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ORIGINAL RESEARCH

Sea level rise adaptation pushes an insular endemic rodent closer to extinction

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Abstract
Understanding how species will respond to a rapidly changing global climate is requisite to conserving biodiversity. Though habitat losses from human development and land use change remain the most critical threats to biodiversity globally, some regions, such as low-lying islands, are particularly vulnerable to the effects of climate change. Despite this vulnerability, there may be opportunities for imperiled species on islands to adapt to the effects of climate-induced sea level rise. To understand how the response to rising seas may influence the amount of future habitat, we investigated shifts in the elevational range of the endangered silver rice rat (*Oryzomys palustris natator;* hereafter "rice rat"), a species endemic to tidal environments of the Lower Florida Keys, USA. We quantified fine-scale habitat use using radio telemetry of collared animals, first in 2004, and again in 2021, thus spanning a 17-year period during which the local sea level rose by 0.142 m. We observed a shift in the elevational range limits of rice rats which closely mirrored the rise in sea level, and that this apparent ability to adapt to rising sea level decreased the extent of habitat loss in subsequent decades. However, over longer time scales (~100 yrs), the extent of habitat loss from sea level rise outpaced rice rats' ability to adapt. As such, the conservation of biodiversity on low-lying islands hinges on the ability of the global community to decrease anthropogenic greenhouse gas emissions and mitigate the associated consequences for the global climate. Otherwise, conservation practitioners will be increasingly forced to make difficult decisions about how to conserve imperiled species on low-lying islands.

Keywords Climate · Rodent · Mangrove · Coast · Elevation · Inundation · Telemetry

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Extended author information available on the last page of the article

Introduction

Human development and land use change, the introduction of exotic species, overexploitation, and pollution currently represent the primary drivers of the global biodiversity crisis (Jackson 2008; Wake and Vredenburg 2008; Davis et al. 2018; Rosenberg et al. 2019; Dobson et al. 2021; Caro et al. 2022). However, as global climate change continues to accelerate, there is increasing concern about its potential to degrade biodiversity, particularly in regions and ecosystems that are vulnerable (Kannan and James 2009; Urban 2015; Nunez et al. 2019; Román-Palacios and Wiens 2020). In addition to some regions being more vulnerable to a changing climate than others, the species within vulnerable areas are likely to vary in their ability to respond to changing conditions.

One way species may respond to climate change is by shifting their elevational range to track the environmental conditions (e.g., temperature). Previous research has documented species shifting upslope in response to climate change and has linked these shifts to the extirpation of species occurring at the highest elevations as they run out of opportunities to shift upslope (Marris 2007; Sekercioglu et al. 2008; Tingley et al. 2012; Freeman et al. 2018). In contrast, species at the lowest elevations may gain habitat as areas at higher elevations become suitable and areas at the lowest elevations remain suitable (Freeman et al. 2018). As such, the net habitat loss resulting from the difference between shifts at the upper extent of a given species' elevational range and that at the lower elevational range is critical to understanding species long-term conservation trajectory (Tingley et al. 2012; Mamantov et al. 2021).

Low-lying islands are particularly vulnerable to the effects of climate change, while contributing disproportionately to global biodiversity (Courchamp et al. 2014; Harter et al. 2015; Russell and Kueffer 2019). Given the small ranges and high rates of endemism among species on islands, as well as the isolated geographical context inherent to islands (Whittaker 1998), even small changes in habitat extent could have dramatic conservation implications. Thus, rapidly rising sea-level is likely to exacerbate on-going threats to biodiversity on islands, such as human development, exotic species, and overexploitation (Clavero and Garcia-Berthou 2005; Clavero et al. 2009; Harper and Bunbury 2015; Wood et al. 2017). Similar to species on mountains, species at the highest elevations of low-lying islands face an escalator to extinction (Marris 2007) as they run out of opportunities to shift upslope. Additionally, however, species occurring at the lowest elevations of islands may face habitat loss resulting from inundation by rising seas (Wetzel et al. 2013; Courchamp et al. 2014; Field et al. 2017). Thus, considering shifts in both upper and lower elevational range limits is critical to understanding the conservation trajectory of species on islands.

