



Native mammals lack resilience to invasive generalist predator

P.J. Taillie^{a,*}, K.M. Hart^b, A.R. Sovie^c, R.A. McCleery^a

^a Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, United States of America

^b Wetland and Aquatic Research Center, U.S. Geological Survey, Fort Lauderdale, FL 33314, United States of America

^c Department of Forestry and Natural Resources, University of Kentucky, Lexington, KY 40506, United States of America

ARTICLE INFO

Keywords:

Mammals
Wetlands
Biodiversity
Multi-species occupancy
Burmese python

ABSTRACT

Invasive predators have caused catastrophic declines in native wildlife across the globe. Though research has focused on the initial establishment, rapid growth, and spread of invasive predators, our understanding of prey resilience to established invasive predators remains limited. As a direct result of invasive Burmese pythons (*Python molurus bivittatus*), medium- to large-bodied native mammals decreased drastically across much of southern Florida as early as 2003. By 2014, most of these mammal species were exceedingly rare within the core invasion area, while pythons expanded outward to newly invaded areas. We used python observations to delineate the core python invasion area from the more recently invaded invasion front, and we compared changes in mammal occurrence from 2014 to 2019 between these two areas. We surveyed mammal communities using camera traps and scat surveys and used these observations to quantify the changes in occurrence among mammal species. As expected, occurrence of medium- and large-bodied mammals declined within the invasion front. However, contrary to our expectation, we observed little evidence of resilience among mammals within the invasion core. Of the 15 species detected in 2019, invasive black rats were the only species to increase in occurrence within the invasion core. Additionally, we observed declines in occurrence among native rodents within the invasion core, which were previously thought to be resistant to the effects of pythons. The continued presence of invasive pythons appears to be shifting the diverse mammal communities of southern Florida to one primarily composed of invasive species.

1. Introduction

Invasive species are a leading cause of global biodiversity loss and homogenization (Clavero and Garcia-Berthou, 2005; Simberloff et al., 2013). The effects of invasive predators have been particularly detrimental to native wildlife (Doherty et al., 2016) with the level of organization of these effects ranging from populations (Gasc et al., 2010; Medina et al., 2011) to communities (Reichert et al., 2017; Wiles et al., 2003) and entire ecosystems (Caves et al., 2013; Rogers et al., 2017). Though the progression of a predator invasion can vary greatly across species and systems, all invasions are thought to broadly occur in three phases. The first phase of initial establishment is characterized by low rates of population growth and spread (Shigesada and Kawasaki, 1997). During the second phase, the introduced species becomes “invasive” when the population rapidly increases in both abundance and distribution as a result of some combination of a lack of predators, naïve prey, and increased movement or dispersal within the invaded system (Anton et al., 2020; Sakai et al., 2001; Salo et al., 2007; Shigesada and

Kawasaki, 1997; Sih et al., 2010). The third phase occurs when prey populations become depleted, intraspecific competition increases, and the abundance of the invasive predator levels off and begins to decline (Carlsson et al., 2010; Pech and Hood, 1998; Shigesada and Kawasaki, 1997; Strayer et al., 2006). This third stage offers an opportunity for understanding how native communities might recover from the potentially catastrophic impact of the invasion.

The concepts of resilience and resistance help to contextualize the variation in responses to invasive predators, both over time and among the species of the native community (Nimmo et al., 2015). For example, some species may be more resistant (no response to predator introduction) to the effects of an invasive predator if they can avoid predation in the case of prey species, or if they can exploit alternative food sources in the case of competing native predators. Thus, traits such as body size and diet breadth may determine the degree of resistance to the invasion (Soto-Shoender et al., 2020; Wiles et al., 2003). Similarly, species of the native community, both prey and competing predators, may begin to rebound and increase in abundance during the third stage of the

* Corresponding author.

E-mail address: paultaillie@ufl.edu (P.J. Taillie).

<https://doi.org/10.1016/j.biocon.2021.109290>

Received 18 January 2021; Received in revised form 28 July 2021; Accepted 1 August 2021

Available online 14 August 2021

0006-3207/© 2021 Elsevier Ltd. All rights reserved.

invasion once the invader begins to decline (Brzeziński et al., 2020; Campbell III et al., 2012; Crooks and Soulé, 1999); however this resilience (recovery following initial decline) to a predator invasion is less well understood, but essential to understanding the long-term effects of predator invasions. As with resistance, the resilience of native species will vary as a function of traits. For example, the capacity for resilience may be greater for species (predators and prey) that remained abundant in adjacent areas less affected by the invasive predator (Gallardo et al., 2017; Plowes et al., 2007). Additionally, after generations of exposure to the invasive predator, native prey may develop behavioral strategies to avoid predation (Brzeziński et al., 2020). Because responses by native wildlife to invasive predators may change over time and as a function of different phases of the invasion, the extensive research on the initial effects of invasive predators and their spread (Arim et al., 2006; Shigesada and Kawasaki, 2002; Sofaer et al., 2018) offer little insight into resilience of native communities following prolonged establishment. To make such inferences, invaded communities must be studied over time (Strayer et al., 2006). However, with few longitudinal investigations of the community response to an invasive predator (but see Brzeziński et al., 2020; Carlsson et al., 2010), we have only a limited understanding of these community dynamics in the long term.

To better understand the effects of persistent invasive predators, we extended previous work documenting the initial declines of mammals in southern Florida, USA linked to the invasion of the Burmese python (*Python molurus bivittatus*; hereafter: pythons). Pythons were introduced to southern Florida and Everglades National Park at least as early as 1990 (Willson et al., 2011). In subsequent decades, several studies documented the near complete absence of mid-to large-bodied mammals in and around Everglades National Park starting in 2003 and continuing through 2014 (M. E. Dorcas et al., 2012; Reichert et al., 2017; Soto-Shoender et al., 2020; Sovie et al., 2016). This collapse of both the python's prey (e.g., marsh rabbit, *Sylvilagus palustris*) and native competitors (e.g., bobcat, *Lynx rufus*) suggests this area has entered the third invasion stage, with the potential for resilience among native mammals. In contrast to larger mammals, rodent populations appear comparatively stable even though they have been observed as python prey since early in the invasion (Snow et al., 2007). This apparent resistance among rodents to predation by pythons (Hoyer et al., 2017; Soto-Shoender et al., 2020) is likely due to high fecundity (Soto-Shoender et al., 2020), but may also be related to other factors, such as predator avoidance.

Our goal for this study was to investigate shifts in native mammal communities exposed to invasive pythons to better understand the response of native wildlife communities at different stages of invasions. Specifically, we quantified the degree to which mammal communities changed by surveying mammals across the Greater Everglades Ecosystem in southern Florida, USA over a 5-year window (2014–2019) following the period of rapid python population growth and associated decline in mammals documented by previous studies (Dorcas et al., 2012; Reichert et al., 2017). We compared the mammal community responses between the invasion core where pythons were established for decades and the invasion front where python occurrence increased over the duration of the study. We predicted that occurrence of species shown to be most sensitive to pythons, such as white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*), and marsh rabbit (M. E. Dorcas et al., 2012; Reichert et al., 2017; Soto-Shoender et al., 2020), would decrease within the newly invaded areas. In contrast, if python relative abundance declined in core invasion areas where these mammals were already rare prior to 2014, we expected highly fecund mammals (rodents, marsh rabbit, and Virginia opossum; *D. virginiana*) to be most resilient, increasing in occurrence within the invasion core (Soto-Shoender et al., 2020). Alternatively, if the effects of pythons were unabated and these species continued to be rare within the core invasion area, the invasion may not yet have transitioned into the third phase.

2. Methods

Our approach to evaluating how mammal communities have changed as a result of the continued invasion of Burmese pythons broadly involved two steps: 1) delineating a core invasion area where pythons have long been established and an invasion front where pythons have recently expanded and 2) sampling mammal communities within these two areas over a 5-year period to determine how they have changed. For the first step, we used a publicly available database of python detections to model their distribution prior to 2014 and in 2019. To measure mammal community change (second step), we conducted presence/absence surveys using camera traps and scat surveys during 2014 and 2019. Within each of these two years, we used detections across multiple sampling occasions to estimate the probability of detecting each mammal species, then used this detection probability to estimate the occurrence probability in each year and then the change in occurrence over the 5-yr period (i.e., the difference between 2014 and 2019). This design allowed us to investigate how mammal occurrence has changed, and importantly, how these changes differed between the core invasion area where we expected to observe resilience, compared to the invasion front where we expected declines across mammal species.

