Habitat use across multiple scales suggests resilience to rising seas for endangered island endemic compared to sympatric invasive species

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Abstract

Wildlife is increasingly threatened by a suite of anthropogenic factors including climate change, habitat loss from human development, and invasive species. These threats are particularly pronounced on islands where species are more likely to go extinct. To better understand how native and invasive species on islands might respond to these threats, we compared habitat use between the endangered silver rice rat (SRR) *Oryzomys palustris natator* and invasive black rat *Rattus rattus* across multiple scales. We used a specialized camera trap design to survey rodents across the Lower Florida Keys, USA, a region vulnerable to emerging threats, such as rising sea level, and persistent threats, such as human development. Additionally, we used a novel modeling approach to investigate temporal variation in rodent activity as a function of lunar tides. Silver rice rat occurrence was greatest in regularly inundated mangroves that could potentially increase in extent as sea level rises. Black rats were widespread and often co-occurred with SRR, but we observed temporal resource partitioning between these species, which suggests competition may be limited. Of the stressors we investigated, we conclude that contjaceinued urban development is the most substantial threat to SRR, and potentially other island species. Our results highlight island species' disparate responses to different aspects of global change and the potential conservation opportunities that may result.

Introduction

Wildlife populations on islands are disproportionately important for global biodiversity conservation (Tershy *et al.*, 2015). The geographic isolation induced by islands can facilitate evolutionarily distinct populations, and ultimately speciation (Whittaker, 1998). However, this isolation may also be detrimental to island populations by limiting population size and genetic variability, rendering them vulnerable to other threats (Frankham, 1997, 1998; Fordham & Brook, 2010). As a result, small island populations are uniquely vulnerable to anthropogenic stressors such as development, invasive species and accelerated sea level rise (Maschinski *et al.*, 2011; Wong *et al.*, 2014).

Human development has long been associated with biodiversity loss on islands (Brooks, Pimm & Collar, 1997; Sodhi *et al.*, 2008). Given the inherently limited area of islands and their proximity to the sea, conservation of island biodiversity now must also consider habitat loss related to rising sea level (Fordham & Brook, 2010; Maschinski *et al.*, 2011). In addition to gradually inundating previously

freshwater-based ecosystems, rising sea level may interact with other disturbances (e.g. development, hurricanes, invasive species) to exacerbate ecosystem change on islands (Ross *et al.*, 2009). Independent of these habitat losses related to development and rising sea level, island biodiversity is also particularly vulnerable to the effects of invasive species (Clavero & Garcia-Berthou, 2005; Clavero *et al.*, 2009; Fordham & Brook, 2010; Medina *et al.*, 2011). As the effects of environmental stressors such as sea level rise and human development worsen, native and invasive species are likely to exhibit disparate responses to these stressors (Marvier, Kareiva & Neubert, 2004). Thus, understanding the relative roles of these various stressors will become increasingly important to island biodiversity conservation as the global climate continues to change.

If invasive species on islands are more resilient than native wildlife to environmental stressors, then anthropogenic global change is likely to exacerbate their detrimental effects on native wildlife (Holmes *et al.*, 2019). In addition to causing direct mortality via predation (Altizer, Foufopoulos & Gager, 2001; Medina *et al.*, 2011), invasive species may

spread diseases or outcompete native species for the same resources (Stokes *et al*., 2009). In the latter case, an understanding of how animals use their environment across multiple scales, is requisite to understand potential competition between native and invasive island wildlife (Lindenmayer *et al*., 2008). Additionally, any assessment of habitat use should consider features that are likely to change on rapidly changing island environments, such as sea level. Native species may be more effective at exploiting available resources if climatic changes such as rising sea level favor the uniquely coastal conditions (Marvier *et al*., 2004). However, if global changes related to the proliferation of humans (e.g. urbanization, invasive species) favor increasing homogenization of environmental conditions on islands, invasive species, that are often generalist, are likely to be favored (McKinney, 2006).

The Lower Florida Keys, USA, and the endemic fauna they support (Lazell, 1989), exemplify the potential threats facing the wildlife of many island systems, including human development, rising sea level and invasive species. The silver rice rat (SRR) *Oryzomys palustris natator* is one of three endangered mammals endemic to this region. Previous studies have shown that SRR primarily use tidally influenced mangroves where they forage for macroinvertebrates, but may nest in the adjacent uplands (Goodyear, 1987; Forys, Frank & Kautz, 1996). They are known to occur on many of the larger islands of the Lower Keys, as well as some of the smaller uninhabited islets (Forys *et al*., 1996; Perry, 2005). SRR appear to occur at lower densities on the Florida Keys compared to mainland rice rats *Oryzomys palustris*, and competition with exotic black rats (BLRA) *Rattus rattus* has been suggested as a possible mechanism for this difference (Goodyear, 1992; Forys *et al*., 1996; Perry, 2006). Black rats are globally distributed and have been implicated in the extinction of many native species, particularly on islands (Harper & Bunbury, 2015). Because of their ability to exploit a wide variety of foods and environmental conditions, BLRA have contributed to the declines of many native taxa via direct predation, competition for resources, spread of disease and alteration of native vegetation (Courchamp, Chapuis & Pascal, 2003; Smith & Banks, 2014). Black rats are generalists and are known to be arboreal (Courchamp *et al*., 2003; Harper & Bunbury, 2015; Sunquist & Sunquist, 2017), whereas rice rats typically occur in treeless areas, are adept swimmers and have a more specialized diet comprised mostly of tidal macroinvertebrates (Esher, Wolfe & Layne, 1978; Goodyear, 1992). Nonetheless, the rapidly changing environment of the Lower Florida Keys might create conditions that allow the generalist BLRA to proliferate and increasingly compete for resources previously only accessed by SRR. A better understanding of the similarities and differences in habitat use between SRR and BLRA will help to elucidate how future stressors will influence these species and ultimately shape biodiversity on the Lower Keys.

