

RESEARCH ARTICLE

Endangered beach mouse resistance to a Category 5 hurricane is mediated by elevation and dune habitat

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Abstract

Coastal ecosystems and their endemic taxa are under threat from hurricanes that are increasingly frequent and severe due to climate change—leading to a need to better understand factors associated with species' resistance (capacity to withstand) and resilience (capacity to rebound) to these storms. The beach mouse species complex (*Peromyscus polionotus* spp.) is a representative endangered group of rodents tightly associated with such coastal habitats. We examined track-tube monitoring data of beach mice from Tyndall Air Force Base, Florida, USA, before and after the 2018 strike of Hurricane Michael, a Category 5 hurricane, and again before and after the 2020 strike of Hurricane Sally, a Category 2 hurricane. We applied dynamic occupancy models to track-tube survey data to assess environmental factors associated with beach mouse initial occupancy and local extinction following Hurricane Michael. Beach mice exhibited high probabilities of detection and initial occupancy across most sites and all representative habitats before Hurricane Michael. Dynamic models revealed that local extinction probabilities of beach mice decreased with increasing elevation and dune habitat, followed by grassland, and scrub—highlighting high elevation dune as the primary driver of beach mouse resistance to storms. Extinction probability was not related to other factors like plant species percent cover or proximity to storm strike. Beach mice occurred at 100% of track-tubes before and after Hurricane Sally. Beach mice are adapted to persist in dynamic coastal environments with regular hurricane strikes, as evidenced by their resistance and resilience following Hurricane Michael to reach 100% occupancy with high resistance to the weaker Hurricane Sally. However, as hurricanes become stronger and more frequent with global change, isolated populations of beach mice may be more susceptible to local extinction with the corresponding loss of elevation and dunes. High elevation, particularly in dune habitats, is an important mediator of resistance and resilience to hurricane impacts and should be considered in habitat restoration and reintroduction strategies, especially if relative elevation decreases with sea-level rise.

KEYWORDS

climate change, disturbance, occupancy, *Peromyscus*, rodents

Plain language summary

Threatened and endangered species that occur in coastal areas are susceptible to the impacts of hurricanes that can destroy and

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reorganize their habitats. We showed that endangered beach mice can survive these impacts by using high elevation dune habitats to stay safe. However, as hurricanes become more frequent and stronger with future climate change projections, the threat may become too strong for hurricane-adapted species and ecosystems.

1 | INTRODUCTION

Coastal ecosystems are dynamic in nature, shaped by the storms, tides, winds, and other abiotic processes (Burke et al., 2001), yet they face diverse threats, including habitat loss and fragmentation due to human development, rising sea-level, and storm surges associated with climate change and major storm events (Schmidt et al., 2012). Hurricanes (tropical cyclones) often play a key role in shaping these coastal dynamics through high winds, storm surge, and heavy rainfall. Atlantic hurricanes are becoming more frequent and intense (Balaguru et al., 2016; Sobel et al., 2016); the 2020 season was the most active in recorded history. Identifying the abiotic aspects of coastal ecosystems most impacted by hurricanes and quantifying their change post-storm can provide valuable insights into priority areas for management toward resistance (weathering the storm) and resilience (rebounding from the storm—Patrick et al., 2022).

Beach mice (*Peromyscus polionotus* spp.) are a species complex of six federally endangered rodent subspecies of oldfield mouse endemic to barrier islands and coastal areas along the Atlantic and Gulf coasts of Florida and Alabama in the United States where they are potentially threatened by strengthening hurricanes (Bird et al., 2002; Falcy & Danielson, 2014; Swilling et al., 1998; Pries et al., 2009). Furthermore, as development has reduced and fragmented their habitat at many sites, the impact of compounding effects from stochastic events like hurricanes and external factors such as invasive predators (*Felis catus*) makes individual populations susceptible to local extirpation (Greene et al., 2017). Beach mice build burrows and regularly occupy the primary dunes that form the initial barrier of coastal ecosystems, but they have also been observed in the secondary scrub dunes and coastal grasslands more interior from the coast that are typically shielded by the primary dunes (Sneckenberger, 2001; Swilling et al., 1998). It is unclear whether these habitats are occupied by beach mice year-round (Pries et al., 2009) or only during hurricanes as refugia from storm surges that overwash or flatten primary dunes (Sneckenberger, 2001). Each of these habitats are characterized by varying levels of vegetation cover, plant species diversity, and abiotic features (i.e., elevation, slope, etc.), all of which may influence beach mouse habitat selection. Investigating the habitat characteristics that most influence beach mouse population dynamics can aid in species

Practitioner points

- Standardized long-term monitoring of endangered species can provide serendipitous opportunities to learn and better understand how species are impacted by extreme weather events by providing baseline data.
- Coastal wildlife and ecosystems are dependent on high elevation dune habitats to avoid the impacts of extreme weather events, so restoration and reintroductions should prioritize these recovery objectives.

recovery through targeted restoration activities in the face of climate change.

