively high spatial activity and diel activity overlap with bobcats, raccoons, and armadillos, although we cannot rule out avoidance on finer temporal scales than diel activity where spatial overlap occurs. Fine-scale resource selection also may have been distinct enough for these species to be unconcerned with wild pigs, but if wild pig density were to increase or if resources are limited, high spatial overlap unmitigated by temporal separation could potentially exceed the tolerance of species. If wild pigs have a strong negative impact in certain seasons or if they outcompete native wildlife for extended time, this could contribute to the decline of populations (Perez Carusi et al., 2017; Singer et al., 1984). With the establishment and growth of wild pig populations across an increasing portion of their introduced range, our findings indicate a need for investigating how season and resource availability affect the responses of specific species to wild pigs and whether those responses could impact the persistence of native species populations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Saldo, 2023) are available from Figshare: <https://doi.org/10.6084/m9.figshare.21901731>.

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