

# Shrub Encroachment Threatens Persistence of An Endemic Insular Wetland Rodent

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## Research Article

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# Abstract

Shrub encroachment is altering the structure and species composition of freshwater wetlands across the globe. These changes are likely to be particularly detrimental for threatened wetland vertebrates. However, little research has focused on how shrub encroachment influences threatened wetland vertebrates. We sought to determine how vegetative structure and shrub cover influenced the occurrence of a threatened semi-aquatic mammal species, the Sanibel Island rice rat (*Oryzomys palustris sanibeli*). Using aerial photography from across the Sanibel Island rice rat's range, we found a 5.5-fold increase in shrub cover over a 71-year period. To link these changes to the current distribution of the species, we evaluated the influence of vegetation and metrics of inundation on probability of occurrence and localized colonization and extinction rates over a three-year period. We found Sanibel Island rice rats on 18 (33.3%) of our 54 sites. Their occurrence was positively associated with elevated sand cordgrass (*Spartina bakeri*) cover and increased elevation, but negatively associated with elevated shrub cover. Their probability of colonization was negatively associated with increased shrub cover. Extinction probabilities for Sanibel Island rice rats were positively associated with increased rainfall totals in the preceding three months and increased shrub cover. Increases in shrub cover reduce sand cordgrass cover, which additively may be driving the decline of this once ubiquitous species. We conclude that shrub encroachment of freshwater wetlands requires greater attention due to its potential to imperil wetland endemic wildlife species.

# Introduction

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). However, anthropogenic induced changes are reducing the extent of freshwater wetlands (Ouyang et al. 2014; Han et al. 2015) and altering the composition of vertebrate species 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), being facilitated by increased atmospheric CO<sub>2</sub> (Ratajczak et al. 2012; Saintial and Rogers 2015). This directional shift in vegetation structure can alter the composition of plant and animal communities (Tesauro and Ehrenfeld 2007; Tape et al. 2018). However, scant research has focused on understanding how directional shifts in wetland vegetation may influence rare and threatened wildlife (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 semi-aquatic 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 (NWRA 2015; FWC 2011; 2013). Although the Sanibel Island rice rat appears to be ecologically distinct from mainland populations of conspecifics (Birkenholz 1963; Forys et al. 1996; Mitchell 1996), marsh rice rats generally are not associated with woody or forested freshwater wetlands (Wolfe 1982; Eubanks et al. 2011; Humphrey et al. 1986).

Nonetheless, it is possible that like other island endemic subspecies of marsh rice rats in south Florida (Goodyear 1992), Sanibel Island rice rats are taking advantage of the mangrove forests that have been expanding in southern Florida (Krauss et al. 2011). However, previous sampling efforts have focused solely on areas of grassy freshwater wetlands (Humphrey et al. 1986), and it is unclear which vegetation communities are used by Sanibel Island rice rats. Recent monitoring efforts (2003-2015) suggest that the Sanibel Island rice rat has become rare but is capable of shifting their use of vegetation communities seasonally and annually (unpublished data). In addition to changes in vegetation, Sanibel Island has undergone extensive changes to its hydrology from construction of canals and water control structures (City of Sanibel 2013). These changes, 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), may increase water persistence and fluctuations in wetlands, both of which appear to harm marsh rice rats (Garrie et al. 2016).

Accordingly, our goals 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 woody vegetation on Sanibel Island. First, we determined the change in woody vegetation coverage on Sanibel Island between 1944 and 2015. Next, we conducted an intensive multi-year, multi-season sampling effort to link measures of vegetation and inundation with Sanibel Island rice rat occurrence and occupancy dynamics. We worked under the assumption that Sanibel Island rice rats are a semi-aquatic wetland specialist that requires habitats dominated by herbaceous groundcover (Wolfe 1982) such as historically-abundant sand cordgrass (*Spartina bakeri*; Humphrey et al. 1986). We predicted that Sanibel Island rice rat (1) occurrence and seasonal colonization would be positively associated with elevated sand cordgrass cover and negatively associated with increased shrub cover, (2) seasonal extinction would increase with elevated shrub cover and decrease with elevated sand cordgrass cover, (3) 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 (4) the Sanibel Island rice rat would be found to inhabit mangrove forests.

## Materials And Methods

### 2.1. Study site

We studied the Sanibel Island rice rat on Sanibel Island; a ~4,900-ha barrier island in southwestern Florida (City of Sanibel 2013). Approximately 50% of the island was designated for conservation and most of the remaining land has 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 (Bogges 1974) vegetated year-round by freshwater plant communities (City of Sanibel 2013). Although historic accounts documented nearly-continuous grasslands (sand cordgrass) within the island's interior (Hammond 1970), woody species (predominately buttonwood; *Conocarpus erectus*) have invaded much of the island's interior (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.

## 2.2. Change in shrub cover

To understand how woody vegetation on the island has changed over the last 70 years, we remotely sensed change in shrub cover from 1944 to 2015 within freshwater interior conservation areas of Sanibel Island. 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 U.S. 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 (version 10.1, Esri, Redlands, California, USA) and merged them into a single raster file using the Create Mosaic Dataset function. We then utilized a supervised approach to classify cover as either shrub or other based on the darkness of each pixel. We considered all woody vegetation to be shrubs. 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 (version 0.7.2.1, Beyer 2018).

We calculated shrub cover in 2015 using publicly available (Lee County 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, and the additional classification data was useful to our land-managing collaborators. 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 9 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 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 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).