To address this need, we systemically sampled coastal wetlands in the Lower Florida Keys to quantify rodent occupancy and activity at multiple spatial scales. In addition, we employed a novel modeling approach to investigate temporal variation in rodent activity as a function of tides and elevation. Specifically, our objectives were to (1) quantify how the most significant threats to the environment of the Lower Keys affect occurrence of SRR and BLRA at multiple scales, and (2) compare variation in these species' activity as a function of lunar tides. Based on the natural histories of these sympatric rodents, we expected that SRR would be more strongly associated with environmental characteristics specific to these islands, such as lower elevation and tidally influenced mangroves. In contrast, we expected BLRA to occur in taller vegetation at higher elevations and closer to development (Cox, Dickman & Cox, 2000; Borroto-Páez, 2009; Harper & Bunbury, 2015).

Materials and Methods

Study area

We conducted the study in the Lower Florida Keys, USA, a subtropical archipelago off the southern coast of mainland Florida comprised of 32 islands >100 ha in size, in addition to hundreds of smaller islets (Fig. 1). The islands support a number of endangered and endemic fauna, many of which are vulnerable to anthropogenic threats including rising sea level, tropical storms, invasive species and human development (Ashton, 1992; Humphrey, 1992; Salvato & Salvato, 2007; Schmidt *et al*., 2012). The effects of these threats are of particular concern in light of continued habitat loss on the Lower Keys resulting from the growth of tourist infrastructure that currently supports over 2 million visitors annually (Clarke, 2002; Schmidt *et al*., 2012). Coupled with development, the Lower Keys is home to several potentially harmful invasive animals, including feral cats *Felis catus* and BLRA (Goodyear, 1992; Cove *et al*., 2018).

At the broadest level, plant communities of the Lower Keys can be differentiated into tidal wetlands and non-tidal uplands (Ross, O'Brien & Flynn, 1992). We limited our study to the tidally influenced areas, as these areas appear most likely to support SRR (Goodyear, 1987; Perry, 2006). The vegetation of the tidally influenced zone of the Lower Florida Keys was comprised predominately of red mangrove *Rhizophora mangle* at the lowest elevations, with more diverse buttonwood *Conocarpus erectus* scrub behind mangroves in the supratidal zone (Ross *et al*., 1992). These two zones were often separated by a band of black mangrove *Avicennia germinans*. At the upper edge of the supratidal zone where soils were deeper, saltmarsh consisting of *Salicornia* and *Distichlis* occurred at the transition to more upland communities (Ross *et al*., 1992).

The rate of sea level rise in the Lower Keys increased throughout the 20th century, to over 0.23 cm year^{-1} in the second half of the century (Maul & Martin, 1993). However, as a result of anthropogenic climate change, sea level could increase by more than 1 m by 2100, which would drastically alter the vegetation zonation of the Lower Keys where much of the islands are below 1 m elevation (Ross *et al*., 1992; Maschinski *et al*., 2011). While upland and freshwater-dependent communities are expected to be negatively affected
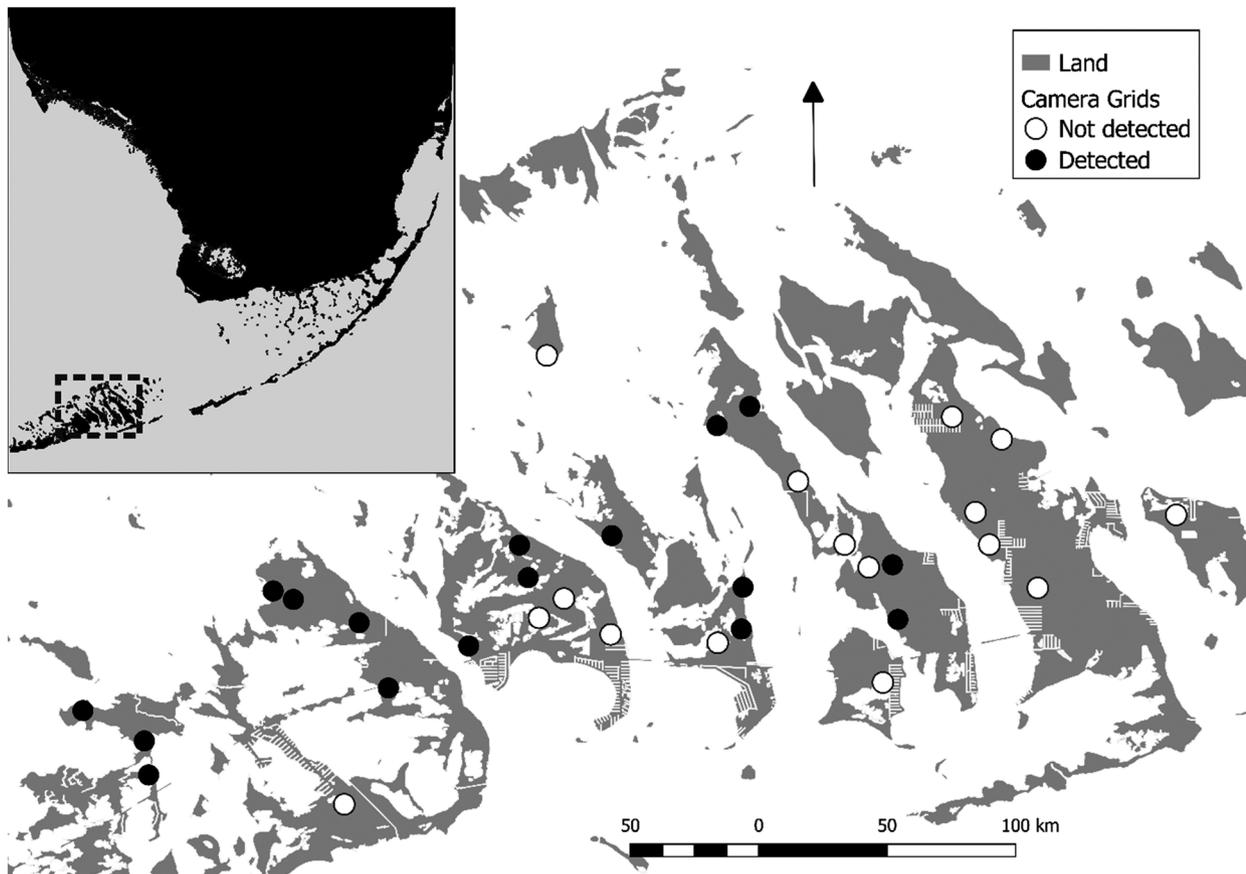
Figure 1 Map of 33 sites, each comprised of 12 camera traps, established to survey silver rice rat and black rats across the Lower Florida Keys, USA, with study area shown with dashed line on inset map of South Florida (2019).