Understanding and addressing the threats to biodiversity on low-lying islands is obscured by a high degree of uncertainty, both in the rate of sea level rise and how animals may respond to a given rate of rise. Global climate change primarily contributes to rising sea level via the thermal expansion of the ocean and the melting of glaciers and ice caps (Church et al. 2013). Uncertainty around future rates of rise results from uncertainty in those physical processes, but also from uncertainty in greenhouse gas emissions and other aspects of sustainable development (Garner et al. 2021). Independent from the factors affecting the rate of rise, the ability of species to persist despite rising sea levels depends on their ability to respond to their changing environment. For species occurring near sea level, their continued persistence requires they shift upslope as the lowest elevations become permanently

inundated from rising sea levels. While inundation drives changes in habitat extent at the lower range limit, expansion at the upslope edge of an animal's range may depend more on factors related to changes in vegetation composition and structure, such as post-disturbance succession, dispersal, and tolerance to changing environmental conditions (Ross et al. 2009; Román-Palacios and Wiens 2020). Furthermore, a species' ability to respond to changing conditions may change over time as they encounter new barriers that impede range shifts.

To understand the potential for species on low-lying islands to adapt to a rapidly changing environment, we assessed the habitat loss trajectory of the endangered silver rice rat (*Oryzomys palustris natator*; hereafter "rice rat"), which is endemic to the low-lying Florida Keys, USA (Indorf and Gaines 2013). This species is both purportedly vulnerable to rising sea level, but may also have potential for upslope migration, and thus resilience. Specifically, its association with tidal environments renders it vulnerable to rising sea levels at its lower elevational range limit, but also offers more potential to shift upslope compared to sympatric endangered species (e.g., lower Keys marsh rabbit [*Sylvilagus palustris hefneri*] and Key deer [*Odocoileus virginianus clavium*]), which are associated with more upland environments. By integrating a high-resolution elevation model with animal locations and sea level rise projections, we aimed to (1) define the rice rat's elevational range, (2) quantify and compare range limit shifts to sea level rise over a 17-year period, and (3) forecast future changes in the amount of potential habitat as a function of sea level rise and the ability of rice rats to shift their range. Given rice rats' association with the lowest elevations (Taillie et al. 2020) and previous work suggesting that these lower-elevation communities may benefit from rising sea level (Ross et al. 2009), we expected rice rats to have shifted upslope in recent decades and that such shifts would mitigate habitat losses caused by rising sea level.

Methods

Our approach to investigating the implications of rising sea level for rice rats involved first determining the extent to which the upper and lower range limits of rice rats have shifted over a 17-year period, and then forecasting how the extent of potential habitat will change under multiple scenarios over the next century. To determine their elevational range, we used radio telemetry to obtain locations of individuals in 2004 and 2021, and then adjusted for the observed amount of sea level rise over that 17-yr period. We then used the 2021 elevational range to map and calculate the extent of potential rice rat habitat across its range during that year, and during each of the 90 successive years under the assumption that initial elevational ranges shifts would be proportional to sea level rise.

Study species

The silver rice rat is a semi-aquatic rodent endemic to the low-lying islands of the Florida Keys, United States. Unlike mainland populations of the marsh rice rat (*Oryzomys palustris*) that are associated with herbaceous wetlands (Wolfe 1982; Cooney et al. 2015; Sunquist and Sunquist 2017), silver rice rats are closely associated with dwarf mangrove (i.e. *Rhizophora mangle* and *Avicennia germinans*) communities at elevations near sea level (Taillie et al. 2020). Specifically, they are most active at the lowest elevations during low tides, likely because they are foraging for exposed macroinvertebrates (Goodyear 1987, 1992; Taillie et

al. 2020). Given their small range and vulnerability to rising sea level, tropical storms, and invasive species, rice rats were listed as federally endangered in 1991, but their population is thought to have remained fairly stable in recent decades (USFWS 2021).

