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BRIEF COMMUNICATION

Stark differences across flood risk zones in the Mississippi River floodplain landscape are revealed by an occupancy survey of Missouri swamp rabbits (*Sylvilagus aquaticus*)

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Abstract
Context Flood protection zones in the Lower Mississippi Alluvial Valley, the often-inundated unprotected side or "batture" and the intermittently flooded protected side, are a juxtaposition of sharply different landscapes and ecological conditions. Swamp rabbits (*Sylvilagus aquaticus*), an indicator species for bottomland hardwood forests, inhabit both zones in the southeastern USA. Though the batture side of the levee offers more habitat and better-connected patches, increased flood severity (frequency and duration) due to climate change or other factors may displace swamp rabbits and other terrestrial vertebrates potentially making the area less habitable.
Objectives We used a habitat model to delineate swamp rabbit habitat patches in the flood zones and conducted occupancy surveys of the patches to determine whether swamp rabbits benefited from conditions on the batture side, despite the flood risk.
Methods The presence of swamp rabbits in habitat patches of southeastern Missouri, USA was ascertained through the observation of latrine logs. Swamp rabbit habitat patches were identified using species distribution modeling and a subset were further characterized using Q1 LiDAR. We evaluated detection and occupancy models which included patch and detection covariates to determine differences across flood risk zones.
Results Patch occupancy was high and similar across zones but detection probability was much higher on the batture side. Habitat patches on the protected side levee were generally smaller with thicker canopy and less understory than those on the batture side of the levee.
Conclusions Since visual obstruction was not an obvious factor, the higher detection rate on the unprotected side may have resulted from greater abundance driven by lower patch isolation. Levees that disconnect rivers from the floodplains have a profound effect on landscapes. Swamp rabbits can thrive in the landscape and habitat of the unprotected floodplain, despite their increased exposure to frequent flooding.

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Introduction

The Lower Mississippi Alluvial Valley (LMAV), which sits below the confluence of the Mississippi and Ohio Rivers in the southeastern United States, receives considerable research and conservation attention due to loss of bottomland hardwood forests and their associated ecosystem services and wildlife habitat (Keddy et al. 2009; Jenkins et al. 2010). Approximately 75% of the original bottomland hardwood forest in this region was cleared for agriculture or altered hydrologically (Abernethy and Turner 1987). Although considerable effort to stem the loss of habitat and restore native vegetation has been invested (Llewellyn et al. 1996; King and Keeland 1999; Stanturf et al. 2000), the ecosystem may face another broader challenge in the form of increased severe flooding (increased frequency and duration) due to climate change (IPCC 2007, Trenberth 2011). Floodplain forest species may be adapted to survive frequent and prolonged flooding but, for many, standing water still prevents movement, foraging, and finding refuge from the elements and predators (Bjorklund and Holm 1997; White et al. 2001; Strickland et al. 2013; Bodmer et al. 2018).

Within the LMAV, the Mississippi River levee system that protects agricultural and residential land from flooding creates two very different landscapes in terms of forest patch configuration. The unprotected side of the levees is called the “batture” side. Batture land may appear to be a harsh environment where wildlife become displaced when the river runs high and swift. But, for wildlife displaced by floods in the short term, the batture land can have benefits over a longer term. First, flood risk and river current exposure on the batture side prevent conventional development and agriculture conversion (Clouse and Lamb 2017), and thus result in larger, more contiguous forested patches than the small, scattered forest tracts on the protected side of the levee where agriculture dominates in the productive soils (Twedt and Loesch 1999). At the patch scale, the flooding regime, pulse of nutrients, scouring, and silt deposition in the batture land are distinct from the surrounding area (Remo et al. 2018). Plant and tree communities differ based on soils and flood regime (De Jager et al. 2012; Stanturf et al. 2001), and wildlife, in turn, may respond positively to the flood disturbance itself or benefit from the community associated with the disturbance regime (reviewed in Klimas et al. 1981). For example, Batzli (1977) observed higher productivity of white-footed mice (*Peromyscus leucopus*) in the floodplain than in the adjacent upland, and Jones et al. (2019) found an increase in body condition of white-tailed deer (*Odocoileus virginianus*) in batture land 1–2 years following a major flood.

