

Climate relict vulnerable to extinction from multiple climate-driven threats

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Abstract

Aim: Over the gradually warming Holocene, many species' range limits shifted poleward. However, some populations persisted in climate refugia, such as mountain tops. These climate relict populations are critical components of regional biodiversity, but their isolation renders them vulnerable to other threats, including changes in environmental conditions indirectly related to a warming global climate. We aimed to quantify the role of these indirect climate effects on Florida saltmarsh vole (*Microtus pennsylvanicus dukecampbelli*; hereafter: "vole"), a poorly understood, endangered climate relict.

Location: The Gulf of Mexico between Sopchoppy and Pine Island, Florida, USA.

Methods: We surveyed for voles broadly across their potential range using camera traps and modelled the relationships between vole occurrence and two climate-driven threats: hurricane storm surge and shifting vegetation communities. We quantified these threats using both field-collected and remotely sensed data at fine (3-m) and coarse (150-m) spatial scales.

Results: Though seemingly suitable habitat exists outside their previously known range, voles appeared restricted to the outer marshes between the Suwannee and Withlacoochee Rivers. Within this range, the sites we surveyed had shorter grass heights, greater *Distichlis* spp. cover, greater potential habitat within 150 m, and were less vulnerable to inundation when compared to sites outside of their range.

Main conclusions: The complex and varied ways in which climate change alters the physical environment can expose small-ranging species to multiple threats. Even climate relicts, which have endured historical changes in the global climate, may fail to cope with the rapid pace of anthropogenic climate change.

KEYWORDS

camera trap, coastal wetland, mammal, mangrove, remote sensing

1 | INTRODUCTION

The climate crisis facing our planet increasingly threatens global biodiversity and has directly contributed to the extinction of species (Pounds et al., 1999; Thomas et al., 2004). To avoid extinction while

their habitats change, species are forced to either adapt to novel conditions within their current range or migrate to new areas to track suitable conditions (Hickling et al., 2006; Ohlemüller et al., 2008). In addition to affecting the distribution of species (Thomas, 2010), climate change can alter species survival through the increasing

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frequency and severity of disturbance such as hurricanes, droughts, floods and fires (Dale et al., 2001; Michener et al., 1997; Stott, 2016; Sun et al., 2014). Though these disturbances have shaped biodiversity for millennia (Brawn et al., 2001; Thom & Seidl, 2016), larger and more severe disturbances could have catastrophic effects for species with ranges that have already been drastically reduced from habitat loss and other anthropogenic sources (List et al., 2010; Oli et al., 2001; Ross et al., 2009).

Populations that have endured a broad range of climate conditions over their evolutionary history can provide valuable insight to our understanding of the implications of this climate crisis for biodiversity (Hampe & Jump, 2011). These so-called climate relicts are populations that have been able to persist in isolated refugia despite range shifts among the larger population, for example poleward shifts in the trailing edge of temperate or high-latitude species (Hampe & Jump, 2011). This stability during past climate changes may serve as evidence of continued resistance to contemporary, anthropogenically exacerbated climate change (Hampe & Jump, 2011). Alternatively, their isolation could render them more vulnerable to the increasing frequency and magnitude of climate-mediated disturbances (e.g. large fires, severe storms, extreme heat and rising sea level; List et al., 2010). Without favourable conditions connecting relict populations to the larger population, they may be more prone to the impacts of these acute disturbances.

The Florida saltmarsh vole (*Microtus pennsylvanicus dukecampbelli*; hereafter: "vole") is a climate relict from the Pleistocene epoch when the global climate was cooler (Woods et al., 1982). Though previously considered a subpopulation of the more widespread meadow vole (*Microtus pennsylvanicus*), more recent genetic analysis indicated that the population likely represents a distinct species (Jackson & Cook, 2020). Meadow voles appear to have been more widespread in Florida during the Pleistocene, but their southern range limit contracted poleward as the climate warmed during the Holocene (Jackson & Cook, 2020; Martin, 1968; Woods et al., 1982). Unlike other climate relicts that persist in areas of climate refugia such as mountain tops and bogs (Hampe & Jump, 2011), voles are uniquely associated with coastal marshes in the subtropics without a clear mechanism for providing refuge from otherwise unsuitable conditions (Hotaling et al., 2010). As such, the mechanism explaining the limited range of voles remains poorly understood. Furthermore, the marshes used by voles (McCleery & Zweig, 2016; US Fish & Wildlife Service, 2008) occur both to the north and south of their previously documented range (E. A. Raabe & Gauron, 2005). As such, voles may be more widespread than currently known, or limited by factors other than the distribution of these vegetation conditions (Hotaling et al., 2010).

Though voles and other climate relicts have persisted in refugia throughout the warming Holocene, anthropogenically exacerbated global climate change may create novel climate-mediated stressors. For example, the increasing frequency of severe tropical storms (Bender et al., 2010) and inundation caused by rainfall, sea-level rise, and storm surge have long been viewed as looming threats to

voles (Hotaling et al., 2010; US Fish & Wildlife Service, 2008; Woods et al., 1982). More recently, the poleward migration of *Avicennia germinans* and *Rhizophora mangle* (hereafter: mangroves) could dramatically alter the vegetation composition and structure of coastal environments at the latitudinal interface between saltmarshes and mangrove forests (Armitage et al., 2015; Cavanaugh et al., 2014; Saintilan & Rogers, 2015; Saintilan et al., 2014). Such shifts have already been observed within the range of voles, and are likely to continue if winters become increasingly mild (Osland et al., 2013, 2020; Stevens et al., 2006). Thus, despite the persistence of voles since the Pleistocene, novel climate-mediated factors may threaten this climate relict (Hotaling et al., 2010; Jackson & Cook, 2020).

