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SHORT COMMUNICATIONS

Abundant and Diverse Terrestrial Vertebrates at the Maritime Forest—salt Marsh Ecotone

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Abstract
Ecotones are areas of transition between ecosystems that often exhibit high habitat heterogeneity. They may serve as habitat in their own right or attract species that exploit ecosystems on either side, thereby facilitating energy flow across systems. Atlantic tidal salt marshes and maritime forests of the southeastern coastal US are adjacent, productive systems. Using motion-triggered wildlife cameras deployed within the narrow forest—marsh ecotone, we quantified visitation of larger (>10 cm body length) terrestrial vertebrate species to the ecotone at 18 locations over 80 km of coastline using over 10,000 h of surveillance in summer 2017. We detected 12 terrestrial species in the ecotone, with the North American raccoon (*Procyon lotor*) comprising 68% of all camera captures. At an average of 1.22 raccoon visits per day per 3–8 m of marsh-forest frontage, raccoon usage of salt marshes represents a potentially underappreciated pathway for cross-boundary ecological interactions. Eastern gray squirrel, white-tailed deer, and red fox were the next most common visitors. Activity of these top four species was positively correlated in space, but raccoons overlapped little with the other three species temporally, visiting the ecotone primarily at night. The presence of diverse, abundant terrestrial vertebrates at this ecotone suggests it functions as habitat or as a corridor linking forest and marsh. As such, the ecotone and the adjacent salt marsh may be undervalued habitats for coastal terrestrial species.

Keywords allochthonous inputs · cross-system migrations · energy transfer · *Spartina alterniflora* · system boundaries

Introduction

Organisms benefit from the habitats they use in regards to energy acquisition (e.g., Yahner 1988; Blouin-Demers and Weatherhead 2008; Wright et al. 2014) and protection from predators (e.g., Byers et al. 2017; Demarais et al. 2017). Here we use the term habitat to refer to a particular physical environment or area of uniform environmental conditions, i.e., a community-centric definition. Access to multiple adjacent habitats can enhance energy acquisition and predator avoidance while minimizing movement costs when habitat boundaries are permeable (Rose and Polis 1998; Hackett et al. 2024). The use of multiple habitats may be particularly advantageous when the habitats occur in close proximity within the landscape and movement costs between the two are minimal (e.g., Richard and Armstrong 2010; Halsey 2016). Highly motile species have been shown to transition between habitats especially when highly desirable, but variable, foraging resources are available in one habitat and not the other (Beasley and Rhodes 2010).

Ecotones, the transition area between two highly distinct habitat types or biomes, may be prominent areas that provide an organism easy access to benefits found within each habitat, and therefore, where such cross-habitat movement is common (Greenwood 2014). For example, ecotones, or edge habitats more generally, may bridge habitats that vary starkly in cover, whereby the open habitat is more productive and the covered habitat has lower predation risk (Grover and Wilbur 2002). Similarly, the two bordering habitats may represent areas where resources from two different habitat types can mix, providing a broader range of benefits to wildlife than a single habitat on its own (Kolasa and Zalewski 1995). This increased opportunity in ecotones is particularly apparent when examining the interface of

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marine and terrestrial environments (e.g., Polis and Hurd 1996; Carlton and Hodder 2003; Talley et al. 2006; Wasson et al. 2021). Energy either deposited by, or extracted from, marine systems has been shown to increase both secondary productivity and consumer diversity within terrestrial systems (Polis et al. 1997). These mechanisms for energy movement likely make terrestrial-marine edges attractive to terrestrial wildlife. However, quantitative data on the frequency and identity of terrestrial vertebrates using salt marsh–forest ecotones remain limited, particularly along the southeastern Atlantic coast.

Ecotones can act as permeable, semi-permeable, or hard barriers for the organisms that meet at these edges (Attrill and Rundle 2002). The ability of an organism to cross the edges at an ecotone depends on its ability to handle the differing abiotic and biotic components in each adjacent habitat (James and Zedler 2000). Furthermore, the ecotone may also be valuable in its own right for its resources, or simply as a corridor for easy passage through—but not across—the landscape (e.g., Lidicker 1999, James and Zedler 2000; Puth and Wilson 2001; Traut 2005). The relatively extreme differences between marine and terrestrial abiotic conditions likely reduces the number of organisms that can take advantage of both systems. The organisms that can utilize both systems are likely important as nexuses for sharing energy and nutrients between the two habitats (Briers et al. 2005). Identifying these organisms and determining the factors that drive their use of this ecotone is important in determining where there may be important connections between two systems across an ecotone.