### **2.3. Trapping**

To select sampling sites, we first used vegetation data from the Florida Natural Areas Inventory in ArcGIS to delineate three vegetation 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 5x5 grid of Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida, USA) 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, USA). We recorded the tag number, age, sex, weight, reproductive status, and body, tail, and foot length 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).

### **2.4. Vegetation**

To link occurrence dynamics of Sanibel Island rice rats with variability in vegetation, we surveyed sand cordgrass cover and mangrove abundance each summer (n = 3) at 9 trapping points per site (Fig. 2) on buttonwood and sand cordgrass grids (n = 36) to account for annual change in these dynamic 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-m<sup>2</sup> quadrat at each trapping point we used a seven-class version (Bailey and Poulton 1968) of Daubenmire's (1959) cover-classification scale. To estimate mangrove abundance, we counted mangrove stems within a 4-m<sup>2</sup> 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 ( $n = 27$ ) as 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 x 5, 15-m spacing). We chose this grid scale because it provided fine-scale inference regarding Sanibel Island rice rat occurrence.

## 2.5. Inundation

To determine if, like other marsh rice rats (Garrie et al. 2016), the Sanibel Island rice rat's seasonal 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 three months before the midpoint of each field season (summer = July 15; winter = January 15). 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 Sanibel Island rice rat occurrence dynamics. 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  $3.05 \times 3.05$ -m pixels contained within the 75-m diameter buffer.

## 2.6. 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 2006; Royle and Dorazio 2008). This flexible and robust Bayesian approach permitted the use of data with sparse detections (Royle and Dorazio 2008). We standardized covariates so their mean was zero. 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 trap day (days 1-4) during each survey. We included survey number (1-6) 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 = 1, winter = 0) accounted for variable detection 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) models modifying occupancy to avoid (1) issues associated with variable collinearity (Graham 2003) and (2) phantom interactions (Jones and Peery 2019) resulting from the back-transformation of parameter estimates from additive and interactive effects models. We calculated the posterior distributions of each parameter using Markov chain Monte Carlo (MCMC) implemented in JAGS (v4.2.0) via program R (v3.4.2, R Core Team 2017) using the R2jags package (Plummer 2011). We used uninformative (uniform) priors (Gelman et al., 1995; Gilks et al., 1996) and for each model generated three chains of 250,000 iterations with 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 ( $R_{hat}$ ), where convergence was reached when  $R_{hat} < 1.1$  (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 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 ( $\gamma$ ) and extinction ( $\epsilon$ ; MacKenzie et al. 2003; MacKenzie 2006; Royle and Dorazio 2008). Based on our previous model, we included relevant predictors of Sanibel Island rice rat detection (MacKenzie et al. 2006). We modeled initial occupancy singularly within each model with the relevant predictors of occupancy from the previous analysis. Then we modeled the influence of vegetation and inundation potential (sand cordgrass cover, shrub cover, mangrove abundance, three 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 then tested three null models that just included one covariate (either sand cordgrass, shrub cover, or elevation) on initial occupancy. We ranked these 18 models separately for colonization and extinction analyses using Akaike's Information Criterion (AIC). We considered models with  $\Delta AIC < 2$  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. Our omission and commission error for shrub cover classification was 13.3% and 2.2% for 1944 imagery and 6.3% and 4.8% for 2015 imagery, respectively.

The Sanibel Island rice rat occurred on 18 (33.3%) of our 54 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) were relevant predictors of detection, so we included no covariate(s) on detection in subsequent models. 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) were positively associated with Sanibel Island rice rat occurrence whereas shrub cover ( $\beta$  -1.32; CRI -1.82 to -0.85; Rhat 1.00) was negatively associated. Occurrence estimates decreased from near 0.93 in areas with no shrub cover to  $< 0.18$  in areas with  $> 60\%$  shrub cover (Fig. 4). Conversely, occupancy increased from 0.27 to 0.89 with an increase from 0 to 100% cordgrass cover and from 0.15 to 0.64 with an increase in elevation from 0 to 4 m. Mangrove abundance ( $\beta$  -0.17; CRI -0.59 to 0.20; Rhat 1.00) was not a relevant predictor of occurrence.

Examining variation in seasonal colonization, we found two competing models (Table 1). 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 ( $\Delta\text{AIC} = 1.93$ ) 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 2). In the best model, seasonal extinction probability of Sanibel Island rice rats was positively associated with three month rainfall total ( $\beta = 0.24$ , 95% CI = 0.05 to 0.42) and shrub cover was negatively associated with initial occupancy ( $\beta = -1.14$ , 95% CI = -2.24 to -0.04). The probability of seasonal extinction increased from 0.09 to 0.79 as rainfall increased from 0 to 40 cm (Fig. 5). The second-best model ( $\Delta\text{AIC} = 1.61$ ) included a positive association between shrub cover and extinction ( $\beta = 1.09$ , 95% CI = 0.09 to 2.09) and negative relationship between shrub cover and initial occupancy ( $\beta = -1.16$ , 95% CI = -2.27 to -0.05). The probability of seasonal extinction increased from 0.17 to 0.85 in areas with zero shrub cover to areas with > 60 percent shrub cover (Fig. 5). The final competing model ( $\Delta\text{AIC} = 1.95$ ) included a positive association similar to that of the best competing model between three month rainfall total and extinction ( $\beta = 0.24$ , 95% CI = 0.05 to 0.43) with sand cordgrass cover ( $\beta = 0.67$ , 95% CI = -0.08 to 1.41) as an uninformative predictor of initial occupancy. As rainfall increased from 0 to 40 cm, we saw a marked increase in extinction probabilities from 0.09 to 0.77 (Fig. 6).