Though forested floodplains host many species that face challenges and opportunities from flooding, the swamp rabbit (*Sylvilagus aquaticus*) of the southeastern United States is an iconic and well-known specialist of floodplain forests and can serve as a model organism for studying this system (Hillard et al. 2017). Swamp rabbits are often studied at the landscape scale: their occurrence is related to patch area (Scheibe and Henson 2003; Robinson et al. 2016; Fantz et al. 2017) and they exhibit relatively low gene flow among patches (Berkman et al. 2015). During floods, they seek high ground or wait out floods in tree canopies (Zollner et al. 2000a; Vale and Kissell 2010; Crawford et al. 2018), but prolonged flooding and more permanently flooded areas are avoided (Hillard et al. 2021, 2024). However, proximity to water is important, potentially for escape from predators (Scharine et al. 2011). Thus, the ultimate relationship between landscapes with increased flood severity and swamp rabbit populations remains unclear.

Southeastern Missouri, an area that supports swamp rabbit populations at the northern edge of their range, has experienced multiple extreme flooding events over the past two decades. In 2011, the New Madrid Floodway, an approximately 53,000-hectare region usually protected from flooding by a federal levee, was purposefully flooded by the US Army Corps of Engineers to alleviate flood damage upstream. Surveys conducted across the region, both in the protected and batture zones, before and after this flood event showed a considerable drop in swamp rabbit occupancy following the inundation (Scheibe et al. 2016). Extreme floods in this region in subsequent years (2018, 2019) exacerbated concerns about renewed declines in patch occupancy of the swamp rabbit, which is designated as a species of conservation concern in the state. It was hypothesized that the batture region may have become a more hazardous place for swamp rabbits, given the recent uptick in flood events. Thus, we re-surveyed this region, taking a landscape approach and incorporating flood risk zones and other variables that might affect swamp rabbit detection and occupancy. By assessing the pattern of patch occupancy we can better understand the impact of severe and prolonged flooding on habitat and resource use and, in turn, inform management and conservation efforts for swamp rabbits and potentially other floodplain-adapted species. A better understanding of flood-prone landscapes and the factors that inhibit or promote wildlife resiliency in the face of severe flooding will help managers respond appropriately to the threats of a changing climate for this important ecosystem.

