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Invasive pythons, not anthropogenic stressors, explain the distribution of a keystone species

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Abstract Untangling the causes of native species loss in human-modified systems is difficult and often controversial. Evaluating the impact of non-native species in these systems is particularly challenging, as additional human perturbations often precede or accompany introductions. One example is the ongoing debate over whether mammal declines within Everglades National Park (ENP) were caused by either the establishment of non-native Burmese pythons (*Python molurus bivittatus*) or the effects of other anthropogenic stressors. We examined the influence of both pythons and a host of alternative stressors—altered hydrology and habitat characteristics, mercury contamination and development—on the distribution of the marsh rabbit (*Sylvilagus palustris*), a once common mammal in ENP. Distance from the epicenter of the python invasion best explained marsh rabbit occurrence in suitable habitat patches, whereas none of the alternative stressors considered could explain marsh rabbit distribution. Estimates of the probability of marsh rabbit occurrence ranged from 0 at the python invasion epicenter to nearly 1.0 150 km from the invasion epicenter. These results support the hypothesis that invasive pythons shape the distribution of marsh rabbits in southern Florida. The loss of marsh rabbits and similar species will likely alter trophic interactions and ecosystem function within the Everglades, an internationally important hotspot of biodiversity. Further, our results suggest that non-native species can have profound impacts on mainland biodiversity.

Keywords North America · Mammals · Distribution modeling · *Python molurus bivittatus* · *Sylvilagus palustris*

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Introduction

Native species are declining at unprecedented rates around the world (Barnosky et al. 2011). Untangling the causes of these declines is difficult because the drivers of biodiversity loss do not occur in isolation (Brook et al. 2008). The role of non-native predators as a driving force behind biodiversity loss in continental ecosystems is particularly unclear (Wilcove et al. 1998; Rosenzweig 2001; Didham et al. 2005; Cox and Lima 2006; Davis et al. 2011). While introduced predators have caused the loss of biodiversity in isolated systems such as lakes and islands (Kaufman 1992; Fritts and Rodda 1998), there is little empirical evidence suggesting similar impacts in mainland terrestrial ecosystems (Gurevitch and Padilla 2004; Clavero et al. 2009). On mainland ecosystems, species introductions are often accompanied or preceded by a host of human-induced stressors such as pollution, habitat destruction and disturbance regime shifts. This complexity makes it difficult to determine whether non-native species cause biodiversity loss or coincidentally proliferate in disturbed areas where native species are already in decline (i.e. the driver/passenger model, Didham et al. 2005; MacDougall and Turkington 2005). Introductions of non-native species are forecasted to increase in the coming decades (Levine and D'Antonio 2003) and assessing their impacts will be increasingly important for the conservation of native flora and fauna. However, disentangling the impacts of non-native species from alternative anthropogenic disturbances remains a challenge. Further complicating matters is the paucity of data on environmental states and species distributions before human disturbance (Gurevitch and Padilla 2004). However, the hypothesized drivers of species decline likely act in predictable ways that can be tested (Quinn and Dunham 1983). By comparing a species current distribution to what we would predict given a hypothesized driver we can elucidate the most probable cause of species loss.

To more effectively focus efforts to conserve native flora and fauna we need a better understanding of how non-native predators and other anthropogenic factors impact native wildlife. The recent loss of native mammals in the Everglades (Dorcas et al. 2012) provides an opportunity to quantify the impact of non-native predators and other anthropogenic factors underlying native species declines. The greater everglades ecosystem (GEE), which includes Everglades National Park (ENP), Big Cypress National Preserve, Loxahatchee National Wildlife Refuge and various storm water treatment areas (Fig. 1) is a highly modified ecosystem and the target of one of the largest restoration efforts to date (Sklar et al. 2005). Threats to the GEE include the invasion of non-native species, alteration of water flow through the system, heavy metal contamination, urbanization and altered disturbance regimes (Light and Dineen 1994; Mitsch and Hernandez 2013). Observations of mammals within ENP have declined by 95 % over the last 20 years while non-native Burmese pythons (*Python molurus bivittatus*) have proliferated in the park over the same timeframe, leading to speculation that pythons drove these declines (Dorcas et al. 2012). Nevertheless, any of number of alternative anthropogenic alterations may have acted as the prevailing stressor or worked synergistically with the python invasion to drive mammal decline on a landscape scale (Brook et al. 2008).