2.1. Study area

We conducted this study in the Greater Everglades Ecosystem, a vast complex of freshwater marsh, forested wetlands, and estuarine coastal wetlands in southern Florida, USA. Specifically, the study was conducted on public properties within the Greater Everglades Ecosystem, including Everglades National Park, the South Glades parcel of the South Florida Water Conservation District ("South Glades"), Big Cypress National Preserve ("Big Cypress"), Everglades and Francis S. Taylor Wildlife Management Area ("Wildlife Management Area"), and Arthur R. Marshall Loxahatchee National Wildlife Refuge ("Loxahatchee"; Fig. 1). The expansive wetlands of the Greater Everglades Ecosystem and much of the surrounding agricultural and urban development are connected by drainage ditches and canals, which likely facilitated the spread of python away from the invasion epicenter near Flamingo, FL (Hart et al., 2015). Though originally introduced in the Greater Everglades Ecosystem prior to 1990, it was not until after 2003 that pythons were encountered in great numbers, marking the beginning of the second stage of their invasion (Willson et al., 2011).

2.2. Python distribution

In order to explicitly link changes in mammals' communities to pythons, we used observations from the University of Georgia Early Detection and Distribution Mapping Service data ("EDDmapS"; EDD-MapS, 2019) to differentiate areas that have long been affected by pythons from newly-invaded areas. Following the methods of Mutascio et al. (2018), we used python observations to model their distribution as a function of environmental predictors. We used python observations between 2000 and 2013 to serve as a baseline python distribution prior to the initial mammal sampling in 2014. Similarly, we used python observations between 2017 and 2019 (i.e., current observations) to compare against the baseline. Splitting the python observations in this way resulted in a comparable number of observations in each of the two time periods ($N = 1927$ and 1872 , respectively). Because these python observations were primarily on or near roads (Willson et al., 2011), we constrained background points to only be within 100 m of a road to minimize the effect of this sampling bias (Mutascio et al., 2018; Phillips et al., 2009). As such, we assumed that the modelled relationships between python detections and environmental covariates (described below), which were based on areas near roads, also applied to areas away from roads.

We incorporated environmental covariates to explain the spatial distribution of python observations. Again, we used Mutascio et al.

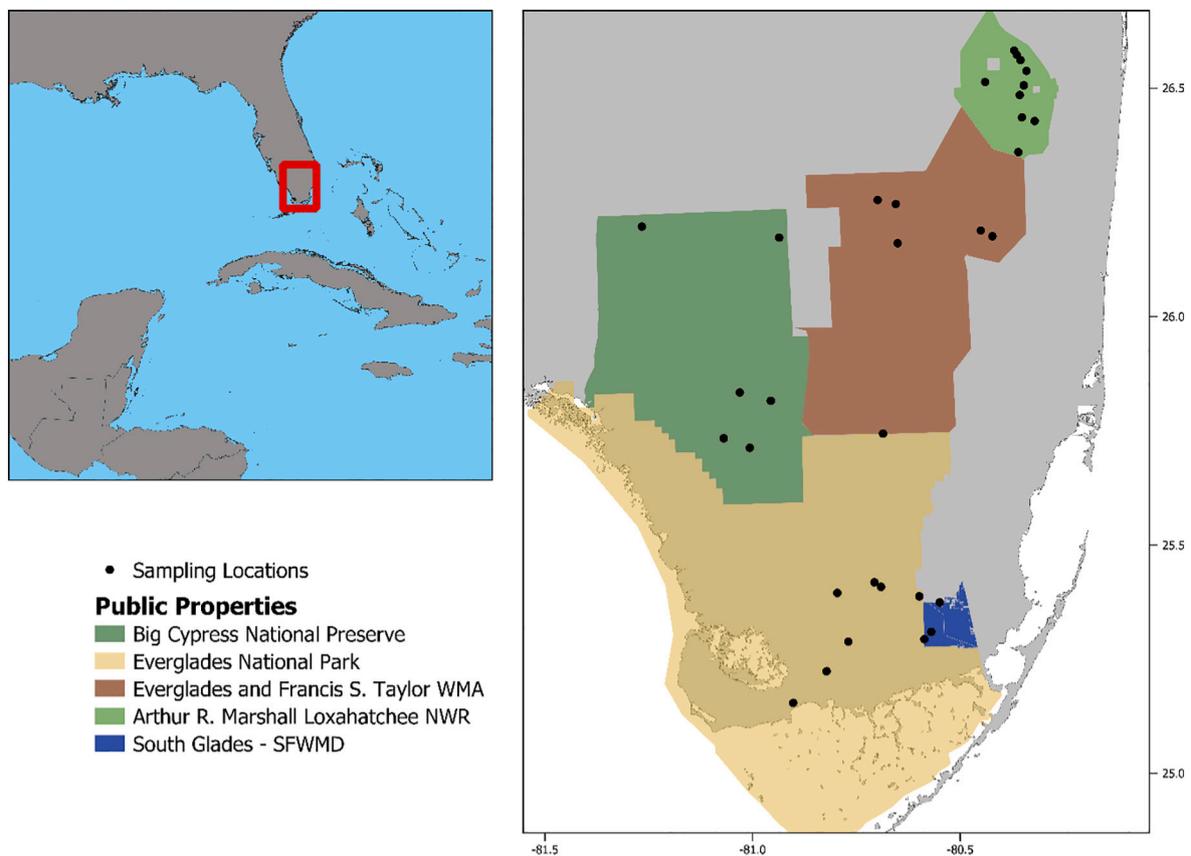


Fig. 1. The distribution of sampling locations where mammals were surveyed in each of 2014 and 2019 on 5 public properties in southern Florida, USA. (WMA = Wildlife Management Area; NWR = National Wildlife Refuge; SFWMD=South Florida Water Management District).

(2018) as a guide to select informative covariates, but focused specifically on the larger scale predictors of python occurrence. First, we incorporated the distance to urban land cover types, which were delineated using the National GAP Analysis Program Landcover Data (USGS 2011). We also used the GAP Landcover data to identify the extent of the land cover types most likely to be used by pythons (estuarine mangrove forest, Florida highlands marsh, and Everglades sawgrass marsh) at the 4-km scale, corresponding to the home range size of pythons in Everglades National Park (Hart et al., 2015). Specifically, we calculated the combined proportion of these three cover types within a 4-km radius of the focal pixel to estimate the amount of python habitat at the home range scale. Given that we expected pythons to have spread north, we incorporated latitude as a predictor of python distribution as well. We performed all spatial analysis using QGIS v.3.4.

Using the python observations, background points, and the three explanatory variables discussed above, we used a maximum entropy (Maxent) framework to model the relative occurrence of pythons within the two time periods (i.e., 2000–2013 and 2017–2019) separately. Models were fit using the R package *dismo* (Hijmans et al., 2017). Because we were interested in broad scale shifts in python distribution (i.e., the location and extent of the invasion front), we tuned the models to only consider linear, quadratic, and interaction relationships, but not hinge or threshold features (Fletcher and Fortin, 2018). We assessed the fit of each model (baseline and current) by plotting the receiver operating characteristic (ROC) curve and calculating the area under this curve (AUC) using the *evaluate* function in *dismo* (Hijmans et al., 2017). Finally, we derived the change in python relative occurrence by subtracting the baseline relative occurrence (i.e., the “logistic” Maxent output) from that in 2019 at each pixel.

We used the modelled change in python relative occurrence to delineate the invasion front from the core invasion area that has been

occupied by pythons for over a decade. We defined the core invasion area as that which had a relative python occurrence greater than 0.5 in 2013, but where the change in python relative occurrence did not increase by at least 0.2. We then defined the invasion front as the areas where the relative occurrence increased by 0.2, resulting in 11 sites within the invasion core, 18 sites in the invasion front, and 3 unclassified sites. We used a threshold of 0.2 because the resulting invasion core area agreed with previous investigations of python distribution and density (Bonneau et al., 2016). Alternatively, a threshold of 0.1 classified areas of southern and eastern Everglades National Park as the invasion front, despite previous studies suggesting pythons have occurred here for over a decade (Bonneau et al., 2016), and a threshold of 0.3 classified only 4 of our sites as occurring along the invasion front.

To investigate potential confounding between the effects of pythons and other environmental characteristics that could influence mammal communities, we compared water levels and vegetation condition between the core area and invasion front, as well as between 2014 and 2019. Given recent work that documented mammal responses to the ongoing hydrological restoration efforts across the Greater Everglades Ecosystem (Romañach et al., 2021), we used the Everglades Depth Estimation Network water depth surfaces (<https://sofia.usgs.gov/eden/models/watersurfacemod.php>) to extract water depth at each of the 32 sampling locations (see “site selection”) during the month of April in both 2014 and 2019. In addition, we investigated differences in vegetation between the core area and invasion front, as well as between years, using satellite imagery. Using Google Earth Engine, we collected all Landsat 8 imagery from the study area during 2014 and 2019 and masked clouded pixels. We then calculated a multi-band composite image for each year according to the median value for each wavelength band at each pixel. Lastly, we calculated the normalized-difference vegetation index (NDVI) and calculated the mean NDVI from all pixels

within 100 m of each of the 32 sampling locations. We used simple linear regression to test for significant differences between 1) sites within the core area and the invasion front 2) all sites in 2014 and all sites in 2019, and 3) an interaction between invasion context and year.

