

Climate change likely to increase co-occurrence of island endemic and invasive wildlife

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ARTICLE INFO

Keywords:

Shrub encroachment
Oryzomys palustris
Sigmodon hispidus
 Climate change
 Sea-level rise
 Invasive species

ABSTRACT

Climate change is altering the distribution of wildlife across the globe. These distributional changes, paired with the environmental and vegetative shifts that spurred them, are likely to change co-occurrence patterns and interspecific interactions of native and invasive wildlife. A mesocosm of global change, we worked on Sanibel Island; a low-lying ~4,900 ha barrier island in southwestern Florida, USA. Sanibel Island possessed a freshwater interior lined with mangrove forests to the north. Sanibel was ~50% developed, ~50% conserved, hydrologically degraded, shrub-encroached, and susceptible to inundation by sea-level rise. We used a Bayesian multispecies occupancy modeling approach to investigate how the effects of climate change might change co-occurrence patterns of 2 native island-endemic species (Sanibel Island rice rat [*Oryzomys palustris sanibeli*]; insular hispid cotton rat [*Sigmodon hispidus insulicola*]) and 1 exotic invasive species (black rat [*Rattus rattus*]). We found that co-occurrence is likely to increase between cotton rats and black rats with unknown impacts on interspecific interactions. We also found that climate change may threaten the persistence of cotton rats and black rats on Sanibel Island, but not rice rats so long as mangrove forests persist. Broadly our research demonstrates the importance of investigating interactions between climate change and co-occurrence when assessing contemporary and future wildlife distributions.

Introduction

As we enter the Anthropocene, an era of rapid human-induced global change, natural wildlife communities face myriad threats [1]. These changes are likely to cause a massive redistribution of wildlife, dramatically altering the composition of many native communities [2, 3]. In particular, wildlife communities are likely to change in response to a rapidly changing climate and to the introduction and growth of populations of invasive species [4,5].

The planet's warming climate has forced wildlife species to move with or track suitable climatic conditions and vegetative communities [3,6]. An additional consequence of climate change that wildlife must contend with has been altered rainfall patterns and increased extreme weather (e.g. drought and floods) [7,8]. Finally, the causative agent of climate change, atmospheric carbon, has been linked to altered vegetative communities with complex and understudied consequences for native wildlife [9,10].

With the redistribution of species from climate change, species' traditional niches are likely to become scarce or unavailable, creating

competition for remaining niche space [11], niche shifts [12], or extirpation [13]. This issue is compounded by the expected climate induced increases in the prevalence and success of invasive species [14]. Invasive species more so than native species tend to be habitat generalists, which may enable them to better-adapt and compete for new niches created by climate change [14]. Interspecific interactions (e.g. competition) between invasive and native species may increase as currently occupied niches are reduced or eliminated [15]. While there has been considerable research on the influence of climate change and invasive species on wildlife distributions and interspecific interactions [16–18], rarely have their individual and combined effects been disentangled [19].

Our goal was to better understand how climate induced changes will singularly and additively influence the occurrence of native and invasive species and their interactions. The effects of climate change and invasive species are of particular concern for dispersal-limited species endemic to low-lying islands. Unlike the mainland, populations on low-lying islands may not be able to track climate-induced shifts in their climate envelope or the vegetative communities they inhabit [20,21]. Islands are also exceptionally vulnerable to invasive species, which are a leading cause

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<https://doi.org/10.1016/j.ecochg.2022.100061>

Received 18 January 2022; Received in revised form 15 June 2022; Accepted 10 July 2022

Available online 15 July 2022

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of extinction and population reduction among island endemic species [22]. To address our goal, we studied the occurrence and co-occurrence of invasive black rats (*Rattus rattus*) and 2 endemic rodents on Sanibel Island: the Sanibel Island rice rat (henceforth “rice rat”; *Oryzomys palustris sanibeli*) [23] and insular hispid cotton rat (henceforth “cotton rat”; *Sigmodon hispidus insulicola*) [24]. We predicted that flooding caused by sea-level rise and severe rain events, expected to increase with climate change [25,26], will alter the distribution of cotton rats, which are not adapted to aquatic environments [27]. We predicted that shrub encroachment, linked to modified hydrology and elevated atmospheric carbon [28,29], will negatively impact all 3 species due to decreased groundcover (cotton rats) and food resources (all 3 species). Likewise, we predicted that increased mangrove density [29,30] will negatively impact cotton rats due to decreased groundcover. Finally, we predicted that interspecific interactions between all species will be more common when conditions are least representative of historic conditions (e.g. wetter and woodier) [31–33].

Materials and methods

Study area

Sanibel Island in southwest Florida (latitude 26.436394, longitude -82.105589) is a ~4,900 ha low-lying barrier island formed by sediment accretion, creating linear dune systems of variable height (~0–3 m above sea level) [34]. Natural sand dune ridges encircle the island’s lower-elevation interior [35] forming freshwater wetlands [36]. Sanibel’s freshwater wetlands rely on osmotic pressure provided by seasonal rainfall, combined with a thin clay deposit that underlies the island, to prevent subsurface saltwater intrusion from the Gulf of Mexico and saline aquifers underlying Sanibel Island, respectively [36]. These wetlands flood during the summer/fall wet season when Sanibel receives 85% of its annual rainfall [37], then water levels recede throughout the winter/spring dry season [36]. Subsequently, conservation lands (~50% of Sanibel’s land-cover) are largely confined to Sanibel’s flood-prone freshwater interior and its bay-ward mangrove forest exterior [34]. Once dominated by sand cordgrass (*Spartina bakeri*) [38], woody species, particularly buttonwood (*Conocarpus erectus*), are now abundant in Sanibel’s freshwater wetlands [39]. Residential, commercial, and infrastructure development dominate upland areas [34].