Methods

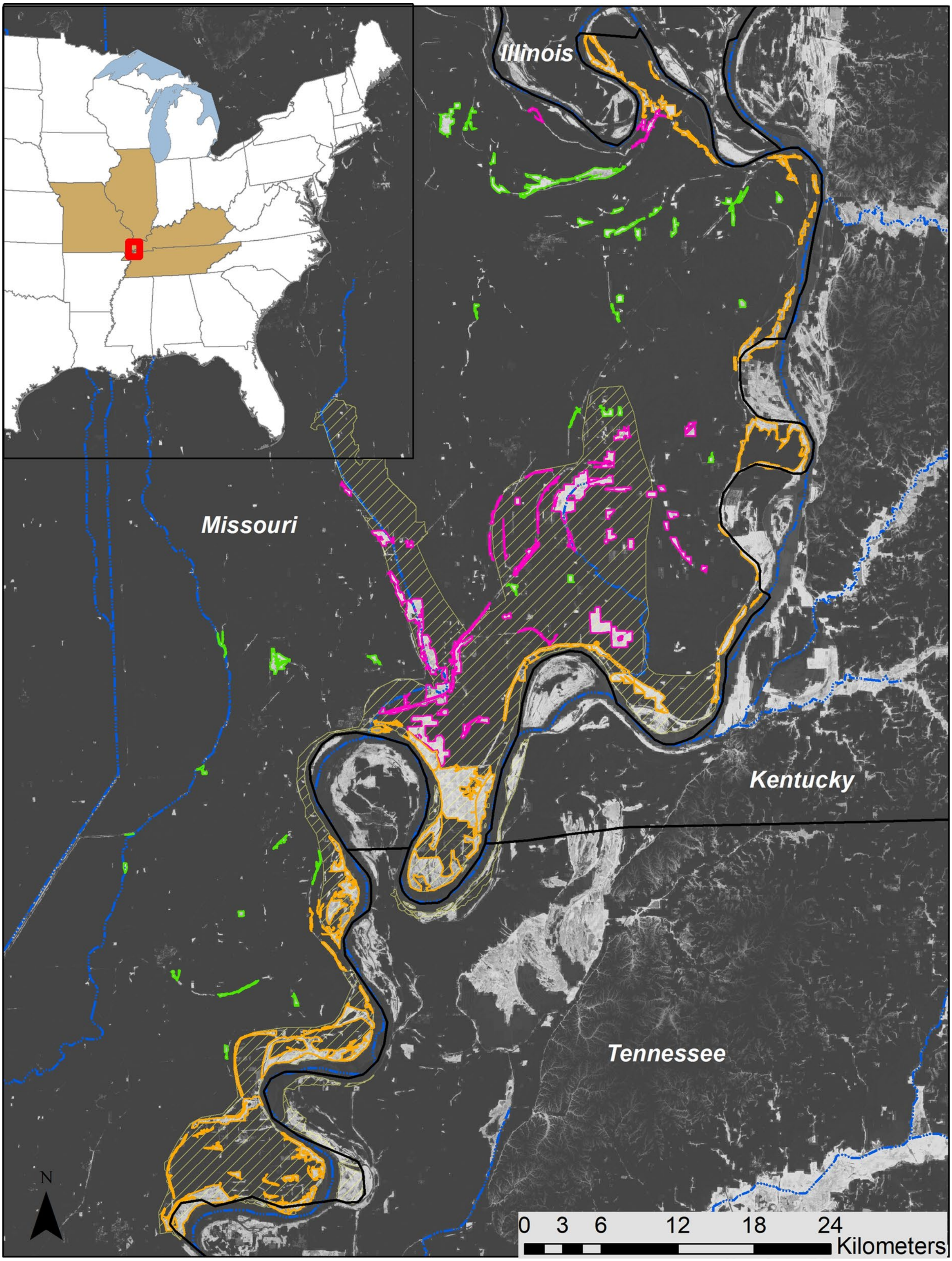
Study area

The flat alluvial plain of southeastern Missouri, colloquially known as the “bootheel”, stands in sharp contrast to the undulating topography of the Ozark Mountains directly to the west. Our study area consisted of the four easternmost counties in this region: Scott, Mississippi, New Madrid, and Pemiscot Counties. These counties contain approximately 85% agriculture landcover, primarily soybeans, corn, cotton, and rice, interspersed with forested patches (USDA National Agricultural Statistics Service 2022). Within part of our study area, a contiguous 62,000 hectares of private and public land are designated as the River Bends Priority Geography by the Missouri Department of Conservation for their importance to statewide biodiversity and their conservation and restoration opportunities. The four counties in our study area contain approximately 9,665 hectares of publicly owned and managed areas. The majority of the study area remains in private ownership, generally for agriculture or hunting lands, but 11,551 hectares of this private land are protected by federal Wetland Reserve Easements (WRE) that take them out of agricultural production.

Forested patches outside the flood protection levees have common canopy dominant trees like sugarberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*), silver maple (*A. saccharinum*), cottonwood (*Populus deltoides*), sweet gum (*Liquidambar styraciflua*), pecan (*Carya illinoiense*), sycamore (*Platanus occidentalis*), and slippery elm (*Ulmus rubra*). Vines are abundant in the forest in canopy gaps, climbing in trees, as part of the ground flora, and in dense mats on the forest floor. The most common vines are poison ivy (*Rhus radicans*), trumpet creeper (*Campsis radicans*), raccoon grape (*Ampelopsis cordata*), greenbrier species (*Smilax spp.*), and crossvine (*Bignonia capreolata*). The herbaceous ground flora diversity is low, with few species being abundant. During flood years when the water recedes late, the herbaceous species will be late to develop. In dry years, the herbaceous flora can develop into dense stands about 1.5 m tall. In areas that are protected by flood control levees, in addition to the tree species mentioned previously, several oak species may be found (*Quercus spp.)*, and ground flora diversity is also generally greater.