Species associated with tidal communities on low-lying islands, like rice rats, are likely more resilient to rising sea level than sympatric species associated with more upland environments (Ross et al. 2009), making them ideal for understanding the potential of endemic wildlife to adapt to rising sea levels on low-lying islands. However, if rising seas permanently inundate tidal areas and animals fail to shift upslope, the resulting habitat loss for coastal fauna could be catastrophic (Bellard et al. 2014). As such, the future extent of habitat for animals associated with coastal environments depends on their ability to adapt to rising sea level (Schuerch et al. 2018).

Study area

The low-lying islands of the Florida Keys are located within the Caribbean Region, whose low-lying islands are particularly vulnerable to climate-induced biodiversity loss (Bellard et al. 2014). We conducted our study on the southern end (i.e., "Lower Florida Keys") of this subtropical archipelago off the southern coast of mainland Florida. The Lower Florida Keys include 32 islands greater than 100 ha in size, in addition to hundreds of smaller islets. Elevations rarely exceed 2 m above sea level, and this subtle elevational gradient plays an important role in determining vegetation community composition (Ross et al. 1992). The distribution of both rice rats and the vegetation conditions with which they are most closely associated are both strongly influenced by elevation (Taillie et al. 2020). As such, we assumed that all undeveloped land within the elevational range of rice rats represented "potential habitat."

The local rate of sea level rise increased throughout the 20th century to over 0.0023 m/yr in the second half of the century (Maul and Martin 1993), and 0.0036 m/yr more recently between 1994 and 2013 (Ogurcak et al. 2019; Table S3). Over the course of our study (i.e., 2004 to 2021) the sea level at Key West, FL rose by 0.142 m, a rate substantially greater than those reported previously (Fig. S3, NOAA 2021). As a result of climate change, local relative 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 land is below 1 m elevation (Ross et al. 1992, 1994, Maschinski et al. 2011, Ogurcak et al. 2019).

Elevation and sea level rise scenarios

Given our focus on the tidal zone, we assigned elevations according to an elevation model developed specifically for the Lower Keys by the National Geophysical Data Center (NGDC) that integrated measurements from both the terrestrial land surfaces and the surrounding submerged aquatic environments (Grothe et al. 2011). As such, the resulting 10-m resolution topo-bathymetry digital elevation model (DEM) provides continuous coverage across the tidal zone, independent of the change in sea level over the duration of the study. Much of the data informing the DEM were collected between 2007 and 2009 (Grothe et al. 2011), and so we considered these elevations to represent the elevation relative to the 2007 sea level. We projected the change in sea level according to the National Aeronautics and Space Administration (NASA) sea level rise projection tool, which accesses the sea level

rise projections resulting from the global development scenarios used in the Inter-governmental Panel on Climate Change (IPCC) 6th Assessment Report (AR6; Garner et al. 2021).

To understand how different sea level rise scenarios might influence the habitat trajectory of rice rats on the Lower Florida Keys, we considered 2 of the 5 Shared Socioeconomic Pathways (ssp's) described in the AR6. The first, ssp119, is considered the most sustainable where global carbon dioxide emissions begin to decrease this decade (Riahi et al. 2017). In contrast, the second ssp. we considered, ssp370, assumes that global carbon dioxide emissions begin to increase less rapidly over the next two decades, but continue to increase through 2100 (Riahi et al. 2017). Hereafter, these ssp's are referred to as the "sustainable development" and "business as usual" scenarios, respectively. In the decades following 2020, the rate of rise in both scenarios is approximately 0.006 m. However, starting around 2050, the rate of rise begins to diverge, such that the sea level in 2110 is 0.317 m higher under the business as usual scenario compared to the sustainable development scenario (Table S1).

