


Urbanization may limit impacts of an invasive predator on native mammal diversity

Brian E. Reichert^{1*} , Adia R. Sovie¹, Brad J. Udell¹,
Kristen M. Hart², Rena R. Borkhataria³, Mathieu Bonneau¹, Robert Reed⁴
and Robert McCleery¹

¹Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611-0485, USA, ²U.S. Geological Survey, Wetland and Aquatic Research Center, Davie, FL 33314, USA, ³Everglades Research and Education Center, University of Florida, 3200 E. Palm Beach Rd., Belle Glade, FL 33430, USA, ⁴U.S. Geological Survey, Invasive Species Branch, Fort Collins CO 80526, USA

ABSTRACT

Aim Our understanding of the effects of invasive species on faunal diversity is limited in part because invasions often occur in modified landscapes where other drivers of community diversity can exacerbate or reduce the net impacts of an invader. Furthermore, rigorous assessments of the effects of invasive species on native communities that account for variation in sampling, species-specific detection and occurrence of rare species are lacking. Invasive Burmese pythons (*Python molurus bivittatus*) may be causing declines in medium- to large-sized mammals throughout the Greater Everglades Ecosystem (GEE); however, other factors such as urbanization, habitat changes and drastic alteration in water flow may also be influential in structuring mammal communities. The aim of this study was to gain an understanding of how mammal communities simultaneously facing invasive predators and intensively human-altered landscapes are influenced by these drivers and their interactions.

Location Florida, USA.

Methods We used data from trail cameras and scat searches with a hierarchical community model that accounts for undetected species to determine the relative influence of introduced Burmese pythons, urbanization, local hydrology, habitat types and interactive effects between pythons and urbanization on mammal species occurrence, site-level species richness, and turnover.

Results Python density had significant negative effects on all species except coyotes. Despite these negative effects, occurrence of some generalist species increased significantly near urban areas. At the community level, pythons had the greatest impact on species richness, while turnover was greatest along the urbanization gradient where communities were increasingly similar as distance to urbanization decreased.

Main conclusions We found evidence for an antagonistic interaction between pythons and urbanization where the impacts of pythons were reduced near urban development. Python-induced changes to mammal communities may be mediated near urban development, but elsewhere in the GEE, pythons are likely causing a fundamental restructuring of the food web, declines in ecosystem function, and creating complex and unpredictable cascading effects.

Keywords

antagonistic interaction, homogenization, invasion, multispecies occupancy.

*Correspondence: Brian E. Reichert, Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611-0485, USA. E-mail: brianereichert@gmail.com

†Present address: Fort Collins Science Center U.S. Geological Survey 2150 Centre Ave, Bldg C Fort Collins, CO 80526-8118 E-mail: breichert@usgs.gov

INTRODUCTION

In the age of the Anthropocene, the planet's native faunal communities have rapidly been lost and homogenized by changing landscapes, human population pressures and novel ecological processes (Ceballos *et al.*, 2015). One of the most prominent drivers of faunal community loss and homogenization has been the introduction of invasive species (Vitousek *et al.*, 1996; Wilcove *et al.*, 1998). Invasive species have been linked to precipitous declines in native populations with effects on biodiversity (Simberloff, 2013). However, evidence for the negative effects of invasive species on vertebrate communities has been mixed (Sax & Gaines, 2003; Fridley *et al.*, 2007), and our ability to predict community-level impacts of invaders remains weak (Ricciardi *et al.*, 2013). Our knowledge of the extent to which invasive species alter the composition of faunal communities is limited for three main reasons. First, few studies have assessed the community-level effects of invasive species using modern methods that account for variation in the sampling process, imperfect detection and the occurrence patterns of rare or elusive species. These considerations are important for making reliable inferences on patterns of biodiversity (Dorazio *et al.*, 2011). Second, studies that simultaneously assessed the impacts of biological invasions at multiple levels of biological organization (e.g. populations to communities) are rare. This leaves us with little understanding of how individual species-level effects scale to community-level impacts (Parker *et al.*, 1999). Third, other drivers of faunal community loss and homogenization, such as landscape modification, can exacerbate or reduce the effects of an invader on native communities (Didham *et al.*, 2005, 2007; Darling & Côté, 2008), yet the relative importance of these interactions is unknown.