Site selection, patch characteristics, and survey methods

To assess differences in landscape use by swamp rabbits across flood protection zones with occupancy rates, we characterized swamp rabbit habitat patches (hereafter “sites”) in the study area and then searched the sites for active swamp rabbit latrines (fecal pellets on elevated surfaces). Survey methods for the present study were based on a combination of previous work (Scheibe et al. 2016; Fantz et al. 2017) and the need to use an occupancy modeling framework that accommodates limited surveying resources and a small population. First, we identified suitable sites from predicted swamp rabbit habitat. We created the habitat model with MaxEnt (Fig. 1; Supplemental Material; Philips et al. 2017). We converted the continuous habitat suitability output from MaxEnt to binary habitat by considering pixels with values of 0.3 and above as habitat based on the ROC reaching a clear plateau at that value (Supplemental Material). Sites were identified and converted to vector format with the Spatial Analyst tool in ArcGIS Desktop (Redlands 2020). The minimum site size remained consistent with previous surveys (> 16 ha). Sites were then digitally edited to correct errors and to split sites connected by habitat corridors narrower than 200 m, which resulted in 150 potential sites. We then divided the study area into three strata based on location


Illinois
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◂**Fig. 1** Study area for swamp rabbit occupancy across different flood risk zones. The inset (upper left) depicts the study area (red rectangle) within the eastern United States. The base map is a swamp rabbit habitat model with lightest shading representing higher likelihood of occurrence. Habitat patches considered for the study are highlighted with orange being the highest flood risk (batture), pink being the medium (floodway) and green being the lowest (ditched and leveed). Blue lines represent major watercourses and the hatched area is the region with LiDAR data coverage

relative to major levee systems (Fig. 1) and relative flood severity (duration and inundation area): ditched and leveed (lowest risk), floodway/non-federal levee protection (medium risk), and batture/no levee protection (highest risk). We identified a stratified random selection of 71 sites (Table 1) and contacted the landowners. If permission to visit the site was not given or no reply was received, we selected an alternative site within the stratum at random.

To achieve a coarse comparison (i.e., estimated means) of forest structure in swamp rabbit patches across the strata we used Q1 LiDAR data in a subsection of the study area which covered 68 sites (Fig. 1) and was collected in the fall of 2022. We estimated mean percent over-(> 9.14 m), mid-(2.45–9.14 m), and understory 0.5–2.44 m) canopy cover as well as basal area (square meters per 168 m^2 plot) for each habitat patch in the LiDAR coverage zone (Fig. 1). We combined sites from the ditched and leveed stratum with those from the floodway stratum to characterize forest structure metrics estimated with LiDAR data. We calculated summary statistics for each estimated metric and included them in a linear discriminant function along with the natural logarithm of patch area (ha) to determine their relative discriminatory ability. Calculations were performed in R (R Core Team 2023).

We standardized search time to one hour per site, regardless of size, based on the observation that larger sites had higher detection probability (Fantz et al. 2017) and the need to conserve resources. The number of observers varied from 1–5 and was included as a detection covariate. Surveys began in November 2021 and concluded in May 2022. Sites were visited twice during the survey period with the first surveys occurring from 4 November to 7 March and the second surveys occurring from 5 December to 29 May. Observers chose the areas to search based on the presence of suitable latrine logs and with an effort to cover the full area (Scheibe and Henson 2003; Fantz et al. 2017). We considered the assumption of closure met because hunting pressure is relatively minimal, the survey was conducted outside the breeding period, and few long-distance movements have been observed during these periods for swamp rabbits (Crawford et al. 2018). Average home range of swamp rabbits is approximately 1–8 ha (Zollner et al. 2000a; Vale and Kissell 2010; Crawford et al. 2018), which is much smaller than the minimum patch size we considered.

