



Shrub encroachment threatens persistence of an endemic insular wetland rodent

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Shrub encroachment is altering the structure and species composition of natural communities across the globe. However, little research has focused on how shrub encroachment influences wetland vertebrates, including small mammals. We sought to determine how vegetative structure and shrub cover influenced the occurrence of a threatened semiaquatic mammalian subspecies, the Sanibel Island rice rat (*Oryzomys palustris sanibeli*). We evaluated the influence of vegetation and metrics of inundation on probability of occurrence and localized seasonal colonization and extinction rates of the Sanibel Island rice rat over a 3-year period. We found Sanibel Island rice rats on 18 (33.3%) of our 54 sites. Their occurrence was positively associated with greater sand cordgrass (*Spartina bakeri*) cover and increased elevation, but negatively associated with greater shrub cover. Their probabilities for Sanibel Island rice rats were positively associated with increased rainfall totals in the preceding 3 months and greater shrub cover. Using aerial photography from across the Sanibel Island rice rat's range, we found 5.5-fold greater shrub cover in 2015 than in 1944. We suggest that increases in shrub cover and reduced cordgrass cover may be driving the decline of this once ubiquitous endemic species and that the encroachment of freshwater wetlands requires greater attention due to its potential to imperil wetland-dependent wildlife.

Key words: Bayesian, *Conocarpus erectus*, dynamic occupancy, Florida, land-cover change, occupancy model, *Oryzomys palustris*, remote sensing, shrub encroachment, *Spartina bakeri*

Freshwater wetlands cover 5.4-6.8% of the Earth's land surface (Lehner and Doll 2004) but harbor 35% of known vertebrate species (Balian et al. 2008) including ~70 mammalian genera (Veron et al. 2008). However, anthropogenic changes including climate change and habitat conversion are reducing the extent of freshwater wetlands (Ouyang et al. 2014; Han et al. 2015) and altering the composition of vertebrate communities within them (Kampichler et al. 2012). Increased woody plant abundance (shrub encroachment) is an example of anthropogenic change in grassy wetlands (Duever 2005; Warren et al. 2007) that is facilitated by increased atmospheric CO₂ associated with climate change (Ratajczak et al. 2012; Saintial and Rogers 2015), altered hydrology (Quintana-Ascencio et al. 2013), and wildfire suppression (Lee et al. 2005). Directional shifts in vegetation structure can alter the composition of both plant and animal communities in wetlands (Tesauro and Ehrenfeld 2007; Tape et al. 2018). However, research focusing on understanding how directional shifts in wetland vegetation may influence rare and threatened wildlife is limited (Pringle et al. 2009).

One species that may be impacted by shrub encroachment in freshwater wetlands is the Sanibel Island rice rat (*Oryzomys palustris sanibeli*), a subspecies of the broadly distributed and common semiaquatic marsh rice rat (*Oryzomys palustris ssp.*). The Sanibel Island rice rat is a genetically distinct and geographically isolated subspecies (Indorf and Gaines 2013) described from Sanibel and Captiva islands along the southwest Florida coast (Hamilton 1955; Indorf and Gaines 2013; Fig. 1). This subspecies is a candidate for listing under the Endangered Species Act as a distinct population segment (FWC 2011, 2013; NWRA 2015). In general, rice rats are known to occupy forested freshwater wetlands (Ivey 1959; Romanach et al. 2021) but rarely occur in freshwater wetlands with dense shrubs (Negus et al. 1961; Wolfe 1982). Additionally, other island endemic subspecies of marsh rice rats use mangrove forest;

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Fig. 1.—ArcGIS (Ver. 10.1) was used to randomly select 18 sites at least 300 m apart in each of three vegetation communities (mangrove, buttonwood, and sand cordgrass; n = 54 sites total) to investigate Sanibel Island rice rat occurrence and colonization/extinction dynamics on Sanibel Island, Florida, United States.

however, it is unclear which vegetative communities are used by Sanibel Island rice rats (Goodyear 1992; Krauss et al. 2011; Taillie et al. 2020). Previous sampling efforts on Sanibel Island have focused solely on areas of grassy freshwater wetlands, excluding shrub-encroached wetlands and mangrove forests (Humphrey et al. 1986). Much of the island's grassy freshwater wetlands appear to be degraded from increased shrub encroachment, potentially a result of changes to the island's hydrology from the construction of canals (Humphrey et al. 1986; City of Sanibel 2013). The construction of canals has decreased the risk of houses flooding on the island while storing water for human use during the dry season (City of Sanibel 2013). However, hydrologic changes have led to shorter inundation duration at higher elevations and longer inundation duration at lower elevations. Coupled with future projections of elevated rainfall (Easterling et al. 2017), increased water level fluctuations, and a rising water table caused by rising sea level (Rotzoll and Fletcher 2013), the island's altered hydrology is likely to increase water persistence and fluctuations in wetlands, both of which harm marsh rice rats (Garrie et al. 2016).