Initial elevational range

Given the strong relationship between elevation and rice rat habitat use (Taillie et al. 2020), quantifying the elevational range limit of rice rats was critical to understanding the extent of their potential habitat. To define the initial (i.e., 2004) elevational range of rice rats, we used USFWS (United States Fish and Wildlife Service) data from the trapping and collaring of rice rats between August and September 2004 (Appendix 1). Using QGIS version 3.4.2-Madeira (QGIS 2018), we overlaid the locations (Table S2) on the DEM to extract the elevation of each location relative to the 2007 sea level. To minimize the effect of outliers, we defined the upper and lower elevational range limits according to the 95th and 5th percentiles, respectively, as opposed to using the true maximum and minimum limits.

Observed range shifts

To evaluate the extent to which the elevational range of rice rats tracked rising sea level after 2004, we collared and tracked rice rats using radio telemetry in 2021 (Appendix 1). All procedures for handling animals during the 2021 fieldwork were reviewed and approved by the University of Florida IACUC on protocol 202,110,390. We collared rice rats on 3 different islands of the Lower Florida Keys and tracked each individual to at least 3 locations between October and December (Table S2). As with the 2004 telemetry locations, we extracted the elevation at each location according to the DEM. We first compared the 2021 elevations to the 2004 locations relative to the 2007 sea level according to the DEM. We then compared the elevations adjusted for the observed rise in sea level by subtracting the 0.142 m of sea level rise observed over the 17-year period from the 2021 locations. We used the *t.test* function in R to compare the mean elevations from 2004 to 2021, for both the relative elevations and the elevations adjusted for sea level rise. Because the upper and lower range limits are subject to different processes (e.g., upslope vegetation migration and sea level rise, respectively) and may shift at different rates, we used quantile regression to compare the upper and lower range limits between years for both the relative elevations and those adjusted for sea level rise. Specifically, we compared the 95th percentile and the 5th percentile, corresponding to the upper and lower range limits, respectively, using the

rq function in the quantreg package (Koenker 2022) in the R computing environment (R Development Core Team 2018). We assumed a range limit had shifted between years if the 95% confidence interval for 2004 did not overlap that of 2021.

Potential habitat modelling

To understand the implications of future sea level rise for potential rice rat habitat, we projected their elevational range 90 years into the future (starting in 2021) according to both a best-case and worst-case rice rat response scenario (Appendix 2). Under the best-case scenario, we assumed that both the upper and lower elevational range limit would track rising sea level. For example, if sea level rose by 0.5 m, the upper and lower elevational limits would shift upslope by 0.5 m. Under our worst-case scenario, we assumed that the lower elevational range limit would track with rising sea level (same as best-case scenario), but the upper limit would remain fixed at its 2021 level. Such a response could result from a lack of landward migration by tidally-influenced vegetation communities, coastal squeeze from human development, tolerance to stress by existing vegetation, or competitive exclusion from uplands by other animal species (e.g., invasive black rats, *Rattus rattus*) (Doody 2004; Schmidt et al. 2012; Field et al. 2016; USFWS 2021). We applied each of these rice rat response scenarios to the two sea level rise scenarios described above ("business as usual" and "sustainable development"), resulting in 4 total scenarios.

For each of the 4 scenarios (i.e., two sea level rise scenarios and 2 rice rat response scenarios), we calculated the areal extent of undeveloped land within the associated range limits in each year from 2021 to 2110 (Table S1). To map and calculate the extent of the initial potential rice rat habitat, we extracted all cells from the DEM with elevations within the observed 2021 elevational range limits of rice rats. In successive years, we added the projected amount of sea level rise to the observed range limits to obtain projected range limits for each year, and recalculated the extent of undeveloped land within those projected range limits. All analyses were performed in R (R Development Core Team 2018), using the stars and sf packages (Pebesma 2018, 2021). In addition, we masked areas of open water and human development from our analysis, as defined by a statewide land use map (FLDEP 2017).