Using a hypothesis-testing approach, we evaluated the relative importance of a non-native species, the Burmese python and alternative factors in driving the distribution of a once common native Everglades mammal: the marsh rabbit (*Sylvilagus palustris*). Marsh rabbits were once found throughout the GEE (Fig. 1) and likely functioned as a keystone species through their role as important primary consumers, seed dispersers and prey base for a variety of predators (Blair 1936; Bond 1994; Delibes-Mateos et al. 2008). Over the last 20 years marsh rabbits have apparently disappeared from much of the southern portion of ENP (Dorcas et al. 2012). This decline has been experimentally linked to pythons (McCleery et al. 2015). However, these experiments were limited in their spatial scale and there were a host of untested hypotheses that could potentially provide better explanations of the loss of marsh rabbits at the landscape level. Clarifying the role of pythons in rabbit distribution in ENP will help to resolve long-standing controversy over the role of non-native species in biodiversity loss (Wilcove et al. 1998; Didham et al. 2005) and assist managers in prioritizing competing threats to biodiversity. To elucidate the potential causes of marsh rabbit decline within ENP, we tested how well different natural and anthropogenic drivers explained the current distribution of the marsh rabbit within the GEE.

Methods

Study area

We conducted the study throughout the GEE, a vast shallow depression wetland that encompasses most of the southern peninsula of Florida (Fig. 1, Wiken et al. 2011). The GEE is a biodiversity hotspot due to the interface of temperate and sub-tropical climates and a

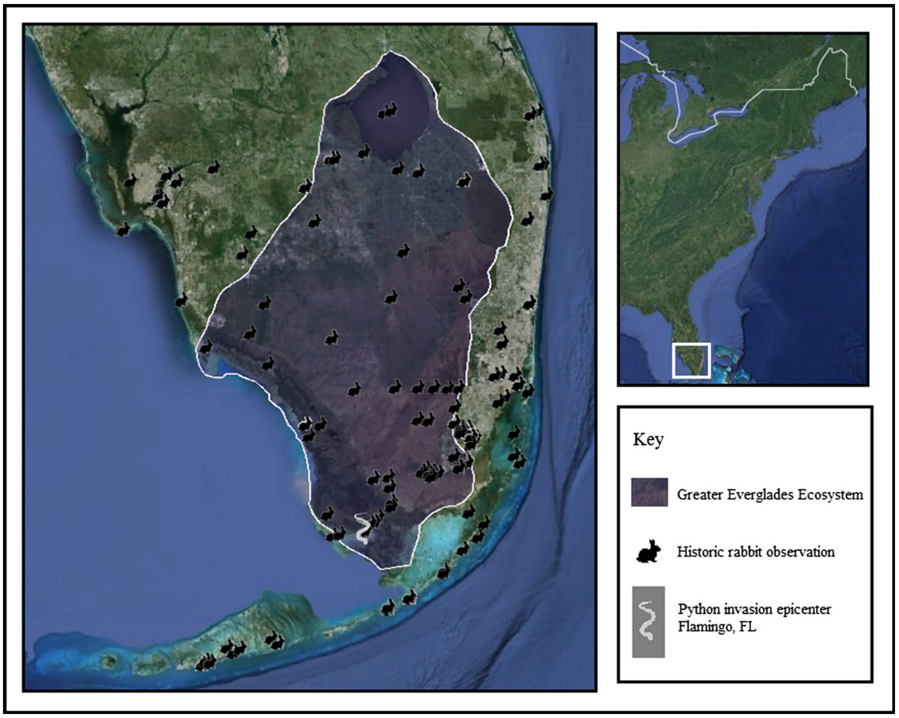

Fig. 1 The Greater Everglades Ecosystem (GEE) and locations of rabbit (*Sylvilagus spp*) observations in southern Florida from 1940–1984, compiled from The USGS Biodiversity Information Serving Our Nation (BISON) project, Everglades National Park Collections and Florida Natural History Museum