We used occurrence of these poorly understood and federally endangered voles (US Fish & Wildlife Service, 2008) to better understand the factors that can limit the range of climate relicts, while also quantifying the roles of emerging threats related to anthropogenic climate change. Specifically, we aimed to (1) determine the current range limits of voles, (2) determine the factor/s limiting those ranges and (3) investigate the relative threats of inundation and the poleward expansion of mangroves to the future conservation of voles. Given the apparent lack of an obvious thermal refuge underlying their long-term persistence and the existence of apparently suitable conditions outside their known range (US Fish & Wildlife Service, 2008), we expected voles to be more widespread than previously documented. If true, this expanded range would alleviate concern regarding the encroachment of mangroves from the south. Furthermore, we expected inundation to represent a minimal, if any, threat to voles, given their long-term persistence in an environment defined by fluctuating water levels. Finally, we expected that mangrove cover would negatively affect vole occurrence, given the dramatically different structure of mangrove forests compared to the marshes known to be used by voles.

2 | METHODS

Given the relationship between range size and extinction vulnerability (Böhm et al., 2016; Cooper et al., 2008), we first aimed to determine the current range of voles. Using camera traps specifically designed for small mammals in tidal environments (McCleery et al., 2014), we surveyed voles across 250 km of coastline along the Gulf of Mexico in western Florida, USA (hereafter, the Gulf Coast), both north and south of the known range of voles (Figure 1). We used the resulting detection/non-detection observations of voles to model their occurrence as a function of environmental conditions to identify factors limiting their range. In addition to quantifying the relationship between these factors and the occurrence of voles, we investigated the broader variation in these metrics to assess their role in limiting the range of voles. Finally, we used repeated sampling to determine the degree to which inundation events affect vole occurrence, both within 2019 and between 2014 and 2019 by comparing our results to those from a previous study (McCleery & Zweig, 2016).

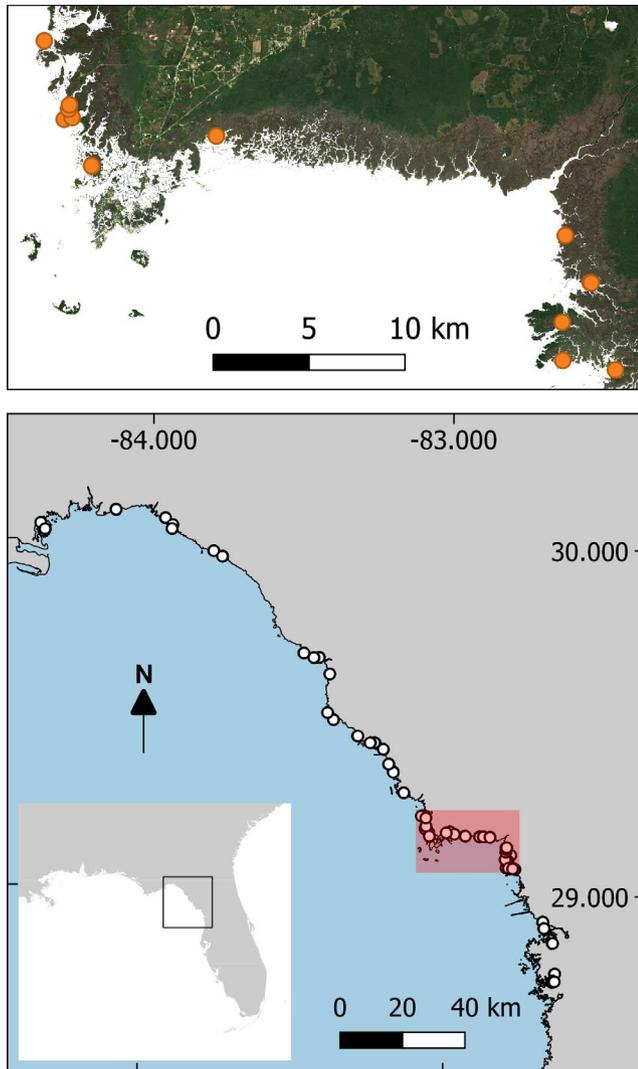


FIGURE 1 Locations of camera trapping grids (bottom—white circles) in 2019 shown in relation to the known range of Florida saltmarsh vole (pink rectangle). All documented detections of voles prior to 2019 (orange) shown in enlarged view (top) over a cloud-free composite of imagery collected from the Sentinel-2 satellite in 2018. Inset map shows the study area in relation to the southeastern United States

2.1 | Study area

Florida's coast along the Gulf of Mexico contains some of the least developed coastal saltmarshes in North America. The low topographical relief and near-shore waters have facilitated the expansion of these marshes over the past 100 years (Ellen A. Raabe & Stumpf, 2016). The distance from the outer marsh edge to the forest edge (i.e. the marsh width) is typically greater than 1 km, but can be greater than 3 km in some locations (Figure 1). Narrow bands of marsh dominated by the salt-tolerant grass *Spartina alterniflora* tend to occur towards the outer marsh edge, whereas the vast majority of marsh is dominated by *Juncus roemerianus* (Pennings et al., 2002). This marsh zonation results from several interacting

factors including salinity, inundation, drought, herbivory and competition (Bertness, 1991; Crain et al., 2004; Pennings et al., 2005; Silliman et al., 2005). In addition to these common saltmarsh plants, mangroves have been established within the range of voles for decades in some locations, thus representing the northern range limit of these cold-intolerant trees (Stevens et al., 2006). Historically, widespread mangrove dieback caused by freezing winter temperatures has limited their extent to a few outer islands at their northern range limit (Osland et al., 2013; Stevens et al., 2006). More recently, however, a series of mild winters in Florida over the past decade has allowed mangroves to spread northward throughout Florida, particularly along the Gulf of Mexico (Osland et al., 2013, 2020).