Southeastern Atlantic salt marshes are highly productive systems characterized by large areas of the marsh cordgrass, *Spartina alterniflora*. These cordgrass marshes exist along a gradient from mid to high intertidal elevations. Variation in tidal inundation along this elevational gradient leads to differences in both the plant and wildlife communities that utilize these habitats (McKinney et al. 2009; Pennings et al. 2005). Estuarine organisms that require longer periods of inundation are usually restricted to the lower vegetated marsh, while the high marsh is more accessible to terrestrial organisms because it is inundated with relatively shallow water for only a few hours per tidal cycle (Weisberg and Lotrich 1982; Smith et al. 2021). The marsh's high productivity and regular periods of accessibility make it a potentially attractive habitat to terrestrial organisms occupying adjacent habitats such as the live oak maritime forest, another relatively productive coastal system (Bellis 1995). Terrestrial species may derive energetic benefits from using the salt marsh, for example by foraging for additional resources such as snails, mussels, crabs, polychaete worms, etc. However, the importance of salt marsh use to these species at a landscape scale is unclear, particularly when considering that the terrestrial system with which these species are associated is productive itself (Carlton and Hodder 2003; Greenberg et al. 2006, Taillie and Moorman 2019; Hines et al. 2026).

Terrestrial mammals have been observed accessing salt marshes along the marsh–forest ecotone (e.g., Thorne et al. 2012; Wasson et al. 2021; Canepuccia et al. 2015, 2023), but such observations are often anecdotal and rarely quantified. We therefore used motion-triggered cameras to systematically document the terrestrial vertebrate community visiting the maritime forest–salt marsh ecotone along the southeastern US coast. Our objectives were to (1) identify the terrestrial species using this ecotone, (2) quantify visitation rates across sites, and (3) characterize daily temporal patterns of ecotone use. By providing a quantitative baseline of visitation frequency and diel activity, we aim to identify relatively large terrestrial species that may play important roles in linking marsh and forest habitats.

We tested two primary hypotheses. First, we predicted that generalist omnivores and mesopredators, particularly raccoons (*Procyon lotor*), would exhibit higher visitation rates to the ecotone than herbivores or dietary specialists, reflecting their flexible foraging strategies and capacity to exploit heterogeneous edge habitats. Second, we predicted that visitation timing would differ among taxa in ways consistent with known diel activity patterns: raccoons would exhibit predominantly nocturnal visitation, deer and fox would peak during crepuscular periods, and squirrels would show primarily diurnal activity. These hypotheses allow us to evaluate whether ecotone visitation is structured by trophic strategy and behavioral timing, thereby strengthening inference about the ecological role of the marsh–forest boundary.

Materials & Methods

To identify the species that visit the salt marsh-maritime forest ecotone, we placed infrared (IR) motion-triggered sensor cameras (Bushnell Trophy Cam) 1–2 m from the upper edge of the marsh oriented to look along the edge of the salt marsh-maritime forest ecotone (Plate 1). The cameras we used are portable devices that record a still image and video when triggered by movement detected in front of the IR sensor. These cameras have been used to measure presence, abundance, and activity of species across many taxa and in many different habitat types (e.g., Cove et al. 2012; Jansen et al. 2014), and are particularly well suited to capturing the visitation of larger terrestrial vertebrates, a relatively under documented, highly mobile community in the maritime forest-salt marsh edge. We deployed cameras in the field from May through July 2017 at three sites

Plate 1 **a**) Camera placed on a camouflaged pvc pipe 1m above the ground and ~1-2m from the high water mark. **b**) Picture of the maritime forest-salt marsh ecotone from directly above a camera placement

spanning 80 km along the Georgia coast: Wormsloe Historic Site (31.979915, -81.069163), Cannon's Point Preserve (31.257845, -81.348114), and Harris Neck National Wildlife Refuge (31.624910, -81.288595). Each site is protected from development and characterized by having maritime forest surrounded by salt marsh.