Model and covariate selection

Though similar surveys have been conducted in the past (Scheibe et al. 2016; Fantz et al. 2017), the current study design accommodated a larger set of candidate models allowing us to untangle the influence of patch characteristics from flood zone classification. For both detection and occupancy, we assessed the natural logarithm of patch area (hereafter "area") estimated with ArcGIS and the flood risk stratum (ditched and leveed, floodway, and batture). We included models with all three strata separate (hereafter, "3-strata" models) and models with the floodway combined with the ditched and leveed (hereafter, "2-strata" models). For detection, we also considered the number of observers and the relative survey date (i.e., the first survey was considered day 1) as seasonal temperatures may affect detection (Fantz et al. 2017). These models were first considered for their strength of information using the R package RMark (Laake 2013). RMark employs program MARK (White and Burnham 1999) to compute maximum likelihood estimates of parameters. We fit 33 models to the survey data with a full suite of covariates and compared them to models that assume constant occupancy and detection (Supplemental Table 2). We discarded models and covariates with consistently low Akaike's information criterion (AICc) rank and proceeded to fit and rank 16 models reflecting a reduced set of hypotheses (Table 3). We identified the top models by the highest AICc weight and calculated evidence ratios (*ER*) for covariates within the top models (Anderson 2008, MacKenzie et al. 2017), regarding *ER* > 1 as supported.

Table 1 Raw number of detections and naïve occupancy of swamp rabbits in habitat patches

Flood risk strata	Sites surveyed	Sites with detection	Naïve occupancy
Batture	26	19	0.73
Floodway	27	8	0.29
Ditched & Leveed	18	5	0.28
Totals	71	31	0.44

Occupancy and detection estimation

Typical estimation procedures used in most occupancy software packages rely on an asymptotic estimate in which it is assumed that the number of sites surveyed represents a relatively small fraction (1/4 or less) of all sites in the study area. Our study system violates the assumption (i.e. the population is infinite) for asymptotic estimators. In other words, our sample size approached the population size, and our standard error was expected to approach zero. Thus, we chose to use standard model comparison methods to select model covariates (detailed above) and Bayesian small population estimates (MacKenzie et al. 2017) to provide detection and occupancy estimates and their credible intervals. A single model was used because model averaging is not feasible when estimating posterior distributions. Estimates were produced from a posterior distribution of occupancy (Ψ) and the detection probabilities (p). From these distributions, Ψ for all surveyed sites (Ψ_{SUR}) as well as the other identified swamp rabbit sites (Ψ_{POP}) were estimated. The different detection probabilities were taken directly into account when estimating Ψ_{SUR} and Ψ_{POP}. The final estimates for both represent the best estimates for the entire swamp rabbit population in the defined areas. Priors were drawn from a non-informative Beta distribution (Beta(1,1)) for p and Ψ. We used the R program and package JagsUI v 1.5.2 (Kellner et al.

Table 2 Characteristics of swamp rabbit habitat patches (sites) as ascertained with LiDAR data. Means of canopy cover percentage in the over-, mid-, and understory; basal area (square meters per 168 m^2 plot); and the natural logarithm of patch area in hectares (ln area) are given with standard deviation in parentheses

Stratum	N	Overstory (%)	Midstory (%)	Understory (%)	Basal area (m^2)	ln area (ha)
Batture	41	49.7 (15.8)	34.3 (9.5)	11.1 (7.0)	0.977 (0.104)	4.53 (1.13)
Floodway/ Ditched and Leveed	27	61.8 (19.0)	38.3 (10.9)	8.8 (3.1)	0.959 (0.068)	4.21 (0.99)

Table 3 A set of 16 occupancy models compared for a survey of swamp rabbit habitat patches in southeast Missouri