## Discussion

Sanibel Island's freshwater wetlands experienced a 5.5-fold increase in shrubby vegetation over 71 years (1944 to 2015) that was linked to reductions of herbaceous wetland vegetation. Meanwhile, the island's threatened and endemic rodent (the Sanibel Island rice rat) showed marked reductions in occurrence and seasonal colonization probabilities, and increased seasonal extinction probabilities (Fig. 4; Fig. 5; Fig. 6) at sites with elevated shrub cover and minimal native grass cover. Combined, our data provides strong evidence that the directional shift towards woody vegetation (i.e. shrub encroachment) in island freshwater wetlands is limiting this once-common subspecies (Humphrey et al. 1986).

The encroachment of freshwater wetlands by woody vegetation is a global trend (Duever 2005; Warren et al. 2007; Colloff et al. 2014) 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, 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 than open, grass-dominated wetlands (Battle and Golladay 2001). Furthermore, increasing woody vegetation is often accompanied by loss of the grassy vegetation associated with increased occurrence of Sanibel Island rice rats in our study. 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 greater 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 (Liston 2006; Corti et al. 1997). Similarly, we found that elevated seasonal rainfall can increase local extinction probabilities, as seen in the central Mississippi River floodplain (Garrie et al. 2016). Seasonal extinctions associated with increased rainfall, like elevation, was likely a function of flooding, forcing Sanibel Island rice rats to utilize areas of higher elevation (Kruczek 2004). However, the upland ridges on Sanibel Island that historically may have provided refuge during flooding are now commonly developed or shrub encroached. These temporal flooding events are only likely to increase in the near future with projections of intense rainfall events and sea-level-rise induced increases to the island's water table (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 salt vs. freshwater community influenced their occurrence, and 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, this would increase the area of conserved potential habitat from 744 to 2,049-ha.

Modifications of vegetation 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 may be a serious risk for 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.

## Declarations

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**Conflict of interest:** The authors declare that they have no conflict of interest.

**Availability of data and material:** Data and materials are available upon written request of the corresponding author.

**Code availability:** Annotated code and corresponding data are available upon written request of the corresponding author.

**Ethics approval:** 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).

**Availability of data and materials:** The datasets and code used during this study are available from the corresponding author on reasonable request.

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## Tables

**Table 1.**—Number of parameters ( $K$ ), AIC,  $\Delta$ AIC, and model weight ( $w$ ) for 18 models investigating Sanibel Island rice rat colonization ( $\gamma$ ) dynamics. The 3 models without covariates on  $\gamma$  were null models. We placed no covariates on extinction ( $\epsilon$ ) or detection ( $p$ ). We conducted trapping across 54 sites during summer (June - August) and winter (December - February) for 3 consecutive years starting summer 2015. We trapped individual sites for 4 consecutive nights per field season.

Model	K	AIC	$\Delta$ AIC	w
$\gamma(\text{shrub}), \epsilon(\cdot), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	370.67	0.00	0.59
$\gamma(\text{shrub}), \epsilon(\cdot), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	6	372.60	1.93	0.22
$\gamma(\text{cordgrass}), \epsilon(\cdot), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	375.16	4.50	0.06
$\gamma(\text{shrub}), \epsilon(\cdot), \text{initial } \psi(\text{elevation}), \rho(\cdot)$	6	375.45	4.78	0.05
$\gamma(\text{cordgrass}), \epsilon(\cdot), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	6	377.16	6.50	0.02
$\gamma(\cdot), \epsilon(\cdot), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	5	378.63	7.97	0.01
$\gamma(\text{elevation}), \epsilon(\cdot), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	379.22	8.56	0.01
$\gamma(\text{cordgrass}), \epsilon(\cdot), \text{initial } \psi(\text{elevation}), \rho(\cdot)$	6	380.01	9.34	0.01
$\gamma(\text{mangrove}), \epsilon(\cdot), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	380.02	9.36	0.01
$\gamma(\cdot), \epsilon(\cdot), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	5	380.65	9.99	0.00
$\gamma(\text{elevation}), \epsilon(\cdot), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	6	381.25	10.59	0.00
$\gamma(\text{mangrove}), \epsilon(\cdot), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	6	382.03	11.37	0.00
$\gamma(\cdot), \epsilon(\cdot), \text{initial } \psi(\text{elevation}), \rho(\cdot)$	5	383.50	12.84	0.00
$\gamma(\text{elevation}), \epsilon(\cdot), \text{initial } \psi(\text{elevation}), \rho(\cdot)$	6	384.09	13.43	0.00
$\gamma(\text{mangrove}), \epsilon(\cdot), \text{initial } \psi(\text{elevation}), \rho(\cdot)$	6	384.86	14.20	0.00

$\gamma(\text{rain}), \epsilon(.), \text{initial } \psi(\text{shrub}), p(.)$	6	473.90	103.24	0.00
$\gamma(\text{rain}), \epsilon(.), \text{initial } \psi(\text{cordgrass}), p(.)$	6	475.25	104.59	0.00
$\gamma(\text{rain}), \epsilon(.), \text{initial } \psi(\text{elevation}), p(.)$	6	482.43	111.76	0.00

\* Model did not converge

**Table 2.**—Number of parameters ( $K$ ), AIC,  $\Delta$ AIC, and model weight ( $w$ ) for 18 models investigating Sanibel Island rice rat extinction ( $\epsilon$ ) dynamics. The 3 models without covariates on  $\epsilon$  were null models. We placed no covariates on colonization ( $\gamma$ ) or detection ( $p$ ). We conducted trapping across 54 sites during summer (June - August) and winter (December - February) for 3 consecutive years starting summer 2015. We trapped individual sites for 4 consecutive nights per field season.