Within each site, we placed one camera at each of six replicate locations that were separated by at least 100 m for six days. The field of view for cameras varied by replicate, with a minimum straight-line sight distance (from camera to obscuring vegetation) of ~3 m and a maximum of 8 m. The width of the field of view was approximately 1.5 m. These distances were all within the maximum trigger range for our cameras; as such, all wildlife greater than ~ 10 cm in length in the field of view would be reliably captured. We acknowledge that differences in sampling area (camera field of view) can affect spatial patterns, but the distribution of the fields of view were haphazardly distributed among cameras and thus should not have introduced any systematic bias to the visitation estimates.

After six days, we recovered cameras, cleared SD memory cards, and checked camera functionality and programming. The next day, we deployed the cameras at six new ecotone replicates at the next field site for a new 6-day camera-trapping session. Thus, after 18 days, we had sampled a 6-day period within all replicate ecotones at each of our three field sites. We then repeated this sequence in the same field site order three more times using all the same ecotone locations, for a total of four 6-day blocks sampled from each of our 18 locations among three field sites. Although sampling was not concurrent among sites, our selected design allowed us to maximize the number of replicates within each site, thereby increasing the total area that was sampled concurrently within each site. Our systematic deployment of cameras across the three sites over a long time period helps to average out a possible influence of tides, which we expected to be minimal anyway since the cameras are placed just above the tidal prism. By measuring over a range of tidal conditions we intended to isolate the influence of time of day on our animal visitation results. The four six-day blocks were separated by sufficient temporal intervals such that visitation events likely represent independent behavioral decisions rather than continuous monitoring of the same animal aggregations. Thus, while local animal populations may have overlapped some across deployments, visitation rates largely reflect repeated, temporally discrete sampling of ecotones. However, because cameras were redeployed at the same ecotone locations across sampling blocks, visitation rates technically represent repeated measures of site use rather than independent population samples. Accordingly, our inference is limited to spatial variation in ecotone visitation rather than estimation of population density.

For each ecotone location, we calculated visitation rates for each species as the number of unique photo captures per 24-hour period averaged over the entire 24 days of deployment at each ecotone location. To be conservative and avoid double-counting organisms that lingered in the field of view, we considered an image to be a unique capture of a species only if an image of that species had not been captured in the previous hour. The one-hour interval threshold was selected to minimize double-counting while retaining biologically meaningful repeat visits (Wagon and Serfass 2016). We considered images of two or more individuals of the same species captured in the same photo to be unique captures. To ensure that all animals traveling in a group were counted, with each IR-triggered photo, the camera also collected a 30 s video to capture slower-moving individuals. When videos revealed additional individuals, each additional individual was considered a unique capture contributing to the activity metric.

We analyzed variation in daily visitation rates within each of the four most abundant species and between these four species across ecotone locations using generalized linear models with a negative binomial distribution with the 'MASS' package in R 3.4.1. Visitation rates were treated as the dependent variable in our model with ecotone location as the independent variable. Significance was tested using an alpha of 0.05. Because we apply a simple generalized linear modeling framework for the main analyses, our inference does not depend on estimating variance components or population parameters at multiple hierarchical levels. Rather, we use models to evaluate broad differences in visitation rates and to describe consistent patterns in activity

timing. We also analyzed the spatial covariance of visitation rates of our most frequently observed species using the 'corrgram' package to determine if there was any overlap in their visitation across ecotone locations. Because visitation rates were right-skewed and included zeros, data were square root transformed for this latter analysis to reduce leverage of high-use locations and stabilize variance prior to computing correlations.

We recorded time stamps of each capture to examine if there was a temporal pattern to the visitation of each species in the ecotone. Analyses on visitation timing were completed using the 'Overlap' package in R 3.4.1. A kernel density estimator was used to generate density plots for time of capture to describe activity patterns in the salt marsh-maritime forest edge. These density plots were used to calculate a coefficient of overlapping as described by (Ridout and Linkie 2009) for the activity patterns of the four top species observed using the salt marsh. This coefficient corresponds to the area of overlap beneath both density curves where a value of 0 means there is no overlap in activity and a value of 1 is identical activity patterns.

Results

A total of 12 vertebrate species were documented within the ecotone habitat across the 18 replicate locations (Table 1, Plate 2). A total of 693 captures of unique individuals were recorded during the camera trapping sessions. Of these captures, the North American raccoon (*Procyon lotor*) accounted for 68.4% ($n=474$) of the total captured images. The next most frequently observed species, Eastern gray squirrel (*Sciurus caroliniensis*), white-tailed deer (*Odocoileus virginianus*), and red fox (*Vulpes vulpes*) accounted for 12.4% ($n=86$), 10.5% ($n=73$), and 3.6% ($n=25$), respectively. Of the remaining eight species observed, none accounted for more than 1% of total captures, and most were only observed at one or two of the 18 replicate ecotone locations.