On 10 October 2018, Hurricane Michael made landfall as a Category 5 storm (exhibiting 1-min sustained wind speeds of >254 km/h) on Tyndall Air Force Base (TAFB) in Panama City, Florida, USA, threatening both the St. Andrew beach mouse (*Peromyscus polionotus peninsularis*) and the Choctawhatchee beach mouse (*Peromyscus polionotus allopshys*). This storm, one of only four Category 5 storms to make landfall in the United States, highlighted the need to understand beach mouse extinction thresholds in terms of resistance and resilience to future storm events, especially with storms predicted to increase in both frequency and intensity in the future. As mandated under the Endangered Species Act (ESA) of the United States, there is a long-term monthly beach mouse track-tube monitoring program at TAFB which gave us a unique opportunity to investigate beach mouse occupancy in relation to several biotic and abiotic factors before and after this catastrophic storm. Effects of extreme climate events such as Hurricane Michael likely pose a more immediate threat to coastal ecosystems than other climate-associated variables such as mean temperature or sea-level rise (Claudino-Sales et al., 2010; Seabloom et al., 2013). Additionally, Hurricane Sally made landfall in nearby Alabama as a Category 2 storm (sustained winds of 154–177 km/h) 2 years later on 16 September 2020, giving us the opportunity to compare how the weaker and more common storm category affected the beach mice relative to their response to Hurricane Michael.

The mitigation and management of major impacts to coastal dune systems requires a better understanding of beach mouse resistance and resilience during and after major storm events. We used the long-term monitoring data collected before and following the two storms' landfalls to estimate beach mouse extinction risk associated with different habitat features under a severe weather event scenario. We hypothesized that beach mouse resistance to hurricane impacts is related to elevation in dune habitat over other factors such as forage availability or cover because beach mice are adapted to these environments and the proximate threat of drowning due to storm surge overwashes is likely the greatest factor influencing individual survival. These effects would be weaker following Hurricane Sally compared to Hurricane Michael due to lower storm surge and habitat damage. We predicted that beach mouse local extinction probability would decline with increasing elevation and in dune habitats over secondary habitats (grasslands and scrub) and local extinction would be higher following the stronger Hurricane Michael.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted beach mouse and plant community surveys at TAFB, located in southeastern Bay County on the Gulf Coast of Florida, USA. The base

is approximately 29 km long and 4.8 km wide, and is surrounded by East Bay, St. Andrew Bay, and the Gulf of Mexico to the north, west, and south, respectively. The property of TAFB includes barrier islands in the Gulf of Mexico (Figure 1) that provide important habitat for populations of federally endangered beach mice and other coastal dependent species. The two subspecies that occur there are the St. Andrew beach mouse on Crooked Island East (CIE), and the Choctawhatchee beach mouse on Crooked Island West (CIW) and the federally owned portion of Shell Island (Shell). The St. Andrew beach mouse population was reintroduced in the 1990s and it is noteworthy that recent genetic evidence suggests that this subspecies may have been from the wrong subspecific source population due to insufficient genetic data at the time (Van Zant & Wooten, 2007). The habitat on these islands is characterized by dunes, grasslands, and scrub and swale.

2.2 | Surveys

Beach mice are monitored in a long-term track-tube survey at TAFB to determine population trends and identify occupancy patterns across the landscape. Presence or absence is determined using track-tubes secured to the ground using metal stakes and baited monthly with a small handful of sunflower seeds (*sensu* Mabey, 1998—Figure 2). An ink pad