Interpreting the net effects of biological invasions on biodiversity requires understanding the potential roles of other drivers such as land use change on species distributions. Biological invasions often occur within urbanizing landscapes where increased disturbance and human development homogenize faunal communities (McKinney, 2006) with both negative and positive influences on the distributions of individual species (McKinney, 2008; Ordeñana *et al.*, 2010). The combined effects of biological invasions and urbanization on native communities can be additive or interactive. Interactive effects can be synergistic or antagonistic (Didham *et al.*, 2007). Synergies occur when disturbance or resource subsidies in urbanized landscapes facilitate the spread or abundance of invaders. In these instances, invasion impacts to native communities increase multiplicatively with increasing influence from urban development. Alternatively, antagonistic interactions result when urban development reduces invasion impacts below expectations from additive effects of independent stressors (Didham *et al.*, 2007). For example, urbanized areas could serve as potential refugia from invasive apex predators (Ritchie & Johnson, 2009) or act as

population sources with increased food subsidies. Under an antagonistic scenario, invasion impacts should diminish near areas of human development.

Despite the recent emphasis on the importance of assessing interactive effects of the drivers of global environmental change (Didham *et al.*, 2007; Brook, 2008), the extent to which interactive effects influence community structure and composition (vs. simple 'main' effects of independent drivers) remains unclear (Darling & Côté, 2008). Accordingly, our goals for this study were to gain an understanding of how faunal communities simultaneously facing invasive species and intensively human-altered landscapes are influenced by these drivers and their interactions and to understand how species-level relationships with environmental drivers affect community structure and composition. To achieve these goals, we studied the mid-to-large mammal community of the Greater Everglades Ecosystem (GEE). The mammal community within the GEE appears to have changed considerably over the last several decades with declines in numerous populations (Dorcas *et al.*, 2012). Since the early 1900s, the GEE has experienced intensive human-induced alterations as a result of urban development, establishment of exotic invasive species, modified hydrology and changes in vegetation communities (Davis & Ogden, 1997) – all of which have the potential to substantially alter mammal communities.

Our specific objectives for the study were to determine the relative influence of introduced Burmese pythons (*Python molurus bivittatus*), urbanization, local hydrology, habitat types, and interactive effects between pythons and urbanization on mammal populations and community diversity. Using a hierarchical community model, we tested for the potential effects of each driver on species occurrence, species richness (α -diversity) and turnover (β -diversity). We distinguished whether each driver of community diversity influenced community composition through species loss ('community dissimilarity due to nestedness') vs. species replacement (Baselga, 2010; Baselga & Orme, 2012).

From mangroves along saltwater shorelines to freshwater marshes, temporally flooded woodland and upland pines, plant communities vary greatly across the GEE. This variation should in turn have a strong influence on mammal communities in the region. Hydrology is an important organizing ecological force in the GEE and a known driver of vegetation, vertebrate and invertebrate communities (Davis & Ogden, 1997). Some mammal species are heavily dependent on shallow permanently flooded wetlands, while upland mammals likely avoid environments with long inundation periods (Brown, 1997). We hypothesized that hydrology and vegetation communities play key roles in determining distribution patterns of mammals in the GEE and expect responses to be species specific. Mammal diversity should be highest at water levels that accommodate semi-aquatic and terrestrial mammals (Brown, 1997). We predicted that vegetation communities would be a strong driver of mammal occurrence and that mammal richness

would increase and intermediate water depths and hydroperiods. We expected that coastal habitats would be the least species rich compared to forested uplands and swamps (Brown, 1997).

Invasive species in novel ecological roles (i.e. as apex predators) can exert major impacts on local biota (e.g. Wiles *et al.*, 2003). Native to Southeast Asia, a Burmese python population has been established in portions of the GEE for at least 20 years. Burmese pythons are generalist predators with a diet primarily composed of mammals and birds (Snow *et al.*, 2007; Reed & Rodda, 2009). Recent studies demonstrated that Burmese pythons are likely responsible for recent declines in native populations of marsh rabbits in the GEE (McCleery *et al.*, 2015; Sovie *et al.*, 2016), while correlative approaches suggest that this may also be the case for other sympatric mammal species (Dorcas *et al.*, 2012). We predicted that negative effects of pythons on mammal distributions likely outweigh the influence of vegetation communities and hydrology. Along the gradient of python density, we expected that change in community composition would be driven primarily by species loss rather than by replacement (Clavero & García-Berthou, 2005).