2.2 | Sampling design

Given our objective of mapping the global range of one of north America's rarest species (McCleery & Zweig, 2016), our first task was to identify the most suitable marsh patches to sample. Within the known range of voles, we sampled all sites with previous detections of voles ($n = 15$; Hotaling et al., 2010; McCleery & Zweig, 2016), as well as 8 sites that were sampled previously, but where voles were not detected. These previous studies revealed that voles use marshes comprised of *S. alterniflora* and *D. spicata*, which are readily discernable from marshes comprised of *J. roemerianus* via aerial imagery (Figure S1). As such, we identified previously unsampled patches of marsh by inspecting high-resolution (3-m) aerial photography collected in the fall of 2017 as part of the National Agricultural Imagery Program (United States Department of Agriculture, 2017). From these potentially suitable patches, we selected 34 previously unsampled sites by attempting to distribute them equally across the study area. This resulted in 57 total sampling sites, almost entirely in remote locations accessed via airboat. These sites were comprised of 28 sites within the known range of voles and 29 additional sites outside of the known range to the north ($n = 22$) and south ($n = 7$; Figure 1).

To understand how voles respond to inundation, we randomly selected four sites where voles were detected during initial sampling to re-sample following the highest high tides of the sampling season (Table S1). In a similar manner, sampling sites where voles were detected in 2014 allowed us to qualitatively assess vole persistence over the 5-year period from 2014 to 2019, during which north-western Florida was affected by two severe hurricanes: Hurricane Hermine in 2016 and Hurricane Michael in 2018.

2.3 | Trapping

We conducted all sampling between February and November, 2019. At each site, we placed a grid of 20 camera traps designed specifically for sampling small mammals in tidal environments (McCleery et al., 2014). These "Hunt traps," consisted of a motion-triggered camera with a short (40 cm) focal distance mounted within a

7-gallon bucket. Three 10-cm openings were cut in the bucket to allow small mammals to access a small cup containing bird seed within the bucket. The bucket assembly was mounted on a floating platform that allowed the trap to move up and down with the tides. We placed individual Hunt traps within a site to maximize the likelihood of detecting voles. Specifically, we spaced traps 20 m apart, roughly following the irregular shape of each focal patch. Each site was sampled for eight consecutive nights. However, due to logistical complications such as faulty batteries, corrupted memory cards and traps dislodged during high winds, some traps were not operational for the entire 8-night deployment and not all sites were ultimately sampled with 20 functional traps (Table S2). Following deployment, we reviewed all photos for detections of voles and recorded the date and trap location to build a nightly detection history for all traps. Compared to other sympatric small rodents (e.g. *Sigmodon* spp., *Peromyscus* spp., and *Oryzomys* spp.), voles are readily identified in photos by their short tail, small ears, and uniform pelage (McCleery et al., 2014, Figure S2).

2.4 | Vegetation conditions

To determine which factors were limiting the range of voles, we quantified vegetation within 3 m of each Hunt trap, by measuring characteristics previously shown to be important to voles (McCleery & Zweig, 2016). First, we measured the herbaceous vegetation height next to the trap location, as well as 3 m away from the trap in each of the cardinal directions and calculated the average of these 5 measurements. We then visually estimated the relative species composition of all plants present within 3 m of the trap to the nearest 5%. Because this metric was relative, the percentages for all species at a trap summed to 100. Though many plant species were detected, we only used the relative cover of two species previously shown to be important to vole habitat use: *S. alternifolia* and *Distichlis spicata*. Additionally, to better understand how the presence of mangroves affect habitat use, we incorporated the combined percent cover of the two species of mangroves present in the study area, *R. mangle* and *A. germinans*.

2.5 | Potential habitat mapping

In addition to local conditions, we expected voles may be limited by larger scale factors, such as the distribution of suitable marsh and mangroves within the broader landscape. To quantify these broader scale factors, we used decision-level fusion of satellite data (Schulte to Bühne & Pettorelli, 2018) and machine learning to classify the study area into the cover types we expected to be relevant to voles. Using the Google Earth Engine cloud-computing platform, we acquired pre-processed (atmospherically corrected and masked of clouds) multispectral reflectance at 10-m resolution from Sentinel-2 for the entire study area. We calculated a median composite of all wavelength bands, as well as the normalized-difference vegetation

index (NDVI), across the entire Sentinel-2 collection from 2016 to 2020. As a measure of “greenness,” we expected NDVI to be important to differentiating between marsh dominated by *S. alterniflora* and *J. romerianus*, given live *J. romerianus* is typically browner in appearance, and has many dead leaves which appear gray. Additionally, NDVI has been shown previously to be important for distinguishing mangroves from other vegetation types (Thomas et al., 2018).