gradient of saline environments which give rise to numerous habitat types (Lodge 2010). Historically, many terrestrial mammals were found throughout the system including marsh rabbits, round-tailed muskrats (*Neofiber alleni*), bobcats (*Lynx rufus*), white tailed deer (*Odocoileus virginianus*) and Florida panthers (*Puma concolor coryi*) (Dorcas et al. 2012). These mammals regularly utilized "tree islands" that provide dry ground even during seasonal flooding events (Sklar and van der Valk 2012). Marsh rabbits were historically found throughout the GEE in fresh and salt water marshes, upland scrub and coastal areas (Blair 1936). They are found in variable habitats south of GEE in the Florida Keys (Schmidt et al. 2011) and are common as far north as Virginia. Marsh rabbits maintain stable home ranges throughout the year (Forys and Humphrey 1996), but may concentrate movements to tree islands and floating vegetation during seasonal flooding events.

Site selection and survey protocol

We surveyed 84 randomly generated 30 m × 30 m sites throughout the GEE for marsh rabbit occurrence. We constrained sites to within 2 km of a road or trail traversable by ATV or truck and discarded sites in open water or shifted sites to the nearest high ground or floating vegetation. To detect marsh rabbits, we conducted systematic fecal pellet counts (Forys and Humphrey 1997; Palomares 2001; Murray et al. 2002; Schmidt et al. 2011) at each survey site during the 2013 southern Florida dry season (November–April). Two observers independently searched each survey site and recorded the presence or absence of rabbit pellets.

Hypothesized drivers of marsh rabbit decline and predictions

Pythons

Sightings and removals of these large-bodied (up to 90 kg) snakes coincided spatially and temporally with the declines in mammal sightings (Dorcas et al. 2012). If pythons were responsible for the decline in marsh rabbit populations, we expected that marsh rabbit occurrence in the GEE would decline in sites where pythons have been established the longest and reached high densities. If python range expansion adhered to the typical spread pattern (linear negative feedback/first-order dynamics) of most invasive species (Arim et al. 2006), we expected marsh rabbit occupancy to be lowest close to the python invasion epicenter, Flamingo, FL (Fig. 1, Snow et al. 2007; Willson et al. 2011). Consequently, we used distance to Flamingo, FL as a landscape-scale metric of relative python impact.

Habitat quality

In the early twentieth century, human activities disrupted fire regimes and water flow in the Everglades, resulting in changes in habitat quality that may have impacted rabbits (Slocum et al. 2003). If changes in habitat quality drove the decline in marsh rabbits, we expected habitat quality to be the best predictor of marsh rabbit occupancy. High-quality marsh rabbit habitat includes open fields with high visual obstruction dominated by Poaceae species and early successional habitat (Blair 1936; Schmidt et al. 2011). Vegetation structures we associated with early successional habitat included high visual obstruction and mid-story cover. Additional habitat variables that likely influence marsh rabbit occupancy is the proximity of both water and cover, which are important escape habitats (Blair 1936).

We evaluated five 1-m^2 plots at each survey site for vegetation structure. We placed our first vegetation plot at the center of the 30 × 30 m site and placed the remaining plots 10 m from the center starting with a randomly generated bearing, and then clockwise at 90° angles. We assessed vegetation species composition, visual obstruction and mid-story cover at each plot. We identified the three dominant plant families on each plot using a modified Daubenmire classification system (Daubenmire 1959). We averaged plant family cover class across the plots and used recursive partitioning for classification trees to determine the families most closely associated with marsh rabbit occurrence in program R version 3.1 using package rpart (S1, Therneau et al. 2005). We classified mid-story cover (vegetation 50–150 cm) using the modified Daubenmire and measured visual obstruction using a Robel pole (Robel et al. 1970). We calculated the mean of each local habitat measure across the 5 1-m^2 plots. We categorized each site into 4 habitat types (freshwater marsh, mangrove forest, salt marsh and upland scrub) using characteristics established by the USGS (S2). We classified distance to water and cover (dense, woody understory vegetation) from the center of each site as either proximate (0–25 m), near (25–50 m), or far (50 m+).