As a low-lying barrier island, Sanibel Island and its wildlife are vulnerable to the effects of climate change. Heavy rainfall events in this region are expected to become more frequent and intense, resulting in increased flooding [26]. Coastal environments are particularly vulnerable to flooding because sea-level rise increases the underlying water table, limiting or preventing rainwater intrusion into the soil and resulting in increased flood potential [40]. Sea-level rise alone, without modified rainfall patterns, can increase the occurrence of surface flooding as the water table rises above that of low-lying areas, resulting in their inundation [40]. Such changes to hydrologic patterns directly influence the distribution of wildlife through flooding [41,42] and indirectly through modifications to vegetative species composition and structure [43]. Prior to development, Sanibel Island’s interior marshes were grass-dominated, seasonally-inundated, and prone to saltwater intrusion from storms and high tides during the dry season when seawater could enter through the wetland’s natural outfall [34,39]. The composition and structure of grassy systems, such as Sanibel Island’s freshwater interior marshes, have been altered by shrub encroachment facilitated by shortened hydroperiods, dewatering projects and the plugging of the wetland’s natural outfall, changes in salinity, suppression of wildfire, and increased atmospheric CO₂ concentrations [28,39,44]. However, this novel vegetative community is likely to be short-lived in Sanibel Island’s freshwater interior wetlands. Sea-level rise is projected to flood Sanibel Island’s freshwater interior wetlands within the next century, facilitating a transition to mangrove forests, as already observed elsewhere in south Florida [25].

Study species

Rice rats, black rats, and cotton rats co-occur on Sanibel Island. Rice rats and cotton rats have unique ecological characteristics that minimize niche overlap, allowing for sympatric distribution throughout much of the southeastern United States [45–47]. Competition for food resources may be diminished because cotton rats are herbivorous [48] and rice rats are omnivorous [45,49]. However, both species exhibit seasonal diet flexibility associated with resource availability [50–52], potentially resulting in seasonal dietary overlap and resource-related competition [53]. Spatial avoidance between cotton rats and rice rats has been speculated [54], but species-specific habitat preference likely accounts for this pattern. Cotton rats are typically associated with drier areas whereas rice rats are characteristic of wetter areas, but substantial spatial overlap occurs [45,55].

Black rats are prolific invaders that likely originated in present day India [56] but are now established on numerous islands [57] and every continent except Antarctica [58,59]. As an invasive species, black rats have depredated [60] and competed with [61] native species, resulting in population crashes [62], extinctions [63], and subsequent trophic cascades [64]. Interspecific interactions between black rats and Sanibel Island’s native wildlife have not been investigated, although they have coexisted since at least 1984 [39]. Additionally, black rat and rice rat competition has been speculated [65] and recently investigated [66] in the Florida Keys (200 km from Sanibel) because of substantial dietary and spatial overlap.

Site selection and trapping

We selected sites by first placing 18 points in each of the 3 dominant vegetative communities on Sanibel Island (sand cordgrass, buttonwood, and mangrove) using available vegetative data from the Florida Natural Areas Inventory [67] in ArcGIS (version 10.4.1, Esri, Redlands, California, USA; Fig. 1). We spaced points > 300 m apart to promote sampling independence. Around each point we established a 0.36-ha trap site of 25 Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida, USA) in a 5 × 5 configuration with 15 m spacing between traps. We secured traps to floating platforms to prevent submersion and secured them in place using wooden stakes. We baited traps with a mix of black oil sunflower seed and millet. We trapped each grid for 4 consecutive

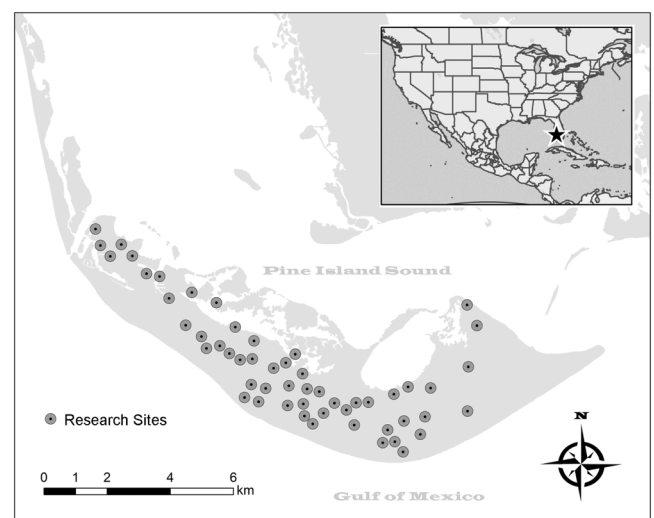


Fig. 1. Location of 54 research sites where we assessed the association between species occurrence, environmental variables associated with climate change, and the co-occurrence of sympatric species on Sanibel Island, Florida, USA. We included invasive black rats (*Rattus rattus*), endemic insular hispid cotton rats (*Sigmodon hispidus insulicola*), and endemic Sanibel Island rice rats (*Oryzomys palustris sanibeli*) in our analyses.

nights once per season (June–August and December–February), for 3 years starting in June 2015. We marked each new capture with a uniquely numbered Monel 1005-1 ear tag (National Band and Tag Co, Newport, Kentucky, USA). In addition to species ID, we recorded tag number, age, sex, weight, reproductive status, and body, tail, and foot length of each capture. We processed and released all animals at their place of origin. Trapping and handling procedures conformed to guidelines established by the American Society of Mammalogists [68] and were approved by the University of Florida's Institutional Animal Care and Use Committee (study #201508922).