To complement the surface reflectance, we acquired C-band synthetic aperture radar (SAR) acquired from the Sentinel-1 satellites to quantify the extent of inundation during Hurricane Michael, a category 5 storm that affected the eastern Gulf of Mexico in October 2018 (Beven et al., 2019). Synthetic aperture radar measures the roughness of the earth's surface and the ability of SAR to penetrate clouds and vegetation makes it particularly useful for mapping inundation of wetlands during storms (Cazals et al., 2016; Kiage et al., 2005). Similar to surface reflectance, we first calculated a median composite of the SAR collection between 2016 and 2020 to serve as a baseline. To represent flooded conditions, we used imagery collected on October 10 when Hurricane Michael made landfall at the Florida panhandle, and when both Cedar Key, FL and Apalachicola, FL reported anomalously water heights (Figure S1). The presence of surface water smooths the land surface relative to exposed marsh vegetation, which translates to a lower SAR backscatter when inundated (Kasischke et al., 2003; Kiage et al., 2005). After preliminary investigation of the four polarization modes available for the Sentinel-1 sensor, we selected the “VH” dual-band cross-polarization mode, as we determined this filter to be least sensitive to roughness in the water surface caused by wind. Because inundated marshes would show less backscatter compared to normal conditions due to the presence of surface water (Kasischke et al., 2003), we used the difference between the backscatter during Hurricane Michael and the median backscatter from 2016 to 2020 as a metric of inundation (hereafter “VHdiff”) and added this metric as an additional band to the surface reflectance, resulting in a single fused image for the entire study area.

We used the random forests classifier (smileRandomForest) within Earth Engine to classify the fused sentinel imagery. After masking open water, we trained the classifier with ground-truthed locations representing three land cover types: potential vole habitat ($n = 48$), other marsh ($n = 321$) and mangrove forest ($n = 89$). The potential vole habitat locations were simply the trap locations where we detected voles, whereas the two remaining cover types were randomly selected points that were ground-truthed in the field for accuracy. The distribution of the spectral band values, as well as NDVI, for all training points are provided in the Figure S3. We evaluated accuracy by randomly selecting 30% of these points to withhold from classifying the image, then calculated the confusion matrix from comparing the classification to the actual classes of these withheld points. Finally, we established a 150-m radius circle around the centroid of all traps at a site to summarize the extent of the classified cover types at each site. We chose this distance because it was large enough to ensure that all traps were included within the circle, but small enough to minimize the effects of non-target cover types, such as upland forest

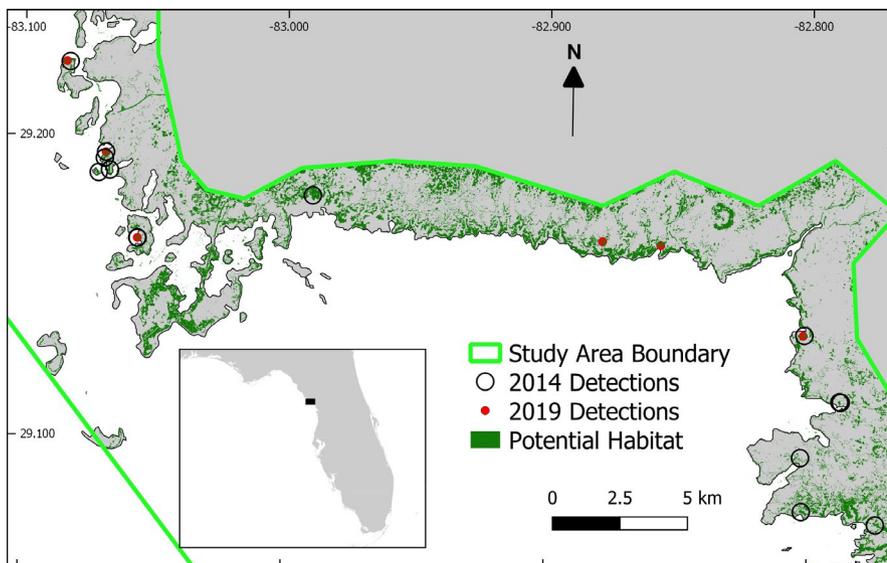


FIGURE 2 Detections of Florida saltmarsh vole in 2014 (McCleery & Zweig, 2016) and 2019 on the coast of Florida, with known range shown on inset map. Green areas show potential habitat defined by applying a random forest classifier to fused Sentinel-1 Synthetic Aperture Radar and Sentinel-2 surface reflectance, using vole detections to train the classifier

and developed areas. Finally, we calculated the area of potential habitat and mangrove forest within these circles to quantify the extent to which these metrics influence the distribution of voles.

2.6 | Occupancy modelling

We used a hierarchical occupancy modelling framework to quantify the extent to which vole occurrence was related to the environmental characteristics we measured. Using the detection histories across nights, this framework accommodates imperfect detection of voles by estimating the detection probability at a trap during a given night of sampling (Kery & Royle, 2016). Incorporating imperfect detection in this way was particularly important for voles, given their elusive nature (Hotaling et al., 2010; US Fish & Wildlife Service, 2008). To accommodate for variation in vole activity over the course of the trapping season, we allowed the detection probability to vary as a second-degree polynomial of Julian date. In the linked model of occurrence, we allowed the occurrence probability at a given trap to vary as a function of the four field-collected vegetation metrics collected at the trap scale, as well as the three metrics derived from remote sensing data at the landscape scale (potential habitat extent, mangrove extent and inundation vulnerability). To account for potential dependence among traps within a site, we included the site at which a given trap was located as a random effect. We analysed the model in a Bayesian setting using the R package rjags (Plummer et al., 2016). To evaluate the relative roles of covariates in explaining variation in occurrence of voles, we compared the magnitudes of the posterior distribution means, and we evaluated uncertainty around these estimates according to the width of the 90% posterior credible interval (CRI). Prior to model-fitting, we standardized each covariate by subtracting the mean and dividing by the standard deviation. Additionally, we investigated correlation among covariates using the cor function in base R (R Development Core Team, 2018). We used non-informative “flat normal” priors for all parameters (Kery & Royle, 2016). We ran 3 Markov

Chain Monte Carlo (MCMC) chains for 40,000 samples, and thinned the resulting samples by every third sample. To assess convergence, we inspected trace plots of the MCMC chains.