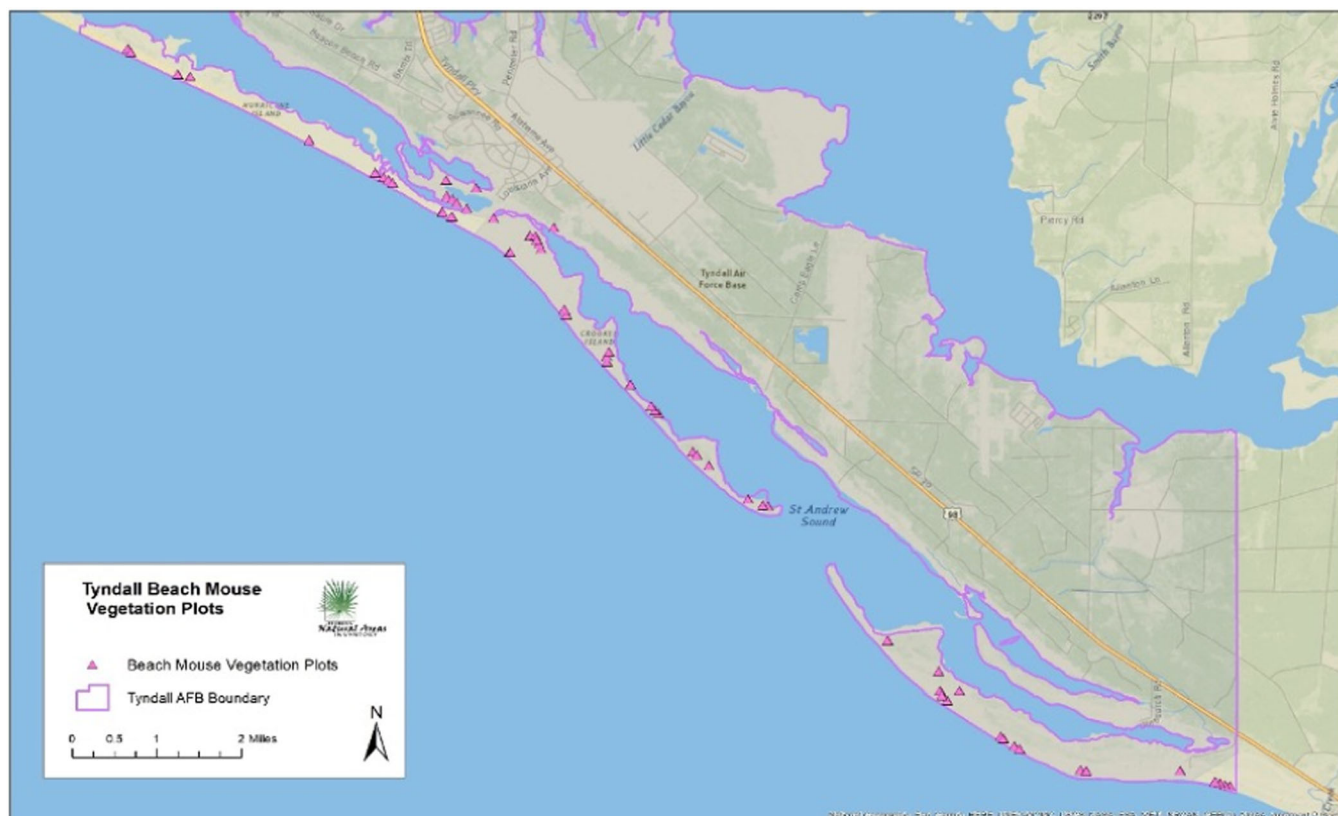


FIGURE 1 Beach mouse track-tube and vegetation sampling plot locations at Tyndall Air Force Base, Panama City, Florida, USA.

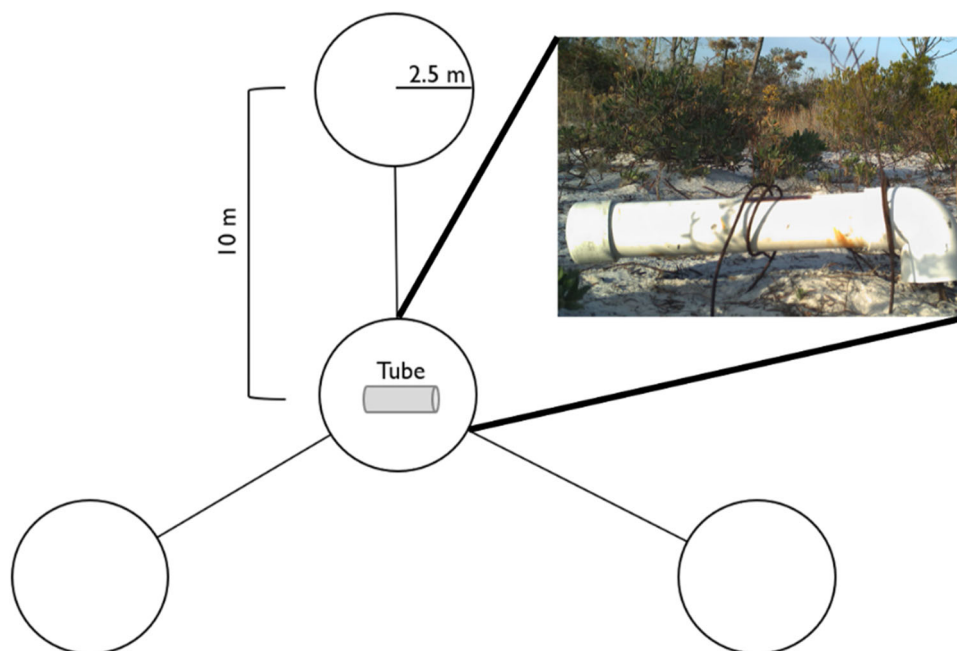


FIGURE 2 Track-tube (with photo) and vegetation subplot array at Tyndall Air Force Base, Panama City, Florida, USA. Vegetation and habitat metrics were measured in each of the four 2.5 m radius subplots.

and paper strip are placed inside the tube such that animal tracks are recorded when they access the tube. The long-term monitoring tubes were placed in linear transects composed of five tubes, each tube placed 100 m apart, for a total transect length of 500 m. In total, 96 track-tubes occur along the barrier islands at TAFB in beach dune, coastal grassland, and scrub communities. Tubes are checked approximately once per month and recorded as detected if beach mice tracks are present on the paper, or not detected if beach mice tracks are absent. Tubes that washed away during the storm surge events were reinstalled 1-month post-hurricane and continued to be monitored monthly.

To understand how beach mouse occupancy dynamics relate to habitat post-hurricane, we collected species-level vegetation data at beach mouse track-tubes. We randomly selected 57 track-tubes (59.4% of the 96 total tubes) across the length of the barrier islands for intensive habitat sampling. Seventeen tubes were located on each island of CIE and Shell, and 23 tubes were located on CIW (Figure 1). We considered track-tubes independent for occupancy surveys because available data show that mean beach mouse home ranges are approximately 100 m in diameter or smaller (Swilling & Wooten, 2002; Van Zant & Wooten, 2003).

To capture variability of the habitat within the area immediately surrounding each track-tube, we sampled four 2.5 m-radius subplots at each tube location (Figure 2). One subplot was centered at the track-tube itself, and three additional subplots were centered approximately 10 m away from the main tube at 0°, 120°, and 240°. This resulted in a total separation distance of 5 m between the edges of the center subplot and each radial subplot. Each plant

rooted in the subplot was recorded to species and either examined independently (e.g., sea oats *Uniola paniculata*) or included in quantification of percent cover of different plant groups (e.g., herbaceous or shrub). We quantified site-specific measures of the percent of herbaceous, shrub, lichen, litter, and bare ground covers across track-tube subplots for inclusion in models to elucidate the potential role of microhabitat factors on initial occupancy and extinction.