Environmental drivers

We quantified 3 environmental drivers projected to increase with climate change (shrub cover, mangrove density, seasonal flooding). Mangrove density is expected to increase within Sanibel Island's interior as sea-level rise facilitates mangrove invasion [25], as has already been observed throughout south Florida's coastal wetlands [69,70]. To quantify mangrove density, we counted the number of mangrove stems within a 4-m² quadrat at a spatially standardized subset of 9 of the 25 trap points per site during the first field season (summer 2015; these 9 points are henceforth termed “environmental sampling points”; Fig. S1). We repeated mangrove stem counts annually on buttonwood and sand cordgrass sites ($n = 36$) because prescribed fire and mechanical shrub removal modified vegetation composition, and because these sites were potentially susceptible to mangrove invasion. We did not repeat stem counts annually on mangrove sites ($n = 18$) because these areas were not subject to fire or mechanical shrub removal and were stable over the course of the study. We did not differentiate between black (*Avicennia germinans*), red (*Rhizophora mangle*), or white (*Laguncularia racemosa*) mangroves. We averaged the 9 stem counts for each site to create a single metric of mangrove density per site.

Continued shrub encroachment of Sanibel Island's interior marshes [34,39] is likely the combined effect of increased atmospheric CO₂ concentrations [44,71], shortened hydroperiods caused by historic dewatering projects [39], and possibly the elimination of wildfire [34]. To quantify shrub cover, we employed a remote sensing approach 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* [72]. Land-cover classes included shrubs, sand cordgrass, leather fern, and open water. Although shrub cover was the only remotely sensed land-cover class of interest, the additional classifications were included because (a) they are widespread in Sanibel Island's freshwater interior and (b) supervised classification requires the designation of alternative land-cover classes present. We then extracted shrub cover estimates in 0.44-ha circular polygons (75-m diameter) at sites not naturally dominated by woody vegetation (i.e. we did not sample mangrove or upland tropical hammock; $n = 27$) so that only areas susceptible to detectable changes in shrub cover were included. We set all other sites to zero. We assessed the accuracy of shrub cover estimates using data collected at the 9 environmental sampling points established on each of the 27 remotely sensed sites. We recorded a binary measure of whether shrub cover was dominant (no = 0; yes = 1) at each point in 2015 and within a 1-m buffer of each point in the remotely sensed data layer. We then calculated omission and commission error rates to assess classification accuracy [73].

Climate change is expected to increase seasonal flooding on Sanibel Island by increasing the severity of individual rain events [26] and decreasing the island's ability to absorb floodwaters due to increased groundwater elevation associated with sea-level rise [40]. To quantify seasonal flooding, we counted the number of environmental sampling points (0–9 points) with standing water during each trap period on each site, creating a flooded point count. We counted any environmental sampling point that was flooded for a portion of the survey period,

including tidally-flooded points.

Modifiers of detection

We included 2 variables (visual obstruction, season) that we predicted would influence rodent detection. Visual obstruction may alter perceptions of fear that influence foraging [74,75], thereby altering detection probability. We measured visual obstruction, a metric of vegetation density, at each environmental sampling point per site annually using a Robel pole [76]. Viewed from 0.7 m height, the approximate height of mammalian predators, and standing 4 m away we recorded the lowest visible point on the Robel pole to the nearest decimeter from each cardinal direction. We averaged measurements across all 9 environmental sampling points per site to create an average annual measure of visual obstruction for each site. Season is associated with changes in temperature and food resources, which influence activity levels or bait attractiveness and thereby change detection probability [75,77,78]. We therefore included a binary measure of season (summer = 1, winter = 0).

Statistical analysis

To understand the response of 3 rodent species to environment factors predicted to change with climate, and to understand how these factors may alter species interactions, we employed a newly-developed occupancy modeling approach [79]. First, we summarized occurrence data across 25 trap points per site, creating a binary daily measure of occurrence for each species at each site in each season. We used this data to assess the association between species occurrence across environmental gradients associated with climate change, and the co-occurrence of sympatric species using a Bayesian multispecies occupancy modeling approach [79]. This model builds on the single-season occupancy model of MacKenzie et al. [80] to investigate patterns of co-occurrence while accounting for imperfect detection (p). The model permits the simultaneous investigation of linear relationships between variables of interest and both single species occurrence (ψ) and co-occurrence of 2 or more species.

To investigate variation in the probability of species occurrence and co-occurrence our models employ a 3-tiered approach in which model complexity varies between tiers but direct comparisons are made within and between tiers [79]. This modeling approach improves on previous occupancy models (1) by enabling the investigation of co-occurrence relationships without assigning dominance or subordination to each species, (2) relationships between environmental variables and species co-occurrence patterns are directly modeled, and (3) a metric of parsimony (WAIC, discussed below) enables model ranking and comparison across all 3 model tiers [79]. First, we developed Tier 1 models which assumed that species occurred in linear association with environmental covariates and independently of each other. Tier 1 models allowed us to understand the individual and combined influence of specific climate related changes on each species' occurrence. Second, we developed Tier 2 models which assumed that species occurred in linear association with environmental covariates and displayed constant dependence on the occurrence of another species. Tier 2 models allowed us to investigate whether the presence or absence of another species resulted in a constant increase or decrease to the linear relationship between climate related change and the occurrence of each species. Finally, we developed Tier 3 models which assumed that species occurred in linear association with environmental covariates and displayed linear dependence on the occurrence of another species in relation to environmental covariates. Tier 3 models allowed us to investigate whether the presence or absence of another species changed the relationship between climate related variables and the occurrence of each species in a non-linear fashion. Within each modeling tier, we tested all possible single variable and additive combinations of shrub cover, mangrove density, and seasonal flooding applied to all species and co-occurrence