Model	K	AIC	$\Delta$ AIC	w
$\gamma(\cdot), \varepsilon(\text{rain}), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	372.94	0.00	0.34
$\gamma(\cdot), \varepsilon(\text{shrub}), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	374.54	1.61	0.15
$\gamma(\cdot), \varepsilon(\text{rain}), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	6	374.89	1.95	0.13
$\gamma(\cdot), \varepsilon(\text{cordgrass}), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	375.03	2.09	0.12
$\gamma(\cdot), \varepsilon(\text{shrub}), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	6	376.59	3.65	0.06
$\gamma(\cdot), \varepsilon(\text{cordgrass}), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	6	377.04	4.10	0.04
$\gamma(\cdot), \varepsilon(\text{elevation}), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	377.53	4.59	0.03
$\gamma(\cdot), \varepsilon(\text{rain}), \text{initial } \psi(\text{elevation}), \rho(\cdot)$	6	377.75	4.81	0.03
$\gamma(\cdot), \varepsilon(\cdot), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	5	378.63	5.70	0.02
$\gamma(\cdot), \varepsilon(\text{shrub}), \text{initial } \psi(\text{elevation}), \rho(\cdot)$	6	379.42	6.49	0.01
$\gamma(\cdot), \varepsilon(\text{elevation}), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	6	379.53	6.59	0.01
$\gamma(\cdot), \varepsilon(\text{cordgrass}), \text{initial } \psi(\text{elevation}), \rho(\cdot)$	6	379.85	6.91	0.01
$\gamma(\cdot), \varepsilon(\text{mangrove}), \text{initial } \psi(\text{shrub}), \rho(\cdot)$	6	380.07	7.13	0.01
$\gamma(\cdot), \varepsilon(\cdot), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	5	380.65	7.72	0.01
$\gamma(\cdot), \varepsilon(\text{mangrove}), \text{initial } \psi(\text{cordgrass}), \rho(\cdot)$	10	382.10	9.16	0.00

$\gamma(\cdot)$ , $\epsilon(\text{elevation})$ , initial $\psi(\text{elevation})$ , $\rho(\cdot)$	6	382.36	9.42	0.00
$\gamma(\cdot)$ , $\epsilon(\cdot)$ , initial $\psi(\text{elevation})$ , $\rho(\cdot)$	5	383.50	10.56	0.00
$\gamma(\cdot)$ , $\epsilon(\text{mangrove})$ , initial $\psi(\text{elevation})$ , $\rho(\cdot)$	6	384.95	12.01	0.00