2.3. Site selection and mammal sampling

Sampling locations were originally established in 2014 to investigate the mammal community composition across a python density gradient (Reichert et al., 2017; Soto-Shoender et al., 2020; Sovie et al., 2016). To investigate how these communities changed over a period of 5 years, we selected a subset of 32 of the original 113 sites sampled in 2014 according to 3 criteria: 1) they covered the gradient of python relative density described by Reichart et al., 2) had previously detected mammals, and 3) were accessible and based in the eastern portion of the study area.; Fig. 1). We sampled the presence/absence of mammals at each site using 3 distinct methods: scat surveys, traditional camera traps, and modified camera traps designed for small mammals. After navigating to the site with a handheld GPS unit, two observers conducted scat surveys by establishing at 30-m by 30-m plot with the sides oriented with the cardinal directions. The first observer walked three evenly-spaced parallel transects within the plot, which was then repeated by the second observer walking the opposite directions. Each scat was identified to species by each observer, and confirmed by a third via photograph. Any scat without consensus among the three observers was classified as “unknown” and not included herein. We then deployed 4 camera traps of two different types near the corners of the plot. The first camera trap type was a motion triggered camera mounted to a tree approximately 30 cm above the ground (hereafter “traditional” camera traps) aimed to maximize detection of mammals (e.g., along an established game trail). The second type of camera trap was better suited to small mammals and consisted of a motion-triggered camera with a short focal distance (40 cm) housed within a 7-gallon bucket mounted on a floating base (McCleery et al., 2014; hereafter “bucket traps”). Holes in the bucket allowed small mammals to enter and exit to access a small cup baited with bird seed.

2.4. Mammal community modelling

We used a multi-species occupancy modelling framework (hereafter: “community model”) to investigate changes in mammal communities across the Greater Everglades Ecosystem (Dorazio and Royle, 2005). This hierarchical modelling framework has several strengths that were particularly relevant to this study. First, in contrast to the presence-only approach to modelling the distribution of pythons we used above, this framework allowed us to use the detection/non-detection history over multiple sampling occasions to estimate the probability that a given species would be detected during a given occasion (MacKenzie and Kendall, 2002). In addition, by considering each species as a random effect of the larger community response, we were able to share data across species and make inferences about less detectable species for which we did not have enough observations to fit a single-species occupancy model (Zipkin et al., 2009, 2012).

Prior to fitting the model, we used the observations of mammals to build a detection history for each species at each site. The observations were pooled between the two cameras of a given type (e.g., the 2 traditional camera traps) at a site within the same year. Both camera types were deployed for a minimum of 7 nights, resulting in a minimum of 16 sampling occasions (2 scat surveys + 7 nights of traditional camera trapping + 7 nights of bucket trapping), with some longer deployments because of access issues, such as weather (Table S1). After manually reviewing all camera trap photos to identify the mammal species observed, we built nightly detection histories at each site in each year using the *detectionHistory* function in the R package *camtrapR* (Niedballa et al., 2016).

Because we were most interested in the change in mammal com-

munity composition between 2014 and 2019, we modified the single-season community model to estimate occurrence in each of 2014 and 2019, where the time- and species-specific occurrences are assumed to be conditionally independent. We parameterized the model to treat each night of camera trapping and each scat survey as sampling occasions $j = 1, 2, \dots, J$ within each year (i.e., 2014 and 2019). Within a year, we assumed that the community was closed to changes in the latent occupancy state z_{ikt} at site $i = 1, 2, \dots, M$, for species $k = 1, 2, \dots, K$, within year $t = 1, 2$, but could vary between these two periods. As such, the observations y_{ijkt} were modelled as a binomial distributed random variable with success probability p_{ijkt} that varied across species, between years, and across sampling methods, given the species was present at the site in that year (Eq. (1)). Following the example of several previous studies that account for variation in detection across sampling methodologies (Ausband et al., 2014; Long et al., 2011; Taillie et al., 2015; Taillie and Moorman, 2019), we estimated a separate detection intercept ($\alpha_{0ikt(surveyTypej)}$) for each species, year, and survey type (scat survey, traditional camera trap, or bucket trap; Eq. (2)). For the linked occurrence component of the hierarchically structured model, the occupancy state z_{ikt} was a binomial-distributed random variable with parameter ψ_{ikt} representing the occurrence probability at each site i , species k , and year t (Eq. (3)). To link any observed change in mammal occurrence to pythons, we included the relative python occurrence in each of the years as a covariate on the logit transform of the occupancy probability ψ_{ikt} (Eq. (4)). We analyzed our model in a Bayesian setting using the R package *rjags* (Plummer et al., 2016). We assumed weakly informative logistic priors, ran 3 MCMC chains for 80,000 iterations after an initial burn-in of 40,000 iterations, and thinned the resulting samples to every fifth iteration. We checked model convergence by inspecting trace plots and confirming the Gelman Rubin diagnostic for all parameters was less than 1.1 (Brooks and Gelman, 1998). Furthermore, we evaluated the fit of the model by comparing model predictions to actual occurrences (Zipkin et al., 2012). Specifically, we fit the model using only the 2014 observations and 2014 python relative occurrence values, used the estimated model parameters to predict mammal species occurrences in 2019 according to the python relative occurrence in 2019, then compared those predictions to the actual occurrence, that we estimated by fitting the model to the 2019 mammal detections. As with the model of python observations, we quantified the predictive performance by calculating the ROC AUC; however, for this model, we calculated the predictions and true occurrences for each species during each MCMC iteration, then calculated the mean AUC from the posterior distributions using the *performance* function within the R package *ROCR* v.1.1-11 (Sing et al., 2005).

$$y_{ijkt} | p_{ijkt}, z_{ikt} \sim \text{Bern}(p_{ijkt} z_{ikt}) \quad (1)$$

$$\text{logit}(p_{ijkt}) = \alpha_{0ikt(surveyTypej)} \quad (2)$$

$$z_{ikt} | \psi_{ikt} \sim \text{Bern}(\psi_{ikt}) \quad (3)$$

$$\text{logit}(\psi_{ikt}) = \beta_{0kt} + \beta_{\Delta kt} * \text{Pythons}_{it} \quad (4)$$

We evaluated the strength of the effect of python relative occurrence by comparing the magnitudes of the slope parameters and evaluated the degree of statistical support for the effect based on the degree to which the posterior distribution overlapped 0. As such, we report 95% credible intervals (CRI) for posterior distributions and considered parameters with 95% CRI's overlapping 0 to have less support as opposed to not “significant.” For each species, we quantified the change in occurrence at a given site by subtracting the occupancy probability in 2014 from that in 2019 at each MCMC iteration, thereby quantifying the associated error around this parameter. We interpreted these changes in occurrence to have more support as less of the posterior distribution overlapped 0, but as with the effect of python relative occurrence, we did not define discrete thresholds of “significance.” Similarly, we computed the change in species richness from 2014 to 2019 at each MCMC iteration by

summing the occurrence across all species within each primary period. To compare changes in occurrence between the invasion front and invasion core, we pooled the model results across sites within each of these areas.

3. Results

3.1. Python model

The presence-only models of relative python occurrence fit well to the EDDmapS python observations, as reflected by the AUC values of 0.968 and 0.953, for the baseline and current periods, respectively. The difference in the predicted relative occurrence between these two periods revealed a substantial expansion of the python invasion to the north and west of the core invasion area (Fig. 2c). Using a relative occurrence threshold of 0.2, the python invasion front was approximately 520,000 ha in 2019, compared with an invasion core of

approximately 440,000 ha. The core area was largely confined to Everglades National Park and South Glades, but also included the extreme southern portions of Big Cypress and the Wildlife Management Area (Fig. 2a). We observed a general northward shift of the front, but the largest increases in python relative occurrence were in the southern half of Big Cypress, as well as the western side of Everglades National Park where we did not sample (Figs. 1 and 2c). Otherwise, increases in the python relative occurrence probability greater than 0.2 were widespread throughout the wetlands of the northern Wildlife Management Area and throughout Loxahatchee (Figs. 1 and 2c). The relative probability of python occurrence remained high (i.e., changed little between time periods) in areas where pythons have been established the longest in the eastern half of Everglades National Park and throughout South Glades (Fig. 2). We did not observe significant differences in either water depth or vegetation conditions (i.e., NDVI) related to invasion context, year, or their interaction, suggesting these factors did not confound the observed mammal responses to pythons.