Visitation rates varied by ecotone location for raccoons ($z=2.84$, $p=0.0045$), squirrels ($z=2.063$, $p=0.039$), and deer ($z=1.97$, $p=0.049$), but not red foxes ($z=-0.73$, $p>0.05$). Visitation rates also varied between these four most common species ($z=2.81$, $p=0.005$). The overall mean of raccoon visitation rate across all sites was 1.22 captures per day (±1.66 SD), with visitation ranging from 0 to 5.16 captures per 24-hour period. Deer had the second highest mean visitation rate at 0.33 captures per day (±0.39 SD), followed by squirrels at 0.26 (±0.38 SD), and foxes at 0.06 (±0.14 SD). Coefficients of variation in visitation rates across space were similar for each species. Visitation rates among species were correlated by ecotone location, where ecotone locations with higher raccoon visitation tended also to exhibit higher visitation by squirrels ($R=0.74$), deer ($R=0.36$), and foxes ($R=0.76$) (Fig. 1).

Table 1 IR-camera trap occurrences of all species observed within the terrestrial-salt marsh ecotone. Cameras were deployed for 24 days in each of 18 ecotone locations and spread evenly among 3 sites for a total of 10,382 h of surveillance

Species	# of captures	# Ecotone locations with captures	Percent of total captures
North American Raccoon (*Procyon lotor*)	474	12	68.40
Eastern Gray Squirrel (*Sciurus carolinensis*)	86	7	12.41
White-tailed Deer (*Odocoileus virginianus*)	73	8	10.50
Red Fox (*Vulpes vulpes*)	25	5	3.61
Rats (subfamily: Sigmodontinae)	7	2	1.01
Nine-banded Armadillo (*Dasypus novemcinctus*)	5	2	0.72
House Cat (*Felis catus*)	4	3	0.58
River Otter (*Lontra canadensis*)	2	1	0.29
Brown Thrasher (*Toxostoma rufum*)	2	2	0.29
Domestic Dog (*Canis lupus*)	1	1	0.14
Virginia Opossum (*Didelphis virginiana*)	1	1	0.14
Great Blue Heron (*Ardea herodias*)	1	1	0.14
Unknown	12	9	1.73
Total captures	693	18	

Raccoons were most active at night, with a large peak in occurrences between twilight and dawn, and a steep drop in activity during the day (Fig. 2). The occurrence of deer and foxes peaked around dawn and dusk with moderate declines in activity during the middle of the day and night (Fig. 2). Squirrel captures peaked around dawn with a steady decline to low levels of activity in the afternoon before declining to zero at night (Fig. 2). The coefficient of temporal overlap in visitation between species pairs was highest for fox and deer (0.74) and fox and squirrel (0.58) pairings. Temporal overlap between the raccoons, the most commonly observed species, and other frequently observed species was low (fox, 0.50; deer, 0.49; squirrel, 0.18).

Discussion

Multiple terrestrial mammals from a variety of taxa visited the salt marsh-maritime forest ecotone. Notably, feral hogs were absent although they are known to thrive in marshes

Plate 2 Representative camera captures of terrestrial wildlife in the salt marsh-maritime forest ecotone. **a**) North American raccoon (*Procyon lotor*) **b**) red fox (*Vulpes vulpes*) **c**) white-tailed deer (*Odocoileus virginianus*), **d**) Eastern gray squirrel (*Sciurus carolinensis*)

of the southeastern US (e.g., Hensel and Hensel 2022). Variation in the visitation rate between ecotone locations indicates that there may be microhabitat characteristics, including slope, productivity, and marsh invertebrate and vegetation density, that make certain areas more attractive. Furthermore, this variation was correlated between species, suggesting that these characteristics act on each species in a similar way. The variety of species observed suggests there is a range of benefits that terrestrial wildlife may draw from the salt marsh proximity (e.g., Lidicker 1999, James and Zedler 2000; Traut 2005; Harding 2002), or they enjoy ease of movement through the corridor the ecotone may provide (Puth and Wilson 2001). The disproportionately high visitation by raccoons suggests that this species may rely more heavily on marsh-adjacent resources or habitat structure than the other terrestrial mammals documented.