\* Model did not converge

## Figures

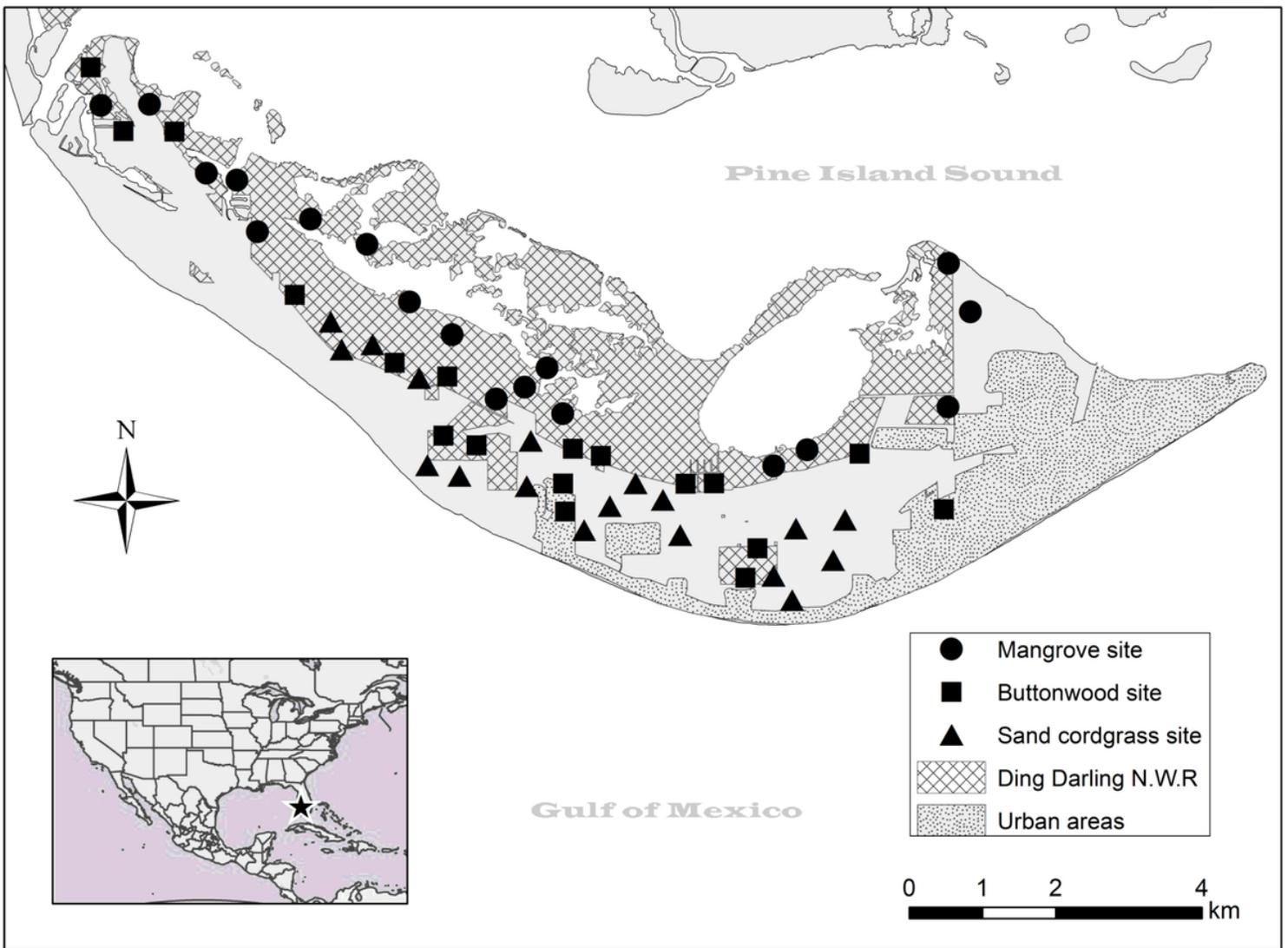
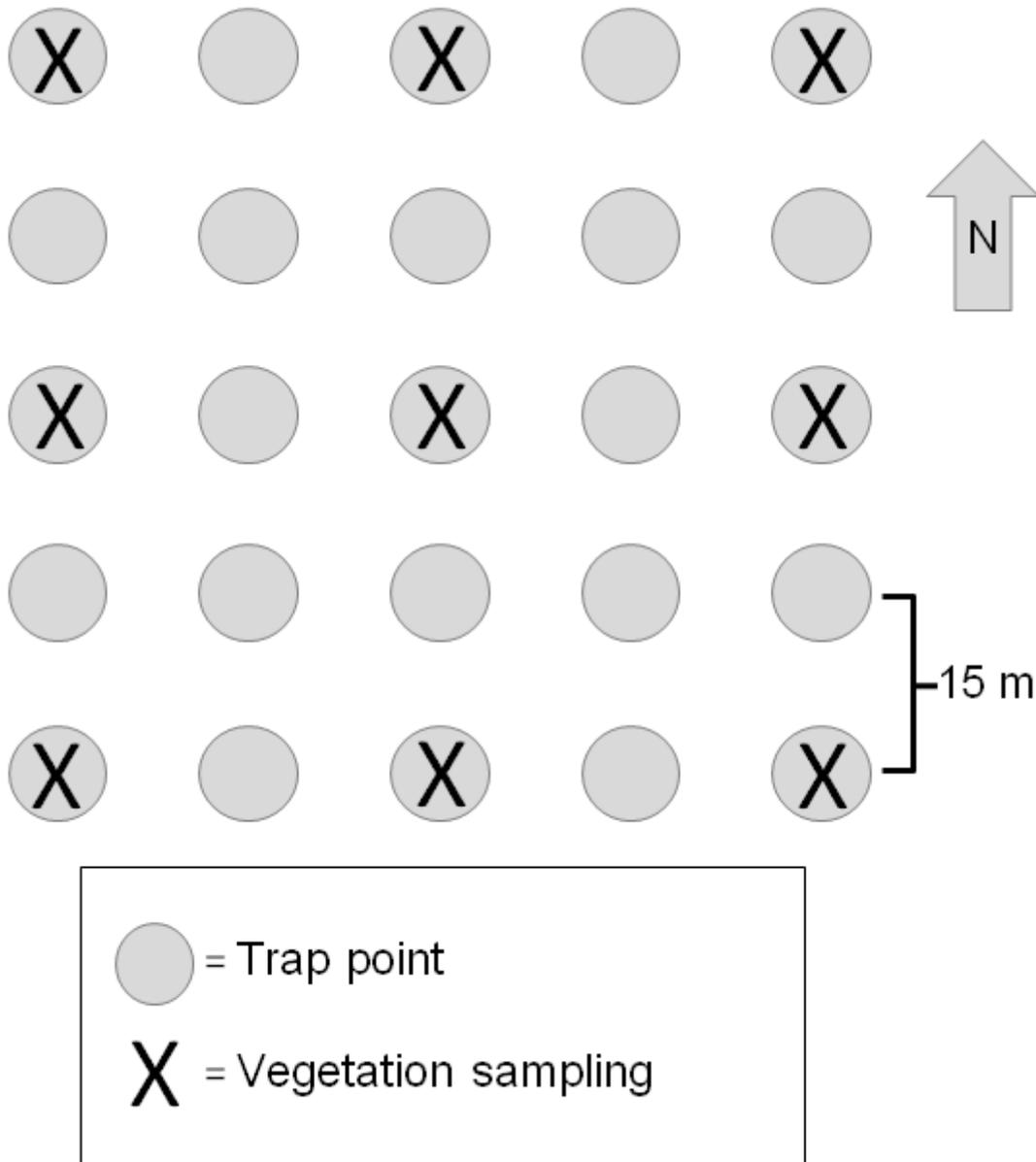