relationships (Supplementary Table S1). Each model included metrics of visual obstruction and season to independently account for the variable detection of each species. We found no evidence of collinearity ($r \geq 0.7$) [81] among the variables used in our model ($r \leq 0.48$). We implemented models in STAN (version 2.19.2) [82] using the RSTAN (version 2.19.2) [83] package in R (version 3.5.1). For each model we ran 2 chains of 3000 iterations with a burn-in of 2000 iterations and no thinning. We assessed convergence using the Brooks-Gelman-Rubin diagnostic (Rhat) where values < 1.1 indicated convergence [84]. We ranked candidate models using Watanabe-Akaike information criterion (WAIC) [84,85], a Bayesian information criterion comparable to Akaike's information criterion (AIC) [86]. To understand which factors best accounted for observed patterns of species occurrence and co-occurrence we considered all models within 10 WAIC units of the model with the lowest WAIC (top model) to be competing models [87]. Within competing models, we considered environmental covariates with 95% Bayesian credibility intervals (CRI) not inclusive of zero to be relevant predictors of species' occurrence or co-occurrence. We evaluated the mean of the posterior distribution to determine the direction (positive or negative) of each relationship.

Results

We captured 501 cotton rats, 66 rice rats, and 236 black rats over 32,400 trap nights. Within a season on the same grid, black rats and cotton rats co-occurred 31 times, black rats and rice rats co-occurred 13 times, and cotton rats and rice rats co-occurred 21 times. Cumulative site naïve occupancy was 0.25 for cotton rats, 0.07 for rice rats, and 0.15 for black rats. The multispecies occupancy analysis yielded 2 competing models of occurrence and co-occurrence in relation to environmental covariates. Both of our top competing models were Tier 3 models, suggesting that interspecific interactions change across environmental gradients [87]. The top competing model (model T-III₁; Supplementary Table S1) was a global model that assessed the relationship between seasonal flooding, mangrove density, and shrub cover and the occurrence (Supplementary Table S2; Fig. 2) and co-occurrence (Supplementary Table S3; Figs. 3 and 4) of each species while accounting for imperfect detection (Supplementary Table S2). The competing model (Δ WAIC 7.08; model T-III₂; Supplementary Table S1) was identical to the top-ranked global model, except that it omitted seasonal flooding when modeling the occurrence (Supplementary Table S4; Fig. S2) and