2.3 | Covariate extraction and development

We used remotely sensed data and field-derived covariates to examine the potential drivers of beach mouse occupancy and extinction before and following Hurricane Michael and Hurricane Sally. We first identified each track-tube to a coarse land classification with one of six potential identities (i.e., mesic flatwoods, coastal scrub, coastal uplands, wet flatwoods, sand beach, and maritime hammock; Florida Natural Areas Inventory [FNAI], 2010) based on the FNAI-modified 2011 National Land Cover Database (NLCD) with 30 m resolution land cover data (Homer et al., 2015). We used the MODIS satellite-derived normalized difference in vegetation index (NDVI) products with USGS Earth Explorer (<https://earthexplorer.usgs.gov>) as a standard index of vegetation cover. For each track-tube site, we classified the natural community types post hoc using the k-means clustering of vegetation species. We determined the optimum number of clusters as four using the elbow method (Ketchen & Shook, 1996), which paralleled our field observations. We then tested

the median rank of the natural community groups using permutational multivariate analysis of variance to determine if clusters were significantly separated. Although, four natural community groups were supported, we combined scrub and swale habitat into a single “scrub” category because swales were a microhabitat feature influenced by wind and protected from inundation within scrub dunes, as well as uneven sampling of these individual habitats compared to dune and grassland tubes. This led us to 36 sites in dunes (primarily vegetated upper beach established by sea oats), 10 sites in grasslands (flat, stable, and sometimes inundated), and 11 sites in scrub (remnant dune, no longer inundated and inland with shrubs, trees, etc.) based on the species present following Florida's Natural Area Inventories Natural Community Guide (FNAI, 2010).

To measure elevation, we downloaded LiDAR data from the US Elevation Data Library (<https://www.coast.noaa.gov/inventory/>). We used aerial LiDAR flown in 2015 with Q2 resolution (1 m) to measure elevation across the islands before Hurricane Michael (covariate on initial occupancy). Aerial LiDAR was reflown in this area on 15 October 2018 which we used to measure elevation post-storm with Q1 resolution (0.76 m). We used the post-Michael LiDAR data to measure elevation before Hurricane Sally and elevation data collected on 04 October 2020 were used as post-Sally metrics. Using these measures, we were able to determine the elevation of each tube both pre- and post-storm, and the change in elevation that resulted from each storm. We used track-tube longitude as an index of distance from the hurricane landfall location, for example, westward sites were further from the direct strike of Hurricane Michael. All remotely sensed geospatial data were extracted using ArcGIS (version 10.6) to field plot locations to assess the effects of each storm on the topography of the islands. All continuous covariates were z-score standardized before analyses (Cove et al., 2018).

2.4 | Analyses

We extracted track-tube survey data to assess the beach mouse occupancy and relevant covariates before the Hurricanes Michael and Sally. We then included the survey data immediately after each storm to estimate local extinction probabilities of sites associated with each hurricane strike, dependent on abiotic and biotic factors, for example, the storm impact was the implicit driver of dynamics between primary survey occasions. To assess the effects of Hurricane Michael, we used track-tube survey data from 3 months before (August, September, and October 2018) and 3 months after the storm (December 2018/January 2019, February, and March 2019). For Hurricane Sally, we used track-tube survey data from 3 months before (June, early August, and late August 2020) and 3 months after

the storm (September, October, and November 2020). We applied dynamic occupancy models using the covariates outlined above to estimate the impacts of the hurricanes on beach mouse population dynamics (MacKenzie et al., 2003).

Dynamic occupancy models use repeated survey data to estimate initial occupancy probability before storms (ψ), colonization probability (γ), extinction probability (ϵ), and detection probability (p) parameters (MacKenzie et al., 2003). The detection history followed a monthly survey occasion (0 = no detection, 1 = detected), such that a detection history of 101 represented that the species was detected in August, not detected in September, and detected again in October for a given track-tube site. Because of high rates of detection previously reported and no a priori hypotheses about factors affecting detection (Falcu & Danielson, 2014), we modeled three simple detection models with p as a function of island-specific effects, natural community effects, or constant which represented monthly survey rates. We ranked those using Akaike Information Criterion (AIC) model selection and then included the most-supported detection covariates in all subsequent models (Burnham & Anderson, 2002).

We used a hierarchical approach, wherein we compared 12 a priori occupancy models with different factors affecting initial occupancy (ψ), including (1) remotely sensed coarse land classification, (2) island-specific, (3) elevation before storm, (4) proximity to storm, (5) NDVI, (6) percent shrub cover, (7) percent herbaceous cover, (8) percent lichen, (9) percent litter cover, (10) percent bare ground, (11) natural community group, and (12) a null model. We ranked these initial occupancy models using AIC model selection to determine if any covariates should be included as predictors of occupancy in the ensuing dynamic models (Table 1—Burnham & Anderson, 2002). We then examined whether the probability of extinction (ϵ) from sites post-storm was affected by similar covariates (14 a priori models), while maintaining the most supported occupancy covariates in the dynamic models (Cove et al., 2018). These models were based on remotely sensed and field-measured habitat covariates as described above and included: (13) natural community group, (14) percent bare ground, (15) elevation after the storm, (16) percent herbaceous cover, (17) percent shrub cover, (18) coarse habitat, (19) NDVI, (20) island-specific, (21) proximity to storm, (22) percent lichen cover, (23) percent sea oat cover, (24) subspecies-specific, (25) binary elevational change, and (26) additive model with natural community group and elevation (Table 1). We ranked all 26 models by their relative AIC value and model weights and considered covariates to have strong effects if their 95% confidence intervals did not overlap zero (Burnham & Anderson, 2002). We conducted all modeling using the “unmarked” package (Fiske & Chandler, 2011) in R (R Core Team, 2022).