Model	Number of Parameters	AICc	Delta AICc	Weight
p(2 Strata) Ψ(.)	3	147.514	0.0000	0.2598
p(2 Strata) Ψ(LnArea)	4	148.086	0.5720	0.1952
p(2 Strata + LnArea) Ψ(.)	4	148.782	1.2676	0.1378
p(2 Strata) Ψ(2 Strata)	4	149.726	2.2123	0.0859
p(3 Strata) Ψ(.)	4	149.749	2.2355	0.0850
p(2 Strata + LnArea) Ψ(LnArea)	5	150.328	2.8139	0.0636
p(3 Strata) Ψ(LnArea)	5	150.397	2.8826	0.0615
p(2 Strata + LnArea) Ψ(2 Strata)	5	151.083	3.5694	0.0436
p(Survey Date) Ψ(2 Strata)	4	151.980	4.4664	0.0278
p(3 Strata) Ψ(2 Strata)	5	152.031	4.5166	0.0272
p(LnArea) Ψ(2 Strata)	4	153.924	6.4103	0.0105
p(Survey Date) Ψ(LnArea)	4	158.359	10.8455	0.0011
p(LnArea) Ψ(.)	3	160.354	12.8396	0.0004
p(LnArea) Ψ(LnArea)	4	160.439	12.9249	0.0004
p(Survey Date) Ψ(.)	3	163.618	16.1042	0.0001

2019) which uses the Bayesian software JAGS (Plummer 2003) for 11,000 iterations with 3 chains and a 1000-iteration burn-in.

Results

The swamp rabbit habitat model resulted in the identification of 150 suitable habitat patches in the study area ranging from 16 to 631 ha in size with a median of 34.5 ha and a skew towards smaller patches. Floodway patches were generally smaller, with less basal area, lower understory cover, higher overstory cover and higher midstory cover than batture patches (Table 2, Fig. 2). The linear discriminant function incorporating all covariates correctly classified patches 61% of the time (Supplemental).

Naïve occupancy ranged from 0.28 in the ditched and leveed region to 0.73 in the batture region (Table 1). From the full suite of models (Supplemental Table 2) we discarded constant detection, observer effect on detection, and 3-strata effect on occupancy. The top 3 models of the reduced set were supported (delta AICc < 2; Table 3). The top model contained the combined 2-strata effect on detection (*ER* = 3.67) and constant occupancy. A positive effect of ln(area) on occupancy appeared in the second-ranked model (delta AICc = 0.57, *ER* = 1.39). The third-ranked model (delta AICc = 1.27) had constant occupancy, an effect of 2-strata on detection, and a positive effect of area on detection (*ER* = 0.34).

Using the variables with *ER* values > 1 for the Bayesian estimates of detection and occupancy, we included the effect of 2-strata on detection and ln(area) on occupancy in the model. In the batture region the detection estimate (p) was 0.606 (95% posterior distribution = 0.450–0.759) while for the floodway/ditched and leveed region p = 0.238 (95% posterior distribution = 0.231–0.387). The coefficient for the effect of ln(area) was 1.642 (95% posterior distribution = -0.298–4.363). Occupancy for the surveyed sites (Ψ_{SUR} = 0.822; SD = 0.092) was nearly