by rising sea level, coastal saline communities like mangroves and saltmarshes may experience a net increase in extent as upland communities are converted to more resilient tidal wetlands (Ross, O'Brien & da Silveira Lobo Sternberg, 1994; Doyle *et al.*, 2010).

Sampling design

We defined our sampling frame as tidally influenced areas in the Lower Keys with native vegetation. We excluded areas of development, roads, upland forest and open water as defined by the Florida statewide land use data (FLDEP, 2017). Additionally, we excluded several islands (Key West, Stock Island, Geiger Key, and Big Coppitt Key) with no recent SRR detections (Perry, 2006). We delineated the remaining sampling frame into a 300 × 300 m grid where a given grid cell would serve as a boundary for a camera trap array. We selected 33 grid cells throughout the Lower Florida Keys to ensure our sample included areas with historical records of SRR (Forys *et al.*, 1996; Perry, 2005), as well as apparently suitable areas that had not been sampled previously (Fig. 1). To capture the variety of vegetation conditions within a cell (hereafter referred to as a 'site'), we assessed the site for the distribution of three distinct vegetation communities: mangrove, saltmarsh and buttonwood. Given all three communities were present, we placed four camera traps within each community. If only two were present at the site, we placed six traps in each. As such, each site consisted of an array of 12 traps, except one site where only seven traps were placed due to inclement weather, resulting in a total of 391 traps (33 sites × 12 traps/site = 396).

Camera trapping

To survey rodents, we used a camera trap specifically designed for aquatic small mammals (McCleery *et al.*, 2014). We mounted a camera with a close focal range (~40 cm) within a 7-gallon plastic bucket, which was mounted on a floating base (Supporting Information Figure S1). Small openings cut into the bucket allowed small mammals to enter and exit the bucket to access a small cup baited with bird seed. This design not only facilitated identification of small mammals that are difficult to detect and identify with more traditional camera trap designs, but also allowed the trap to float up and down with the changing tides (McCleery *et al.*, 2014). Traps were deployed for five consecutive nights per site between 22 February and 24 May

2019. Each camera was set to capture three images when triggered, followed by a 1-min delay before the next potential trigger. We manually reviewed all photos and used the R package *camtrapR* to compile detection histories for BLRA and SRR (Niedballa *et al.*, 2016).

Trap scale covariates

We considered a suite of variables collected in the immediate vicinity (<3 m; hereafter 'trap scale') of the individual camera traps because microhabitat conditions are important to explaining rodent habitat selection (Dueser & Shugart, 1978). To broadly characterize each trap location, we estimated the percent cover of each of woody cover, herbaceous cover and bare ground as seen from above. We then added compositional complexity to these metrics by also measuring the percent cover of the three dominant woody plant species and the three dominant herbaceous plant species within 1 m of the ground surface. Because more than one species could cover the same portion of the plot, these species-specific percentages could total >100%. Among this set of plant species that were dominant at a trap location, only mangroves and *Salicornia* were well-represent across all traps, and thus other species were not informative in regards to explaining variation in rodent occurrence (Supporting Information Table S1). In addition to these metrics of vegetation composition, we quantified variation in vegetation structure by estimating woody vegetation density within three, height intervals (i.e. 0–1 m, 1–2 m, 2–5 m). We expected these metrics of vegetation structure would further describe differences in habitat selection between SRR and BLRA because of their documented differences in habitat associations. For example, because SRR are semi-aquatic, they should require more cover near the ground/water surface, whereas BLRA are more arboreal, and thus should occur in areas with more vegetation above the ground (Goodyear, 1992).

Among this full set of vegetation metrics, many were correlated with each other. To avoid issues related to collinearity, we calculated the correlation coefficient between all variable using the cor function in base R version 3.5.1 (R Development Core Team, 2018), and defined a threshold of 0.5 above which we did not include both variables in the same model (Supporting Information Table S2). Additionally, despite some plant species being dominant at a given trap locations, these species were poorly represented across all traps, and thus were not considered appropriate for explaining variation in rodent occurrence across traps. We did not consider any plant species that were not present at >20% of trap locations (Supporting Information Table S1).

In addition to these field-collected metrics, we used existing data to incorporate elevation and human development (Table 1). We estimated the elevation at trap locations using a LiDAR-derived digital elevation model at 5-m resolution from the National Oceanic and Atmospheric Administration's Coastal Management's Digital Coast Data Access Viewer (NOAA, 2017). We used statewide land use data to identify human development across the Lower Keys (FLDEP, 2017). We then calculated the distance from each trap to the nearest human development using QGIS version 3.4 (QGIS, 2019). To ensure parameter estimates were comparable across covariates, we standardized all trap-scale covariates by subtracting the mean and dividing by the standard deviation.