TABLE 1 Model selection statistics for dynamic occupancy models explaining variation in extinction probability of beach mice (*Peromyscus polionotus* spp.) from track-tube surveys in Tyndall Air Force Base, Florida, USA, pre- and post- the Category 5 Hurricane Michael landfall.

Model	K	AIC	Δ AIC	ω_i	$\Sigma (\omega_i)$	LogLike
ϵ (natural community + elevation)	9	350.18	0.00	0.55	0.55	-166.09
ϵ (elevation)	7	350.79	0.61	0.41	0.96	-168.39
ϵ (island)	8	355.87	5.69	0.03	0.99	-169.94
ϵ (subspecies)	7	358.25	8.07	0.01	1.00	-172.13
ϵ (natural community)	8	362.67	12.48	0.00	1.00	-173.33
ϵ (binary elevation change)	8	365.04	14.86	0.00	1.00	-174.52
ϵ (shrub cover)	7	366.40	16.22	0.00	1.00	-176.20
ϵ (sea oats)	7	366.97	16.79	0.00	1.00	-176.48
ψ (island)	8	368.10	17.92	0.00	1.00	-176.05
ϵ (proximity to storm)	7	369.88	19.70	0.00	1.00	-177.94
null	6	371.07	20.89	0.00	1.00	-179.54
ψ (proximity to storm)	7	371.17	20.98	0.00	1.00	-178.58
ψ (shrub cover)	8	371.33	21.14	0.00	1.00	-178.78
ϵ (NDVI)	7	371.57	21.38	0.00	1.00	-178.82
ψ (litter cover)	7	371.63	21.45	0.00	1.00	-179.00
ψ (natural community)	7	372.00	21.82	0.00	1.00	-177.66
ψ (herbaceous cover)	11	372.11	21.92	0.00	1.00	-179.28
ϵ (lichen cover)	7	372.56	22.38	0.00	1.00	-179.30
ψ (NDVI)	7	372.61	22.42	0.00	1.00	-179.48
ϵ (herbaceous cover)	7	372.96	22.77	0.00	1.00	-179.48
ψ (elevation)	7	372.96	22.78	0.00	1.00	-179.48
ψ (bare ground)	7	372.97	22.79	0.00	1.00	-179.49
ϵ (bare ground)	7	372.97	22.79	0.00	1.00	-179.53
ψ (lichen cover)	7	373.06	22.87	0.00	1.00	-179.54
ψ (coarse habitat)	7	373.07	22.89	0.00	1.00	-175.05
ϵ (coarse habitat)	11	373.29	23.11	0.00	1.00	-175.65

Note: Included are the number of model parameters (K), the Akaike Information Criterion (AIC), the information distance from the top model (Δ AIC), the Akaike weight (ω), the cumulative Akaike weight ($\Sigma (\omega_i)$), and model log-likelihood (LogLike). All models included an island-specific effect on detection. Abbreviation: NDVI, normalized difference in vegetation index.

3 | RESULTS

We detected beach mice at 48 of the 57 track-tube sites before Hurricane Michael (naïve occupancy = 84.2% of sites). After Hurricane Michael, we detected beach mice at only 39 of the 57 track-tube sites (naïve occupancy = 68.4% of sites). Hurricane Michael strongly influenced and shaped the habitat of TAFB, by causing a 40% decline (loss of 150 ha) in vegetated dune to nonvegetated sandy beach or open water, that each increased by 139% (121 ha) and 99% (41 ha), respectively. Although the mean elevation across our track-tubes was not significantly different pre- (2.25 m \pm 2.27 SD, range = 0.95–5.56 m) and post-Michael (2.33 m \pm 2.34 SD, range = 1.0–6.9 m), 24 of the sites experienced declines in elevation ranging up to a loss of 1.51 m of elevation.

Island-specific detection was the most-supported model in preliminary detection analyses, so we included island effects in all subsequent models. The average probability of detecting beach mice given their presence was ($p = 0.81 \pm 0.03$ SE) per month, leading to a cumulative detection probability from three survey months equivalent to 0.99. Beach mice were least detectable on CIE ($p = 0.72 \pm 0.04$ SE), followed by CIW ($p = 0.83 \pm 0.04$ SE), and most detectable on Shell island ($p = 0.91 \pm 0.03$ SE).

We modeled occupancy as constant in all dynamic models due to no strong covariate relationships among the 12 initial occupancy models, which were retained for comparison in Table 1. The top dynamic model to predict beach mouse local extinction following Hurricane

Michael received 0.55 of the Akaike weight and included natural community grouping and elevation. The next best model received 0.41 of the Akaike weight (cumulative Akaike weight = 0.96) and only included elevation as a covariate on extinction. We present the results from the top model for simplicity and because the second most supported model was nested in the top model. The probability of beach mouse extinction declined with increasing elevation ($\beta = -5.09 \pm 2.19\text{SE}$ —Table 2). The probability of extinction was higher across sites located in grassland habitats ($\varepsilon = 0.91 \pm 0.09\text{SE}$) and scrub habitats ($\varepsilon = 0.96 \pm 0.06\text{SE}$) compared to dunes ($\varepsilon = 0.72 \pm 0.23\text{SE}$) at low elevations (<0.8 m), but all habitats approached 0 probability of extinction at the mean elevation (~2.3 m—Figure 3). No other models received substantial support (cumulative Akaike weight <0.04—Table 1).