Due to the combined effects of species loss and the facilitation of a few generalist species (Olden, 2006), we predicted that urbanization, from the vast expansion of residential development in the region, should influence β -diversity through species turnover, without significantly impacting site-level species richness (i.e. α -diversity) (McKinney, 2006; Ordeñana *et al.*, 2010). We also predicted that urbanization would lead to the homogenization of mammal communities (McKinney, 2006), such that community composition becomes increasingly similar as distance to urbanization decreases. Additionally, we hypothesized that by providing benefits to some species, urbanization would reduce the net impacts of pythons on site-level mammal diversity (i.e. 'antagonistic interaction', Didham *et al.*, 2007), such that the negative effects of invasive pythons should be less apparent at sites located closer to urbanization.

METHODS

Study area

We conducted this study throughout the GEE, a 800,000 ha wetland that encompasses most of southern Florida, from near Orlando to the Florida Bay (Wiken *et al.*, 2011) (Fig. 1). The GEE is considered a biodiversity hotspot because of its endemic flora and fauna, its numerous vegetative communities created by the interface of temperate and subtropical climates and a gradient of saline environments (Lodge, 2010), and because of its greater than 70% loss of primary vegetation (Myers *et al.*, 2000). Historically, the GEE had a diverse medium- to large-sized mammal community (hereafter mammals) that utilized the region's variety of aquatic and terrestrial habitat.

Data collection

Site selection & survey protocol

During the southern Florida dry season (November–April, 2014), we surveyed 113 randomly generated sites (via random point generator in ArcGIS) throughout the GEE to sample for mammal occurrence within 1.5 km of a road or trail traversable on foot, by ATV or airboat. To detect mammals, we conducted systematic faecal counts (Forys & Humphrey, 1997; Palomares, 2001; Murray *et al.*, 2002; Schmidt *et al.*, 2011) at each survey site. Two observers independently searched each 30 m \times 30 m area survey site and recorded the number and species type of feces observed. In addition to faecal counts, we installed two trail cameras (Bushnell HD Trophy Cam, Overland Park, KS, USA) within each survey site. Observers placed cameras to maximize mammal detections (e.g. along game trails) and removed vegetation that would interfere with mammal detection from within 10 m in front of the camera. We collected cameras after 14 days in the field. To measure visual obstruction at each site, the observers recorded Robel pole readings (Robel, 1970) at the centre of the survey site and four locations 10 m from the centre. At a height of 1 m, from four cardinal directions 4 m away from the poll, observers recorded Robel measurements to the nearest decimetre. We averaged Robel readings across the five locations to produce a mean visual obstruction index.

Burmese pythons

To test for the potential effects of pythons, we used estimates of python density (pythons per km²) from a recently developed Reaction-Diffusion (R-D) model from Bonneau *et al.* (2016). The python R-D model was parameterized using 15 years of presence-only data, but makes a number of assumptions (random walk process, homogeneous landscape, a single point of invasion, logistic population growth and constant detection) which may limit its utility for fine-scale inferences. R-D models assume that at any space and time, a population is growing because of animal dispersion and reproduction. Given these assumptions and lack of standardized empirical data on python abundance and/or occupancy, this estimate of python density may be best interpreted as a spatially explicit measure of the 'time since establishment' or 'residence time' of pythons in southern Florida. R-D models have been criticized for oversimplifying the invasion process, but despite their simplicity may have the ability to make reliable predictions for a wide range of important processes including animal dispersal, the spread of disease and biological invasion (Holmes, 1993). Previous studies on the impacts of pythons on mammals in the GEE have relied on related indices representing the relative impacts of pythons, including distance to the assumed invasion epicentre (Dorcas *et al.*, 2012; Sovie *et al.*, 2016) and opportunistic presence-only python data (collected primarily along roads) (Dorcas *et al.*,