Accordingly, our objectives for this study were to understand seasonal associations of Sanibel Island rice rats with wetland vegetation and metrics associated with inundation, and to determine the long-term shifts in the distribution of woody vegetation on Sanibel Island. First, to provide context we determined the change in woody vegetative coverage on Sanibel Island between 1944 and 2015. Next, we conducted an intensive multiyear, multiseason sampling effort to compare measures of vegetation and inundation with Sanibel Island rice rat occurrence and occupancy dynamics. To accomplish our objectives we used occurrence data and a dynamic occupancy approach because they allowed us to examine the influence of site-specific factors on habitat selection and patch dynamics while accounting for imperfect detection (MacKenzie et al. 2003, 2006). We assumed that Sanibel Island rice rats were semiaquatic wetland specialists that required habitats dominated by herbaceous groundcover such as historically abundant sand cordgrass (Spartina bakeri; Wolfe 1982; Humphrey et al. 1986). We predicted that Sanibel Island rice rat (i) occurrence and seasonal localized colonization would be positively associated with greater sand cordgrass cover and negatively associated with lesser shrub cover, (ii) seasonal localized extinction would increase with greater amounts of shrub cover and decrease with elevated sand cordgrass cover, (iii) occurrence would be reduced and seasonal extinctions would increase in wetlands at lower elevations and during seasonal increases in rainfall because of increased inundation, and (iv) the Sanibel Island rice rat would be found to inhabit mangrove forests.

MATERIALS AND METHODS

Study site.—We studied the Sanibel Island rice rat on Sanibel Island; a ~4,900-ha barrier island in southwestern Florida (Fig. 1; City of Sanibel 2013). Approximately 50% of the island was designated for conservation, and most of the remaining land has

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been developed (City of Sanibel 2013). Sanibel Island experiences a distinct wet season in summer and fall, when ~85% of annual rainfall occurs (Kushlan 1987). Remnant sand ridges ~1-2 m above mean sea-level trap rainwater within the island's interior, creating seasonal wetlands (Boggess 1974) vegetated year-round by emergent freshwater plant communities (City of Sanibel 2013). Historically, high tides and storm surges periodically inundated these freshwater wetlands with saltwater, limiting the extent of salt-intolerant plant species (Humphrey et al. 1986). However, the natural outfall of the island's freshwater wetlands was capped in 1951 to store freshwater and prevent saltwater intrusion (Humphrey et al. 1986). Although historic accounts documented nearly continuous grasslands (sand cordgrass) within the island's interior (Hammond 1970), woody species (predominantly buttonwood; Conocarpus erectus) have invaded much of the island's interior potentially because of reductions in freshwater persistence and reduced saltwater intrusion (Humphrey et al. 1986). Additionally, giant leather fern (Acrostichum danaeifolium) is now abundant in areas with prolonged freshwater inundation. Northern portions of the island (areas along Pine Island Sound), largely contained within J.N. Ding Darling National Wildlife Refuge (Fig. 1), consist of saline mangrove forests.

Change in shrub cover.—We assessed changes in woody vegetation within the range of the Sanibel Island rice rat over the preceding 71 years using remotely sensed data from Sanibel's interior freshwater conservation areas. We selected 1944 because it was the earliest year for which aerial imagery of Sanibel Island was available, and because it predated the large-scale development of Sanibel Island (City of Sanibel 2013). We selected 2015 because it was the first year of our field research on the Sanibel Island rice rat.