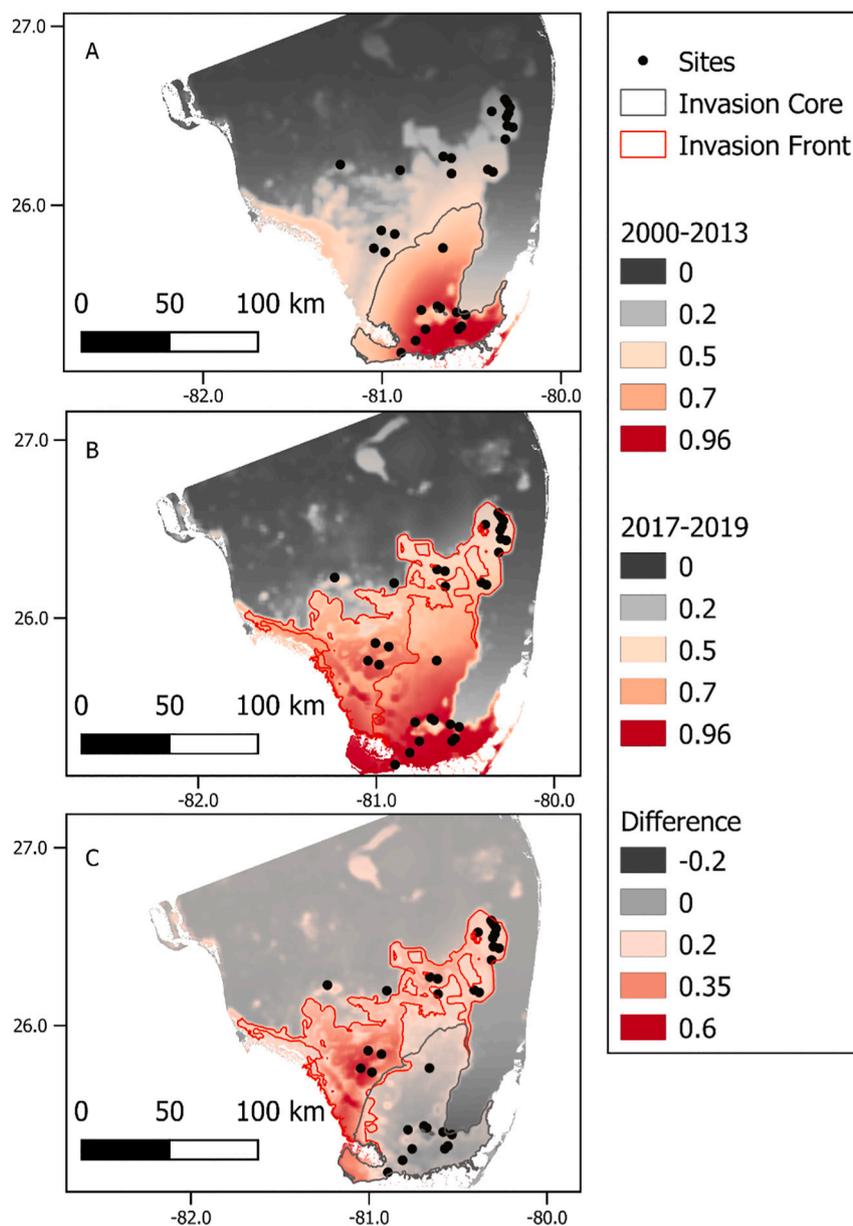


Fig. 2. The relative python occurrence estimated with a Maxent model of python presence observations from 2000 to 2013 (A), 2017–2019 (B), and the difference between the two (C) in southern Florida, USA. The invasion core (outlined in gray) was defined as areas with a relative python occurrence greater than 0.5 in 2013 and the invasion front was defined as areas where the difference in relative python occurrence between the two time periods was greater than 0.2.

3.2. Mammal community model

We detected 15 mammal species at the 32 sampling locations in 2019 and 4 additional species in the original 2014 sampling (Soto-Shoender et al., 2020; Table 1). Six of the 15 species were exceedingly rare or elusive and only detected on fewer than 10 occasions (Table 1). The predictive performance of the model for rarely-detected species was poor, with the posterior mean AUC values ranging from 0.51 to 0.61 for river otter (*Lontra canadensis*) and round-tailed muskrat (*Neofiber alleni*), respectively. Of the seven most commonly detected species, AUC values reflected better predictive performance for medium to large mammals, than for rodents. Specifically, Bobcat (*Lynx rufus*), white-tailed deer, marsh rabbit and raccoon all had AUC values greater than 0.8, while those for rodents did not exceed 0.68. Bobcat, white-tailed deer, marsh rabbit, and raccoon were less likely to occur in areas where python relative occurrence was greater, independent of year (Fig. 3; posterior means for the effect of python occurrence were -6.5 , -7.0 , -6.6 , and -6.7 , respectively). Four rodent species, black rat, cotton rat (*Sigmodon* spp.), cotton mouse (*Peromyscus* spp.), and rice rat (*Oryzomys palustris*) were all more likely to occur where pythons were more likely to occur, though the posterior mean for cotton mouse was near 0 (Fig. 3). The posterior distributions of the effects of python relative occurrence for infrequently encountered species were mostly negative, but with a high degree of uncertainty (Fig. 3).

These temporally independent responses of mammals to python occurrence translated to shifts in community composition over the 5-yr period. As pythons became more common along the invasion front, occurrence of medium- to large-bodied mammals like deer, marsh rabbit, and bobcat decreased (Fig. 4). In contrast, small mammals decreased only slightly (e.g., rice rat), did not change (e.g., cotton rat), or increased in occurrence (e.g., black rat) within the invasion front (Fig. 4). Across all mammals, species richness decreased by an average of 2 species across the invasion front over 5 years (Fig. 5).

Changes in occurrence within the core invasion area were largely contrary to our predictions. Species that were rare at the beginning of the study, such as white-tailed deer, bobcat, raccoon, and marsh rabbit, remained very unlikely to occur (mean occurrence probability <0.2 ; Fig. S1). Though the probability of raccoon occurrence increased slightly within the invasion core (Fig. 4), this was likely an artifact of increased uncertainty around the estimated occurrence in 2019 (Fig. S1), as only one raccoon was detected within the invasion core, at the northernmost sampling location within the invasion core. Invasive

Table 1

The number of detections summed across sampling occasions at all 32 sites for all species detected, ordered according to increasing body size. Species listed with 0 detections in either year were detected in the 2014 sampling, but not at the 32 sites included in this study.

Species	Scientific name	2014	2019
Cotton mouse	<i>Peromyscus</i> spp.	0	10
Rice rat	<i>Oryzomys palustris</i>	53	39
Cotton rat	<i>Sigmodon</i> spp.	36	18
Black rat	<i>Rattus rattus</i>	8	8
Eastern gray squirrel	<i>Sciurus carolinensis</i>	0	0
Fox squirrel	<i>Sciurus niger</i>	0	0
Round-tailed muskrat	<i>Neofiber alleni</i>	1	2
Marsh rabbit	<i>Sylvilagus palustris</i>	25	30
Striped skunk	<i>Mephitis mephitis</i>	1	0
Virginia opossum	<i>Didelphis virginiana</i>	2	1
Nine-banded armadillo	<i>Dasypus novemcinctus</i>	0	0
Raccoon	<i>Procyon lotor</i>	30	11
Bobcat	<i>Lynx rufus</i>	5	4
River otter	<i>Lontra canadensis</i>	1	0
Coyote	<i>Canis latrans</i>	2	0
Florida panther	<i>Puma concolor</i>	1	0
White-tailed deer	<i>Odocoileus virginianus</i>	23	60
Domestic pig	<i>Sus scrofa</i>	0	1
Black bear	<i>Ursus americanus</i>	0	6

black rats actually appeared to be both resistant and resilient, increasing in occurrence in both the invasion core and front (Fig. 4), while native cotton rats and rice rats decreased in occurrence within the core invasion area. Species richness appeared to decline in both the core invasion area and the invasion front over the 5 years (Fig. 5).