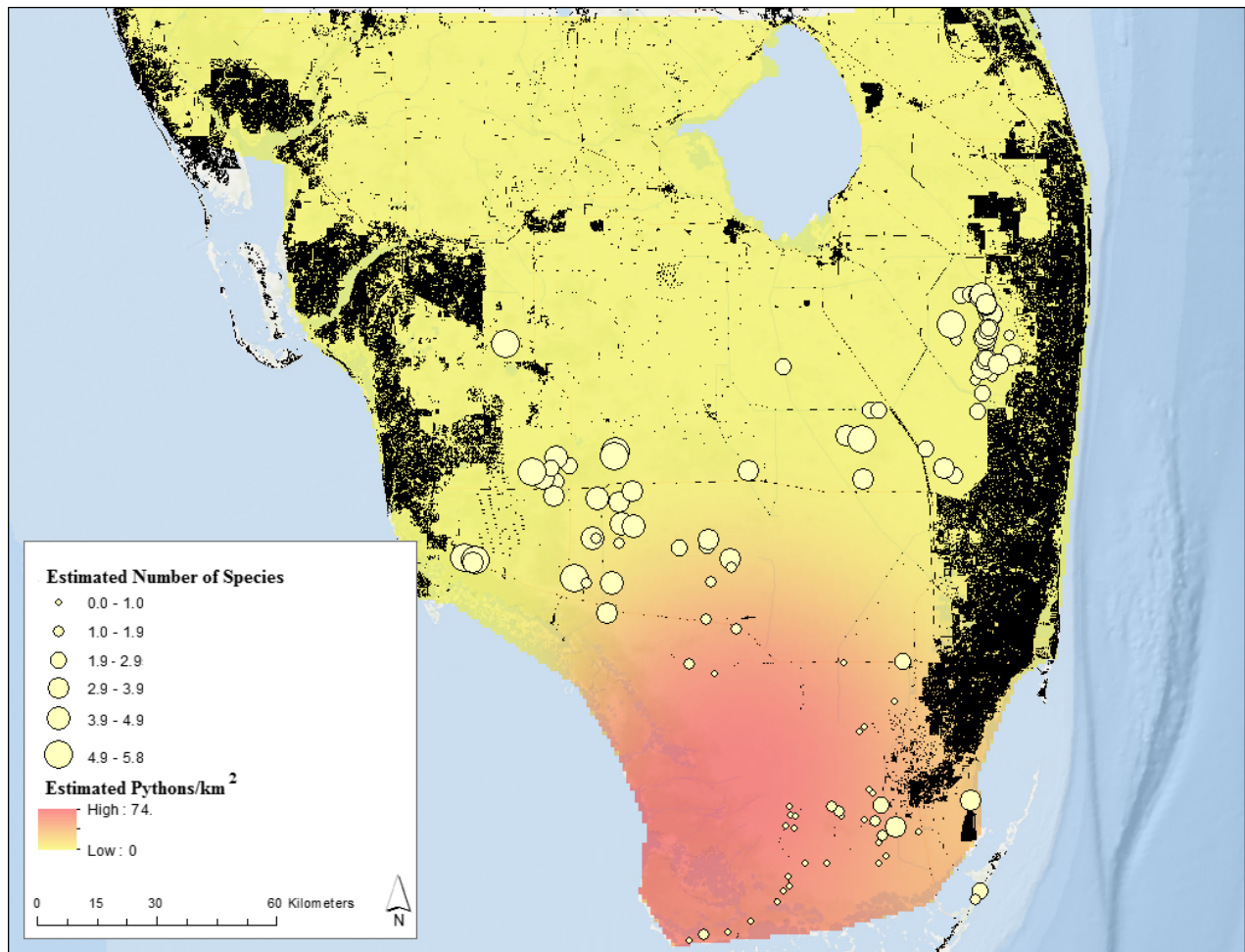


Figure 1 Map of study area (Greater Everglades Ecosystem in Florida, USA) including sampling locations (circles). Size of circles is proportional to estimated site-specific species richness, based on posterior distribution from multispecies occupancy model. Also included are the predicted python densities for 2014 (per km²) and areas of high-density urbanization (black) used to calculate distance to urbanization for each sampling location. [Colour figure can be viewed at wileyonlinelibrary.com]

2012). While imperfect, estimates from the R-D model improve upon previous python indices by incorporating both sources of information along with an explicit consideration of time since invasion (Bonneau *et al.*, 2016).