We obtained 1944 monochromatic aerial photographs (n =12) of Sanibel Island from the online Map and Imagery Library at the University of Florida where they were catalogued on behalf of the US Department of Agriculture. These photographs were single-band black and white with 0.3-m resolution taken in January and February. We georeferenced the 1944 photographs in ArcGIS (ESRI 2012) and merged them into a single raster file using the Create Mosaic Dataset function. We then utilized a supervised approach, which uses training polygons identified as each possible cover type, to classify cover as either shrub or other based on the darkness of each pixel. We excluded areas with dense tree cover from our study and, because we were unable to differentiate between shrubs and trees, we considered all woody vegetation, including any mangroves occurring in freshwater wetlands, to be shrubs. We believe the absence of trees observed in these wetlands in historical records supports this decision (Hammond 1970). We created a shapefile of current conservation areas dominated by freshwater plant communities by modifying a conservation lands shapefile from the Florida Natural Areas Inventory (FNAI 2015) to omit saltwater and upland vegetative communities, which are naturally dominated by woody vegetation. Finally, we calculated the area of each category, shrub or other, within the freshwater conservation lands shapefile using the Isectpolyrst function in Geospatial Modeling Environment (Beyer 2018).

We calculated shrub cover in 2015 using publicly available (Lee County, Florida government) true color (red, blue, and green bands) georeferenced aerial imagery with 0.15-m resolution from January 2015. We used a supervised approach to classify images based on true color spectral reflectance values in ArcGIS, enabling the selection of land-cover classes a priori (Ozesmi and Bauer 2002). Land-cover classes included shrubs, sand cordgrass, giant leather fern, and open water. We differentiated between additional cover classes with the 2015 imagery because the additional bands allowed for a more thorough classification of vegetative communities. We then calculated the area of each category within the previously created shapefile of freshwater conservation lands using the Isectpolyrst function in Geospatial Modeling Environment.

We assessed the accuracy of our remotely sensed 2015 shrub cover estimates using data collected at nine points in a grid format with 30-m spacing on each of the 27 grids not occurring in saltwater and upland vegetative communities (Fig. 2). We recorded a binary measure determined using on-site visual inspection of whether shrub cover was dominant (no = 0; yes = 1) at each point during the 2015 field season and then within a 1-m buffer of each point in the remotely sensed data layer. We then calculated omission and commission error rates to assess the accuracy of our classification (Jensen 2005). We then assessed the accuracy of our remotely sensed 1944 shrub cover



Fig. 2.—Trapping was conducted at each site on a 5×5 trapping grid with 15-m spacing between traps. We sampled vegetation at a standardized subset of nine nonadjacent points on each grid. We used these same nine vegetation sampling points to assess shrub cover omission and commission classification errors using 2015 aerial imagery on a subset of 27 grids not occurring in communities naturally dominated by woody species.

estimates by visually inspecting the 1944 imagery for shrub cover dominance (no = 0; yes = 1) at 200 points randomly generated in ArcGIS. We then compared this to shrub dominance within a 1-m buffer in the 1944 remotely sensed data layer and calculated omission and commission error rates (Jensen 2005).

Trapping.—To select sampling sites, we first used vegetation data from the Florida Natural Areas Inventory in ArcGIS to delineate three vegetative communities (mangrove, buttonwood, and sand cordgrass) that were dominant on Sanibel Island. We then used ArcGIS to select 18 points spaced >300 m apart within each vegetation community (54 sites total; Fig. 1). Around each point, we created a trapping site to investigate use of these areas by Sanibel Island rice rats. Due to the highly interspersed nature of the vegetative communities, individual sites frequently had some components of other vegetative communities.

At each site we constructed a 5×5 grid of Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida) with 15-m spacing between traps (0.36 ha; Fig. 2). We attached traps to floating platforms to prevent submersion and secured them in place using wooden dowels. We baited traps with a black oil sunflower seed and millet mix. To capture annual and seasonal variation, we trapped each grid for four consecutive nights in summer (June-August) and winter (December-February) for three consecutive years starting June 2015. Upon capture each morning, we removed the animal from the trap and handled it in a mesh bag. We marked each new capture with a uniquely numbered Monel 1005-1 ear tag (National Band and Tag Co., Newport, Kentucky). We recorded the tag number for each capture. We released all rodents at their place of capture immediately following processing. Trapping and handling procedures conformed to guidelines established by the American Society of Mammalogists (Sikes et al. 2016) and were approved by the University of Florida's Institutional Animal Care and Use Committee (study #201508922).

Vegetation.—To assess possible associations between occurrence dynamics of Sanibel Island rice rats and variability in vegetation, we surveyed sand cordgrass cover and mangrove abundance each summer (n = 3) at nine trapping points per site (Fig. 2) on buttonwood and sand cordgrass grids (n = 36) to account for annual change in these sites. We conducted identical vegetation surveys on mangrove grids (n = 18), but only during the first summer because visual inspection revealed negligible vegetation change between summers. To estimate percent cover of sand cordgrass within a 0.25-m² quadrat at each trapping point we used a 7-class version (Bailey and Poulton 1968) of Daubenmire's (1959) cover-classification scale. To estimate mangrove abundance, we counted mangrove stems within a 4-m² quadrat around the nine trapping points. We averaged vegetation variables for all nine points at each site to create a single measurement for each variable of interest at each site.