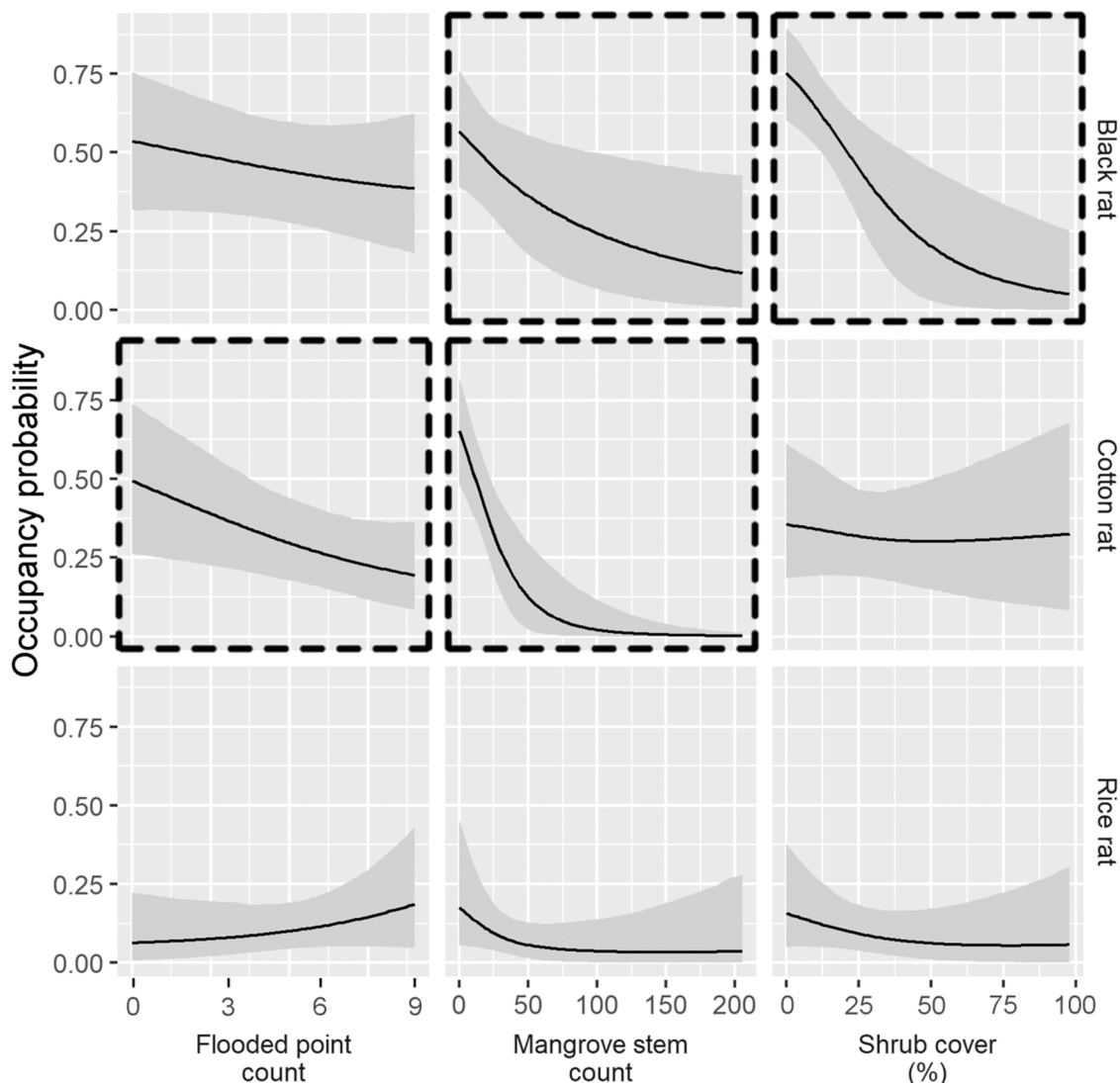


Fig. 2. Results from the top-ranked competing model of predicted occupancy probability independent of co-occurrence relationships of invasive black rats (*Rattus rattus*), endemic insular hispid cotton rats (*Sigmodon hispidus insulicola*), and endemic Sanibel Island rice rats (*Oryzomys palustris sanibeli*) in relation to the number of flooded survey points (0 – 9), average mangrove stem count (density) measured within nine 4-m² quadrats, and percent shrub cover within a 0.44 ha circular polygon (75-m diameter) at each site. Black dashed-line boxes denote significance. Black lines depict posterior means and shaded areas signify 95% credible intervals.

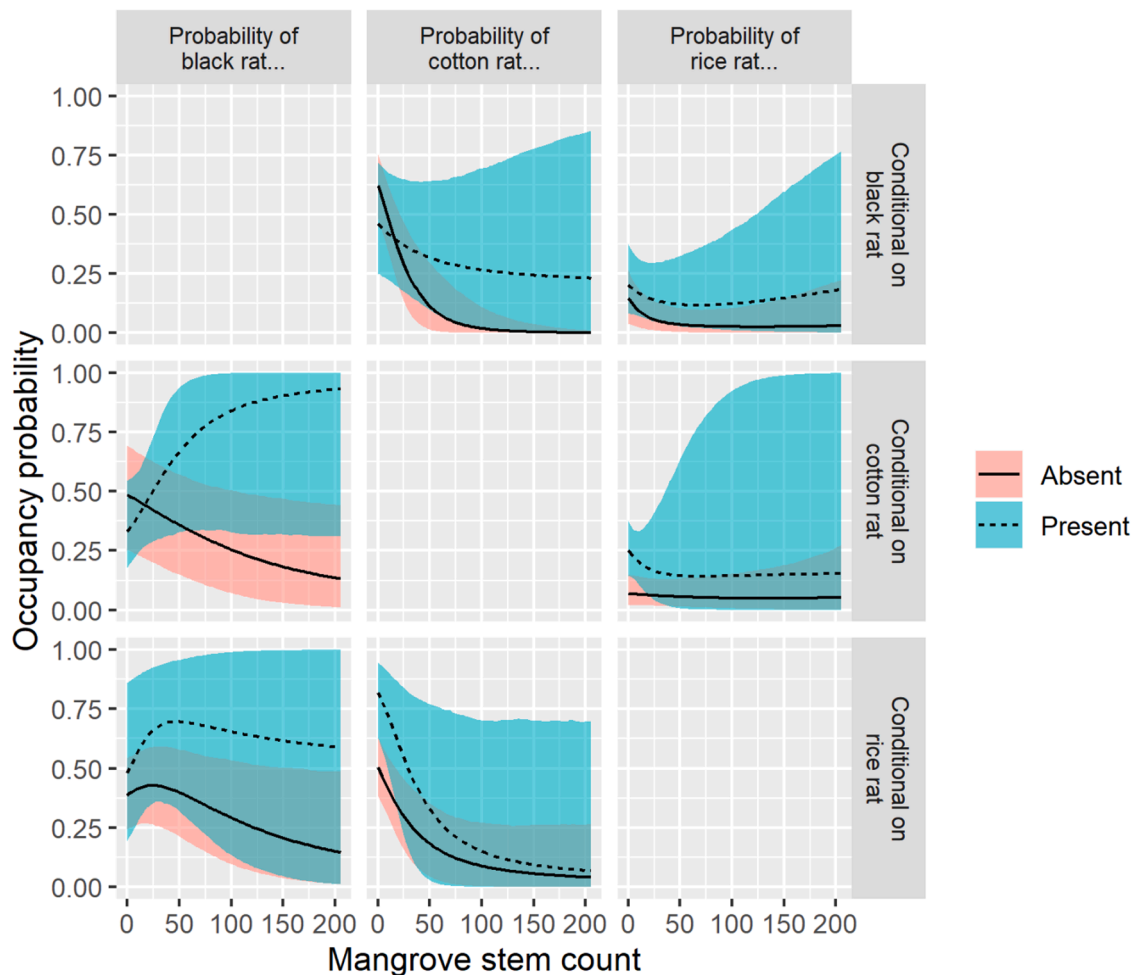


Fig. 3. Results from the top-ranked competing model of predicted occupancy probability of invasive black rats (*Rattus rattus*), endemic insular hispid cotton rats (*Sigmodon hispidus insulicola*), and endemic Sanibel Island rice rats (*Oryzomys palustris sanibeli*) conditional on the presence or absence of each other species and in relation to the average mangrove stem count (density) measured within nine 4 m² quadrats at each site. Black lines (solid and dotted) depict posterior means and shaded areas signify 95% credible intervals.

co-occurrence of each species (Supplementary Tables S4 and S5; Figs. S3 and S4). Accordingly, below we present the statistically significant results from the best model only.