Figure 1

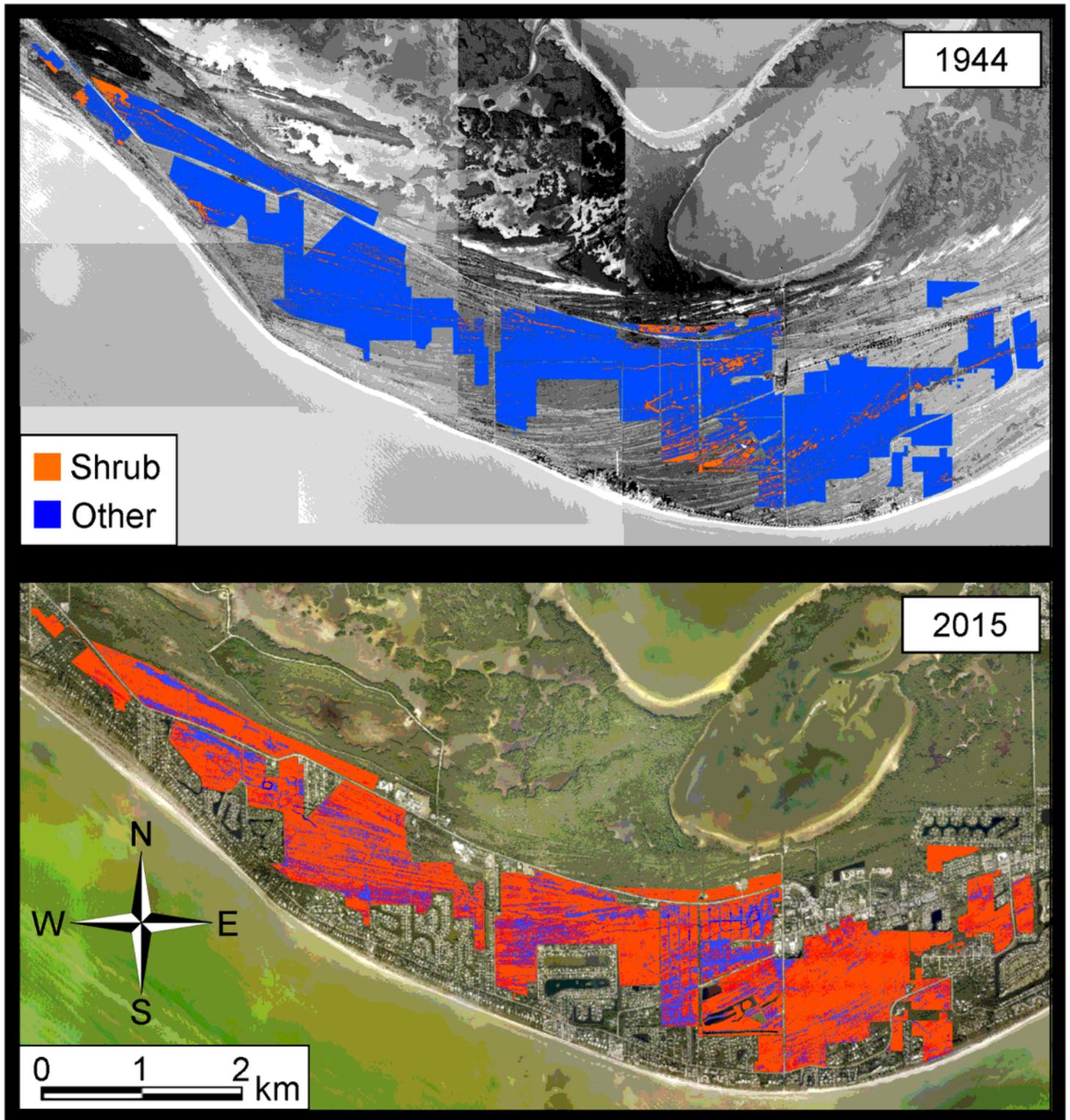
We used ArcGIS to select 18 sites > 300 m apart in each of three vegetation communities (mangrove, buttonwood, and sand cordgrass; n = 54 sites total) to investigate Sanibel Island rice rat occurrence and

colonization/extinction dynamics on Sanibel Island, Florida, USA. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 2**