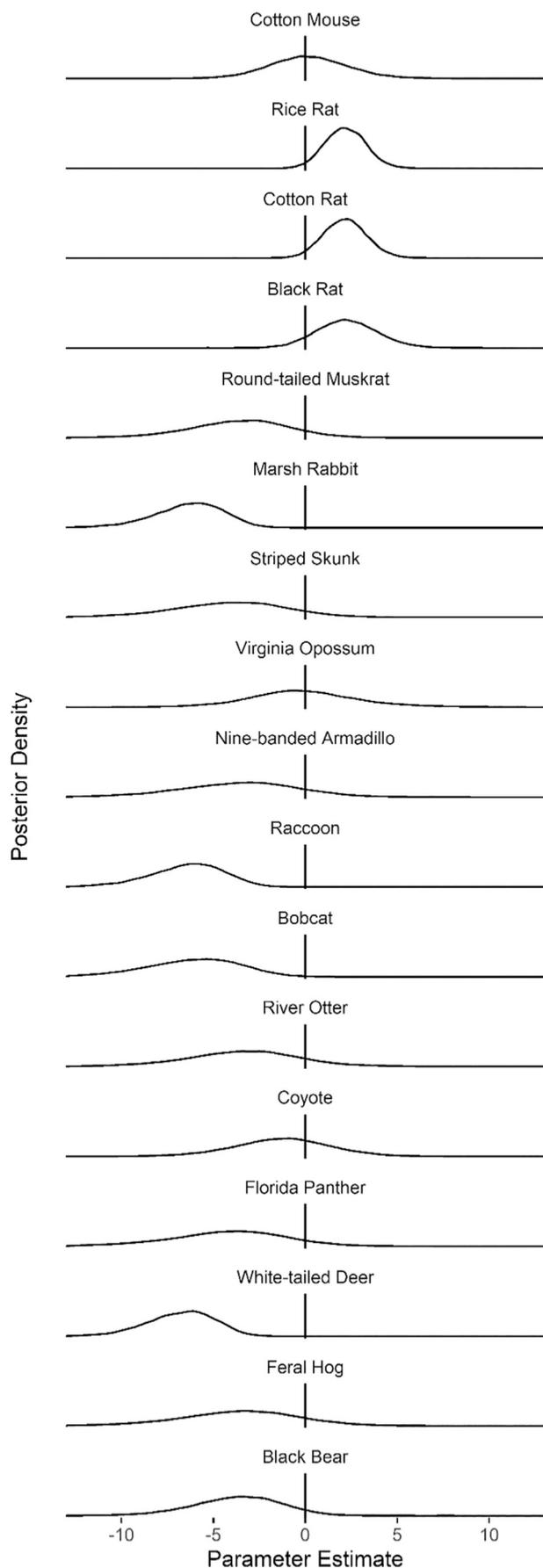
4. Discussion

Over a 5-yr period, the spatial extent of the python-linked declines of southern Florida's native mammals approximately doubled. Meanwhile, in areas with the longest exposure to invasive pythons (i.e., the core area), the loss of mammal diversity documented by previous studies (Dorcas et al., 2012; Reichert et al., 2017) continued, with all mid-sized mammals remaining absent or rare and native rodents declining as well. We observed no evidence of resilience to the effects of pythons among native mammal populations within areas of prolonged exposure. However, the black rat, a globally distributed invasive species (Borroto-Páez, 2009; Courchamp et al., 2003; Harper and Bunbury, 2015; Stokes et al., 2009) was the only mammal to increase in occurrence within the invasion core over the 5-year period.

Despite extirpation of many of their documented prey species, pythons and their associated effects on mammals do not appear to have abated. One explanation for this result is that pythons are persisting on alternative prey (Caut et al., 2008), thereby protracting the second phase of the invasion. Despite evidence that pythons had not reduced native rodent populations (Hoyer et al., 2017; Soto-Shoender et al., 2020), we observed declines in occupancy within the invasion core for both rice rats and cotton rats. While there may have been some initial resistance to pythons among rodents, the absence of medium-bodied mammal prey species (e.g., marsh rabbits) may have caused pythons to consume more rodents. Similar shifts to alternative prey have been observed in other systems (Caut et al., 2008). On the island of Guam, smaller birds were initially most vulnerable to predation by the invasive brown tree snake (*Boiga irregularis*), but over time larger birds began to decline as well (Wiles et al., 2003). The ability of pythons to consume alternative prey could have negative consequences, not only for rodents, but also for other taxa consumed by pythons, such as birds and herpetofauna (Dove et al., 2011; Orzechowski et al., 2019; Snow et al., 2007). However, the loss of mammals in southern Florida could contribute to the success of other invasive reptiles such as black and white tegu (*Salvator merianae*) and green iguana (*Iguana iguana*) by releasing them from competition from native mammals (Meshaka et al., 2009). The combined effects of these multiple invasive species thus reflect the broader pattern of global homogenization where diverse communities are replaced by generalists (McKinney and Lockwood, 1999).

Previous work has shown that black rats were more resistant to the effects of invasive predators compared to native rodents (Fukasawa et al., 2013). This resistance is likely related to high fecundity and broad habitat breadth, which have both been shown to moderate the effects of invasive predators (Soto-Shoender et al., 2020). Alternatively, or perhaps in addition, the increases in black rat occurrence in the core invasion area may be due to immigration from adjacent urban areas (Reichert et al., 2017). Regardless of the drivers, the combined resistance and resilience of black rats to the effects of pythons suggest the observed shifts in mammal communities will persist without concerted management.

As expected, the mammals that were previously shown to be more sensitive to pythons became less likely to occur along the invasion front where pythons have recently invaded. While previous work has shown that predation drives negative responses among some species, namely marsh rabbit (McCleery et al., 2015), the mechanisms explaining negative response among other species, such as raccoon, white-tailed deer, and bobcat, are less clear. Further research may allow for a more comprehensive understanding of these mechanisms driving the negative responses to pythons among the various species of native mammals, but for carnivorous species competition for food resources is likely to be at



(caption on next column)

Fig. 3. Posterior distributions for the effect of python relative occurrence, independent of the year of sampling, on the occurrence probability of mammal species, ordered according to increasing body size, in southern Florida, USA (2014–2019). A taller, narrow distribution reflects a stronger relationship between mammal occurrence and python relative occurrence, where positive values indicate mammals are more likely to occur where pythons are likely to occur and negative values indicate mammals are less likely to occur where pythons are more likely (vertical line at 0 shown for reference).

least partially responsible (McCleery et al., 2015). Alternatively, the dramatic restructuring of native mammal communities could result from other indirect effects of pythons, such as trophic cascades (White et al., 2006). Though the likelihood of pythons spreading outside of Florida to neighboring U.S. states is low (Avery et al., 2010; Dorcas et al., 2011), the degree to which they continue to spread remains uncertain (Rodda et al., 2009). Given their susceptibility to cold winter temperatures, climate is likely to be a primary factor limiting the northward spread of pythons outside of Florida (Michael E. Dorcas et al., 2011; Mazzotti et al., 2011). Additionally, the availability and connectivity of wetland habitats used by pythons may also limit their ability to spread north of Lake Okeechobee (Mutascio et al., 2018). While spreading north is of primary concern, given the potential area affected, the spread of pythons to the Upper and Lower Florida Keys would be similarly devastating to a number of unique and endangered mammals (Reed, 2005; Reichert et al., 2017; Soto-Shoender et al., 2020).

We acknowledge that a measure of python density, rather than relative occurrence, may be a better predictor of mammal responses. For example, two sites with different python densities would be expected to differ in regard to the effects on mammals, despite both being occupied by pythons. However, the elusive nature of pythons has precluded accurate estimates of python density across the Greater Everglades Ecosystem (Hunter et al., 2015; Nafus et al., 2020). In addition, the remote nature of many wetlands within the Greater Everglades Ecosystem presents additional challenges for estimating python density at moderate spatial scales. For example, few python detections exist for the interior of Loxahatchee where access is limited, yet recent passive sampling methods have revealed that pythons are widespread throughout this wetland (Hunter et al., 2019). By using these uncertain estimates of python relative occurrence as predictors in our model of mammal occurrence, that uncertainty likely propagated, which could contribute to the poor predictive power of the model for some species. Despite these limitations, we believe our approach of quantifying the change in python relative occurrence was the best available method for identifying the python invasion front and core areas across broad scales. In the future, advances in the quantification of python density are requisite to further understanding their continued effects on the Greater Everglades Ecosystem.

With little evidence of resilience among southern Florida's native mammals more than 15 years after their collapse, it remains to be seen if, and after how much time, invaded systems reach the third stage of the invasion and begin to recover. Understanding the mechanisms that facilitate this transition will be critical to mitigating the severe and persisting effects of invasive predators that threaten the conservation of native fauna globally. Regardless, it appears unlikely that mammal communities in southern Florida will rebound from the python invasion without drastic management intervention.