Results

Elevational range shifts

In 2004, the 188 locations from 12 collared rice rats (Table S2) represented an elevational range between −0.188 and 0.258 m relative to the 2007 sea level (Fig. 1a). In 2021, we collared and tracked 17 rice rats for a total of 278 locations (Table S2). The elevational range according to the 5th and 95th percentiles was 0.018 to 0.469 m. Thus, compared to the 2004 locations, the 2021 locations revealed a substantial shift in the elevational ranges of rice rats (Fig. 1). When comparing the means using a T-test, the upslope shift we observed between 2004 and 2021 was significant at the 0.05 level for the unadjusted elevations ($p<0.01$), but was also significant after adjusting for the rise in sea level ($p=0.04$). This difference in mean elevations adjusted for sea level rise between 2004 and 2021 was 0.023 m, suggesting that

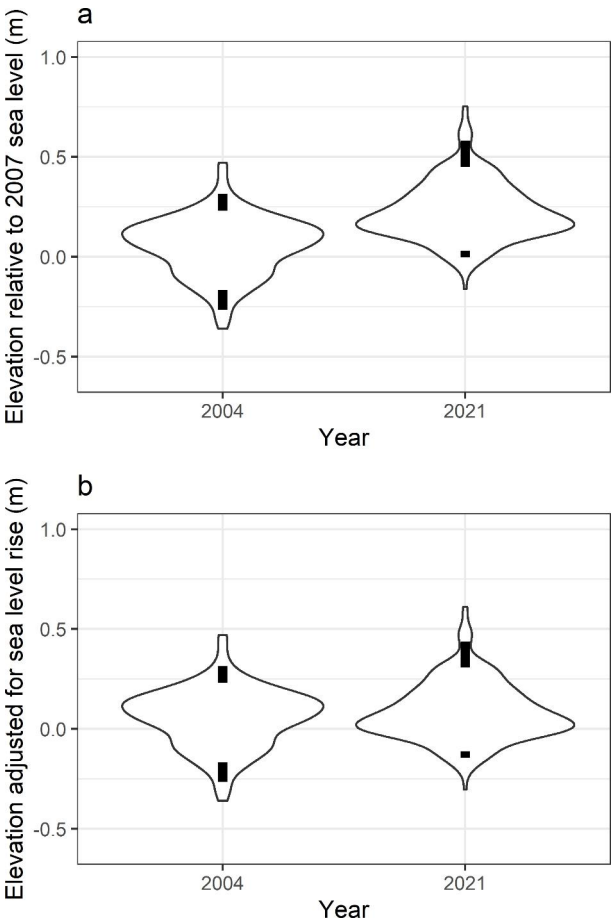

Fig. 1 Radio telemetry was used to obtain locations of silver rice rats in the Lower Florida Keys, USA in each of 2004 ($n=188$) and 2021 ($n=278$). From these locations, the elevation relative to sea level in 2007 **(a)**, as well as the elevation adjusted for the rise in sea level between 2004 and 2021 **(b)**, was extracted and the distributions are shown as violin plots. In addition, the black vertical lines show the 95% confidence intervals for the 95th percentiles and 5th percentiles, which were derived using quantile regression, to compare the upper and lower range limits, respectively

rice rats shifted upslope by an amount greater than the observed rise in sea level (0.142 m). Moreover, both the upper and lower range limits shifted upwards. The 95th and 5th percentiles shifted upwards by 0.205 and 0.206 m, respectively, which corresponded to shifts of 0.063 and 0.064 m, respectively, after adjusting for sea level rise (Fig. 1).

After excluding open water and developed areas, 16,525 hectares of land remained within the Lower Florida Keys. Of this undeveloped land, approximately 8,210 ha (50%) was within elevational range of rice rats in 2004. Because most of the undeveloped land on the Lower Keys occurs near sea level (Fig. 2), the upward shift in the elevational range in rice rats resulted in a decrease in potential habitat. Specifically, the amount of potential habitat remaining in 2021 was 5,530 ha, representing a loss of potential habitat between 2004 and 2021 of approximately 2,680 ha (33%).