Landscape scale covariates

To understand how rodents were influenced by the features of their environment at other biologically relevant scales, we considered three larger scales (referred to collectively hereafter as 'landscape scales') by aggregating trapping information within a given site. At the smallest of these landscape scales, we buffered trap locations at a distance of 70 m and then dissolved them into one polygon per site. We chose 70 m because the area of the resulting polygons approximately matched the home range size of SRR (Perry, 2005). In a similar manner, we created polygons at buffer distances of 500 and 1000 m. We chose the 1000-m scale based on

Table 1 Vegetation and environmental covariates investigated to influence silver rice rat occupancy and activity in the Florida Keys, USA (2019)

Scale	Covariate	Description	Source
Trap[a]	*Salicornia*	% cover of *Salicornia* spp.	Field collected
	Mangrove	% cover of both red and black mangrove	Field collected
	Struct1	Woody vegetation density 0–1 m above ground	Field collected
	Elevation	Elevation above sea level	NOAA
	Distance	Distance to human development	FL DEP
Landscape[b]	Water	% cover of open water	FL DEP
	Tidal flats	% cover of unvegetated tidal sand flats	FL DEP
	Short veg	% cover of vegetation <1.5 m tall	LiDAR
	Tall veg	% cover of vegetation >1.5 m tall	LiDAR
	Urban	% cover of human development	FL DEP
Trap hourly	Elevation	Same as trap-level	NOAA
	Tide stage	Hourly water height relative to mean sea level	NOAA

[a] 3-m radius circle around trap location.
[b] Each of these covariates was calculated with each of three scales: 70, 500 and 1000 m.

the maximum observed movement of SRR in previous studies (Perry, 2006). Finally, the 500 m scale was chosen to capture the influence of environmental factors outside the home range, but less than the longest distances travelled.

To quantify landscape composition at these larger scales, we used a statewide land use layer to delineate four land cover types that we expected would disparately influence SRR and BLRA habitat selection: (1) open water, (2) tidal sand flats, (3) vegetated land and (4) human development (FLDEP, 2017). Given the known swimming abilities of SRR and the association with human development of BLRA (Goodyear, 1992), we expected disparate effects for these non-vegetated metrics. Within the vegetated areas, we used a LiDAR-derived canopy height to further delineate vegetated land into two additional land cover types, short vegetation (<1.5 m tall) and tall vegetation (>1.5 m tall), for a total of five land cover types (FDEM, 2007). We chose this height threshold to correspond to the definition of dwarf mangrove (Lugo & Snedaker, 1974). The LiDAR data acquisition flights occurred in 2007 and the vertical accuracy of the resulting data were 0.18 m at the 95% confidence level (FDEM, 2007). At each scale, we calculated the percent cover of each of these five land cover types within the polygon created by buffering the trap locations at a given site at the specified scale distances (70, 500 and 1000 m). Unlike the trap-scale covariates, these landscape scale variables were not standardized, because they were already on the same scale (proportion of total area).

Preliminary analysis revealed little variation in open water, tidal flats and urban areas at the 70-m scale. Specifically, there were few sites that included these land cover types at all. As such, we also quantified the influence of these land cover types by measuring the distance from the 70-m scale polygon to the closest area of the given land cover type.

Occupancy modeling

At the trap scale, we used the R package *unmarked*, version 0.12-2, to fit single-season, single-species occupancy models to investigate relationships between environmental covariates and occupancy of both SRR and BLRA (Fiske & Chandler, 2011). This framework allowed us to jointly estimate detection and occupancy probability, thereby accounting for imperfectly detecting rodents at a given trap during a given night (MacKenzie *et al.*, 2017). Specifically, we considered each night to be a sampling occasion, and then used the five-night detection history to model the probability of detecting a SRR on a given occasion. We included the Julian date of the sampling occasion as a continuous observation covariate on detection probability. We fit models with all possible combinations of the trap-level measurements of elevation, distance to development and the vegetation metrics as covariates on occupancy probability. From the resulting model set, we considered only those models within 2 Akaike information criterion (AIC) of the minimum AIC to be competitive, and calculated model-averaged parameter estimates from these competitive models (Burnham & Anderson, 2002). We considered model-averaged covariate effects to be significant if the 95% CI did not overlap 0.

At the landscape level scales, we summarized SRR and BLRA detection histories across nights and across all traps within a site, thereby assuming that a site was not occupied if a species was not detected. Preliminary analysis revealed that for both SRR and BLRA, the cumulative detection probability across the 12 traps over five nights was >0.99. We then used logistic regression to model whether or not a site was occupied as a function of the land use percent cover metrics using the *glm* function in R (R Development Core Team, 2018). To avoid overfitting models with only 33 observations at the landscape scales, we only fit univariate models of each covariate, as well as the null model. Within a given scale for each species, we ranked models according to minimum AIC and considered all models within 2 AIC of the top-ranked model to be competitive.

Temporal activity modeling

The third model type we used aimed to investigate variation in SRR and BLRA activity as a function of lunar tides. Given the twice-daily tide schedule, we considered each hour to be a sampling occasion in order to better match the temporal scale of tides. We then considered the number of photos of a given species taken within a given hour as the response variable, thus serving as a metric of activity. This approach allowed us to investigate temporal variation in activity, and whether that activity was driven by diel or tidal cycles. The tidal height data were acquired from the National Oceanic and Atmospheric Administration via the R package *rnoaa* (Chamberlain, 2019). We modeled rodent activity as a zero-inflated poisson random variable with a conditional mean parameter λ_{ijk} and fixed effects of both tide height at trap i during hour j and the elevation at trap i within site k (equation 1). In addition, we incorporated an interaction effect between elevation and tidal height because we expected the effect of tide height might be more pronounced at either high or low elevation. Finally, we included a random intercept of site k to account for the clustered sampling design where traps are clustered together within a site. We analyzed this model in a Bayesian framework using the *rjags* package, because this framework allowed us the most flexibility in regards to parameterizing different distributions for our response, accommodating longitudinal data, and incorporating random effects (Plummer, Stukalov & Denwood, 2016). We ran three Markov Chain Monte Carlo (MCMC) chains for 30 000 iterations after an initial burn-in of 5000 iterations. We thinned the MCMC chains to every 3rd iteration to account for autocorrelation between adjacent MCMC samples. We evaluated model convergence by investigating trace plots. We evaluated effect strength by comparing means of the posterior distributions and considered an effect significant if the 95% Bayesian credible interval (CRI) for the posterior distribution did not include zero.