The species documented in the salt marsh-maritime forest ecotone were terrestrial. To the extent that species are moving in and extracting resources from the marsh (e.g., food resources that are only found in the marsh such as marsh cordgrass, snails, mussels, crabs, polychaete worms, and even acorns that fall from extended canopies of forest dwelling oaks), the asymmetrical composition of terrestrial species at the salt marsh-maritime forest ecotone implies this may be another example of a marine system subsidizing a terrestrial system (Polis et al. 1997). We emphasize that this is only a working hypothesis. Although ecotone visitation creates the potential for cross-boundary energy transfer, our study does not measure consumption, nutrient flux, or net subsidy magnitude. However, previously, asymmetric energy flows have been documented in systems where the terrestrial environment was far less productive than the marine system. In our system, the maritime forest is itself productive in food resources (Bellis 1995), yet no large marine species (e.g. blue crabs, diamondback terrapins, horseshoe crabs) were ever found in the ecotone.

Although our study was designed only to detect larger organisms, other studies have examined the movement of a

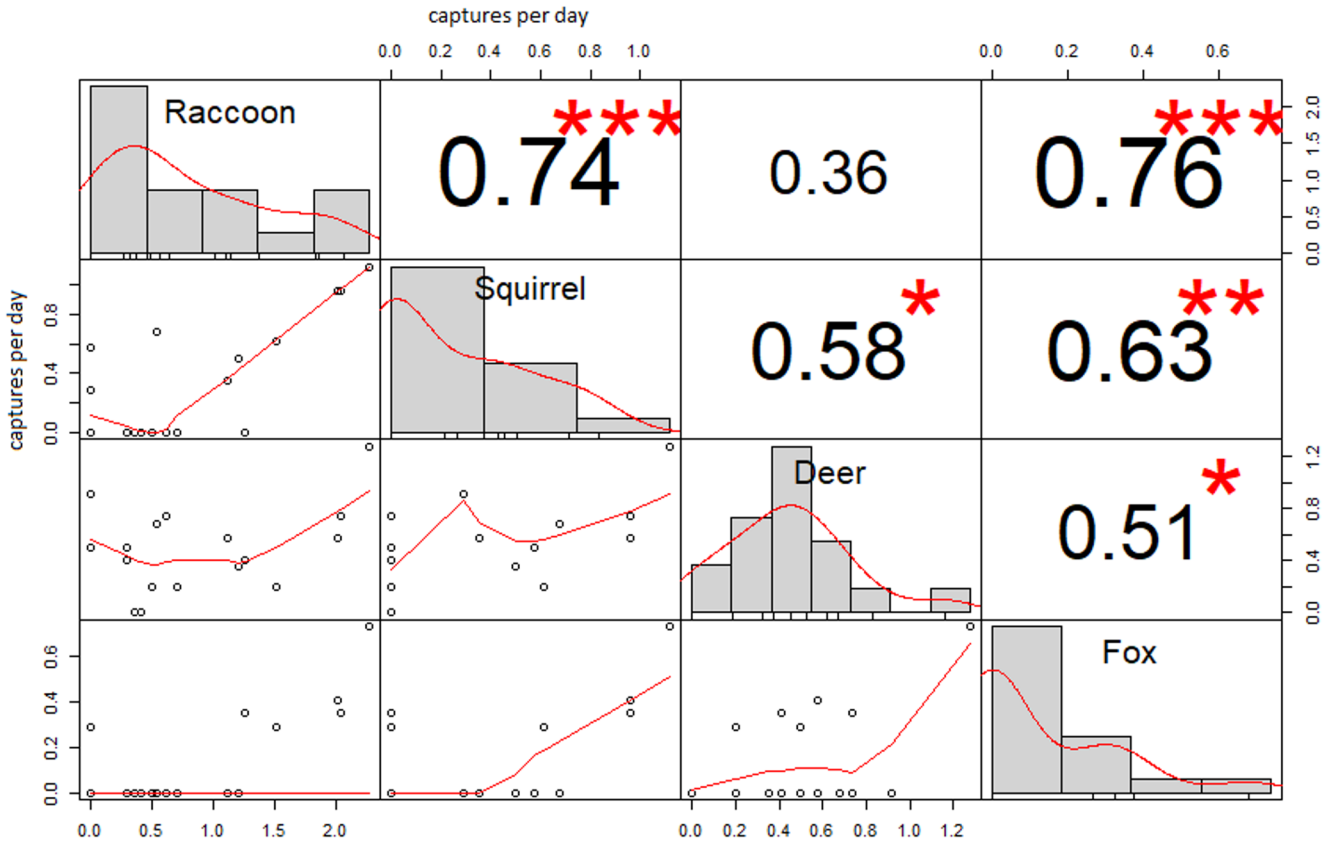

Fig. 1 Spatial correlation matrix of visitation rate for the four most commonly observed species (North American raccoon, Eastern gray squirrel, white-tailed deer, red fox) at all 18 ecotone locations. Histograms are the distribution of average captures per day for each species across locations. White dots represent the average camera captures per day at a location (square root-transformed) compared to the other species' average daily capture at the same location. All 18 locations are present in each plot, but in a few cases the points overlap exactly. Asterisks indicate levels of significance of R values (*** $p<0.001$, ** $p<0.01$, * $p<0.05$). Also, font size is graduated with a larger font indicating a higher level of significance