Urbanization

Using GIS, we calculated ‘distance to urbanization’ based on Euclidean distance from each survey site to the centroid of the nearest cell characterized as *high intensity urban* by the Florida Cooperative Land Cover map (Knight, 2015).

Hydrology

Anthropogenic changes in water flows of the last 20 years have reshaped the flow of water across the GEE (Davis & Ogden, 1997) and may also be affecting changes in the GEE mammal community along with it. To model the potential effects of local hydrology on mammal occurrence and

community structure, we included site-specific covariates for hydroperiod (number of days of continuous inundation) to summarize recent hydrology and mean water depth from 2008 to 2014 to capture longer-term hydrological conditions. Both hydrology metrics were based on water-level data from the Everglades Depth Estimation Network (EDEN <http://sofia.usgs.gov/eden/>). When hydrology records were not available for particular sites (for locations outside of the EDEN domain), we used the global mean of all the observations (mean imputation) to ensure that these sites would not bias our conclusions.

Habitat

We classified the 113 study sites into four broad habitat types that included ‘freshwater marsh-prairie’ ($n = 41$ sites), ‘coastal’ ($n = 10$ sites), ‘scrub and forested swamp’ ($n = 38$ sites), ‘briefly flooded woodland and hammock’ ($n = 21$ sites), and ‘disturbed’ ($n = 3$). We did not include a

covariate for ‘disturbed’ sites in the community model because of a limited sample. These four habitat types were broader classifications of 15 vegetation communities identified previously by Sovie *et al.* (2016) which were determined based on species composition, structure and inundation period (see Table S1 in Supporting Information).

Multispecies occupancy model

We constructed a multispecies occupancy model (Dorazio & Royle, 2005; Dorazio *et al.*, 2006) using BUGS language adapted from code by Kery & Royle (2016) to assess the biotic and abiotic factors influencing the species distributions and community structure of mammals in the GEE. Multispecies occupancy models have several advantages over more traditional approaches commonly used to assess patterns in biological communities (Iknayan *et al.*, 2014). The most notable of these advantages is the explicit consideration of species-level variation in occurrence and imperfect detection, both of which we modelled as linear functions of covariates of interest. Namely, our model incorporates the use of random effects, using community-level hyperpriors and hyperparameters to govern species-level intercepts and covariate effects. This assumes that intercepts and drivers of species-specific variation in detection (β_k) and occurrence (α_k) share a common community-level distribution (Dorazio & Royle, 2005). By leveraging information from species with relatively high rates of detection, this approach provides the ability to make inferences regarding patterns of occurrence for rare or cryptic species for which probabilities of detection are low (Dorazio & Royle, 2005).

We accounted for the occurrence of undetected species using parameter-expanded data augmentation (Royle *et al.*, 2007; Royle & Dorazio, 2008, 2012). This involves the inclusion of an arbitrarily large, yet computationally tractable number of ‘all-zero’ encounter histories ($n_{zeroes} = 5$) representing a pool of undetected, but previously recorded species in the study area (Dorazio *et al.*, 2006). The model then estimates the probability that an undetected species was available to be observed during the study period (i.e. the ‘super-population’ process) (Dorazio *et al.*, 2006).

In our model, we defined species occurrence z_{ik} as a binary, partially observable state variable, such that $z_{ik} = 1$ if species k was observed at site i in at least one of two camera traps placed at the location or their scat was identified during systematic line-transect surveys ($n = 2$ per site) (see Section Data collection). We assumed that if a species occurred at the site during at least one survey period (1 day), it was present and available at that site during all 14 consecutive days. Violation of this assumption can lead to an overestimation of occupancy (Rota *et al.*, 2009). Each value of z_{ik} was modelled as an outcome of a Bernoulli trial with a single parameter (ψ_{ik}), the probability of occupancy, for each species k at location i , with the likelihood of occurrence described by: $Z_{ik} \sim \text{Bernoulli}(\psi_{ik})$.