$$\log(\lambda_{ijk}) \sim \beta 0_k + \beta 1 \times \text{tideheight}_{ij} + \beta 2 \times \text{elevation}_i + \beta 3 \times \text{tideheight}_{ij} \times \text{elevation}_i. \quad (1)$$

Results

At both the trap and landscape scales, the naïve occupancy (proportion of sampling locations where species was detected) was very similar to the model-averaged occupancy intercepts after accounting for imperfect detection for both SRR and BLRA. Specifically, the naïve occupancy and model-averaged occupancy probability (setting all covariates to 0) across all traps for SRR were 0.15 and 0.16 (SE = 0.02), respectively, at the trap scale, and 0.54 and 0.51 (SE = 0.08), respectively, at the landscape scale. For BLRA, the naïve occupancy and model-averaged occupancy probability were 0.56 and 0.57 (SE = 0.02), respectively, at the trap scale and were both 0.88 (SE = 0.05) at and the landscape scale. The probability of detecting SRR and BLRA at a trap during a given sampling occasion (i.e. averaged across date) was 0.15 (SE = 0.07) and 0.70 (SE = 0.04), respectively. The effect of date on detection of SRR was positive (mean = 0.02, SE = 0.005), whereas detection of BLRA decreased as date increased (mean = −0.006, SE = 0.003).

Of the seven trap-level covariates we considered, four had model-averaged confidence intervals that did not overlap zero for SRR (Table 2). Specifically, the probability that a trap was occupied by SRR increased with decreasing elevation, increasing mangrove and *Salicornia* cover, as well as increasing distance from urban development (Table 2). The strongest of these effects was elevation, with SRR most likely to occur at the lowest elevations that were regularly inundated by tides (Table 2). Neither buttonwood cover nor vegetation density in either height class were included in any of the competitively ranked models. Consistent with these results from the trap scale, SRR were most likely to occur in landscapes comprised of little or no human development, particularly at the 500-m scale, which was the top-ranked landscape model according to AIC, followed by the analogous model at the 1000-km scale (Table 3). Other than the percent cover of human development at the 500-m and 1000-m scales, all other landscape scale metrics had 95% CIs that overlapped zero.

Similar to SRR, BLRA occupancy was associated with increasing mangrove cover and increasing distance from development at the trap scale; parameter estimates for these

effects were 0.70 (95% CI: 0.41–0.98) and 0.36 (95% CI: 0.09–0.63), respectively, which were similar in magnitude to those observed for SRR (Table 2). In contrast to SRR, the parameter estimate for the effect to elevation on BLRA occupancy was positive (mean = 0.38, 95% CI = 0.12–0.63). However, even at low elevations where BLRA occupancy was lowest, it was still greater than the maximum occupancy probability for SRR (Fig. 2). Black rats did not appear to respond to environmental characteristics at the landscape scale; at all three scales, the null model was competitive with the top-ranked model (Table 4).

The temporal model of rodent activity revealed an interaction between elevation and tidal height for SRR. Though the linear effect of tidal height was not significant (95% CRI: −0.02 to 0.09), both the linear effect of elevation, and the interaction between tidal height and elevation were significant (95% CRI's: −0.99 to −0.75 and 0.05 to 0.16, respectively; Fig. 3). SRR were more active at lower elevations independent of tidal height, but they were most active in these low elevations at low tide (Fig. 4). Neither of the linear effects nor the interaction were significant for BLRA. Instead, BLRA activity was approximately uniform across the tidal gradient (Fig. 4). The posterior means for the zero-inflation parameters were 0.81 (CRI: 0.74, 0.89) and 0.51 (CRI: 0.42, 0.59) for SRR and BLRA, respectively.

Discussion

Silver rice rat occurrence was best explained by uniquely coastal characteristics, namely regularly-inundated mangroves, suggesting this species likely is well-suited to adapting to rising sea level. Unlike upland and freshwater-dependent coastal communities that will decrease in extent

Table 2 Model-averaged estimates (on logit scale), SE and bounds (lower and upper) of 95% CIs calculated for all parameters included in competitively-ranked occupancy models for silver rice rat (SRR) and black rat (BLRA) at the trap scale.

Species	Parameter	Estimate	SE	Lower	Upper
SRR	Intercept	−2.06	0.2	−2.45	−1.66
	Distance	0.59	0.15	0.29	0.88
	Elevation	−0.68	0.2	−1.08	−0.27
	Mangrove	0.61	0.17	0.27	0.96
	Salicornia	0.35	0.15	0.05	0.65
BLRA	Intercept	0.36	0.11	0.13	0.58
	Distance	0.36	0.13	0.09	0.63
	Elevation	0.38	0.13	0.12	0.63
	Mangrove	0.7	0.14	0.41	0.98

Table 3 Parameter estimates, lower and upper bounds of 95% CIs, Akaike information criterion (AIC) and the difference in AIC from the top-ranked model for all landscape-scale univariate models of silver rice rat occupancy across its range in the Lower Keys, FL (2019). Descriptions for of covariates can be found in Table 1