Evaluating the top model (summarized in Table 1), we found that independent of co-occurrence relationships, cotton rat occurrence was negatively associated with elevated mangrove density (mean -2.33; CRI -4.09 to -0.94; Fig. 2) and seasonal flooding (mean -0.65; CRI -1.19 to -0.15; Fig. 2). Cotton rat occurrence estimates decreased from 0.66 in areas devoid of mangroves to <0.01 in areas with 200 mangrove stems per 4-m². Cotton rat occurrence also decreased from 0.49 in areas without flooding to 0.19 in areas where all 9 points were flooded. Black rat occurrence was negatively associated with elevated mangrove density (mean -0.52; CRI -1.01 to -0.08; Fig. 2) and shrub cover (mean -1.74; CRI -3.36 to -0.54; Fig. 2). Black rat occurrence decreased from 0.57 in areas devoid of mangroves to 0.12 in areas with 200 mangrove stems per 4-m². Black rat occurrence also decreased from 0.76 in areas without shrub cover to 0.05 in areas with 100% shrub cover. No environmental covariates were relevant predictors of rice rat occurrence (Supplementary Table S2; Fig. 2).

In the top model (summarized in Table 2), black rats and cotton rats displayed positive co-occurrence in relation to increasing mangrove density (mean 1.91; CRI 0.28 to 3.87; Fig. 3) and percent shrub cover (mean 2.14; CRI 0.71 to 3.92; Fig. 4). Cotton rat's negative association with mangrove density was less pronounced when black rats were present than when they were absent (Fig. 3). Inversely, black rat association

with mangrove density switched from negative when cotton rats were absent to positive when cotton rats were present (Fig. 3). Black rat and cotton rat occurrence flipped from a negative association with elevated percent shrub cover in the absence of the other species to a positive association with elevated shrub cover in the presence of the other species (Fig. 4). Flooding was not associated with any statistically relevant interspecific interactions (Supplementary Table S3).

Cotton rat and rice rat detection probabilities within the top model were highest during summer trapping (mean 0.96; CRI 0.71 to 1.22 and mean 0.66; CRI 0.22 to 1.12, respectively). Black rat detection probability was negatively associated with increased visual obstruction (mean -0.90; CRI -1.25 to -0.55) and summer trapping (mean -0.31; CRI -0.58 to -0.01). Visual obstruction was not a relevant predictor of cotton rat or rice rat detection probability (mean -0.12; CRI -0.49 to 0.29 and mean -0.52; CRI -1.47 to 0.44, respectively).

Discussion

We investigated the potential for variable environmental conditions and invasive species to alter the distribution of island endemic wildlife. We found environmental conditions associated with climate change were likely to reshape the distribution of native and invasive wildlife. We also found interspecific interactions between invasive and native species were likely to increase with environmental conditions predicted under future climate change scenarios. Specifically, we found that