2.7 | Regional comparisons

We further investigated the relationships between vole occurrence and vegetation characteristics with regional comparisons to understand how broader patterns of marsh composition might be influencing the distribution of voles. In addition to making these comparisons for the four field-collected metrics (*S. alterniflora* cover, *D. spicata* cover, herbaceous vegetation height, and mangrove cover) and two landscape composition metrics (potential habitat extent and mangrove extent), we also made these regional comparisons for the SAR inundation metric, VHdiff, to make inferences about regional differences in inundation vulnerability. To evaluate differences in each of these metrics, we first defined the range of the voles according to all historic detections and treated sampling locations north and west of that range (i.e. up the coast) as a separate region, and sampling locations south and east (i.e. down the coast) as a third region (Figure 1). We used analysis of variance to determine if the range of voles differed significantly from those regions outside their range, both to the north and south and then performed pairwise comparisons between groups using a Tukey Honest Significant Differences (HSD) test. We conducted these analyses in R, version 3.5.1 (R Development Core Team, 2018), using the aov and TukeyHSD functions.

3 | RESULTS

3.1 | Detection

We detected voles at 48 of 1,176 trap locations (4%) distributed across only 6 of the 57 sites (10.5%). None of the 6 sites where voles

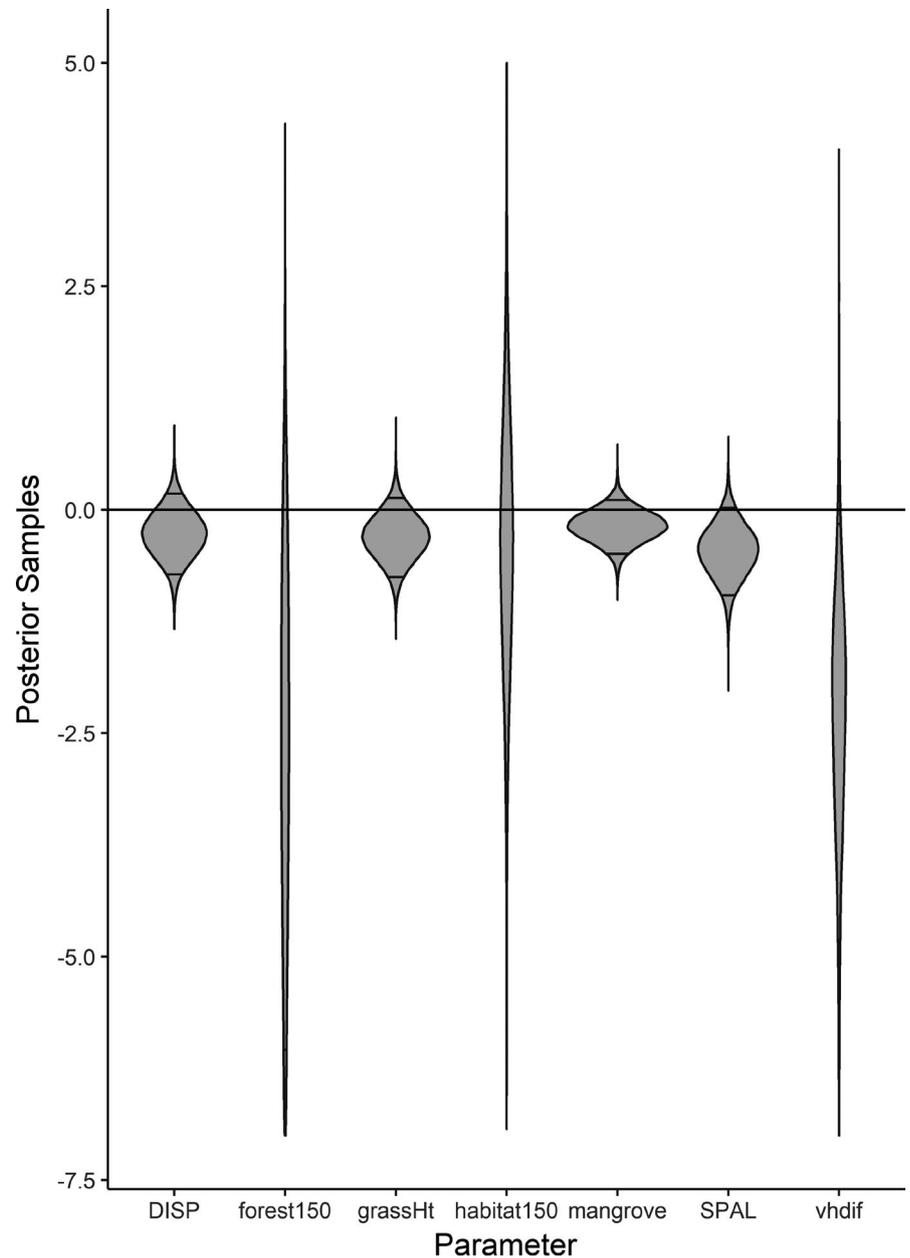


FIGURE 3 Samples of the posterior distributions (horizontal lines within shaded areas correspond to 90% credible intervals) of the 6 vegetation metrics (*D. spicata* cover, forest area within 150 m, grass height, potential habitat within 150 m, mangrove cover, *S. alterniflora* cover, and the departure of the synthetic aperture radar backscatter during Hurricane Michael compared to baseline) incorporated as covariates in a model of Florida saltmarsh vole occurrence from camera trap observations in 2019 near Cedar Key, Florida