We assumed that occupancy varied among species and was influenced by site-specific environmental factors. After standardizing the covariate data (z -transformation) and using a logit link function, we modelled species-specific site occupancy as a function of nine covariates (none of the variables were highly correlated, Pearson $r < 0.41$) representing hypotheses regarding the potential drivers of mammal species distributions which we formulated as follows:

$$\begin{aligned} \text{logit}(\psi_{ik}) = & \beta_k + \beta_{1k}\text{python} \cdot \text{density}_i + \beta_{2k}\text{urbanization}_i \\ & + \beta_{3k}(\text{python} \cdot \text{density}_i * \text{urbanization}_i) \\ & + \beta_{4k}\text{hydroperiod}_i + \beta_{5k}\text{water} \cdot \text{depth}_i \\ & + \beta_{6k}\text{habitat1}_i + \beta_{7k}\text{habitat2}_i + \beta_{8k}\text{habitat3}_i \\ & + \beta_{9k}\text{habitat4}_i. \end{aligned}$$

Similar to occupancy, we allowed detection to vary among species, but also expected that it had increased during periods when we collected scat samples. To account for variation in detection resulting from this increase in sampling effort, we included a binary survey-specific covariate (1 = days with scat surveys, 0 = days without scat survey). Vegetation can obscure visibility of mammals in camera traps such that detection in habitats with dense vegetation may be lower than in those with sparse vegetative structure. To account for possible variation in detection due to site-specific vegetative structure, we also included measurements of visual obstruction taken at each site (see Section Data collection). We assume that species detections (y_{ijk}) follow a Bernoulli distribution with parameter (p_{ijk}) which is the detection probability for species k at site i during sampling period (day) j , and are conditional on the latent occupancy status of the site (z_{ijk}). Covariate effects on detection (p_{ijk}) were modelled via a logit link. Therefore, the likelihood is specified as follows:

$$y_{ijk} \sim \text{Bernoulli}(z_{ijk} * p_{ijk})$$

$$\text{logit}(p_{ijk}) = \alpha_k + \alpha_{1k}\text{scat} \cdot \text{survey}_j + \alpha_{2k}\text{veg} \cdot \text{density}_i$$

Using species-specific mean daily probabilities of detection from the posterior distribution, we computed the probability of detecting a species at least once over the 14-day study (p_k^*), as follows:

$$\hat{p}_k^* = ((1 - p_{jk}^{\text{scat+camera}})^2 \times (1 - p_{jk}^{\text{camera only}})^{12})$$

where $p_{jk}^{\text{scat+camera}}$ and $p_{jk}^{\text{camera only}}$ are the survey-specific detection probabilities for each species with and without additional scat survey efforts, respectively. Covariates on detection were modelled as random effects, with species-level variation drawn from a common distribution with an estimated mean and variance (i.e. hyperparameters).

For both occupancy and detection, we determined the influence of each covariate based on the direction and significance of the associated model coefficients (β_{1k} , α_{1k} , ...), such that the effect of a covariate was considered to be

significant if its 95% credible interval (CRI) did not include zero (Russell *et al.*, 2009). We used weakly informative priors for parameters of interest, for example $\mu_{\beta} \sim \text{normal distribution}$ and $\mu_{\sigma} \sim \text{uniform distribution}$ (see Appendix S1 for model code with all prior specifications), and implemented models in JAGS 4.0 (Plummer, 2005) via R (R Core Team, 2015) using the R-package ‘JAGSUI’ (Kellner, 2014). Inferences were based on 6000 samples from five chains from a total of 60,000 MCMC iterations after a burn-in of 5000 and a thin rate of 50. We assessed convergence by inspecting the MCMC chains and the Gelman-Rubin statistic, assuming convergence when Rhat was <1.1 (Gelman *et al.*, 2013). We assessed model adequacy using a posterior predictive check (Kéry, 2010; Gelman *et al.*, 2013), monitoring the Bayesian *P*-value (0.468) and *c*-hat (0.999) statistics to ensure goodness-of-fit.