We did not model factors associated with occupancy or extinction following Hurricane Sally in 2020. Beach mice occupied 100% of the 57 track-tube sites before and following the Category 2 storm, rendering us unable to model the results due to no variation or change. However, this suggests we can differentiate between the effects of stronger hurricanes and lower category storm impacts on endangered beach mice with high resilience after the Category 5 storm and higher resistance (e.g., 100% persistence) to the weaker Category 2 storm.

TABLE 2 Estimated logit-scale coefficients (β) with standard errors (SE), lower (LCI) and upper (UCI) 95% confidence intervals, and p -values for covariate effects from the top-ranking dynamic occupancy model explaining variation in extinction probability of beach mice (*Peromyscus polionotus* spp.) from track-tube surveys in Tyndall Air Force Base, Florida, USA, pre- and post- the Category 5 Hurricane Michael landfall.

	β	SE	LCI	UCI	p Value
Occupancy					
Intercept	1.70	0.37	0.98	2.43	0.000
Extinction					
Intercept	-4.13	1.45	-6.97	-1.290	0.004
Grassland	1.42	1.12	-0.78	3.62	0.207
Scrub	2.23	1.16	-0.04	4.50	0.054
Elevation	-5.09	2.19	-9.38	-0.80	0.020
Colonization					
Intercept	0.24	0.69	-1.11	1.59	0.733
Detection					
Intercept	0.92	0.22	0.48	1.35	0.000
Shell	1.38	0.46	0.48	2.28	0.003
CIW	0.67	0.39	-0.09	1.43	0.083

Note: The extinction intercept represents dune habitat and the detection intercept represents CIE.

Abbreviations: CIE, Crooked Island East; CIW, Crooked Island West.

4 | DISCUSSION

This study offers an assessment of the effects of a Category 5 hurricane, one of only four in recorded history to make landfall, on an endangered species complex of beach mice along the Gulf Coast of the southeastern United States. Although we explored various biological drivers of beach mouse occupancy before Hurricanes Michael and Sally, we were unable to identify any habitat associations most likely due to the high observed occupancy (85% and 100% of sites, respectively). However, we observed strong evidence of two key variables mediating the effects of Hurricane Michael on the distribution dynamics of these rodents. Increasing elevation was the most important factor associated with reduced beach mouse local extinction probabilities after the storm. Our results suggest that habitat elevations greater than two meters are the most protective from and influential in species resistance to a Category 5 hurricane. Habitat type further mediated extinction risk, where dunes were the most important habitat for beach mice to persist after the storm, followed by grasslands, and to a lesser extent scrub habitat.

The impacts of tropical storms on protected species are of great concern to scientists and resource managers because of the predicted increase in severity and frequency of these events due to climate change (Sobel et al., 2016). Here, we provide quantitative thresholds of extinction probability by elevation and habitat type that can help inform models predicting the effects of future storm events on at-risk species. Both elevation and habitat are easily attained through remote sensing. LiDAR flights, which can provide digital elevation models, are usually available shortly after a storm event in coastal areas. Similarly, habitat models based on spectral imagery could be completed with relative ease post-storm when new aerial imagery becomes available. Taken together, remote sensing could provide initial estimates of storm impacts to beach mouse populations relatively rapidly with assumptions informed by our findings. These remotely sensed products could also be powerful for tracking and informing management and restoration objectives in the face of rapid global change. Even so, we caution that these results should be confirmed for additional storm events and using additional coastal species to provide more robust conclusions.

The hierarchy of habitat (dune > grassland > scrub) associated with beach mouse persistence supplements existing knowledge of habitat requirements for the species complex (Sneckenberger, 2001; Swilling et al., 1998). This knowledge can aid beach dune recovery and restoration efforts when managers must provide a rationale for which habitats will provide protection from future storm events. Additionally, there is some debate in the literature about the extent to which beach mice use other coastal plant communities, such as scrub. Here, we provide evidence that prestorm occupancy was equivalent