were detected were outside the previously known range of voles (Figure 2). All of the six sites where we detected voles in 2019 were previously sampled in 2014, but only at four of those were voles detected in 2014. As such, we detected voles at two sites where they had not previously been documented. We did not detect voles at seven additional sites where they were detected in 2014, and did not detect them at any of the three locations where they were detected prior to 2014. Four of the sites where voles appeared to be extirpated comprised the four southernmost sites where voles were detected in 2014 (Figure 2). Overall, we estimated the average occurrence probability to be at most 0.13 (95% CRI: -23.8 to -1.9 on logit scale). Similarly, the average detection probability, given a trap was occupied, was at most 0.09 (95% CRI: -23.9 to -2.3 on logit

TABLE 1 Confusion matrix and accuracy statistics when 30% of the data used to classify surface reflectance from Sentinel-2 into potential vole habitat, other marsh and forest habitat types along the northwest coast of Florida, USA were withheld to serve as validation data for the classification algorithm

	Potential vole habitat	Other marsh	Forest	Producer's accuracy
Potential vole habitat	15	2	0	0.88
Other marsh	0	87	0	1
Forest	0	0	24	1
Consumer's accuracy	1	0.98	1	

scale). Thus, voles were both rare and seldomly detected where they did occur.

3.2 | Vegetation

Although we only detected voles at a small proportion of traps and sites, the vegetation conditions we measured did not appear to be related to vole occurrence. We observed little difference in vegetation conditions between traps and sites where voles were detected when compared to those where they were not. This similarity was reflected in the occupancy model parameter estimates of vegetation conditions, none of which were significant. At the 90% level, the CRI's of the posterior distributions of all occurrence covariates, except VHdiff, overlapped 0; however, there was high uncertainty around the landscape-scale covariates of potential habitat and forest cover within 150 m, as well as VHdiff (Figure 3). The posterior means for all effects were negative, even for covariates we included specifically because we expected them to be positively related to vole occurrence, such as the amount of *D. spicata* cover (Figure 3). As a result of the similarity between traps where voles were detected/not detected, 758 of the 1,204 (63%) trap locations were classified as potential vole habitat according to the classification of satellite imagery. This occurred despite training the classification algorithm with only the trap locations where we detected voles ($n = 48$). After withholding 30% of the training points for validation, the overall classification accuracy was 92.7%, and the producer's and consumer's accuracy for the potential vole habitat class were 88% and 100%, respectively (Table 1). Sample maps of the classified imagery are included in Figure S4.

Comparing vegetation conditions more broadly between the known range of voles and the areas outside that range helped to understand factors that may limit the range of voles. As expected, the amount of potential vole habitat within 150 m was greatest at sites within, or near, the known range of voles (Figure 4b). Otherwise, we did not observe any significant (p -value $< .05$) differences between sites within the range of voles and sites to the south. Within the areas we sampled, mangrove cover at the trap scale (within 3 m) did not differ between the known range of voles and sites to the south; however, the sites within both of these regions had significantly more mangrove cover when compared with sites to the north of the voles' range (Table 2). Specifically, mangroves were only detected within 3 m of traps at one site north of the known range of voles (Figure 4c). The lack of mangroves at sites north of the range of voles was further reflected at the landscape scale (150 m) where forest cover was mostly 0 (Figure 4a); however, this difference was not significant according to the Tukey HSD test (Table 2). Regarding herbaceous plant species, we observed several significant differences between sites within the range of voles and the sites we sampled to

the north (Table 2). Herbaceous vegetation was taller (Figure 4e) and *S. alterniflora* cover was greater (Figure 4f) at sites to the north of the range of voles when compared to those within their range, whereas *D. spicata* cover was lower north of their range (Figure 4d).

3.3 | Inundation

High water events within 2019 did not appear to affect vole occupancy, but the effect of Hurricane Michael is less clear. Despite two high-water events (April 19 and October 16) occurring during the 2019 sampling season where the measured water height at the NOAA tide station in Cedar Key, FL was greater than 1.83 m (Figure S5), we detected voles again during resampling at all four sites that were resampled. The extent to which inundation during these 2019 events compared to that during Hurricane Michael is not clear because comparable SAR imagery was not available for these 2019 high-water events. During Hurricane Michael, vast extents of coastal marshes along the coast of northwestern Florida were inundated according to the SAR-derived inundation metric (Figure S6). However, lower VHdiff values were observed along the outer marsh edge within the range of voles, compared to the northern portion of the study area where marshes were inundated more uniformly (Figure S6). In addition, the CRI for the effect of VHdiff in the occupancy model was negative (-4.8 , -0.2), which suggests voles are more likely to occur in marshes that were less vulnerable to inundation.

4 | DISCUSSION

Greater range sizes are key to the adaptive capacity of unique and isolated populations, such as climate relicts (Böhm et al., 2016; Cooper et al., 2008). Our results suggest that this population of vole, an endangered climate relict, is restricted to a small (~40 km) stretch of the coast between the Suwannee and Withlacoochee Rivers (Figure 1). Furthermore, their range appears to be contracting as a result of multiple threats, including shifting vegetation communities and severe weather events. Despite persisting through substantial climatic shifts since the Pleistocene, our results suggest that the voles may no longer be able to keep pace with the rapid pace of climate-induced changes to their environment.