Species richness, turnover and nestedness

As described by Kéry & Royle (2016), Bayesian hierarchical multispecies occupancy models provide ‘a detection-error-corrected estimate of the true presence–absence matrix \mathbf{Z} for every site and species’ (p. 709). We used \mathbf{Z} to calculate metrics of community diversity. First, we calculated site-level species richness (α -diversity) and species richness by habitat type by summing across presence–absence values for all species at each of the 113 sites and five broad habitat types ($\alpha\text{-diversity}_{\text{habitat}}$), respectively (Dorazio & Royle, 2005; Dorazio *et al.*, 2006, 2011; Kéry *et al.*, 2009). Then, based on the equation from Baselga & Orme (2012), we assessed β -diversity, or dissimilarity in community composition, by calculating the components of Jaccard dissimilarity due to turnover, J_{tu} , (i.e. species replacement) vs. Jaccard dissimilarity due to nestedness, J_{ne} (species loss or gain). Jaccard dissimilarity is the sum of J_{tu} and J_{ne} , and ranges from 0 to 1, where 1 indicates that sites have no species in common and 0 indicates that species composition is identical between sites (Baselga & Orme, 2012). Using a similar approach as Kéry & Royle (2016), who instead used total Jaccard similarity, we calculated J_{tu} and J_{ne} separately for all sites relative to four reference sites, one for python density, urbanization, hydroperiod and water depth, respectively. We chose reference sites that corresponded to the minimum values for each of the environmental variables.

We assessed directional changes in community diversity across each environmental gradient by regressing J_{tu} , J_{ne} and α -diversity onto each environmental variable using linear regression (for J_{tu} and J_{ne}) and generalized linear models (GLMs) with Poisson error distributions (for α -diversity), such that $\log(\alpha\text{-diversity}) = \beta_0 + \beta_1 x_i$, where x is the continuous covariate of interest at site i . We included a quadratic term, $\beta_2 x_i^2$, to test for nonlinear effects of hydrology (Table S2). Effects of a covariate were considered significant if the CI for its parameter estimate did not include zero. To assess the rate of change in diversity measures along each

gradient, we evaluated the slope of each regression (Nekola & White, 1999). We tested for interactive effects of pythons and urbanization on diversity measures by including an interaction term, and compared predicted rates of change in diversity along the python gradient between sites located at minimum vs. maximum distance from urbanization (Anderson *et al.*, 2011). Community metrics based on modelled presence–absence data may be sensitive to model assumptions (Dorazio *et al.*, 2011). To account for sampling and model uncertainty, we performed regressions on each of the 6000 iterations and assessed significance based on the degree to which the distribution of slope coefficients overlapped zero.

RESULTS

From camera traps and scat surveys combined, we detected 14 total species of mammals across all 113 sites (Table 1). Based on the mean of the posterior distribution of the multispecies occupancy model, we estimated 16 total species, $SD = 1.44$ (γ -diversity). Data from scat surveys provided information on seven species; two of these species [Florida panther (*Felis concolor coryi*) and round-tailed muskrat (*Neofiber alleni*)] we detected via scat sampling only. Observed site-level species richness ranged from 0 to 5 species, while values of estimated site-level species richness from the posterior distribution of the multispecies occupancy model ranged from 0 to 6 species (mean = 2.5, $SD = 1.69$). Five species were observed (via scat or camera) at only one of the 113 total sites (nine-banded armadillo, fox squirrel, coyote, river otter, Florida panther and round-tailed muskrat).

Species-level effects

We found evidence for the effects of pythons and urbanization on distributions of mammals while accounting for variation due to habitat. Negative effects of python density were significant for all observed species except coyotes for which the effect was negative but not significant based on credible intervals overlapping zero (Table 2, see Figure S1 for full summary of coefficients by species). Main effects of urbanization varied among species – occurrence of marsh rabbits and raccoons significantly increased as distance to urbanization decreased, but the opposite was observed for most other species (Table 2, Fig. 2). The python–urbanization interaction term, hydroperiod and water depth were not significantly correlated with species occurrence (see Figure S1). Habitat effects varied, especially among species where ‘freshwater marsh-prairie’ (hab3) had the most consistent (negative) effect on species occurrence followed by ‘scrub and forested swamp’ (hab4), while ‘briefly flooded woodlands and hammocks’ (hab1) were not correlated with any species and ‘coastal’ habitat (hab2) was negatively correlated with marsh rabbit occurrence (Table 2 and see Figure S1).