Contaminants

The GEE has high concentrations of mercury (Hg) and methylmercury (MeHg) (Osborne et al. 2011) in the soil, which pose a serious threat to fish and wildlife in the region (Facemire et al. 1995). Marsh rabbits consume aquatic vegetation potentially containing high concentrations of Hg and MeHg, which may lower fecundity and survival (Cleckner et al. 1998). If contamination caused the decline in marsh rabbits we expected marsh rabbit occurrence to increase with distance from a Hg or MeHg contamination hot spot. For each survey site, we calculated the distance to the nearest soil mercury and methylmercury sediment hotspot using maps developed by Osborne et al. (2011).

Development

The Miami-Fort Lauderdale metropolitan area bordering the GEE experienced high population growth, adding over half a million residents between 2000 and 2010 (Mackun et al. 2011). The resulting development is encroaching on the remnant GEE, introducing stressors on wildlife (i.e. cats and dogs, pollutants, lighting, traffic) that likely result in species loss and biotic homogenization (Czech et al. 2000; McKinney 2008). If development is influencing marsh rabbit distributions we expected their occurrence to decline with proximity to human development. To measure the influence of urbanization on marsh rabbits we utilized the 2013 Florida Natural Areas Inventory land cover map (Knight 2010), and calculated the shortest distance from each survey site to the nearest cell categorized as "urban".

Hydrology

Humans have controlled the timing and flow of water through the GEE for over a century, with marked changes occurring in the last 20 years (Light and Dineen 1994). Changes that may have impacted wildlife include the permanent inundation of large areas of land and the disruption of seasonal flooding (Nilsson and Dynesius 1994). Alterations in total yearly flow and maximum water depth may significantly interrupt important mammal life-history stages (i.e., unseasonal flooding may drown altricial young), make high-quality food unavailable or alter vegetation composition (Zweig and Kitchens 2008). Finally, flood stage at the time of our survey may drive marsh rabbit occupancy, with mammals moving to high ground when wetlands were periodically inundated (McCarthy and Fletcher 2015). We expected that if extreme flow events caused marsh rabbit decline sites with the highest total yearly flow, maximum daily flow and flood stage would not be occupied by rabbits. We assessed the influence of changing water regimes on marsh rabbit occurrence on sites in the GEE that fell within the Everglades Depth Estimation Network (EDEN). For each survey site we used EDEN daily surface raster maps to calculate the 2012 yearly total flow and daily max flow (Henkel 2012). Further, for all sites we measured water depth at each vegetation plot and averaged the values to arrive at a mean site water depth as a proxy for flood stage.

Synergistic and additive effects

In addition to the main effects of human induced changes in the environment, it is recognized that stressors can work synergistically or additively to impact species (Gurevitch and Padilla 2004; Sih et al. 2010). For example, marsh rabbits select areas near water as refuge from native predators (Blair 1936); however, pythons are highly aquatic (Reed et al. 2012). We expected that if synergistic effects drive marsh rabbit occurrence, in the presence of pythons, proximity to water may be negatively associated with marsh rabbit occurrence. Similarly, pythons prefer wetlands and if synergistic effects were shaping marsh rabbit distribution, we expected that in the presence of pythons marsh rabbits would be associated with higher elevated habitat types like pine flatland and dry prairies.

Data analysis

We used an occupancy-modeling framework (MacKenzie et al. 2002) to calculate marsh rabbit detectability based on our replicate surveys. We found that pellet detectability was very high ($p = 0.85$, thus the probability of missing rabbits after two searches was $(1–0.85) \times (1–0.85) = 0.02$) and focused on logistic regression modeling to reduce model complexity. If marsh rabbits were detected during either survey the site was deemed occupied, if neither survey documented marsh rabbits the site was deemed unoccupied. We analyzed a suite of candidate models (Table 1) representing our hypothesized drivers of mammal decline to predict the presence of marsh rabbits at a given site. We did not include correlated covariates ($r > 0.60$) in interactive models and Z-transformed environmental covariates to improve model convergence. Additionally, we developed two sets of models because 26 survey sites were not covered by the EDEN domain. First, we evaluated one set of models using data from all sites but not considering water flow. We then took the most parsimonious model and refit it to the subset of sites with available EDEN data and compared that model to a set of candidate models incorporating water flow on those sites.