Potential habitat projections

The relative roles of the rate of sea level rise and the adaptability of rice rats on the trajectory of habitat loss depended on the temporal scope (Fig. 3). In the near-term (i.e., 2021 to 2040), there was little difference in the amount of potential habitat lost under the sustainable

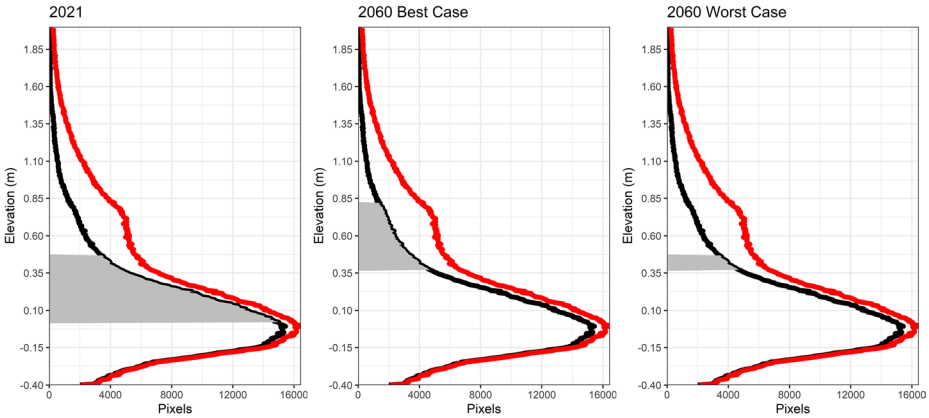

Fig. 2 The elevational distribution of the Lower Florida Keys (red) as well as that of just the un-developed areas (solid black line). The gap between the black line and red line represents additional potential habitat that is unavailable due to human development. The shaded area represents the potential habitat within the elevational range of the endemic silver rice rat observed using radio telemetry in 2021 (left panel), the projected range in 2060 assuming they continue to shift their range ("best case response"; middle panel) as sea level rises according to the ssp119 shared socioeconomic pathway and the worst case response where their upper range limit remains fixed (right panel)