We remotely sensed shrub cover in 0.44-ha circular polygons (75-m diameter) at each site in ArcGIS using the classified 2015 aerial imagery data layer created above. We discarded shrub cover calculations from sites dominated by mangrove or upland tropical hammock vegetation (n = 27) because these areas are

naturally dominated by woody vegetation. Instead, we inserted the mean shrub cover value from the remotely sensed sites (n = 27) in place of the discarded shrub cover calculations to avoid positively or negatively skewing the data distribution. We classified all woody vegetation as shrubs. We selected a scale of 75 m because it captured the extent of our grids (5×5 , 15-m spacing). We chose this grid scale because it provided fine-scale inference regarding occurrence of Sanibel Island rice rats.

Inundation.-To determine if, like other marsh rice rats (Garrie et al. 2016), the Sanibel Island rice rat's seasonal occupancy dynamics were influenced by measures of relative inundation such as rainfall and elevation, we obtained rainfall data for Sanibel Island from the National Oceanic and Atmospheric Administration. We then calculated the cumulative rainfall total for the 3 months before the midpoint of each field season (summer = 15 July; winter = 15 January). Therefore, rainfall totals varied between field seasons but not between sites. We measured average elevation within a 75-m diameter buffer centered around each site in ArcGIS to determine if elevation, used as an inverse measure of inundation potential or water depth, was associated with occurrence dynamics of Sanibel Island rice rats. We calculated average elevation using publicly available LiDAR data (South Florida Water Management District) with >0.01-m resolution by averaging the elevation of all 3.05×3.05 -m pixels contained within the 75-m diameter buffer.

Statistical analysis.--We investigated the relationship among vegetation, inundation metrics, and Sanibel Island rice rat occurrence using a Bayesian occupancy modeling approach that accounted for imperfect detection (MacKenzie et al. 2006; Royle and Dorazio 2008). This flexible and robust Bayesian approach is useful for data sets with sparse detections (Royle and Dorazio 2008). We recorded a binary measure of detection (observed = 1, not observed = 0) for Sanibel Island rice rats cumulatively for 25 trap grids at each site (n = 54) for each trapday (days 1-4) during each survey. We included survey number 1 through 6, with summer 2015 being survey 1 and winter 2017-2018 being survey 6, as a random effect to account for the lack of independence associated with sampling the same sites during multiple surveys (Kéry and Schaub 2012). We first investigated if trap-day or season (summer = one, winter = zero) accounted for variable detection (p) and included significant predictors in subsequent analysis (MacKenzie et al. 2006). We then built single-variable (sand cordgrass cover, shrub cover, mangrove abundance, and elevation; variable descriptions in Table 1) models modifying occupancy (ψ) to avoid (i) issues associated with variable collinearity (Graham 2003) as denoted by pairwise absolute correlation coefficients > 0.7(Dormann et al. 2013) and (ii) phantom interactions (Jones and Peery 2019) resulting from the back-transformation of parameter estimates from additive and interactive effects models. We standardized covariates, so their mean was zero. We calculated the posterior distributions of each parameter using Markov chain Monte Carlo (MCMC) implemented in JAGS (Plummer 2011) via program R (R Development Core Team 2017). We used uninformative (uniform) priors (Gilks et al. 1996) and for each model generated three chains of 250,000 iterations with

Variable	Description
Abbreviation	
Elevation	Elevation of each site, averaged within a 75-m diameter buffer centered around each site
Mangrove abundance	Count of all mangrove stems per 4-m ² quadrat, averaged across nine points per site
Sand cordgrass cover	Cover (%) of sand cordgrass (Spartina bakeri) within 0.25-m ² quadrats, averaged across nine
-	points per site
Shrub cover	Shrub cover (%) remotely sensed (aerial imagery analyzed in ArcGIS) within a 75-m diameter
	buffer centered around each site
Three-month rainfall total	Total rainfall in 3 months before midpoint of the field season (summer = 15 July; winter = 15
	January)

Table 1.—Description	of variables included in Sanibel Isla	nd rice rat (Oryzomys palustris	sanibeli) occupancy analyses
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a burn-in of 50,000 iterations and a thinning rate of 10. We assessed model convergence by visually inspecting trace plots and using the Gelman–Rubin diagnostic (Rhat), where convergence was reached when Rhat < 1.1 (Gelman and Hill 2007). We considered covariates significant when their 95% Bayesian credibility interval (CRI) was not inclusive of zero.