CRediT authorship contribution statement

PJT, KMH, and RAM conceived the ideas and designed methodology; ARS and PJT collected the data; PJT analyzed the data; PJT and RAM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PJT: Conceptualization, Methodology, Investigation, Formal Analysis, Writing – Original Draft.

KMH: Project Administration, Funding Acquisition, Writing –

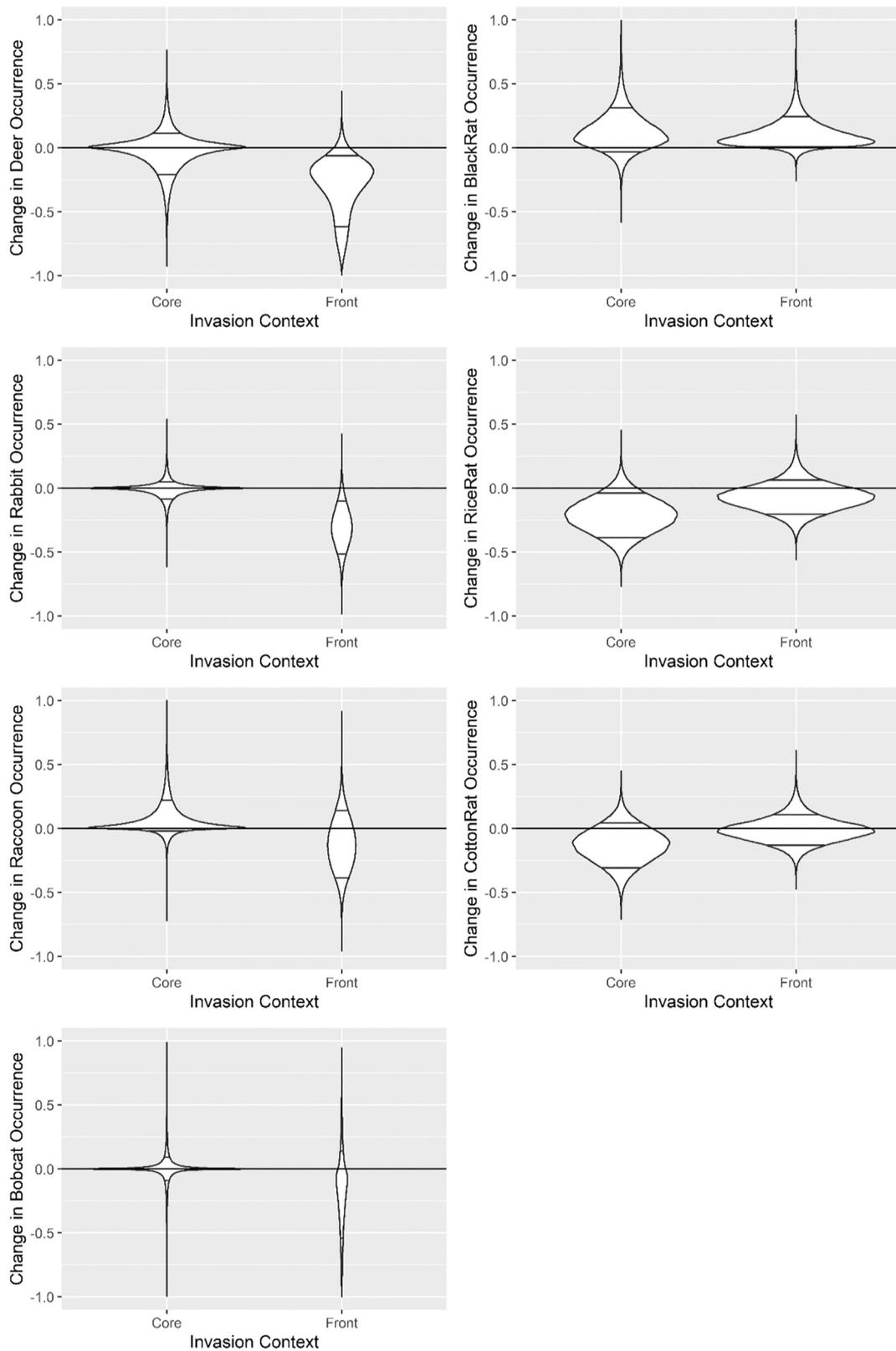


Fig. 4. Violin plots showing the posterior distribution of the change in occurrence probability from 2014 to 2019 within the core Burmese python invasion area compared to the invasion front for the 7 most commonly detected mammal species in the Greater Everglades Ecosystem in southern Florida, USA. Horizontal lines within violins represent the 0.1 and 0.9 quantiles.

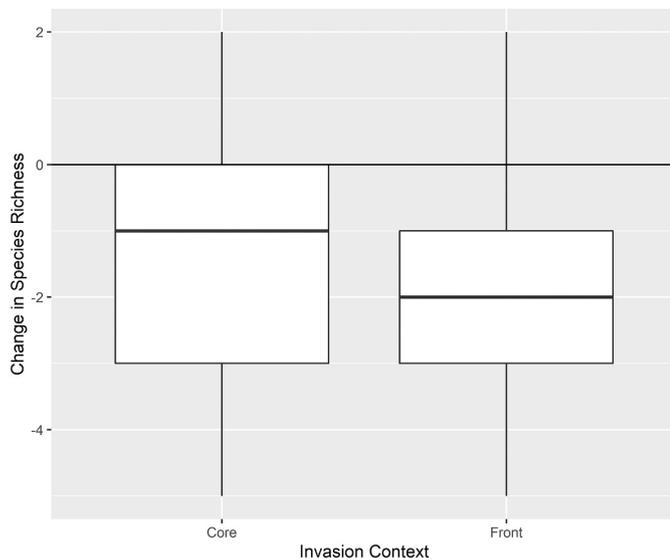


Fig. 5. The posterior distribution of the change in mammal species richness between 2014 and 2019 pooled across sites within the Burmese python invasion core and invasion front in southern Florida, USA.

Review & Editing.

ARS: Methodology, Investigation, Writing – Review & Editing.

RAM: Conceptualization, Methodology, Project Administration, Funding Acquisition, Writing – Review & Editing.

Data availability statement

The pythons observations from EDDmapS and the landcover data are both freely available via the linked resources. We will make our mammal detection data and analysis code available via an online repository such as Zenodo.

Declaration of competing interest

We submit this manuscript for review and exclusive publication in Biological Conservation. All of the work in this paper is original research carried out by the authors. All of the authors agree with the contents of the manuscript and its submission to the journal. This manuscript has not been published elsewhere, has not been submitted to Biological Conservation previously, and has not been submitted simultaneously for publication elsewhere.

Acknowledgments

This research was made possible by the United States Geological Survey (Grant G19AC00432 & G18AC00358), with funding from the Priority Ecosystem Science Program. We thank R. Gibble, M. Juntunen, S. Schulze, and B. Garrett for assisting with access to field sites. In addition, we thank all technicians involved with collecting field data. None of the authors have a conflict of interest to declare. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109290>.