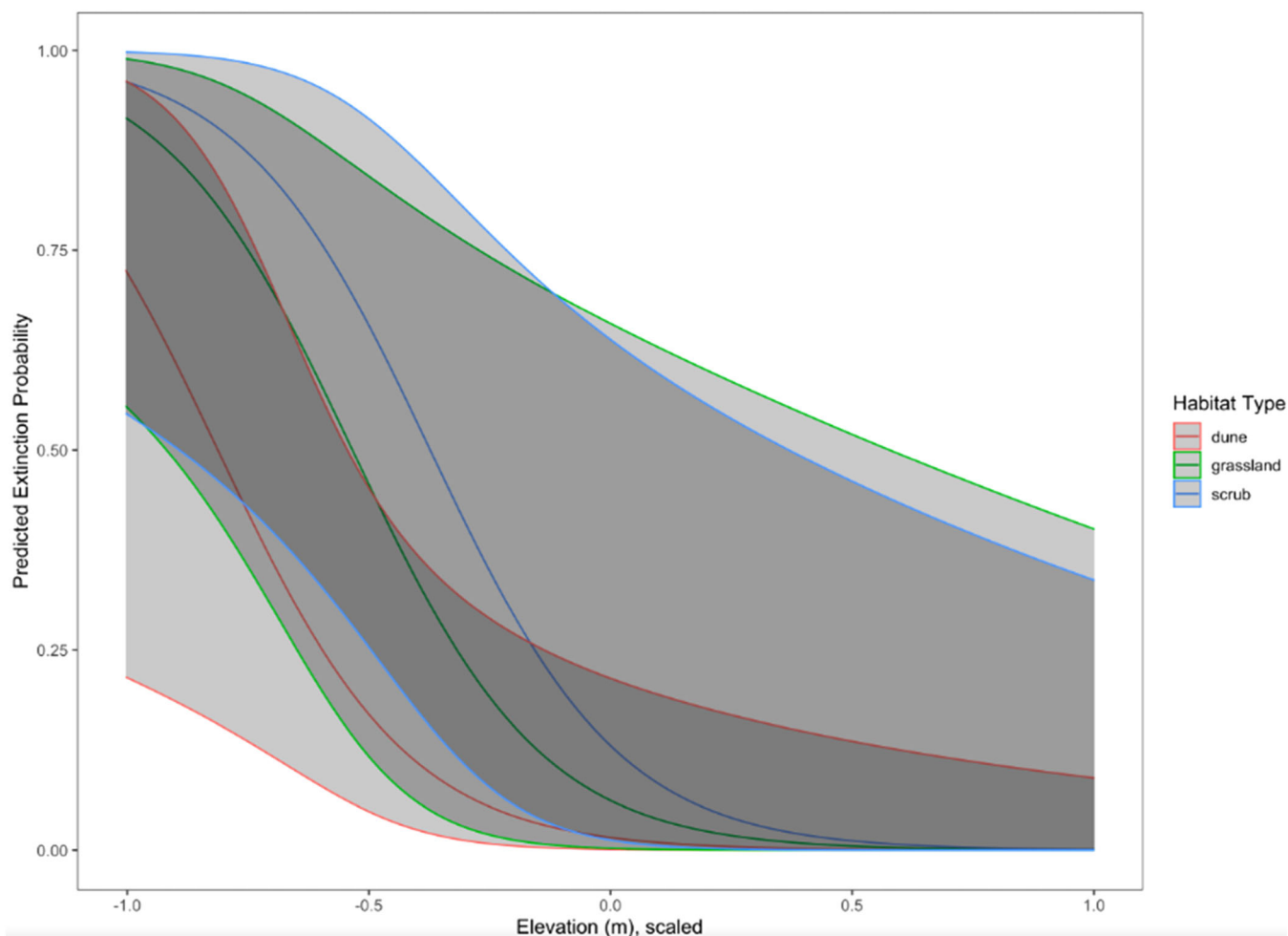


FIGURE 3 Predicted beach mouse (*Peromyscus polionotus* spp.) extinction probability (with 95% confidence intervals) across a standardized elevation gradient for each habitat group from the top-ranking dynamic occupancy model from track-tube surveys at Tyndall Air Force Base, Florida, USA, pre- and post- the Category 5 Hurricane Michael landfall.

across all potential habitat types. Pries et al. (2009) observed that dune habitat was the strongest predictor of Santa Rosa beach mouse occupancy pre- and post-Hurricane Ivan, a Category 3 storm when it struck Florida in 2004. Although it has been suggested that scrub habitats act as refugia for tagged individuals retreating during hurricanes (Snekenberger, 2001; Swilling et al., 1998), our data do not necessarily suggest this. However, our data do provide occupancy estimates under pre- and post-storm conditions which account for detectability. Our study design tracking species presence (e.g., dynamic occupancy models) suggests that mouse persistence was highest in dunes, though it is possible that the apparent extinctions in scrub habitat could be driven by individuals recolonizing vacant dune habitats between primary survey occasions (e.g., when dynamics occur). This alternative mechanism possibly underlying our extinction model results requires further examination and should be considered as a next step to examine how survival of individual mice varies by habitat and is directly affected by hurricane strikes.

Our results also inform and support other beach mouse conservation strategies. One of the preeminent recovery strategies for beach

mice (e.g., Perdido Key beach mice *Peromyscus polionotus trissyllepsis*) is to reintroduce mice from captive-breeding colonies. Indeed, reintroduction programs have proven successful with apparent recruitment following initially steep declines (Greene et al., 2017). Our insights here aid in the identification of suitable reintroduction sites based on the importance of elevation for mouse resiliency. The beach mouse populations at TAFB represent some of the more well protected and managed areas with limited human influence compared to other beach mouse populations, so inferences from these results could help managers when selection criteria of reintroduction sites are complicated by other external factors such as fragmented beaches and invasive predators.

Finally, few studies have examined the detection probability of beach mice using the current methods implemented across the subspecies' ranges in the Florida panhandle (e.g., Falcu & Danielson, 2014). Our results revealed that there was an island-specific effect on beach mouse track-tube detection with the St. Andrew beach mouse exhibiting lower detection than the Choctawhatchee beach mouse on their respective islands. This warrants further investigation in case

detection is related to abundance or other differences in biological processes among the different sub-species, especially considering genetic evidence that the St. Andrew population was likely introduced from an inappropriate source population due to insufficient genetic data at the time (Van Zant & Wooten, 2007). Yet, we demonstrate that 3 monthly replicates of occupancy sampling results in a near certain probability of detection, assuming true occupancy does not change over the course of 3 months. This suggests that year-round sampling on a monthly basis may be redundant and resources used for this purpose may be better directed to supplemental monitoring needs via live-trapping or camera trapping or direct coastal restoration objectives. Our findings suggest a need to review current sampling protocols with a power analysis to optimize the frequency of track-tube sampling when resources are limited. Even with reduced sampling, we expect track-tube detections will reliably inform managers of trends over time or of the status of the species at any given site before and after hurricane strikes. This study also highlights the need for baseline monitoring as it can be used in before-after experimental designs when disturbance events occur more frequently under future climate change scenarios. We suggest continued monitoring of beach mice and other coastal-tied species that builds off the insights gained through this case study to best prepare and adapt for future global change.