Although our Bayesian models provided insight into Sanibel Island rice rat occurrence, we were also interested in temporal patterns of seasonal localized colonization and extinction. To understand how occupancy dynamics were associated with vegetation, rainfall, and inundation potential, we modeled change in Sanibel Island rice rat occurrence between surveys (n = 6)using a dynamic occupancy modeling approach implemented in program R using the unmarked package (Fiske and Chandler 2011). This approach accounted for imperfect detection when modeling Sanibel Island rice rat colonization (γ) and extinction (ɛ; MacKenzie et al. 2003; MacKenzie et al. 2006; Royle and Dorazio 2008). Based on our previous model, we included significant predictors of Sanibel Island rice rat detection (MacKenzie et al. 2006). We first tested three null models that included just one covariate (either sand cordgrass, shrub cover, or elevation) on initial occupancy (initial ψ). Then, we modeled the influence of vegetation and inundation potential (sand cordgrass cover, shrub cover, mangrove abundance, 3-month rainfall total, and elevation) on colonization or extinction with each of the three initial occupancy covariates (sand cordgrass cover, shrub cover, and elevation), yielding 15 colonization and 15 extinction models. We ranked these 18 models separately for colonization and extinction analyses using Akaike's Information Criterion (AIC). We considered models with ΔAIC < 2 to be competing models (Akaike 1973; Burnham and Anderson 2002). We considered covariates in competing models with model averaged 95% confidence intervals not intersecting zero to be important predictors of Sanibel Island rice rat colonization or extinction.

RESULTS

We found that shrub cover increased in currently protected freshwater wetlands from 9.8% in 1944 to 63.3% in 2015 (Fig. 3). This increase in shrub cover equates to shrub encroachment of 398 ha of potential rice rat freshwater habitat on Sanibel Island.



Fig. 3.—ArcGIS (Ver. 10.1) was used to remotely sense change in shrub cover from 1944 to 2015 within freshwater interior conservation areas of Sanibel Island. Buttonwood (*Conocarpus erectus*) was the dominant invading shrub. The "other" classification was a catch-all category including sand cordgrass (*Spartina bakeri*), giant leather ferm (*Acrostichum danaeifolium*), and open water. Shrub cover increased from 9.8% in 1944 to 63.3% in 2015, a ~5.5-fold increase in 71 years.

Our omission and commission error for shrub cover classification was 13.3% and 2.2% for 1944 imagery, respectively, and 6.3% and 4.8% for 2015 imagery, respectively.

The Sanibel Island rice rat occurred on 18 (33.3%) of our 54 sites, including five mangrove, three buttonwood, and 10 sand cordgrass sites. Neither trap-day ($\beta = 1.26$; CRI = -11.95 to 17.54; Rhat = 1.03) nor season ($\beta = -0.24$; CRI = -0.76 to 0.26; Rhat = 1.00) was a significant predictor of detection, so we included no covariate(s) on detection in subsequent models. Occurrence of Sanibel Island rice rats was positively associated with sand cordgrass cover ($\beta = 0.74$; CRI = 0.44 to 1.05; Rhat = 1.00) and elevation ($\beta = 0.37$; CRI = 0.02 to 0.73; Rhat = 1.00)

but negatively associated with shrub cover ($\beta = -1.32$; CRI = -1.82 to -0.85; Rhat = 1.00). Occurrence estimates ranged from near 0.93 in areas with no shrub cover to <0.18 in areas with >60% shrub cover (Fig. 4). Conversely, we found occupancy as high as 0.89 at sites with 100% sand cordgrass cover, up from 0.27 at sites with 0% sand cordgrass. Occupancy ranged from 0.15 to 0.64 across an elevational gradient from 0 to 4 m. Mangrove abundance ($\beta = -0.17$; CRI = -0.59 to 0.20; Rhat = 1.00) was not a significant predictor of occurrence.