Covariate	Estimate	Lower	Upper	AIC	ΔAIC
urban500	−43.8	−88.58	−16.79	30.77	0
urban1000	−25.9	−51.07	−8.6	38.28	7.51
distance_urban70	0.72	−0.09	1.94	46.76	15.99
tallVeg1000	−7.11	−17.31	1.9	47.35	16.58
null model	0.06	−0.63	0.75	47.72	16.95
tidalFlat500	3.97	−1.86	11.49	48.01	17.24
water500	2.39	−1.46	6.69	48.26	17.49
tidalFlat1000	4.46	−3.24	13.51	48.46	17.69
water1000	2.28	−1.92	6.95	48.6	17.83
tallVeg70	−2.37	−7.88	2.61	48.86	18.09
tallVeg500	−3.2	−10.56	3.59	48.87	18.1
shortVeg1000	3.21	−3.64	10.55	48.88	18.11
distance_water70	−0.19	−0.98	0.52	49.43	18.66
shortVeg500	1.16	−3.67	6.23	49.5	18.73
elevation70	−0.06	−0.78	0.64	49.69	18.92
shortVeg70	0.14	−3.02	3.31	49.71	18.94
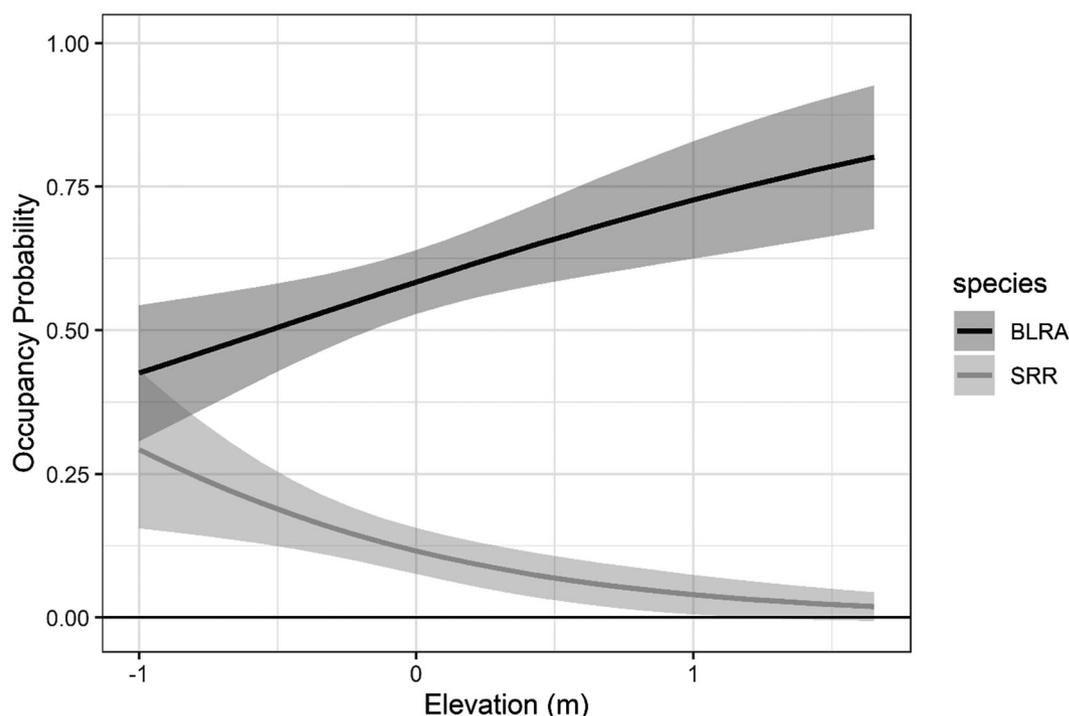
Figure 2 Predicted occupancy probability in the Lower Florida Keys (2019) for black rat (BLRA; black) and silver rice rat (SRR; gray) as a function of elevation according to model-averaged parameter estimates from all models with an AIC < 2. Dashed lines show 95% CIs. AIC, Akaike information criterion.

Table 4 Parameter estimates, lower and upper bounds of 95% CIs, Akaike information criterion (AIC) and the difference in AIC from the top-ranked model for all univariate models of black rat occupancy across the range of silver rice rat in the Lower Keys, FL (2019). Descriptions for of covariates can be found in Table 1

Covariate	Estimate	Lower	Upper	AIC	ΔAIC
distance_urban70	2.84	−0.22	10.24	25.61	0
distance_water70	2.3	−0.3	10.34	26.06	0.45
null model	1.98	1.05	3.2	26.38	0.77
urban500	−3.98	−11.47	3.67	27.13	1.52
shortVeg500	3.08	−4.42	12.23	27.77	2.16
tidalFlat500	−2.72	−9.83	5.72	27.87	2.26
shortVeg1000	2.79	−7.74	14.81	28.11	2.5
urban1000	−2.39	−10.89	9.36	28.11	2.5
tallVeg500	2.7	−7.71	14.57	28.12	2.51
water500	1.49	−4.35	8.15	28.13	2.52
elevation70	0.24	−0.86	1.28	28.16	2.55
water1000	1.57	−4.76	9.56	28.16	2.55
tidalFlat1000	−2.3	−12.47	10.2	28.2	2.59
tallVeg1000	−2.79	−16.95	10.92	28.21	2.6
shortVeg70	0.91	−4.1	5.55	28.23	2.62
tallVeg70	1.22	−6.21	9.91	28.28	2.67

as sea level rises (Ross *et al.*, 1994; Schmidt *et al.*, 2012), increasing inundation by sea water may facilitate the landward migration of coastal wetlands (Doyle *et al.*, 2010; Kirwan *et al.*, 2016), increasing their extent and benefiting associated species (Traill *et al.*, 2011). Not only did we find

SRR using the lowest elevations, but we showed a clear link between their activity and tides, suggesting they are foraging for food resources exposed during low tide, such as macroinvertebrates (Goodyear, 1992). Although previous work has suggested climate change and land conversion may benefit the same suite of species (Frishkoff *et al.*, 2016), our results suggest disparate effects of these stressors for the endangered SRR and potentially other island species.