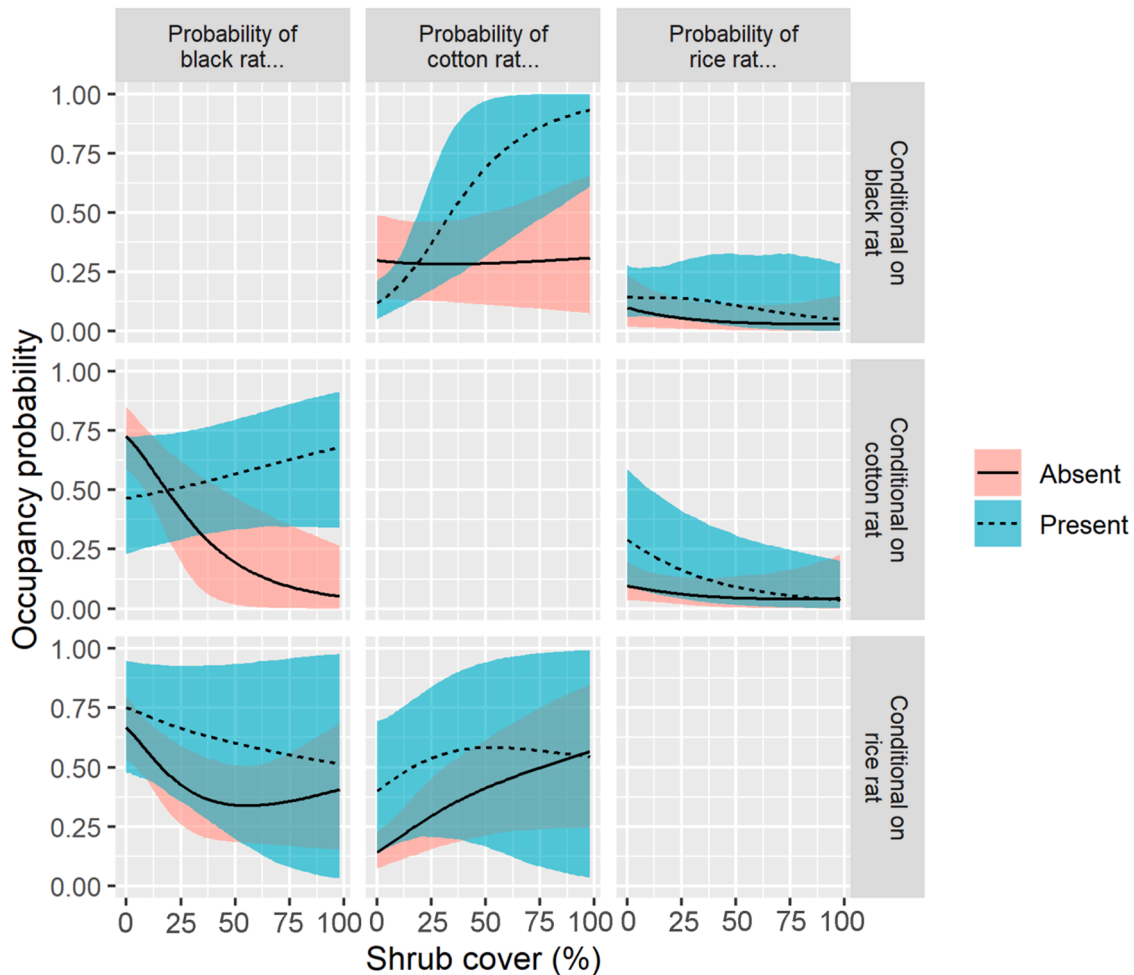


Fig. 4. Results from the top-ranked competing model of predicted occupancy probability of invasive black rats (*Rattus rattus*), endemic insular hispid cotton rats (*Sigmodon hispidus insulicola*), and endemic Sanibel Island rice rats (*Oryzomys palustris sanibeli*) conditional on the presence or absence of each other species and in relation to the percent shrub cover within a 0.44 ha circular polygon (75-m diameter) at each site. Black lines (solid and dotted) depict posterior means and shaded areas signify 95% credible intervals.

Table 1

Summarized results from the top-ranked competing model (T-III1) of predicted occupancy probability of invasive black rats (*Rattus rattus*), endemic insular hispid cotton rats (*Sigmodon hispidus insulicola*), and endemic Sanibel Island rice rats (*Oryzomys palustris sanibeli*) independent of co-occurrence relationships. Environmental parameters included flooded point count (0 – 9), average mangrove stem count (mangrove density) within nine 4-m² quadrats, and percent shrub cover within a 0.44 ha circular polygon (75-m diameter) at each site. Response depicts whether an increase in the environmental parameter elicited an increase or decrease in the species' occupancy probability. Significant conveys whether the 95% Bayesian credibility interval excluded zero (yes) or crossed zero (no).

Species	Environmental Parameter	Response	Significant
Black rat	Flooded point count	Negative	No
	Mangrove density	Negative	Yes
	Shrub cover	Negative	Yes
Cotton rat	Flooded point count	Negative	Yes
	Mangrove density	Negative	Yes
	Shrub cover	Positive	No
Rice rat	Flooded point count	Positive	No
	Mangrove density	Negative	No
	Shrub cover	Negative	No

interspecific interactions between invasive black rats and endemic cotton rats were likely to become more common with increases in both mangroves and shrub cover, with mangrove distribution expected to

increase on Sanibel Island through at least 2100 [25].

We posit that black rats and cotton rats co-occurred more under increasingly novel conditions (i.e. increased mangrove (Fig. 3) and shrub cover (Fig. 4) on Sanibel Island because they selected the same previously sub-optimal [45,55] environments (e.g. sink population) as optimal environments became limited (Supplemental material, Supplementary Table S2). Differences in space use and dietary flexibility may have facilitated coexistence without competitive exclusion. Black rats are capable of accessing arboreal food and nesting resources [65,88] that may be less accessible to cotton rats [89]. Additionally, while cotton rats are predominately herbivorous [48], black rats are omnivorous with a substantial component of their diet composed of invertebrates and other non-vegetative food sources [90,91]. Within mangrove forests, black rats further reduce the potential for dietary overlap with cotton rats by taking advantage of novel food sources such as mollusks [92]. Alternatively, a mutualistic relationship could account for the observed co-occurrence patterns. While mutualism is unlikely because of the black rat's history of outcompeting numerous native species [62,63], and the absence of an apparent mechanism for either species to facilitate the occurrence of the other, it cannot be ruled out. Facilitative habitat modification and dilution of predatory pressure are plausible mechanisms [93], but further research is needed to assess their validity.

As predicted, increased mangrove density and flooding, factors associated with climate change [7,21], may threaten the persistence of cotton rats on Sanibel Island. As sea-level rise facilitates a gradual

Table 2

Summarized results from the top-ranked competing model (T-III1) of predicted occupancy probability of invasive black rats (*Rattus rattus*), endemic insular hispid cotton rats (*Sigmodon hispidus insulicola*), and endemic Sanibel Island rice rats (*Oryzomys palustris sanibeli*) conditional on the presence or absence of each other species and in relation to an environmental parameter. Environmental parameters included flooded point count (0–9), average mangrove stem count (mangrove density) within nine 4-m² quadrats, and percent shrub cover within a 0.44 ha circular polygon (75-m diameter) at each site. Change in response depicts whether an increase in the environmental parameter elicited an increase or decrease in the species' occupancy probability when the co-occurring species was present compared to when it was absent. Significant conveys whether the 95% Bayesian credibility interval excluded zero (yes) or crossed zero (no).