We considered competing hypotheses using an information-theoretic approach (Anderson and Burnham, 2002), and evaluated the parsimony of models using Bayesian Information Criterion (BIC) and BIC weight (ω_i) (where the ω_i of any particular model depends on the set of candidate models, and varies from 0 (no support) to 1 (complete support)). We considered models within 2 BIC units of the best model as competing models, and calculated the evidence ratios between the highest ranked models (Anderson and Burnham 2002). We evaluated model goodness of fit by calculating a χ^2 statistic and the AUC (the area under the receiver curve statistic) using leave-one-out cross-validation (Fielding and Bell 1997). We then examined the individual covariates in the most parsimonious model to determine if their 95 % CI included 0.

Results

During the 2013 dry season we surveyed 84 sites for marsh rabbit occurrence and detected marsh rabbits at 29 of the sites. Our sites ranged 2.5–157.5 km from the python invasion epicenter, and marsh rabbits were only detected at sites >50 km from the epicenter (Fig. 2). The most parsimonious model of rabbit occurrence indicated that the relative influence of pythons was the best predictor of marsh rabbit distribution in southern Florida and none of the models representing alternative stressors were supported by the data (Table 1). Without sub-setting data to consider hydrology, the python-only model was sixteen times more likely to be the best model

Table 1 Ranking of single-season logistic regression models, excluding water flow models, used to describe the probability of marsh rabbit occurrence in the Greater Everglades Ecosystem, Florida, USA

Driver model	K[a]	BIC[a]	ΔBIC[a]	ωi[a]
Invasive pythons (P[b])	2	87.4	0.00	0.88
Additive effect (P[b] + C[c])	4	93.1	5.64	0.05
Additive effect (P[b] + W[d])	4	93.3	5.87	0.05
Synergistic effect (P[b] × C[c])	6	96.5	9.05	0.01
Additive effect (P[b] + H[e])	5	98.90	11.46	0.00
Habitat quality (veg[f])	3	100.11	12.68	0.00
Synergistic effect (P[b] × W[d])	6	100.91	13.47	0.00
Contaminants (MeHg[g])	2	103.80	16.37	0.00
Contaminants (Hg[h])	2	107.97	20.53	0.00
Synergistic effect (P[b] × H[e])	8	109.75	22.31	0.00
Development (D[i])	2	109.83	22.40	0.00
Habitat (C[c])	3	110.52	23.08	0.00
Hydrology (WD[j])	2	111.48	24.08	0.00
Intercept only	1	112.70	25.26	0.00
Habitat quality (VO[k])	2	113.88	26.45	0.00
Habitat quality (M[l])	2	116.95	29.55	0.00
Habitat quality (H[e])	4	117.12	29.68	0.00
Habitat quality (M[l] + VO[k])	3	118.29	30.89	0.00
Habitat quality (W[d])	3	120.19	32.75	0.00

[a] *K* number of variables in model, *BIC* Bayesian information criterion, *ΔBIC* difference between the BIC value of each model and the lowest BIC model, *ωi* BIC weight

[b] Distance to the python invasion epicenter (Flamingo, FL, USA), a continuous variable

[c] Distance to cover, a categorical variable with three levels proximate (0–25 m), near (25–50 m), or far (50 m+)

[d] Distance to water, a categorical variable with three levels proximate (0–25 m), near (25–50 m), or far (50 m+)

[e] Habitat type, a categorical variable with four levels (freshwater marsh, mangrove forest, salt marsh and upland scrub)

[f] Vegetation composition a categorical variable with four levels (Arecaceae present at >34.69, Arecaceae present at <34.69, Arecaceae present at <34.69 with Cupressaceae <24.7 and Arecaceae present at <34.69 with Cupressaceae >24.7)