Examining variation in seasonal colonization, we found two competing models with $\Delta AIC < 2$ (Table 2). In the best model, initial occupancy ($\beta = -1.13, 95\%$ CI = -2.23 to -0.03) and colonization ($\beta = -1.01, 95\%$ CI = -1.67 to -0.35) were negatively associated with shrub cover. The probability of colonization

was reduced from 0.43 in areas with no shrub cover to <0.05 in areas with >50% cover (Fig. 5). The second-best colonization model ($\Delta AIC = 1.93$) included a similar negative association between shrub cover and colonization ($\beta = -1.01$, 95% CI = -1.67 to -0.35; Fig. 6), with sand cordgrass cover ($\beta = 0.66$, 95% CI = -0.08 to 1.41) as an uninformative predictor of initial occupancy.

Examining variation in seasonal extinction dynamics, we found three competing models (Table 3). In the best model, seasonal extinction probability of Sanibel Island rice rats was positively associated with 3-month rainfall total ($\beta = 0.24$, 95% CI = 0.05 to 0.42) and initial occupancy was negatively associated with shrub cover ($\beta = -1.14$, 95% CI = -2.24 to -0.04). The probability of seasonal extinction changed from



Fig. 4.—Predicted relationships of (a) shrub cover, (b) sand cordgrass cover, and (c) elevation with Sanibel Island rice rat occurrence. Solid lines depict model averages and dotted lines depict 95% credibility intervals from the Bayesian analysis performed in JAGS (Ver. 4.2.0).

Table 2.—Number of parameters (*K*), AIC, Δ AIC, and model weight (w) for 18 models investigating Sanibel Island rice rat colonization (γ) dynamics. The three models without covariates on γ were considered null models. We placed no covariates on extinction (ε) or detection (*p*). We conducted trapping across 54 sites during summer (June–August) and winter (December–February) for three consecutive years starting summer 2015. We trapped individual sites for four consecutive nights for each summer and winter field season.

Model	K	AIC	ΔΑΙΟ	W
γ (shrub), ε (.), initial ψ (shrub), p (.)	6	370.67	0.00	0.59
γ (shrub), ε (.), initial ψ (cordgrass), p (.)	6	372.60	1.93	0.22
γ (cordgrass), ε (.), initial ψ (shrub), p (.)	6	375.16	4.50	0.06
γ (shrub), ε (.), initial ψ (elevation), p (.)	6	375.45	4.78	0.05
γ (cordgrass), ε (.), initial ψ (cordgrass), p (.)	6	377.16	6.50	0.02
$\gamma(.), \varepsilon(.), \text{ initial } \psi(\text{shrub}), p(.)$	5	378.63	7.97	0.01
γ (elevation), ε (.), initial ψ (shrub), p (.)	6	379.22	8.56	0.01
γ (cordgrass), ε (.), initial ψ (elevation), p (.)	6	380.01	9.34	0.01
γ (mangrove), ε (.), initial ψ (shrub), p (.)	6	380.02	9.36	0.01
$\gamma(.), \varepsilon(.), \text{ initial } \psi(\text{cordgrass}), p(.)$	5	380.65	9.99	0.00
γ (elevation), ε (.), initial ψ (cordgrass), p (.)	6	381.25	10.59	0.00
γ (mangrove), ε (.), initial ψ (cordgrass), p (.)	6	382.03	11.37	0.00
$\gamma(.), \varepsilon(.), \text{ initial } \psi(\text{elevation}), p(.)$	5	383.50	12.84	0.00
γ (elevation), ε (.), initial ψ (elevation), p (.)	6	384.09	13.43	0.00
γ (mangrove), ε (.), initial ψ (elevation), p (.)	6	384.86	14.20	0.00
γ (rain), ε (.), initial ψ (shrub), p (.)	6	473.90	103.24	0.00
γ (rain), ε (.), initial ψ (cordgrass), p (.)	6	475.25	104.59	0.00
γ (rain), ε (.), initial ψ (elevation), p (.)	6	482.43	111.76	0.00

0.09 to 0.79 as seasonal rainfall ranged from 0 to 40 cm (Fig. 5). The second-best model (Δ AIC = 1.61) included a positive association between shrub cover and extinction (β = 1.09, 95% CI = 0.09 to 2.09) and negative relationship between shrub cover and initial occupancy (β = -1.16, 95% CI = -2.27 to -0.05). We found elevated probabilities of seasonal extinction (from 0.17 to 0.85) when cover ranged from 0 to >60% (Fig. 5). The final competing model (Δ AIC = 1.95) included a positive association between 3-month rainfall total and extinction (β = 0.24, 95% CI = -0.08 to 1.41) as an uninformative predictor of initial occupancy. As more rainfall was recorded (from 0 to 40 cm), we saw a shift in extinction probabilities from 0.09 to 0.77 (Fig. 6).