AUTHOR CONTRIBUTIONS

Michael V. Cove: Formal analysis; conceptualization; methodology; data curation; writing—original & review. **Samantha L. Dietz:** Writing—original & review; data curation; conceptualization. **Chad T. Anderson:** Conceptualization; methodology; formal analysis; writing—original & review; project administration; data curation. **Amy M. Jenkins:** Data collection; conceptualization. **Katie R. Hooker:** Methodology; writing—review & editing; project administration; data curation. **Melanie J. Kaeser:** Methodology; writing—review & editing; funding acquisition.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

- Balaguru, K., Judi, D.R. & Leung, L.R. (2016) Future hurricane storm surge risk for the U.S. gulf and Florida coasts based on projections of thermodynamic potential intensity. *Climatic Change*, 138, 99–110.
- Bird, B., Branch, L. & Hostetler, M. (2002) Beach mice. *EDIS*, 165, 1–5. Available from: <https://doi.org/10.32473/edis-uw173-2002>
- Burke, L., Kura, Y., Kassem, K., Revenga, C., Spalding, M., McAllister, D. et al. (2001) *Coastal ecosystems*. Washington, DC: World Resources Institute, p. 77.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*, 2nd edition, New York: Springer.
- Claudino-Sales, V., Wang, P. & Horwitz, M.H. (2010) Effect of Hurricane Ivan on coastal dunes of Santa Rosa Barrier Island, Florida: characterized on the basis of pre-and poststorm LIDAR surveys. *Journal of Coastal Research*, 26(3), 470–484.
- Cove, M.V., Gardner, B., Simons, T.R. & O'Connell, A.F. (2018) Co-occurrence dynamics of endangered Lower Keys marsh rabbits and free-ranging domestic cats: prey responses to an exotic predator removal program. *Ecology and Evolution*, 8(8), 4042–4052.
- Falcy, M.R. & Danielson, B.J. (2014) Post-hurricane recovery and long-term viability of the Alabama beach mouse. *Biological Conservation*, 178, 28–36.
- Fiske, I. & Chandler, R. (2011) unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43(10), 1–23.
- Florida Natural Areas Inventory (FNAI). (2010) *Guide to the natural communities of Florida*, 2010 edition, Tallahassee, FL: Florida Natural Areas Inventory.
- Greene, D.U., Gore, J.A. & Austin, J.D. (2017) Reintroduction of captive-born beach mice: the importance of demographic and genetic monitoring. *Journal of Mammalogy*, 98(2), 513–522.
- Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G. et al. (2015) Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*, 81(5), 345–354.
- Ketchen Jr., D.J. & Shook, C.L. (1996) The application of cluster analysis in strategic management research: an analysis and critique. *Strategic Management Journal*, 17(6), 441–458.
- Mabee, T.J. (1998) A weather-resistant track-tube for small mammals. *Wildlife Society Bulletin*, 26, 571–574.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, 84(8), 2200–2207.
- Patrick, C.J., Kominoski, J.S., McDowell, W.H., Branoff, B., Lagomasino, D., Leon, M. et al. (2022) A general pattern of trade-offs between ecosystem resistance and resilience to tropical cyclones. *Science Advances*, 8(9), eabl9155.
- Pries, A.J., Branch, L.C. & Miller, D.L. (2009) Impact of hurricanes on habitat occupancy and spatial distribution of beach mice. *Journal of Mammalogy*, 90(4), 841–850.
- R Core Team. (2022) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/> [Accessed 2nd May 2022].
- Schmidt, J.A., McCleery, R., Seavey, J.R., Cameron Devitt, S.E. & Schmidt, P.M. (2012) Impacts of a half century of sea-level rise and development on an endangered mammal. *Global Change Biology*, 18(12), 3536–3542.
- Seabloom, E.W., Ruggiero, P., Hacker, S.D., Mull, J. & Zarnetske, P. (2013) Invasive grasses, climate change, and exposure to storm-wave overtopping in coastal dune ecosystems. *Global Change Biology*, 19, 824–832.
- Sneckenberger, S.I. (2001) *Factors influencing habitat use by the Alabama beach mouse (Peromyscus polionotus ammobates)*. MS Thesis, Auburn University.
- Sobel, A.H., Camargo, S.J., Hall, T.M., Lee, C.Y., Tippet, M.K. & Wing, A.A. (2016) Human influence on tropical cyclone intensity. *Science*, 353(6296), 242–246.
- Swilling Jr., W.R. & Wooten, M.C. (2002) Subadult dispersal in a monogamous species: the Alabama beach mouse (*Peromyscus polionotus ammobates*). *Journal of Mammalogy*, 83(1), 252–259.

- Swilling, W.R., Wooten, M.C., Holler, N.R. & Lynn, W.J. (1998) Population dynamics of Alabama beach mice (*Peromyscus polionotus ammobates*) following Hurricane Opal. *The American Midland Naturalist*, 140(2), 287–298.
- Van Zant, J.L. & Wooten, M.C. (2003) Translocation of Choctawhatchee beach mice (*Peromyscus polionotus allophrys*): hard lessons learned. *Biological Conservation*, 112(3), 405–413.
- Van Zant, J.L., & Wooten, M.C. (2007) Old mice, young islands and competing biogeographical hypotheses. *Molecular Ecology*, 16(23), 5070–5083.

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