[g] Distance to a methylmercury contamination hotpot, a continuous variable

[h] Distance to a mercury contamination hotpot, a continuous variable

[i] Distance to human development, a continuous variable

[j] Water depth measured at site, a continuous variable

[k] Visual obstruction, a continuous variable

[l] % mid-story cover, a continuous variable

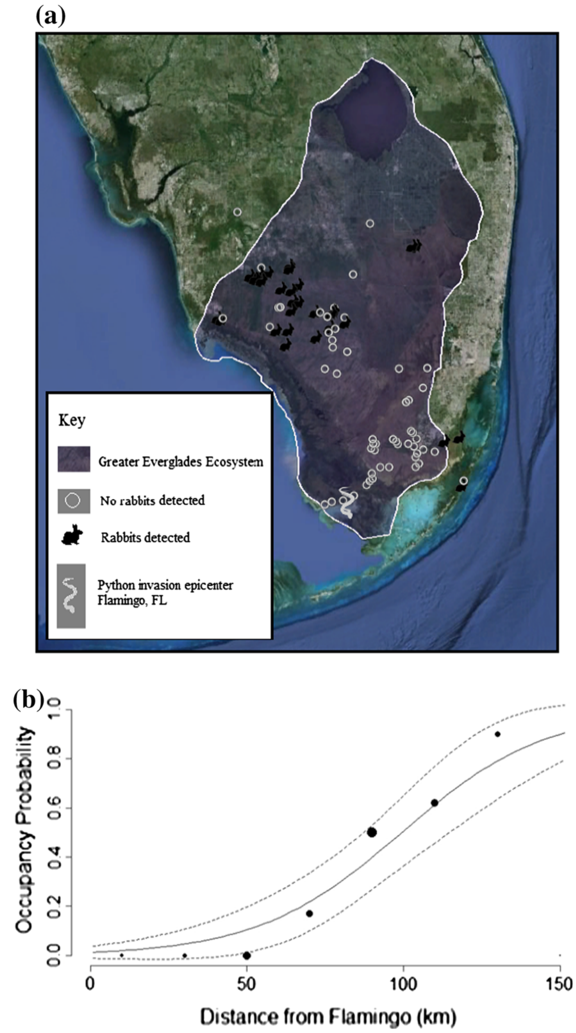

Fig. 2 **a** Location of 2013 marsh rabbit pellet survey sites in southern Florida. **b** Relationship between distance (km) from the python invasion epicenter (Flamingo, FL, USA) and the probability of marsh rabbit occurrence in the Great Everglades Ecosystem, Florida, USA, with 95 % confidence interval. Points represent the proportion of sites occupied in 20 km bins, size of point proportional to number of sites sampled in that bin

compared to the next highest ranked models including python and habitat additive effects (evidence ratio of 16.81). Marsh rabbit occurrence was positively correlated with distance from the python invasion epicenter; Flamingo, FL ($\beta = 1.638 \pm 0.75$), with occurrence probabilities rising from 0 to nearly 1 as distance from Flamingo increased to over 150 km (Fig. 2). The Chi square test indicated there was no evidence of lack of fit ($p = 0.68$) and the AUC test indicated the model accurately predicted presences and absences (AUC = 0.84). When tested on the subset of sites for which we had water flow data (61 sites), the python-only model was still the most parsimonious model (Table 2). The python-only model was over six times more likely to be the best model than the models including the additive effects of pythons and hydrology (evidence ratio 6.72).

Discussion

Our results indicate that even in complex continental ecosystems faced with extreme anthropogenic stressors, the impacts of non-native predators cannot be discounted. The drivers of global change rarely occur in isolation (Brook et al. 2008). Nevertheless, identifying the primary drivers of species distributions in complex and disturbed systems is critical for preserving ecosystem functioning. We found that marsh rabbits are absent from a significant portion of their historic range, highlighting the potential landscape-wide impacts invasive predators can have.

Our results are inconsistent with the hypothesis that mainland species are resilient to non-native predators due to their evolutionary history with multiple predator archetypes (Cox and Lima 2006; Sih et al. 2010).