smaller salt marsh invertebrate across this ecotone (Hubner et al. 2015). *Armases cinereum* is a salt marsh crab that has been documented to use forested habitats at the edge of salt marshes (Seiple 1979). Despite utilizing the terrestrial habitat extensively, *Armases* have been shown to derive most of their diet from the salt marsh (Hubner et al. 2015). Thus, *A. cinereum* is one known example of a species that resides in the marsh but visits the terrestrial environment, opposite of the organisms captured in our study. Similar to the terrestrial species we have documented using this ecotone, the role of *A. cinereum* in the transfer of energy between the two systems remains unclear.

Although there was a large amount of spatial overlap between species in the ecotone among locations, there was relatively little temporal overlap of visitation between raccoons and the other frequently observed species. This differentiation indicates that even at high use sites there was little opportunity for direct interactions between raccoons and other terrestrial species using the ecotone. The lack of temporal overlap is likely indicative of differences in species' activity patterns. Raccoons are nocturnal, and the other commonly observed species are crepuscular and diurnal; our data along the coast reaffirms the established understandings of these species' behavior. These observations suggest that the high activity of raccoons at the study locations is driven by factors related to the habitat or its population density, and is not due to avoidance of the other terrestrial species frequenting the ecotone.

Wildlife cameras were useful to document the community utilizing the ecotone between the salt marsh and live oak maritime forest, but we were only able to calculate relative visitation rates at our sites and not the relative abundances of the species documented. Due to the unobtrusive methods of this study that were intentional so as not to perturb natural movement patterns, and the fact that the most common species we documented typically do not have distinguishing characteristics, we could not reliably identify individuals returning to our camera sites. This issue precluded us from using mark-resight and unmarked models (McClintock and White 2009), which have become popular tools to determine the relative abundance of species monitored using wildlife cameras. Instead, we report a measure of activity (average visitation