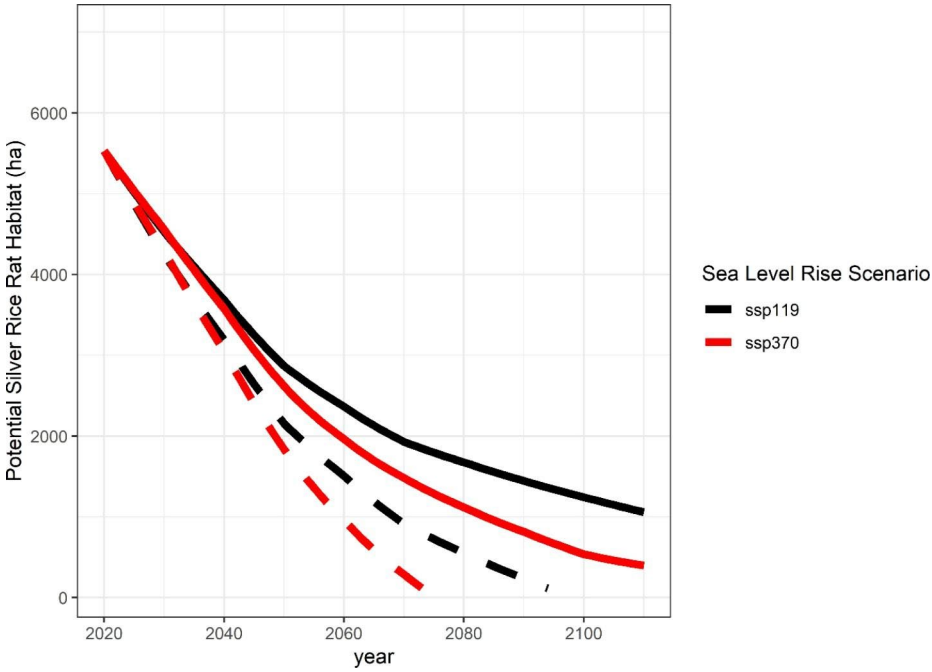

Fig. 3 The amount of potential silver rice rat habitat (i.e. undeveloped land within the observed elevational range limits) in the Lower Florida Keys, USA for 2 sea level rise scenarios based on the Shared Socioeconoic Pathways (ssp.) described by the Intergovernmental Panel on Climate Change. For each sea level rise scenario, we considered two rice rat response scenarios: a best-case scenario (solid lines) where their upper and lower elevational ranges track rising sea level and a worst-case scenario (dashed lines) where the lower limit tracks rising sea level due to inundation, but the upper limit remains fixed

development sea level rise scenario (1,846 ha) and business as usual scenario (1,953 ha). However, the habitat lost over this period under the worst-case rice rat response scenario was 2,340 ha and 2,475 ha under the sustainable development and business as usual sea level rise scenarios, respectively. Thus, the amount of near-term habitat loss due to the adaptability of rice rats was more than 3x greater that that due to the rate of sea level rise. Furthermore, human development played an important role in the trajectory of habitat loss over this timeframe, as most human development existed above the 2021 upper elevational range limit (Fig. 2). Thus, habitat loss related to a shift upslope was dramatically exacerbated by extent of human development at higher elevations.

Starting around 2040, the rate of potential habitat loss began to slow, especially under the sustainable development sea level rise scenarios (Fig. 3). Between 2040 and 2060 (i.e., the same duration as the near-term period above), the additional amount of potential habitat loss ranged from 1,317 ha under the sustainable development sea level rise and best-case rice rat response scenario to 2,090 ha under the business-as-usual sea level rise scenario and worst-case rice rat response scenario. In contrast to the previous 20-year period where the difference in potential habitat loss between the sustainable development and business as usual sea level rise scenarios was approximately 107 ha, this difference increased to 293 ha between 2040 and 2060 (Fig. 3), assuming the best-case rice rat response. Nonetheless, the amount of potential habitat reached 0 ha under both of the worst-case rice rat response scenarios (i.e., regardless of the rate of sea level rise; Fig. 3). In contrast, if rice rats continue to shift their ranges in proportion to sea level rise, there will be approximately 400 ha and 1,060 ha of potential habitat remaining in 2110 under the sustainable development and business as usual sea level rise scenarios, respectively.

Discussion

Our results demonstrate that animals occurring at the lowest elevations of low-lying islands are shifting their ranges to accommodate rising seas and that these shifts can mitigate habitat loss associated with contemporary rates of sea level rise. However, this adaptive response resulted in a 33% loss of potential habitat over the course of our study. Thus, continued sea level rise over the next century is likely to result in dramatic habitat losses for species on low-lying islands. This habitat loss almost certainly equates to an elevated risk of extinction as anthropogenic climate change accelerates sea level rise rates (Bellard et al. 2014). As such, mitigating greenhouse gas emissions and sequestering atmospheric carbon present a critical and growing challenge for biodiversity conservation on low-lying islands and coastal systems.

Our results show that the ability of species to shift their elevational ranges upslope is critical to the persistence of coastal communities (Smith 2013; Kirwan and Megonigal 2013; Kirwan et al. 2016b), particularly in areas like the Florida Keys where vertical accretion rates are slow (Callaway et al. 1997). The comparable shifts in the upper range limit (0.205 m) and lower range limit (0.206 m) suggest that rice rats faced few obstacles to shifting upslope over the duration of our study, but it remains to be seen if these shifts will continue. A smaller shift in the upper range limit compared to the lower limit would suggest that characteristics of the landscape (e.g., human infrastructure) or vegetation community (ability to disperse/colonize upslope areas) were limiting the ability of rice rats to shift.