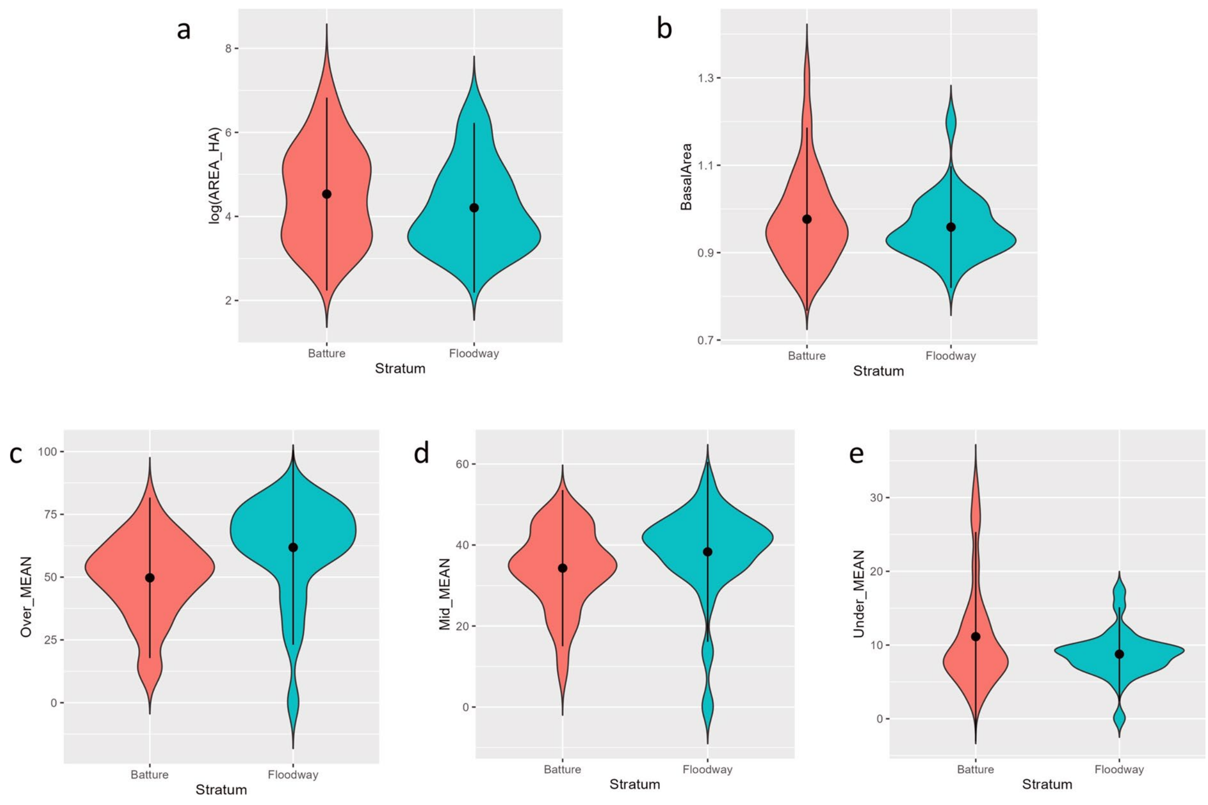

Fig. 2 Violin plots of the natural logarithm of habitat patch area **a** and LiDAR-derived estimates for basal area **b** mean overstory cover **c** mean midstory cover **d** and mean understory cover **e**

the same as occupancy estimated for the population ($\Psi_{POP}=0.817$; SD = 0.063).

Discussion

Forested floodplains in the US provide critical habitat needs for many imperiled species (Llewellyn et al. 1996; Twedt and Loesch 1999), but many have lost resilience and become highly degraded due to human activities (Morrison et al. 2023) such as the construction of artificial levees (Knox et al. 2022). For the first time, we examined the association of swamp rabbits, a bottomland hardwood forest specialist and indicator species (Hillard et al. 2017), with flood risk zones, to account for the effect of levees. We also included factors that have had a demonstrated effect on swamp rabbit detectability, including patch area (Scharine et al. 2011) and day of survey (Fantz et al. 2017) to ensure any effect we observed was not confounded with differences across the flood zones. We found drastic differences in swamp rabbit detection by latrine surveys among flood risk zones with detection being the highest in the highest flood risk region (the batture) and lower in the medium and low-risk regions (floodway/ditched and leveed).