References

- Anton, A., Gerald, N.R., Ricciardi, A., Dick, J.T.A., 2020. Global determinants of prey naiveté to exotic predators. *Proc. R. Soc. B Biol. Sci.* 287 (1928), 20192978 <https://doi.org/10.1098/rspb.2019.2978>.
- Arim, M., Abades, S.R., Neill, P.E., Lima, M., Marquet, P.A., 2006. Spread dynamics of invasive species. *Proc. Natl. Acad. Sci.* 103 (2), 374–378. <https://doi.org/10.1073/pnas.0504272102>.
- Ausband, D.E., Rich, L.N., Glenn, E.M., Mitchell, M.S., Zager, P., Miller, D.A.W., Waits, L.P., Ackerman, B.B., Mack, C.M., 2014. Monitoring gray wolf populations using multiple survey methods: monitoring wolf populations. *J. Wildl. Manag.* 78 (2), 335–346. <https://doi.org/10.1002/jwmg.654>.
- Avery, M.L., Engeman, R.M., Keacher, K.L., Humphrey, J.S., Bruce, W.E., Mathies, T.C., Mauldin, R.E., 2010. Cold weather and the potential range of invasive Burmese pythons. *Biol. Invasions* 12 (11), 3649–3652. <https://doi.org/10.1007/s10530-010-9761-4>.
- Bonneau, M., Johnson, F.A., Romagosa, C.M., 2016. Spatially explicit control of invasive species using a reaction–diffusion model. *Ecol. Model.* 337, 15–24. <https://doi.org/10.1016/j.ecolmodel.2016.05.013>.
- Borroto-Páez, R., 2009. Invasive mammals in Cuba: an overview. *Biol. Invasions* 11 (10), 2279–2290. <https://doi.org/10.1007/s10530-008-9414-z>.
- Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.* 7 (4), 434–455. <https://doi.org/10.1080/10618600.1998.10474787>.
- Brzeziński, M., Żmihorski, M., Nieoczym, M., Wilniewczyc, P., Zalewski, A., 2020. The expansion wave of an invasive predator leaves declining waterbird populations behind. *Divers. Distrib.* 26 (1), 138–150. <https://doi.org/10.1111/ddi.13003>.
- Campbell III, E.W., Adams, A.A.Y., Converse, S.J., Fritts, T.H., Rodda, G.H., 2012. Do predators control prey species abundance? An experimental test with brown treesnakes on Guam. *Ecology* 93 (5), 1194–1203. <https://doi.org/10.1890/11-1359.1>.
- Carlsson, N.O.L., Jeschke, J.M., Holmqvist, N., Kindberg, J., 2010. Long-term data on invaders: when the fox is away, the mink will play. *Biol. Invasions* 12 (3), 633–641. <https://doi.org/10.1007/s10530-009-9470-z>.
- Caut, S., Angulo, E., Courchamp, F., 2008. Dietary shift of an invasive predator: rats, seabirds and sea turtles. *J. Appl. Ecol.* 45 (2), 428–437. <https://doi.org/10.1111/j.1365-2664.2007.01438.x>.
- Caves, E.M., Jennings, S.B., HilleRisLambers, J., Tewksbury, J.J., Rogers, H.S., 2013. Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. *PLoS One* 8 (5), e65618. <https://doi.org/10.1371/journal.pone.0065618>.
- Clavero, M., Garcia-Berthou, E., 2005. Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* 20 (3), 110. <https://doi.org/10.1016/j.tree.2005.01.003>.
- Courchamp, F., Chapuis, J.-L., Pascal, M., 2003. Mammal invaders on islands: impact, control and control impact. *Biol. Rev.* 78 (3), 347–383. <https://doi.org/10.1017/S1464793102006061>.
- Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400 (6744), 563–566. <https://doi.org/10.1038/23028>.
- Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., Dickman, C.R., 2016. Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci.* 113 (40), 11261–11265. <https://doi.org/10.1073/pnas.1602480113>.
- Dorazio, R.M., Royle, J.A., 2005. Estimating size and composition of biological communities by modeling the occurrence of species. *J. Am. Stat. Assoc.* 100 (470), 389–398. <https://doi.org/10.1198/016214505000000015>.
- Dorcas, Michael E., Willson, J.D., Gibbons, J.W., 2011. Can invasive Burmese pythons inhabit temperate regions of the southeastern United States? *Biol. Invasions* 13 (4), 793–802. <https://doi.org/10.1007/s10530-010-9869-6>.
- Dorcas, M. E., Willson, J. D., Reed, R. N., Snow, R. W., Rochford, M. R., Miller, M. A., Meshaka, W. E., Andreadis, P. T., Mazzotti, F. J., Romagosa, C. M., & Hart, K. M. (2012). Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proc. Natl. Acad. Sci.*, 109(7), 2418–2422. doi: <https://doi.org/10.1073/pnas.1115226109>.
- Dove, C.J., Snow, R.W., Rochford, M.R., Mazzotti, F.J., 2011. Birds consumed by the invasive Burmese python (*Python molurus bivittatus*) in Everglades National Park, Florida, USA. *Wilson J. Ornithol.* 123 (1), 126–131.
- EDDMapS. (2019). *Early detection and distribution mapping system*. The University of Georgia - Center for Invasive Species and Ecosystem Health. <https://www.eddmaps.org/>.
- Fletcher, R., Fortin, M.-J., 2018. *Spatial Ecology and Conservation Modeling*. Springer.
- Fukasawa, K., Miyashita, T., Hashimoto, T., Tataru, M., Abe, S., 2013. Differential population responses of native and alien rodents to an invasive predator, habitat alteration and plant masting. *Proc. R. Soc. B Biol. Sci.* 280 (1773), 20132075 <https://doi.org/10.1098/rspb.2013.2075>.
- Gallardo, B., Aldridge, D.C., González-Moreno, P., Pergl, J., Pizarro, M., Pyšek, P., Thuiller, W., Yesson, C., Vilà, M., 2017. Protected areas offer refuge from invasive species spreading under climate change. *Glob. Chang. Biol.* 23 (12), 5331–5343. <https://doi.org/10.1111/gcb.13798>.
- Gasc, A., Duryea, M.C., Cox, R.M., Kern, A., Calsbeek, R., 2010. Invasive predators deplete genetic diversity of island lizards. *PLoS One* 5 (8), e12061. <https://doi.org/10.1371/journal.pone.0012061>.
- Harper, G.A., Bunbury, N., 2015. Invasive rats on tropical islands: their population biology and impacts on native species. *Glob. Ecol. Conserv.* 3, 607–627. <https://doi.org/10.1016/j.gecco.2015.02.010>.
- Hart, K.M., Cherkiss, M.S., Smith, B.J., Mazzotti, F.J., Fujisaki, I., Snow, R.W., Dorcas, M. E., 2015. Home range, habitat use, and movement patterns of non-native Burmese