DISCUSSION

Sanibel Island's protected freshwater wetlands experienced a 5.5-fold increase in shrubby vegetation and a simultaneous reduction in herbaceous wetland vegetation over 71 years prior to the initiation of our field work (1944–2015). Our 2015–2018 trapping data of the island's endemic Sanibel Island rice rat showed markedly lesser occurrence and seasonal colonization probabilities and greater seasonal extinction probabilities (Figs. 4–6) at sites with greater shrub cover and minimal native grass cover. Combined, our data provide evidence that the directional shift toward woody vegetation (i.e., shrub encroachment) in island freshwater wetlands may be limiting this once-common subspecies (Humphrey et al. 1986).

The encroachment of woody vegetation into freshwater wetlands is a global trend (Duever 2005; Warren et al. 2007) with complex and largely unknown implications for endemic vertebrate species. However, there are several ways that changes in woody vegetation may deter small mammals. Specifically, rodents that evolved in open grassy environments may perceive an increased risk of predation with increased woody vegetation (Schooley et al. 1996; Jayadevan et al. 2018) and corresponding reductions of herbaceous cover (Coleman and Hill 2014; Riginos 2015; Loggins et al 2019). With more perches for raptors, minimal cover, and few escape routes from predators such as barn owls (Tyto alba; Horner at al. 1974) and bobcats (Lynx rufus; Thornton et al. 2004), Sanibel Island rice rats may avoid or reduce their activity in these areas (Wolfe 1982). Additionally, woody vegetation in wetlands may alter macroinvertebrate communities (De Szalay and Resh 2000), an important food source for marsh rice rats (Wolfe 1982). Macroinvertebrates can be less abundant and diverse in wooded wetlands compared to open, grass-dominated wetlands (Battle and Golladay 2001). Increasing woody vegetation is also often accompanied by loss of the grassy vegetation. Grasses are an important component of the marsh rice rat's diet (Negus et al. 1961; Hamilton and Whitaker 1979). Grasses are also used to weave nests (Hamilton 1946; Goodpaster and Hoffmeister 1952) and attach nests to elevated marsh vegetation, particularly grasses and reeds in flooded areas (Audubon and Bachman 1854; Sharp 1967; Wolfe 1982).

We found associations of Sanibel Island rice rats with measures of inundation. They were more likely to occur in areas at higher elevation (Fig. 4c). Areas below 0.98 m often experience prolonged flooding from the island's canal and weir system (City of Sanibel 2013). Prolonged flooding may sustain predators of invertebrates (i.e., fish), reducing one of the Sanibel Island rice rat's potential food sources (Corti et al. 1997; Liston 2006). Similarly, we found that elevated seasonal rainfall can



Fig. 5.—Predicted relationships between (a) shrub cover and Sanibel Island rice rat colonization, and (b) shrub cover and (c) 3-month rainfall total and Sanibel Island rice rat extinction. Solid lines depict model averages and dotted lines depict 95% confidence intervals.

increase local extinction probabilities, likely as animals retreat to higher, dry ground. This aligns with research from freshwater (Garrie et al. 2016) and tidal saltwater (Kruchek 2004) systems where local extinctions were caused by flooding, forcing rice rats to utilize areas of higher elevation. However, the upland ridges on Sanibel Island that historically may have provided refuge during flooding are now commonly developed or dominated by woody vegetation. These flooding events are only likely to increase in the near future with projections of intense rainfall events and increases to the island's water table due to sea-level rise (Rotzoll and Fletcher 2013; Easterling et al. 2017). As predicted, the Sanibel Island rice rat did occur in mangrove forests. We found no evidence that a salt versus freshwater community influenced their occurrence, and we were unable to determine the relative importance of mangrove forests. Although we captured Sanibel Island rice rats in mangrove forests during summer and winter, we do not know if they persisted throughout the year or used these areas intermittently. This finding is noteworthy because this subspecies was not previously known to inhabit mangrove forests. If mangrove forests represent viable long-term habitat, as was recently found for another island endemic subspecies of rice rat in south Florida (Taillie et al. 2020), this would increase the



Fig. 6.—Predicted relationships between (a) shrub cover and Sanibel Island rice rat colonization, and (b) 3-month rainfall total and Sanibel Island rice rat extinction. Solid lines depict model averages and dotted lines depict 95% credibility intervals. These relationships are similar to those found in higher-ranked competing models (Fig. 5).