Detectability can be related to temporal factors that make a species more noticeable at certain times (e.g., nighttime calling of frogs), spatial factors that affect the ability to observe a species (e.g., thick brush impeding vision), and the abundance of the species at a site. Increased canopy cover has been associated with increased detectability of swamp rabbits via trapping (Scharine et al. 2011) and presence of latrines (Zollner et al. 2000b). We did not observe drastic differences in canopy and basal area that might influence detectability of swamp rabbit latrines in floodway patches based on visual obstruction. In the absence of factors that could impede the observation of latrines, higher detection in the batture could result from increased pellet deposition due to a higher abundance of swamp rabbits (McCarthy et al. 2013). This result was surprising given the short-term potential for displacement from floods and high water (Hillard et al. 2024). Our results agree with a recent study by Bosch (2024) across the swamp rabbit range in Missouri that found patch extinction and colonization over the long term (~12 years) was not related to flood severity or frequency. Abundance and density of small, non-volant mammals generally declines as a result of floods (Golet et al. 2013; Bodmer et al. 2018) but may rebound shortly after (Batzli 1977; Zhang et al. 2007; Balčiauskas et al. 2012; Price and Berkowitz 2020) potentially due to renewed resources or displaced competitors and predators. Our survey captured the swamp rabbit population three years following a major flooding event and it is possible that patches were recolonized and abundance may have reached a peak.

It also may be possible that the batture regularly supports higher abundances of swamp rabbits due to better metapopulation connectivity with patches being closer to one another and closer to large patches that may serve as mainlands (Brown and Kodrick-Brown 1977). Smaller (Fantz et al. 2017) and more isolated (Bosch 2024) habitat patches are less likely to be occupied by swamp rabbits. We did not observe an effect of flood risk zones on patch occupancy, but we noted a positive influence of patch area on occupancy similar to Sheibe and Henson (2003) and Fantz et al. (2017). This effect seemed more pronounced in the floodway/ditched and leveed region where patches were smaller (Supplemental Table S4).

Our study was limited by sample size and the number of covariates we could include in a model simultaneously, so we did not address possible interactions among covariates. Further, though we were able to address site area and vegetation structure in our study, we did not evaluate a full suite of site-level and landscape-level factors coincident with the flood zones that could affect swamp rabbit populations. In addition to interpatch distance, distribution and size of upland habitats affect relative abundance (Scharine et al. 2009) and these may vary across the flood zones. Also, plant and tree species composition, which could not be assessed with remotely sensed data, may vary based on soils and flood duration (De Jager et al. 2012) and its relationship to swamp rabbit abundance is still unknown.

Regardless of some of these limitations, our results suggest that levees, through the highly different landscape they create, influence swamp rabbit populations in southeastern Missouri. More broadly, surveys that do not account for the presence of levees in large river systems may be getting an incomplete picture or inefficiently using resources for swamp rabbit surveys. Levees have a profound effect on terrestrial environments by reducing habitat heterogeneity, preventing lateral exchange of nutrients and organisms, altering ecological communities, and encouraging urban and agricultural development once flood protection is in place (i.e. part of “the levee effect”) thus reducing forested landcover (reviewed in Knox et al. 2022). All of these factors may shape swamp rabbit habitat at the patch and landscape scale but, in particular, intensive agricultural use of the protected region of our study area strongly affects the amount of swamp rabbit habitat and configuration of habitat patches (i.e. size and isolation). Further changes in flooding and associated distributions of floodplain vegetation and soils are expected to occur during the next 100 years due to climate change (Olsen et al. 1999; Milly et al. 2002; Palmer et al. 2008) challenging the resilience of flood-prone landscapes (Morton and Olson 2014). Our results emphasize that, despite exposure to more flooding, expanded floodplains could benefit swamp rabbits and potentially other terrestrial wildlife that inhabit bottomland hardwood forests.

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Author contributions SRT, LKB, IWV, KB, and JSS designed the study and wrote the proposal for funding. SRT administered contracts and data curation. LKB, SRT, and KB did site selection, GIS, and landowner contacts. JSS supervised and performed field work. LKB and IWV did statistical analysis. XZ and TWB did LiDAR collection, processing, and analysis. LKB, IWV, and KB wrote the main manuscript text. All authors reviewed the manuscript.

Data availability Swamp rabbit locations are available from the Missouri Natural Heritage Database.

Declarations

Competing Interest The authors declare no competing interests.

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