- pythons in Everglades National Park, Florida, USA. *Anim. Biotelem.* 3 (1), 8. <https://doi.org/10.1186/s40317-015-0022-2>.
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). R package “dismo” for species distribution modelling (1.1-4) [Computer software]. <http://rspatial.org/sdm>.
- Hoyer, L.J., Blosser, E.M., Acevedo, C., Thompson, A.C., Reeves, L.E., Burkett-Cadena, N. D., 2017. Mammal decline, linked to invasive Burmese python, shifts host use of vector mosquito towards reservoir hosts of a zoonotic disease. *Biol. Lett.* 13 (10), 20170353 <https://doi.org/10.1098/rsbl.2017.0353>.
- Hunter, M.E., Oyler-McCance, S.J., Dorazio, R.M., Fike, J.A., Smith, B.J., Hunter, C.T., Reed, R.N., Hart, K.M., 2015. Environmental DNA (eDNA) sampling improves occurrence and detection estimates of invasive Burmese pythons. *PLoS One* 10 (4), e0121655. <https://doi.org/10.1371/journal.pone.0121655>.
- Hunter, M.E., Meigs-Friend, G., Ferrante, J.A., Smith, B.J., Hart, K.M., 2019. Efficacy of eDNA as an early detection indicator for Burmese pythons in the ARM Loxahatchee National Wildlife Refuge in the greater Everglades ecosystem. *Ecol. Indic.* 102, 617–622. <https://doi.org/10.1016/j.ecolind.2019.02.058>.
- Long, R.A., Donovan, T.M., MacKay, P., Zielinski, W.J., Buzas, J.S., 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. *Landsc. Ecol.* 26 (3), 327–340. <https://doi.org/10.1007/s10980-010-9547-1>.
- MacKenzie, D.I., Kendall, W.L., 2002. How should detection probability be incorporated into estimates of relative abundance? *Ecology* 83 (9), 2387–2393. [https://doi.org/10.1890/0012-9658\(2002\)083\[2387:HSDPBI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2387:HSDPBI]2.0.CO;2).
- Mazzotti, F.J., Cherkiss, M.S., Hart, K.M., Snow, R.W., Rochford, M.R., Dorcas, M.E., Reed, R.N., 2011. Cold-induced mortality of invasive Burmese pythons in south Florida. *Biol. Invasions* 13 (1), 143–151. <https://doi.org/10.1007/s10530-010-9797-5>.
- McCleery, R.A., Zweig, C.L., Desa, M.A., Hunt, R., Kitchens, W.M., Percival, H.F., 2014. A novel method for camera-trapping small mammals: a novel camera trap method. *Wildl. Soc. Bull.* 38 (4), 887–891. <https://doi.org/10.1002/wsb.447>.
- McCleery, R.A., Sovie, A., Reed, R.N., Cunningham, M.W., Hunter, M.E., Hart, K.M., 2015. Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. *Proc. R. Soc. B Biol. Sci.* 282 (1805), 20150120 <https://doi.org/10.1098/rspb.2015.0120>.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14 (11), 450–453. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1).
- Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C., Keitt, B.S., Corre, M., Horwath, S.V., Nogales, M., 2011. A global review of the impacts of invasive cats on island endangered vertebrates. *Glob. Chang. Biol.* 17 (11), 3503–3510. <https://doi.org/10.1111/j.1365-2486.2011.02464.x>.
- Meshaka, W.E., Smith, H.T., Cress, H.L., Sekscienski, S.R., Mapp, W.R., Cowan, E.M., Moore, J.A., 2009. Raccoon (*Procyon lotor*) removal and the rapid colonization of the green iguana (*Iguana iguana*) on a public land in South Florida: a conservation opportunity for the Caribbean. *Caribb. J. Sci.* 45 (1), 15–19. <https://doi.org/10.18475/cjos.v45i1.a4>.
- Mutascio, H.E., Pittman, S.E., Zollner, P.A., D’Acunto, L.E., 2018. Modeling relative habitat suitability of southern Florida for invasive Burmese pythons (*Python molurus bivittatus*). *Landsc. Ecol.* 33 (2), 257–274. <https://doi.org/10.1007/s10980-017-0597-5>.
- Nafus, M.G., Mazzotti, F.J., Reed, R.N., 2020. Estimating detection probability for Burmese pythons with few detections and zero recaptures. *J. Herpetol.* 54 (1), 24. <https://doi.org/10.1670/18-154>.
- Niedballa, J., Sollmann, R., Courtiol, A., Wilting, A., 2016. camtrapR: an R package for efficient camera trap data management. *Methods Ecol. Evol.* 7 (12), 1457–1462. <https://doi.org/10.1111/2041-210X.12600>.
- Nimmo, D.G., Mac Nally, R., Cunningham, S.C., Haslem, A., Bennett, A.F., 2015. Vive la résistance: reviving resistance for 21st century conservation. *Trends Ecol. Evol.* 30 (9), 516–523. <https://doi.org/10.1016/j.tree.2015.07.008>.
- Orzechowski, S.C.M., Romagosa, C.M., Frederick, P.C., 2019. Invasive Burmese pythons (*Python bivittatus*) are novel nest predators in wading bird colonies of the Florida Everglades. *Biol. Invasions* 21 (7), 2333–2344. <https://doi.org/10.1007/s10530-019-01979-x>.
- Pech, R.P., Hood, G.M., 1998. Foxes, rabbits, alternative prey and rabbit calicivirus disease: consequences of a new biological control agent for an outbreaking species in Australia. *J. Appl. Ecol.* 35 (3), 434–453. <https://doi.org/10.1046/j.1365-2664.1998.00318.x>.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19 (1), 181–197. <https://doi.org/10.1890/07-2153.1>.
- Plowes, R.M., Dunn, J.G., Gilbert, L.E., 2007. The urban fire ant paradox: native fire ants persist in an urban refuge while invasive fire ants dominate natural habitats. *Biol. Invasions* 9 (7), 825–836. <https://doi.org/10.1007/s10530-006-9084-7>.
- Plummer, M., Stukalov, A., & Denwood, M. (2016). Rjags Version 4-6.
- Reed, R.N., 2005. An ecological risk assessment of nonnative boas and pythons as potentially invasive species in the United States. *Risk Anal.* 25 (3), 753–766. <https://doi.org/10.1111/j.1539-6924.2005.00621.x>.
- Reichert, B.E., Sovie, A.R., Udell, B.J., Hart, K.M., Borkhataria, R.R., Bonneau, M., Reed, R., McCleery, R., 2017. Urbanization may limit impacts of an invasive predator on native mammal diversity. *Divers. Distrib.* 23 (4), 355–367. <https://doi.org/10.1111/ddi.12531>.
- Rodda, G.H., Jarnevich, C.S., Reed, R.N., 2009. What parts of the US mainland are climatically suitable for invasive alien pythons spreading from Everglades National Park? *Biol. Invasions* 11 (2), 241–252. <https://doi.org/10.1007/s10530-008-9228-z>.
- Rogers, H.S., Buhle, E.R., HilleRisLambers, J., Fricke, E.C., Miller, R.H., Tewksbury, J.J., 2017. Effects of an invasive predator cascade to plants via mutualism disruption. *Nat. Commun.* 8 (1), 14557. <https://doi.org/10.1038/ncomms14557>.
- Romañach, S.S., D’Acunto, L.E., Chapman, J.P., Hanson, M.R., 2021. Small mammal responses to wetland restoration in the Greater Everglades ecosystem. *Restor. Ecol.* 29 (3) <https://doi.org/10.1111/rec.13332>.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O’Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 32 (1), 305–332. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114037>.
- Salo, P., Korpimäki, E., Banks, P.B., Nordström, M., Dickman, C.R., 2007. Alien predators are more dangerous than native predators to prey populations. *Proc. R. Soc. B Biol. Sci.* 274 (1615), 1237–1243. <https://doi.org/10.1098/rspb.2006.0444>.
- Shigesada, N., Kawasaki, K., 1997. *Biological Invasions: Theory and Practice*. Oxford University Press.
- Shigesada, N., Kawasaki, K., 2002. Invasion and the range expansion of species: effects of long-distance dispersal. In: Bullock, J., Kenward, R., Hails, R. (Eds.), *Dispersal Ecology, The 42 Symposium of the British Ecological Society*. Blackwell Pub, pp. 350–373.
- Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S., Vonesh, J.R., 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* 119 (4), 610–621. <https://doi.org/10.1111/j.1600-0706.2009.18039.x>.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., Garcia-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M., 2013. Impacts of biological invasions: what’s what and the way forward. *Trends Ecol. Evol.* 28 (1), 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>.
- Sing, T., Sander, O., Beerenwinkel, N., Lengauer, T., 2005. ROCr: visualizing classifier performance in R. *Bioinformatics* 21 (20), 3940–3941. <https://doi.org/10.1093/bioinformatics/bti623>.
- Snow, R.W., Brien, M.L., Cherkiss, M.S., Wilkins, L., Mazzotti, F.J., 2007. Dietary habits of the Burmese python, *Python molurus bivittatus*, in Everglades National Park, Florida. *Herpetological Rev.* 101, 5–7.
- Sofaer, H.R., Jarnevich, C.S., Pearse, I.S., 2018. The relationship between invader abundance and impact. *Ecosphere* 9 (9), e02415. <https://doi.org/10.1002/ecs2.2415>.
- Soto-Shoender, J., Gwinn, D.C., Sovie, A.R., McCleery, R.A., 2020. Life-History Traits Moderate the Susceptibility of Native Mammals to an Invasive Predator. *Biological Invasions*.
- Sovie, A.R., McCleery, R.A., Fletcher, R.J., Hart, K.M., 2016. Invasive pythons, not anthropogenic stressors, explain the distribution of a keystone species. *Biol. Invasions* 18 (11), 3309–3318. <https://doi.org/10.1007/s10530-016-1221-3>.
- Stokes, V.L., Banks, P.B., Pech, R.P., Spratt, D.M., 2009. Competition in an invaded rodent community reveals black rats as a threat to native bush rats in littoral rainforest of south-eastern Australia: competition in an invaded rodent community. *J. Appl. Ecol.* 46 (6), 1239–1247. <https://doi.org/10.1111/j.1365-2664.2009.01735.x>.
- Strayer, D.L., Eviner, V.T., Jeschke, J.M., Pace, M.L., 2006. Understanding the long-term effects of species invasions. *Trends Ecol. Evol.* 21 (11), 645–651. <https://doi.org/10.1016/j.tree.2006.07.007>.
- Taillie, P.J., Moorman, C.E., 2019. Marsh bird occupancy along the shoreline-to-forest gradient as marshes migrate from rising sea level. *Ecosphere* 10 (1), e02555. <https://doi.org/10.1002/ecs2.2555>.
- Taillie, P.J., Peterson, M.N., Moorman, C.E., 2015. The relative importance of multiscale factors in the distribution of Bachman’s sparrow and the implications for ecosystem conservation. *Condor* 117 (2), 137–146. <https://doi.org/10.1650/CONDOR-14-137.1>.
- White, E.M., Wilson, J.C., Clarke, A.R., 2006. Biotic indirect effects: a neglected concept in invasion biology. *Divers. Distrib.* 12 (4), 443–455. <https://doi.org/10.1111/j.1366-9516.2006.00265.x>.
- Wiles, G.J., Bart, J., Beck, R.E., Aguon, C.F., 2003. Impacts of the brown tree snake: patterns of decline and species persistence in Guam’s avifauna. *Conserv. Biol.* 17 (5), 1350–1360. <https://doi.org/10.1046/j.1523-1739.2003.01526.x>.
- Willson, J.D., Dorcas, M.E., Snow, R.W., 2011. Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in Southern Florida. *Biol. Invasions* 13 (7), 1493–1504. <https://doi.org/10.1007/s10530-010-9908-3>.
- Zipkin, E.F., DeWan, A., Royle, J.A., 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *J. Appl. Ecol.* 46 (4), 815–822.
- Zipkin, E.F., Grant, E.H.C., Fagan, W.F., 2012. Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. *Ecol. Appl.* 22 (7), 11.