Table 3.—Number of parameters (*K*), AIC, Δ AIC, and model weight (w) for 18 models investigating Sanibel Island rice rat extinction (ε) dynamics. The three models without covariates on ε were considered null models. We placed no covariates on colonization (γ) or detection (*p*). We conducted trapping across 54 sites during summer (June–August) and winter (December–February) for three consecutive years starting summer 2015. We trapped individual sites for four consecutive nights for each summer and winter field season.

Model	K	AIC	ΔΑΙC	W
$\gamma(.), \epsilon(rain), initial \psi(shrub), p(.)$	6	372.94	0.00	0.34
$\gamma(.), \epsilon(\text{shrub}), \text{ initial } \psi(\text{shrub}), p(.)$	6	374.54	1.61	0.15
$\gamma(.), \epsilon(rain), initial \psi(cordgrass), p(.)$	6	374.89	1.95	0.13
$\gamma(.), \epsilon(\text{cordgrass}), \text{ initial } \psi(\text{shrub}), p(.)$	6	375.03	2.09	0.12
$\gamma(.), \epsilon(\text{shrub}), \text{ initial } \psi(\text{cordgrass}), p(.)$	6	376.59	3.65	0.06
$\gamma(.), \epsilon(\text{cordgrass}), \text{ initial } \psi(\text{cordgrass}), p(.)$	6	377.04	4.10	0.04
$\gamma(.), \epsilon$ (elevation), initial ψ (shrub), $p(.)$	6	377.53	4.59	0.03
$\gamma(.), \epsilon(rain), initial \psi(elevation), p(.)$	6	377.75	4.81	0.03
$\gamma(.), \varepsilon(.), \text{ initial } \psi(\text{shrub}), p(.)$	5	378.63	5.70	0.02
$\gamma(.), \epsilon(\text{shrub}), \text{ initial } \psi(\text{elevation}), p(.)$	6	379.42	6.49	0.01
$\gamma(.), \epsilon$ (elevation), initial ψ (cordgrass), $p(.)$	6	379.53	6.59	0.01
$\gamma(.), \epsilon(\text{cordgrass}), \text{ initial } \psi(\text{elevation}), p(.)$	6	379.85	6.91	0.01
$\gamma(.), \epsilon(\text{mangrove}), \text{ initial } \psi(\text{shrub}), p(.)$	6	380.07	7.13	0.01
$\gamma(.), \varepsilon(.),$ initial ψ (cordgrass), $p(.)$	5	380.65	7.72	0.01
$\gamma(.), \epsilon(\text{mangrove}), \text{ initial } \psi(\text{cordgrass}), p(.)$	10	382.10	9.16	0.00
$\gamma(.), \epsilon$ (elevation), initial ψ (elevation), $p(.)$	6	382.36	9.42	0.00
$\gamma(.), \epsilon(.), \text{ initial } \psi(\text{elevation}), p(.)$	5	383.50	10.56	0.00
$\gamma(.), \varepsilon(\text{mangrove}), \text{ initial } \psi(\text{elevation}), p(.)$	6	384.95	12.01	0.00

Modifications of vegetative composition in shrub-encroached systems like Sanibel Island have been associated with altered wildlife communities in terrestrial (see Stanton et al. 2018) and wetland (Austin and Buhl 2013; Dorado-Rodrigues et al. 2015) systems. Our findings indicate that shrub encroachment of freshwater wetlands is a serious risk for the Sanibel Island rice rat, and should be assessed for other wetland endemic wildlife species. This observation is particularly concerning because globally, wetlands are home to numerous rare and threatened wildlife species (Niering 1988; Junk et al. 2006).

Conservation efforts for the Sanibel Island rice rat should focus on increasing the coverage of herbaceous vegetation within freshwater wetlands by removing encroaching buttonwood shrubs from Sanibel's freshwater interior and increasing the extent of sand cordgrass marshes. Methods successfully employed to remove woody species from wetlands should be tested and evaluated. Specifically, mechanical removal, herbicide use, and prescribed fire application have successfully aided the removal of shrubs from other wetland systems (Clark and Wilson 2001; Paynter and Flanagan 2004; Klimkowska et al. 2010). Restoration and conservation efforts must include upland areas in addition to areas of prolonged flooding. Conservation efforts in upland areas should restore native grasses and tropical hammock, and remove buttonwood shrub cover and lawns. Restoring these uplands could provide refuge for Sanibel Island rice rats during future floods.

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