Black rats were widespread and responded positively to mangrove cover and distance to human development in a similar manner to SRRs, indicating a high degree of overlap in occurrence between these species. Furthermore, the estimated occurrence probability of BLRA in areas below sea level where they were least likely to occur, was comparable to that of SRR (~0.3). However, despite this spatial coexistence, our results show substantial temporal resource partitioning, which has been shown to facilitate coexistence by related species (Adams & Thibault, 2006). While both rodents are nocturnal, SRR were most active at low tides, whereas we did not observe a relationship between BLRA activity and tides. This temporal partitioning is consistent with the diets of these species, where SRR specialize on ephemerally exposed resources, while BLRA are more generalist (Goodyear, 1992). Although BLRA have been implicated in the declines of many island species (Courchamp *et al.*, 2003; Harper & Bunbury, 2015) the threat of BLRA competition for SRR appears to be limited.

Although BLRA occurrence increased at higher elevations as we expected, they did not appear to respond to vegetation
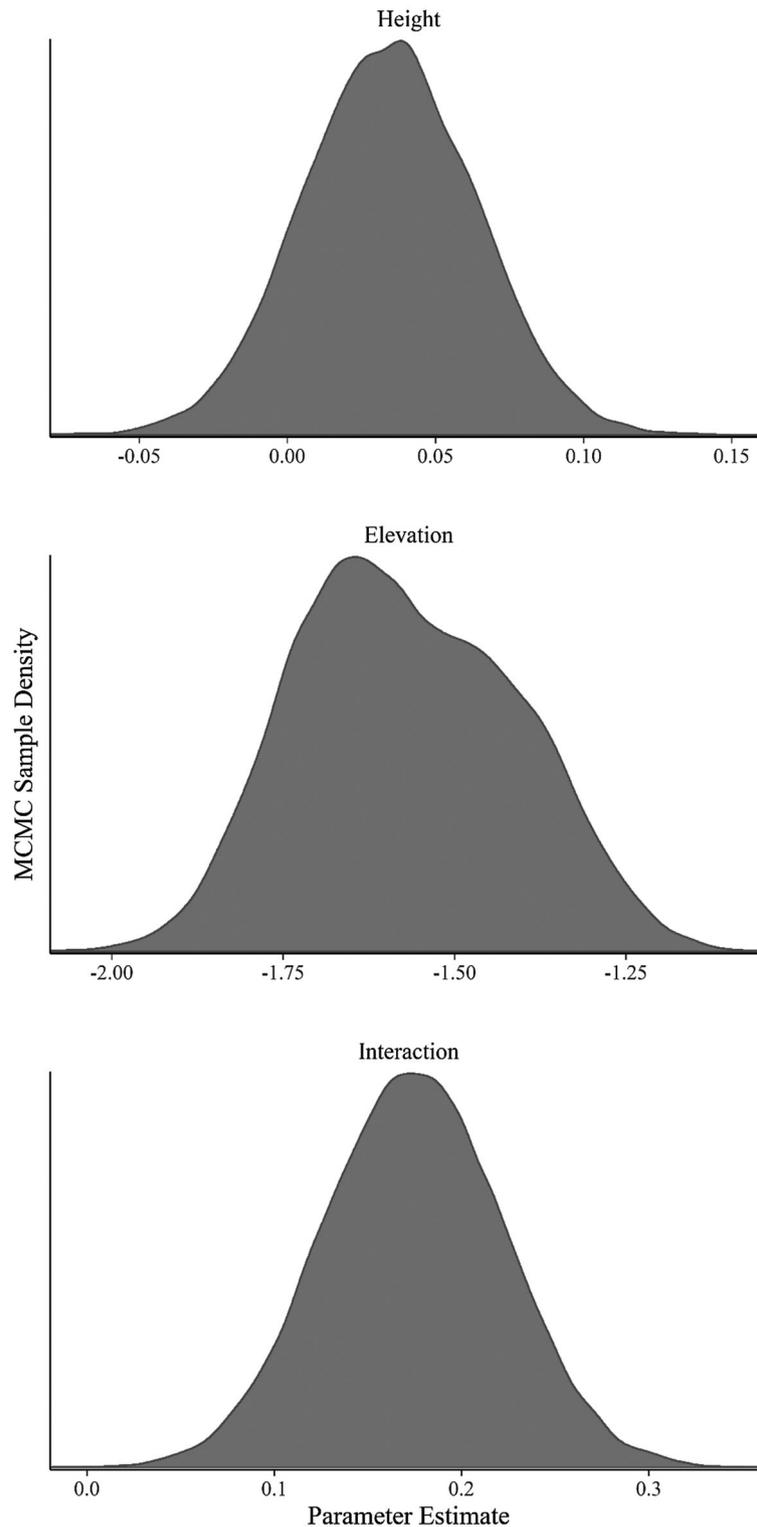
Figure 3 Posterior distributions for the linear effects of tidal stage and elevation, as well as an interaction between these two covariates, on hourly silver rice rat activity across their range in the Lower Florida Keys (2019).