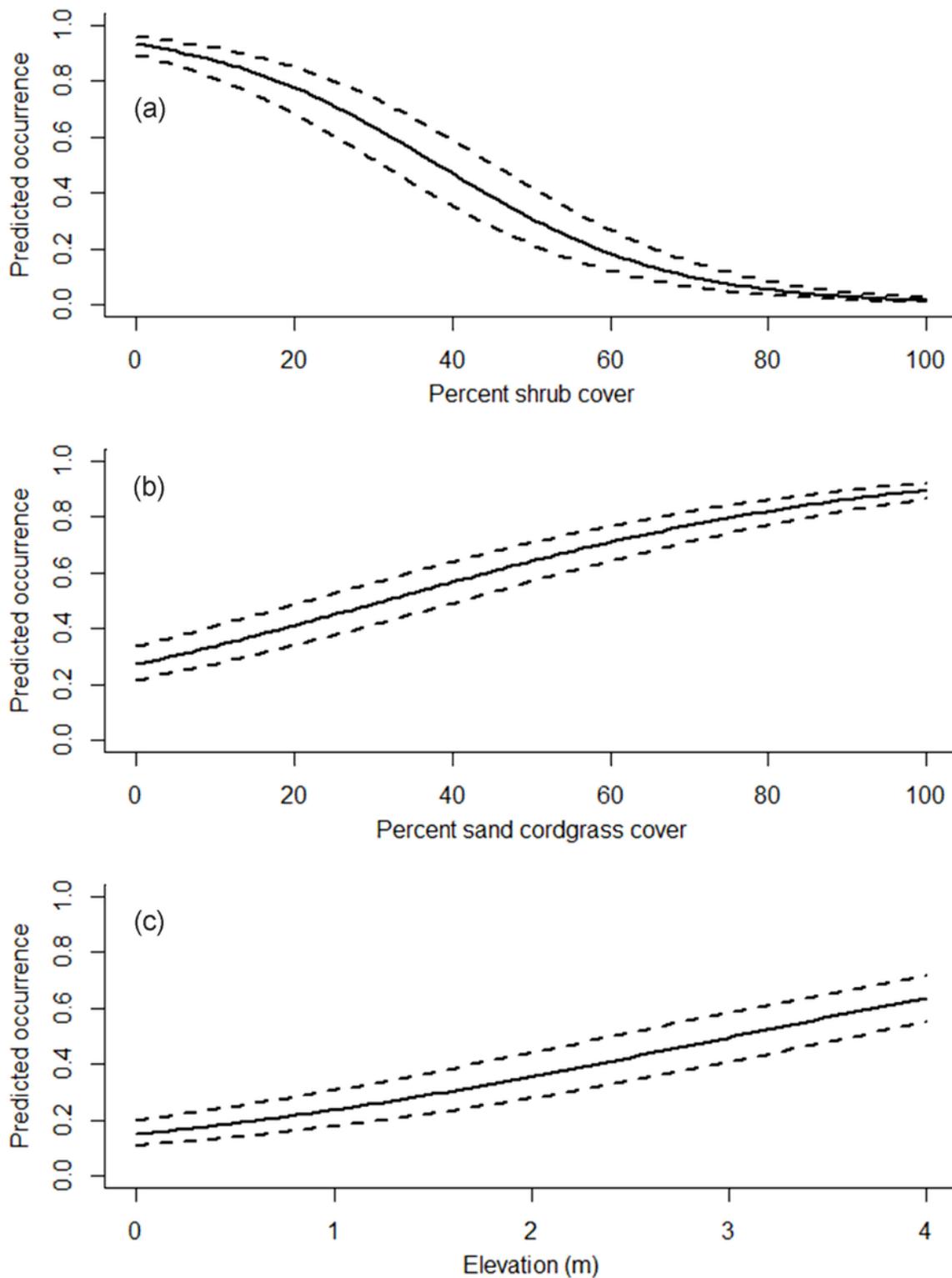
We conducted trapping at each site on a 5x5 trapping grid with 15-m spacing between traps. We sampled vegetation at a standardized subset of nine non-adjacent points on each grid. We used these same nine vegetation sampling points to assess shrub cover omission and commission classification errors using 2015 aerial imagery on a subset of 27 grids not occurring in communities naturally dominated by woody species.



**Figure 3**

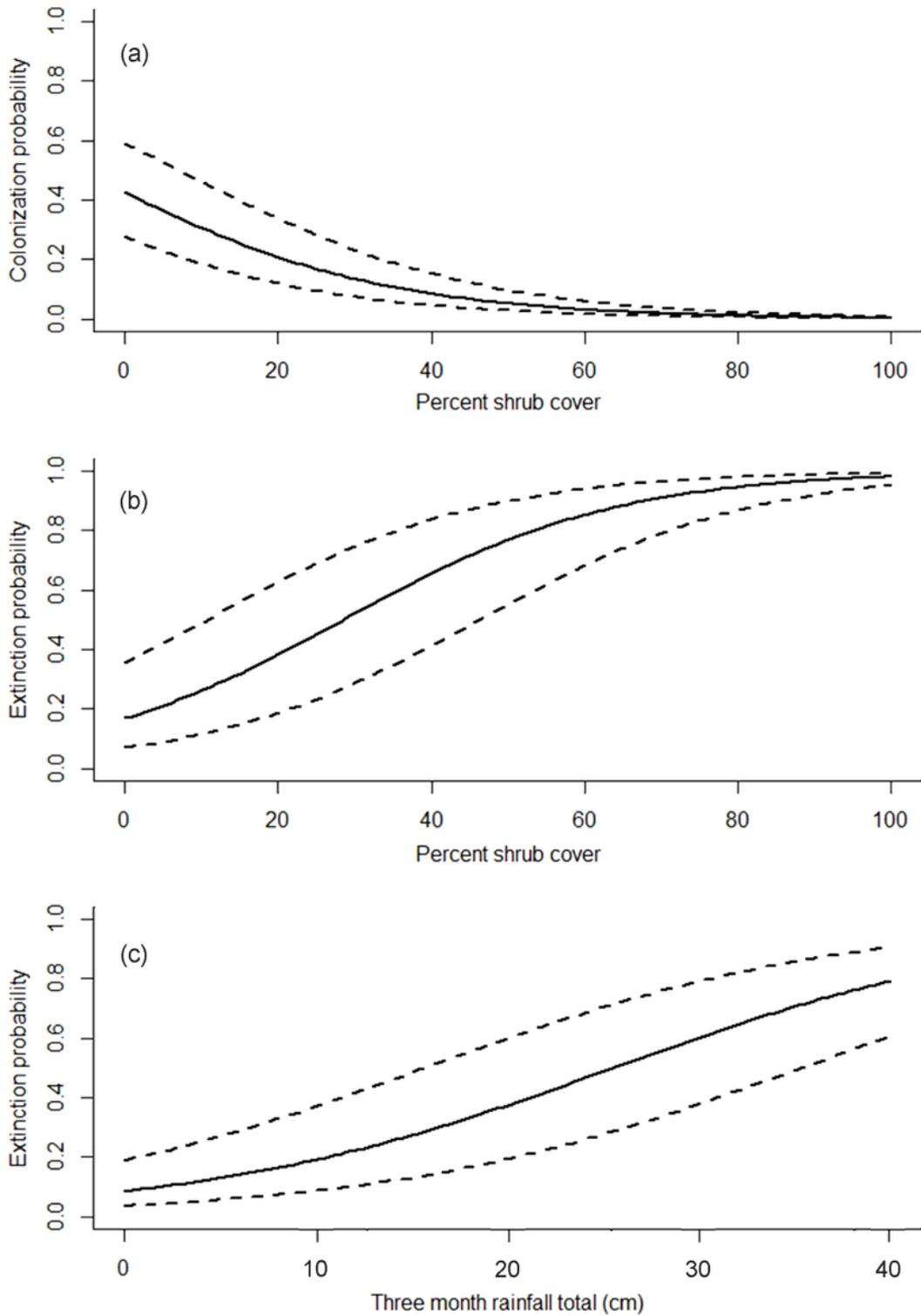
We used ArcGIS to remotely sense change in shrub cover from 1944 to 2015 within freshwater interior conservation areas of Sanibel Island. Buttonwood (*Conocarpus erectus*) was the dominant invading shrub. The “other” classification was a catch-all category including sand cordgrass (*Spartina bakeri*), giant leather fern (*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. Note: The designations employed and the presentation