Response Species	Co-occurring Species	Change in Response	Environmental Parameter	Significant	
Black rat	Cotton rat	Cotton rat	Flooded point count	Less negative	No
			Mangrove density	Turns positive	Yes
			Shrub cover	Turns positive	Yes
	Rice rat	Rice rat	Flooded point count	Less negative	No
			Mangrove density	Less negative	No
			Shrub cover	Less negative	No
Cotton rat	Black rat	Black rat	Flooded point count	Less negative	No
			Mangrove density	Less negative	Yes
			Shrub cover	Turns positive	Yes
	Rice rat	Rice rat	Flooded point count	Less negative	No
			Mangrove density	Less negative	No
			Shrub cover	More positive	No
Rice rat	Black rat	Black rat	Flooded point count	Turns negative	No
			Mangrove density	Less negative	No
			Shrub cover	Less negative	No
	Cotton rat	Cotton rat	Flooded point count	More positive	No
			Mangrove density	Less negative	No
			Shrub cover	Less negative	No

increase in mangrove distribution along Sanibel Island's northern margins [25,30], cotton rat occurrence may decrease in those areas. However, the most abrupt change to cotton rat distribution on Sanibel Island may occur within the next century when rising seas inundate the interior wetlands [30,94], permitting mangrove forest expansion. The resulting combination of flooding and mangrove encroachment, 2 factors negatively associated with cotton rat occurrence in our analysis, may extirpate cotton rats from the interior freshwater wetlands where they have historically been most abundant [39].

Rice rat occurrence was not substantially influenced by flooding. Rice rats possess water-resistant fur that retains body heat and increases buoyancy, readily disperse and move through water, and are most commonly associated with wetlands [27,45]. Contrary to our predictions, based on how other subspecies of cotton rats are closely, if not entirely, associated with grasses and areas of dense groundcover with minimal shrub cover [reviewed in 55], increased shrub cover was not associated with rice rat or cotton rat occurrence. Within shrub-encroached areas, cotton rats were typically captured in small

grass patches that remained between encroaching shrubs.

Black rats were not substantially influenced by flooding, but were negatively associated with shrub cover. In the short-term, black rats may benefit from efforts to reduce shrub cover intended to aid rice rats and cotton rats. However, the eventual conversion of Sanibel Island's freshwater interior to mangrove forests caused by sea-level rise may offset this increase. This assertion is supported by the negative association between black rats and mangrove density. Goodyear [65] revealed extensive use of mangrove forests by black rats. However, mangrove forests on Sanibel Island may have differed in structure from those observed by Goodyear [65] because Sanibel Island's mangrove forests were severely damaged by category 4 Hurricane Charley in 2004 (11 years prior to initiation of our research) [95]. Sanibel Island's mangrove forests were still recovering during this research, potentially providing less mast and arboreal nesting opportunities [96].

Limited rice rat detection and capture (66 individuals; 149 captures) and lower trap success (0.46%) compared to previous research (1.94%) [39] suggest rice rats were rare on Sanibel Island during our study. However, we found little indication that climate-induced environmental changes would alter their future distribution. The rice rat's semi-aquatic nature [27] and persistence in mangrove forests in the Florida Keys [66] suggests future conditions (e.g. increased flooding and mangrove density) should not limit their distribution. However, it is not known if rice rats can persist solely in tidal mangrove forests, or if their persistence requires exploitation of upland or non-salt tolerant species that may not be available in the future. Although extinctions of other island endemic species within the oryzomine genera have been credited to competition with black rats [97–99] we found no support for increased spatial overlap associated with climate change. The ~500 year co-occurrence of black rats and rice rats in the Florida Keys [65] suggests that, without increased interaction, black rats are unlikely to exclude rice rats from Sanibel Island. While our rice rat and black rat co-occurrence models did rely on sparse data (13 co-occurrences), these models did converge and were informed by a robust sampling effort of an exceptionally rare species. Co-occurrence models using as few as 5 co-occurrences have provided insights into the activity patterns of rare species [100]. While informative, the sparseness of co-occurrence data between certain species combined with the data-hungry nature of our analyses sometimes resulted in wide credibility intervals. Additional research would further validate our findings.

Our results highlight the importance of considering the interaction between climate change and invasive species when assessing their influence on contemporary wildlife distributions. Increased co-occurrence of native and invasive species under future conditions, as found between native cotton rats and invasive black rats in our study, could have substantial implications for future conservation efforts. Revealing these potential future associations now provides managers with the information and time necessary to plan for problems caused by increased co-occurrence before they are realized. Studies that fail to account for synergistic effects of climate change and invasive species may be poor predictors of future wildlife distributions and therefore misinform management and conservation actions. While this research was confined to an island, the importance of investigating future changes in wildlife co-occurrence related to climate change are broadly relevant to any place where invasive and native species co-occur, especially when native species are already imperiled.

CRedit authorship contribution statement

Wesley W. Boone: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Robert A. McCleery:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

None.

Acknowledgments

We thank the Florida Fish and Wildlife Conservation Commission's State Wildlife Grants Program (agreement number 15043) and their Aquatic Habitat Restoration and Enhancement subsection, as well as the University of Florida's Institute of Food and Agricultural Science, the USDA National Institute of Food and Agriculture, Hatch project FLA-WEC-005125, for funding this research. We thank the staff at J.N. "Ding" Darling National Wildlife Refuge, "Ding" Darling Wildlife Society, Sanibel-Captiva Conservation Foundation, City of Sanibel, and the Sanctuary Golf Club for allowing us to access their property and supporting this research in countless ways. We thank the Florida Fish and Wildlife Conservation Commission's Upland Habitat Research team for conducting annual vegetative surveys. We thank the numerous volunteers, technicians, and lab members that helped with field research. In particular, we would like to thank Joelle Carbonell, Modeline Celestin, José Daniel Rodrigues Oliveira Filho, Hanna Innocent, Tre'Nard Morgan, and Brittany Sumner for their immeasurable commitment to this project.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.ecochg.2022.100061](https://doi.org/10.1016/j.ecochg.2022.100061).

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