structure, which was unexpected given their arboreal nature (Goodyear, 1992; Courchamp *et al.*, 2003; Sunquist & Sunquist, 2017). Additionally, BLRA occurrence increased with mangrove cover and distance from development, whereas we expected opposite responses to these habitat characteristics. Given BLRA and SRR represent opposite ends of the specialist-generalist
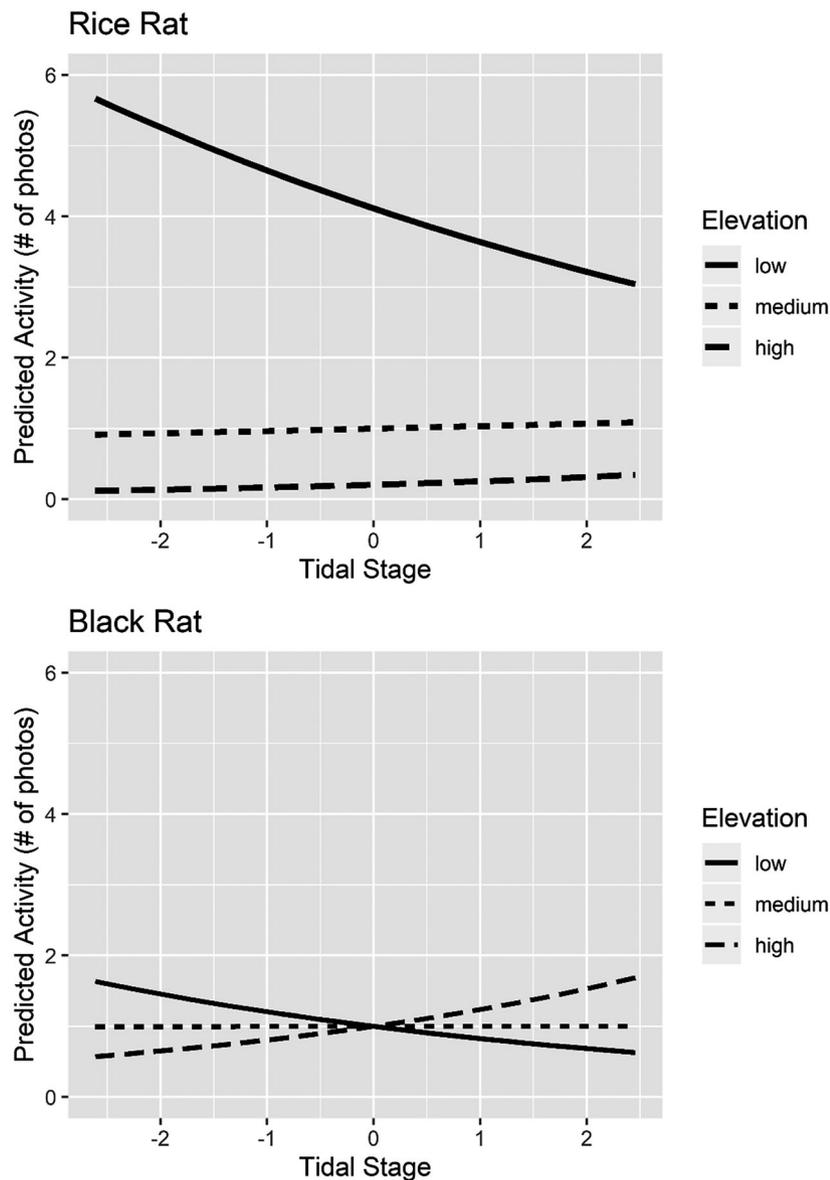
Figure 4 Predicted activity measured by the number photos taken per hour with remote cameras and modeled as a function of tidal stage, at each of three elevations (low = −0.9 m, medium = 0 m, and high = 1.0 m relative to mean sea level) for silver rice rat (top) and black rat (bottom) on the Lower Florida Keys, USA (2019).

spectrum and generalist mammals thrive in urban areas (Rodewald & Gehrt, 2014), it was surprising that both species appeared to be sensitive to development. A previous study from mainland Florida showed that occurrence of generalist mammals increased with decreasing distance to urban development, but at a scale an order of magnitude greater than that which we considered (Reichert *et al.*, 2017). Furthermore, we selected sampling locations based on expected suitability for SRR, but where BLRA also happen to occur. Thus, our results for BLRA are limited to only these areas and distributing sampling locations across the Lower Keys more broadly may reveal more expected responses of BLRA to factors such as urban development and upland vegetation conditions.

Human development of the Lower Keys appears to be the primary threat to SRR. Though we observed SRR to select habitat primarily at the trap scale, the proximity and amount of human development negatively influenced SRR habitat selection across scales. In addition to lacking tidal or freshwater wetlands required by SRR (Goodyear, 1987), the urban developments of the Lower Keys typically consist of highly altered environments with limited native vegetation, consistent with broader patterns of urbanization-induced biotic homogenization (McKinney, 2006). Furthermore, these changes in vegetation can alter other ecosystem processes, such as disturbance dynamics, which could ultimately facilitate woody encroachment and vegetation maturation

(Marzluff & Rodewald, 2008). Compounding these effects of altered vegetation, feral cat occurrence on the Florida Keys was higher near human development and was previously shown to be detrimental to another endangered mammal endemic to the Lower Keys (Cove *et al.*, 2018). Regardless of the mechanisms, limiting future development will be essential to conserving the endangered mammals of the Lower Florida Keys (Lopez *et al.*, 2004).

While island species associated with coastal environments may potentially benefit from rising sea level in the coming decades, this resilience depends on the landscape context and the ability of coastal island environments to migrate landward (Gilman *et al.*, 2006; Mazaris, Matsinos & Pantis, 2009; Saunders *et al.*, 2013; Borchert *et al.*, 2018). In addition to directly threatening native species, such as SRR, human development such as buildings and roads, but also shoreline protection infrastructure, like breakwalls and bulkheads, can impede the landward migration of tidal environments resulting in net habitat loss (Enwright, Griffith & Osland, 2016). Even for island species that may be resilient to rising sea level in the short-term, long-term conservation will require reducing the anthropogenic contribution to rising sea level, particularly on islands with small area and topographic relief (Maschinski *et al.*, 2011; Wetzel *et al.*, 2013).

Acknowledgments

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Floating bucket trap.

Figure S2. Residuals correlelegram for top-ranked trap-level occupancy model for silver rice rat.

Figure S3. Histogram of silver rice rat detection times of day.

Figure S4. Comparison of cumulative detection probabilities from floating bucket camera traps and traditional live traps.

Table S1. Summaries of environmental variables.

Table S2. Correlation table for trap-level covariates.

Table S3. Summary of the number of nights during which rodents were detected.