At their northern range limit, voles appear to be limited by herbaceous vegetation conditions. Though there was little support for marsh grass (*S. alterniflora*, *D. spicata*) influencing local occurrence, broader patterns revealed that marshes north of the voles' range contained less *D. spicata*, which is an important food source for voles in coastal marshes (Harper et al., 2020; Hotaling et al., 2010;

FIGURE 4 The distribution of 7 environmental covariates at 57 sites as a function of the distance from the centre of the range of Florida saltmarsh vole along the coast near Cedar Key, Florida. Positive distances represent sites to the north of the range voles' range (shown with gray vertical lines) and negative distances are to the south. The data are fitted with a Loess smoothing function (solid line) with 95% confidence interval shown in shaded region

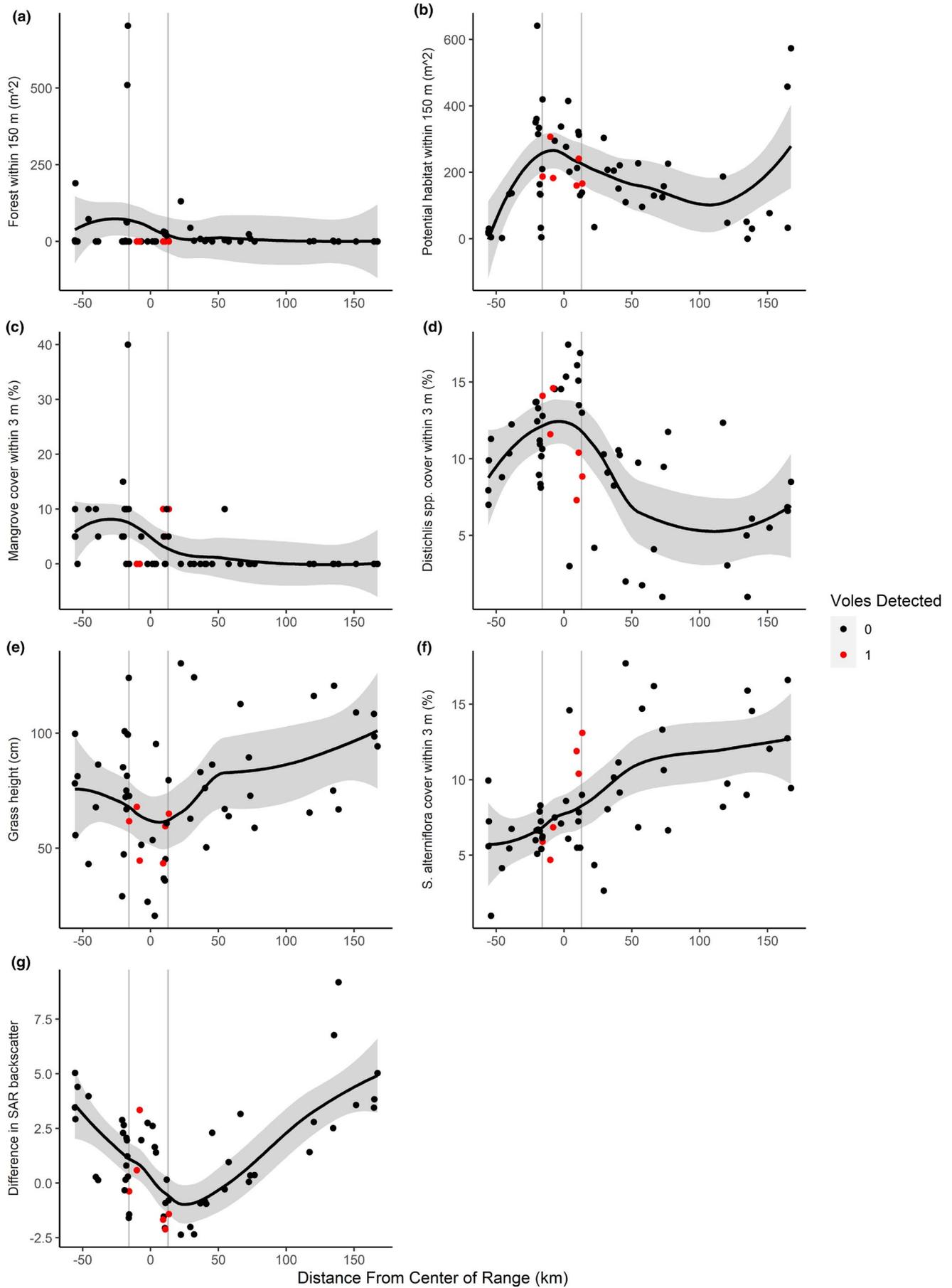


TABLE 2 Pairwise comparisons of covariate effect sizes between sites within the range of voles and those sites to the North and South of this range according to a Tukey HSD test

Variable	Scale	North	p-Value	South	p-Value
Grass height	Average across traps in a site	0.84	.01	0.18	.88
Spartina cover	Average across traps in a site	0.98	<.01	-0.42	.41
Distichlis cover	Average across traps in a site	-1.31	<.01	-0.4	.42
Mangrove cover	Average across traps in a site	-0.75	.02	0.22	.82
Forest cover	Landscape (150-m radius from middle of site)	-0.41	.34	-0.24	.81
Potential habitat	Landscape (150-m radius from middle of site)	-0.55	.13	-0.89	.05