of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



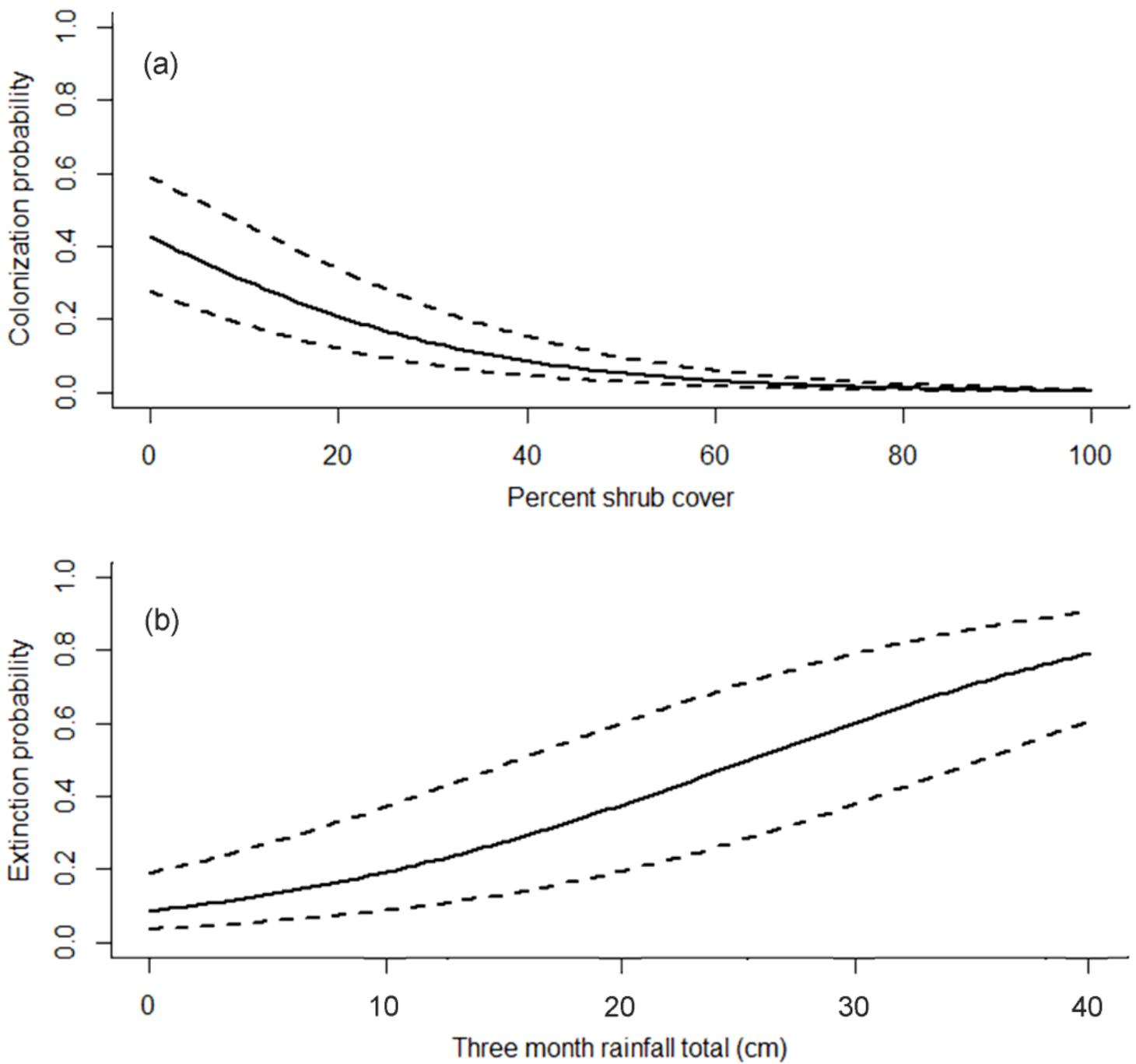
**Figure 4**

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.



**Figure 5**

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



**Figure 6**

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