Instead, we observed rice rats shifted more than sea level rose at both the upper and lower range limits (0.063 and 0.064 m, respectively). This response may result from the nonlinear nature of sea level rise or an interaction with more acute extreme weather events. For example, the local sea level was over 0.04 m higher in 2019 and 2020 (Fig. S3), which could have contributed to the elevational shifts we observed. Alternatively, storm surge from hurricanes like Hurricane Irma in 2017 could facilitate the upslope migration of coastal communities, while contributing little to the annual average sea level (Doyle et al. 2003, 2010; Field et al. 2017). Regardless of the cause, these shifts greater than the observed rise in sea level pushed rice rats further along the escalator to extinction. A greater temporal resolution revealed through more frequent longitudinal sampling of elevational shifts would be better able to reveal these non-linear processes than simply comparing between two years.

Though the difference in potential habitat loss between the two sea level rise scenarios in the near term was negligible, the role of the rate of sea level rise increased over time. In addition to topography and an island's elevation profile, which determines the potential for communities to shift upslope (Elsen and Tingley 2015), several local factors may influence the habitat loss trajectory related to rising sea level. Independent of the global rate of sea level rise, ocean currents, temperature, and geological factors influence the change in sea level experienced in a given location (Church et al. 2013). However, increased inundation associated with a rise in sea level could increase the rate of vertical accretion of sediments (Kirwan and Megonigal 2013; Kirwan et al. 2016a). Thus, the vulnerability of islands to rising sea levels varies geographically (Webb et al. 2013), with some coastal wetlands accreting material fast enough to keep pace with local sea level (Callaway et al. 1997). The conservation trajectories of imperiled species on low-lying islands are likely similarly dependent on these local factors and processes. Regardless, these feedbacks between sea level rise and vertical accretion are unlikely to keep pace with the accelerated rates of sea level rise that are projected from unmitigated rates of greenhouse gas emissions (Sasmito et al. 2016).

One of the key limitations of our study is the difference between potential rice rat habitat and actual rice rat habitat. Though we considered all vegetated areas within the elevational range of rice rats to represent potential habitat, much of that is not actually used by rice rats (Taillie et al. 2020). Thus, our estimate of potential habitat likely represents an overestimate of rice rate habitat, which may partly explain why the rice rat population appears stable despite our estimate of a 33% decrease in potential habitat over the duration of the study. Additional factors such as vegetation composition and structure, food availability, and predation pressure likely contribute to habitat use among rice rats and thus should be considered in future efforts to estimate population dynamics. Additional monitoring of rice rat habitat use and movement would also help to quantify habitat loss at finer scales with less uncertainty.

Even under the most optimistic scenarios, our results suggest a dire future for species on low-lying islands. Given the inevitability of rising sea level, we make three recommendations for conserving imperiled species on low-lying islands. First, we recommend that future conservation actions (e.g., habitat restoration, invasive species eradication) be concentrated in areas with the potential to serve as future climate refugia (Michalak et al. 2018, Morelli et al. 2020). Second, we suggest that managers develop strategies and trial methodologies for the translocations and assisted migrations that will likely be needed to save threatened populations (Thomas 2011). Finally, though highly contentious, we recommend that policy

makers and communities plan for the eventual withdrawal of people and subsequent restoration of currently developed areas (Hauer 2017; Lincke and Hinkel 2021).

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Authors' contributions All authors contributed in conceptualization of the study. P.T., N.P., and R.M. designed the study and collected the data. P.T. led data analysis, with input from R.M. Writing of the manuscript and preparation of the figures was led by P.T., with input from all co-authors.

Data Availability The data and analysis code are available in an R project archived at the Zenodo Data Repository. DOI: https://doi.org/10.5281/zenodo.8144287

Declarations

Ethics approval and consent to participate Protocols for capturing, collaring, and tracking animals were approved by Texas A&M Institutional Animal Care and Use Committee (IACUC) on protocol 2003 – 271 and the University of Florida IACUC on protocol 202110390.

Competing interests The authors do not have any competing interests to claim. However, the findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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