Note: The effect size differences are relative to the site within the range of voles, unitless because covariates were standardized, and shown with their associated *p*-values. Sample sizes for the range of voles, the region to the north of the voles' range and the region to the south of the voles' range were, 175, 161 and 63, respectively

Howell, 1984; McCleery & Zweig, 2016). Because *S. alterniflora* and *D. spicata* are competitively inferior to *J. romerianus* and *S. patens*, they are often restricted to the outer marsh where harsher conditions (e.g. salinity) limit competition from *J. romerianus* and *S. patens* (Pennings et al., 2002). Additionally, patches of bare marsh created by disturbance are readily colonized vegetatively by *D. spicata* and are thus important to *D. spicata* persistence (Bertness, 1991). Therefore fire, a historically important disturbance in coastal marshes (Frost, 1995), may serve to maintain abundance of *D. spicata* in the high marsh zone (Mitchell et al., 2006). Alternatively, the observed variation in *D. spicata* cover may result from nutrient availability, which can shift the competitive hierarchy from *J. romerianus* to favour *D. spicata* and *S. alterniflora* (Pennings et al., 2002). Given the disproportionate role of the Suwannee River in delivering sediment to marshes where voles occur (Wright et al., 2005), these freshwater inputs could also supply nutrients that promote the establishment and persistence of *D. spicata* within the range of voles.

At the southern range limit of voles, the poleward expansion of mangroves presents an emerging threat. Several recent studies have documented the expansion of mangroves across the Gulf Coast, including around this southern range limit (Osland et al., 2013; Stevens et al., 2006). In addition, four of the seven sites from which voles were likely extirpated since 2014 represent the four southern-most vole detections (Figure 2). Thus, these extirpations may represent a contraction of the voles' range caused by the expansion of mangroves. If mild Florida winters persist as the climate continues to change (Hartmann et al., 2013), a continued poleward expansion of mangroves will likely continue to replace the saltmarshes used by voles. In addition to these stands of mangroves visible from space, our trap scale (3 m) measurement of mangroves revealed that small mangrove seedlings have established at many of the sites that currently or formerly supported voles. In the absence of freezing winter temperatures across Florida, these young mangroves are likely to persist and spread at the expense of marshes used by voles. With only one remaining site known to support voles south of the Waccasassa River, future monitoring of voles and mangrove expansion around this southern range limit will be critical to future conservation of voles.

Our results suggest that only the most severe inundation events are likely to threaten voles, if at all. Vole occurrence did not change

after 2019 high water events, despite inundating shorter marsh grasses used by voles (Figure S7). However, these events were not as extreme as that which occurred during Hurricane Michael, when water heights were approximately 0.6 m higher (Figure S5). Compared to the marshes north of the Suwannee River, the marshes we sampled where voles occurred appeared to be less vulnerable to inundation during severe storms, according to our SAR metric (Figure S6). As such, these marshes may serve as refugia for terrestrial animals like voles when surrounding marshes are inundated. Small mammals endemic to coastal wetlands have been shown to readily move through inundated environments (Abuzeineh et al., 2007; Geissel et al., 1988), but they may require escape cover or other refugia from predators when inundation is widespread. Thus, as sea levels continue to rise, conservation of the unique animals associated with coastal wetlands may increasingly depend on targeted management, such as creating impoundments with water control structures (Braun de Torrez et al., 2020; Shellhammer, 1989).

The future persistence of voles remains uncertain, in part due to some important limitations of our study. Populations of small mammals are known to be highly dynamic, in part due to high fecundity and high predation pressure (Lima et al., 2002; Stenseth, 1999; Turchin, 1993). Studies of other voles in coastal marshes have shown interannual fluctuations may be related to widespread inundation during storms (Bias & Morrison, 2006; Longenecker et al., 2018). Because our study was limited to one year, we have limited information about the potential for annual or seasonal population fluctuations. This inability to link environmental changes to specific demographic processes likely limited our understanding of their importance (Johnson, 2007; Van Horne, 1983). Specifically, we have no real understanding of the features that promote fecundity in voles and there are likely complex interactions between vegetation, inundation and predation risk. Trade-offs between foraging and predation risk are common in most small mammals (Loggins et al., 2019; Potash et al., 2019), and in coastal environments animals face trade-offs between avoiding predation and avoiding reproductive failure related to inundation (Hunter et al., 2016). In addition to these factors, our study was conducted within a single year (2019) and compared against one previous year (2014). Because we have no information about the years between 2014 and 2019, our ability

to draw inferences from extirpated sites is limited. Given the potentially dire consequences of these related threats for the voles and other species associated with coastal marshes, continued monitoring is warranted.

Despite a gradually warming global climate throughout the Holocene, climate relicts from the Pleistocene have persisted in isolated regions of the globe for millennia (Hampe & Jump, 2011). Thus, unlike the “canary in the coal mine,” one might expect these relict populations to be less vulnerable to the current climate crisis when compared to other imperiled species. However, the isolation inherent to relict populations exposes them to the indirect effects of climate change, including shifts in vegetation communities and extreme weather. As such, the implications of climate change for the persistence of climate relicts are likely more dire when these indirect effects are considered.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13380>.

DATA AVAILABILITY STATEMENT

The camera trapping detection/non-detection data, trap locations and vegetation data are archived in a Zenodo repository (<http://doi.org/10.5281/zenodo.4779434>). Also included in the repository are the locations of the training data used to classify the satellite imagery. The satellite imagery are publicly available and accessible via Google Earth Engine, as well as the Sentinel Open Access Hub (<https://sentinels.copernicus.eu/web/sentinel/sentinel-data-access>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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