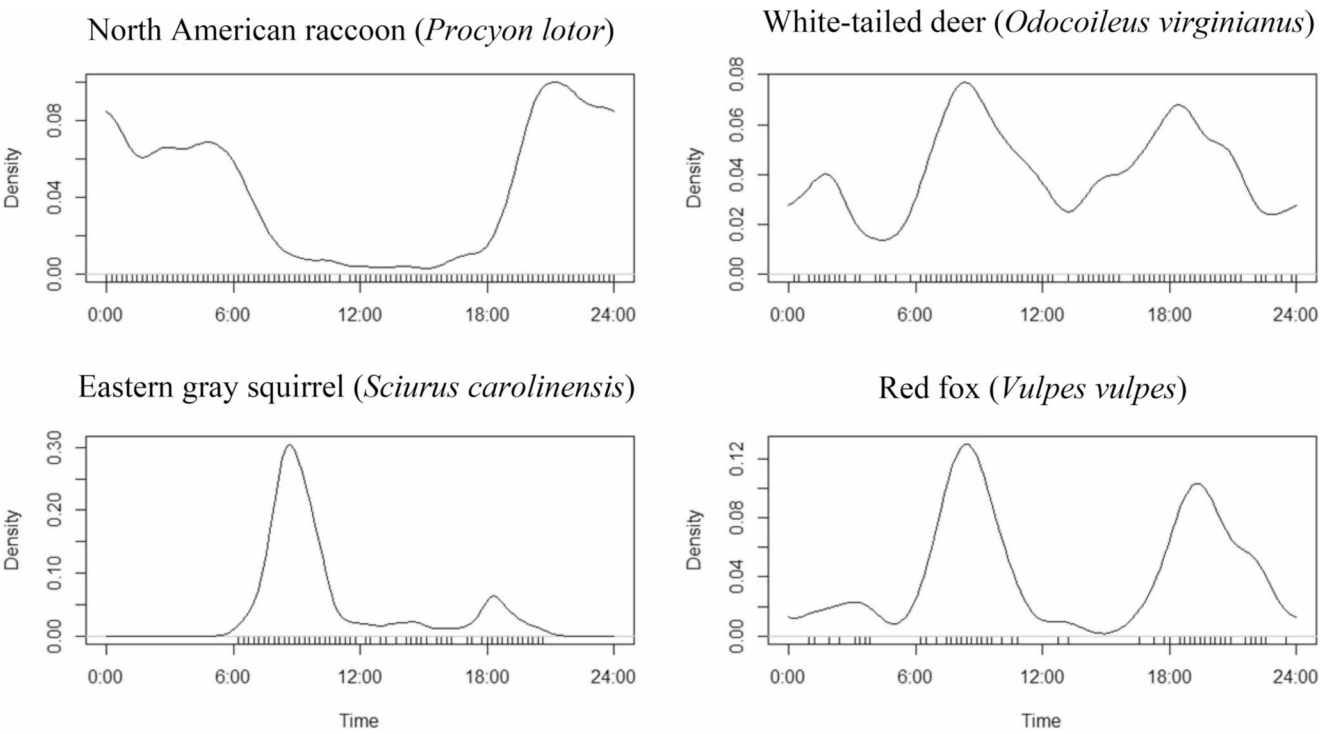

Fig. 2 Kernel density plots from data aggregated across all 18 ecotone locations from three field sites for (**a**) North American raccoon (*Procyon lotor*), (**b**) white-tailed deer (*Odocoileus virginianus*), (**c**) Eastern gray squirrel (*Sciurus carolinensis*), (**d**) red fox (*Vulpes vulpes*) showing the hourly temporal variation in observations of each species within the salt marsh-maritime forest edge

rate) to describe the community of terrestrial wildlife utilizing the maritime forest—salt marsh ecotone. Although we cannot determine the relative importance of ecotone use to terrestrial wildlife populations along the southeastern Atlantic coast, our visitation metric does represent an index of use of the ecotone by terrestrial species. Importantly, these visitation rates were measured over a relatively small frontage area of marsh (3–8 m). But, if the average rate of 1.22 raccoon visits per day per location observed within our 3–8 m frontage is representative of other marsh–forest interfaces, raccoon activity at the marsh scale could be substantial, representing a potentially important mode of energy flow between the two systems. However, spatial heterogeneity in marsh structure and resource availability likely produces variability beyond the extent captured here. Accordingly, we interpret broader implications for marsh-wide raccoon activity as hypotheses for future study rather than definitive conclusions.

Of the twelve species documented, only four were observed with regularity (i.e., raccoon, squirrel, deer, fox, in order of frequency). One of these species, the North American raccoon, was observed with such high activity relative to the other documented species, that it could play a more important role in the dynamics of the maritime forest-salt marsh edge habitat than the other terrestrial species. The North American raccoon is a common, generalist mesopredator, well known for its ability to exploit resources within a landscape (Rosatte et al. 1991; Bateman and Fleming 2012). As active foragers, raccoons likely move from refugia in the forest down into the salt marsh during low tides to forage on the various small invertebrates that occupy the temporarily drained environment (Dorney 1954; Lafferty and Dunham 2005; Smith et al. 2025). This coupled behavior of movement to the salt marsh and foraging within the habitat makes this species a potentially important connection in the energy dynamics between the salt marsh and maritime forest of the US southeastern coast. Broadly, our quantification of the terrestrial species that use the maritime forest—salt marsh ecotone along the US southeastern coast is a baseline from which we can begin to explore questions related to how wildlife, energy, and nutrients are linked across the ecotone between the maritime forest and salt marsh.

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Authors' contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Darren Fraser, an early career researcher, Kimberly Andrews, and James E. Byers. The first draft of the manuscript was written by Darren Fraser and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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