Table 2 Ranking of single-season logistic regression models used to describe marsh rabbit distribution within the Everglades Depth Estimation Network, Greater Everglades Ecosystem, Florida, USA

Driver model	K[a]	BIC[a]	ΔBIC[a]	ω_i^a
Invasive pythons (P[b])	2	48.2	0	0.74
Additive effect (P[b] + flow[c])	3	52.0	3.81	0.11
Additive effect (P[b] + max[d])	3	52.1	3.85	0.10
Synergistic effect (P[b] × flow[c])	4	56.1	7.90	0.01
Synergistic effect (P[b] × max[d])	4	56.2	7.95	0.01
Hydrology (max[d])	2	56.5	8.31	0.00
Hydrology (flow[c])	2	58.0	9.81	0.00
Intercept only	1	80.5	32.25	0.00

[a] *K* number of variables in model, *BIC* Bayesian information criterion, *ΔBIC* difference between the BIC value of each model and the lowest BIC model, ω_i weight

[b] Distance to the python invasion epicenter (Flamingo, FL, USA), a continuous variable

[c] Total water flow for 2013, a continuous variable

[d] Maximum daily water flow for 2013, a continuous variable

Marsh rabbits have evolutionary history with predators similar to pythons including Eastern diamondback rattlesnakes (*Crotalus adamanteus*) (Blair 1936; McCleery et al. 2015), yet marsh rabbits still appear to be highly vulnerable to python predation (McCleery et al. 2015). Understanding if and how the mammalian fauna of southern Florida recognize and respond to novel predators will be critical in mitigating the impacts of pythons and other invasive species.

Our results contradict previous research where bottom up—and not top down—pressures explain lagomorph distributions. In contrast to most research on rabbit distributions (Virgos et al. 2003; Sarmento et al. 2011; Kontsiotis et al. 2013), we found habitat type, vegetation composition and vegetation structure to be poor predictors of marsh rabbit occurrence. In fact, high-quality rabbit habitat likely remains close to the python invasion site. Marsh rabbits reintroduced near Flamingo, FL persisted for several months and produced offspring before being extirpated by pythons in the summer (McCleery et al. 2015), highlighting the suitability of these sites for marsh rabbits when pythons are inactive. Although we focused on marsh rabbits, our results are likely generalizable to a large portion of the vertebrate community in southern Florida. Of the Everglades' midsized mammals, marsh rabbits should theoretically be among the most resilient to introduced predators due to their generalist habitat requirements and high reproductive rate (Blair 1936; Pech et al. 1992).

Some of our results may be limited by the inherent difficulty of quantifying environmental stressors and landscape-scale processes. For example, quantifying the distribution and density of pythons in southern Florida is challenging due to a lack of reliable detection methods for pythons (Piaggio et al. 2013). By assuming pythons followed a linear spread pattern from the hypothesized introduction site (Arim et al. 2006), we are discounting the importance of habitat, subsequent introductions and connectivity in the dynamics of python spread. However, the use of straight-line distance to the python introduction site (Flamingo, FL, USA; Willson et al. 2011) is likely less problematic than the use of opportunistic reports to estimate python densities which are highly biased towards road, levees and canals. Further, distance from a Hg or MeHg hot spot may be an overly coarse measure of the availability of these heavy metals. Concentrations of MeHg and Hg in vegetation and the water column are highly variable in space at time (Cleckner et al. 1998); nevertheless, the landscape distribution of hot spots can be an appropriate indicator of chronic exposure and elevated risk (Evers et al. 2005). Given the strength of the observed relationship between marsh rabbit occurrence and distance from the python introduction site, more nuanced measures of anthropogenic disturbances would not likely produce different results. Further, we did not consider the effects of latitude on marsh rabbit occupancy, because it would be largely confounded with distance to the python epicenter. Also, there is substantial anecdotal evidence that marsh rabbits historically occurred in large numbers throughout the GEE (Dorcas et al. 2012, Fig. 1), and a population of Lower Keys marsh rabbits persists far to the south of our study area (Schmidt et al. 2011), lending little support to the role of latitude in shaping marsh rabbit distribution.

The current distribution of marsh rabbits, combined with the failure of reintroduced rabbit populations to reestablish in ENP due to python predation (McCleery et al. 2015), supports the hypothesis that pythons are responsible for the decline of marsh rabbits in southern Florida. Further, our data do not support the hypotheses that alternative factors such as habitat quality, water flow or contamination explain the distribution of marsh rabbits, nor did we find evidence for synergistic effects. While chronic environmental stressors such as water management, heavy metal contamination and habitat destruction will have profound impacts on the long term functioning of the Everglades (Sklar et al. 2005), for marsh rabbits, the acute impact of pythons appears to overshadow the influence of such anthropogenic threats.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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