Table 1 Summary of observations, estimated species occurrence and detection for all observed mammal species.

Species	Proportion of sites observed		Model estimates			
	Cameras	Scat	$\hat{\psi}$	SD	\hat{p}^*	SD
Nine-banded armadillo	0.009	0.000	0.043	0.072	0.440	0.210
Florida black bear	0.018	0.000	0.056	0.077	0.471	0.195
Bobcat	0.071	0.000	0.241	0.186	0.350	0.137
White-tailed deer	0.292	0.124	0.476	0.123	0.763	0.049
Big Cypress fox squirrel	0.009	0.000	0.050	0.085	0.406	0.199
Virginia opossum	0.124	0.009	0.325	0.178	0.428	0.103
Marsh rabbit	0.195	0.265	0.464	0.123	0.812	0.059
Raccoon	0.274	0.027	0.404	0.127	0.769	0.061
Eastern grey squirrel	0.018	0.000	0.078	0.103	0.401	0.174
Striped skunk	0.009	0.009	0.074	0.101	0.389	0.187
Coyote	0.009	0.000	0.034	0.067	0.501	0.205
River Otter	0.009	0.000	0.053	0.093	0.382	0.193
Florida panther	0.000	0.009	0.039	0.066	0.448	0.208
Round-tailed muskrat	0.000	0.009	0.052	0.090	0.420	0.202

Included are the proportion of sites at which species were observed using camera traps and scat surveys, estimated mean occupancy ($\hat{\psi}$) with standard deviations (SD) and probability of detecting species during at least one survey period (\hat{p}^*) with standard deviations (SD). Occurrence and detection probabilities are mean values from the posterior distribution of a multispecies occupancy model that includes effects of python density, distance to urbanization, python–urban interaction, hydrology (mean depth and hydroperiod in number of days) and habitat type ($n = 4$) on species occurrence; effects of local vegetation density and survey method ('cameras only' vs. 'camera and scat') on species detection.

Community-level effects

Urbanization

The effects of urbanization (measured as distance to urbanization) on species distributions varied among species (Table 2 and Fig. 2). As a result, site-level species richness remained unchanged with distance to urbanization (see Table S2), but community dissimilarity due to turnover significantly increased ($\beta_{\text{urban}}^{\text{tu}} = 0.133$, CRI = 0.063, 0.198) (Fig. 2) and dissimilarity due to nestedness decreased ($\beta_{\text{urban}}^{\text{nc}} = -0.0496$, CRI = -0.085 , -0.012) with distance to urbanization.

Burmese python

Impacts of pythons on community diversity were consistent with the negative effects found on species occurrence. Site-level species richness was negatively correlated with python density ($\beta_{\text{python}}^{\alpha\text{-diversity}} = -0.85$, CRI = -1.03 , -0.66) (Fig. 3), such that the site with the greatest estimated python density (70.2 pythons per square km) had zero species in 5857 of the 6000 total MCMC iterations of our multispecies occupancy model. Across the python gradient, the rates of turnover and community dissimilarity due to nestedness were not significantly different from zero (see Table S2).

Python–urbanization interaction

We found a significant interactive effect of pythons and urbanization on species richness ($\beta_{\text{python-urban}}^{\alpha\text{-diversity}} = -0.22$,

CRI = -0.462 , -0.0004). While the interactive effect was considerably weaker compared to main effects of pythons on species richness, predicted rate of change (slope) in species richness due to change in python density was significantly lower at the minimum vs. maximum observed distance to urbanization (Fig. 3). We did not find interactive effects of python density on either Jaccard dissimilarity measure (see Table S2).

Hydrology

We found evidence that hydrology influenced mammal community diversity in the GEE. Site-level species richness was significantly correlated with a nonlinear effect of water depth ($\beta_{\text{waterdepth}}^{\alpha\text{-diversity}} = -0.222$, CRI = -0.301 , -0.143), such that richness was greatest at sites that averaged ~ 55 cm of water depth (Fig. 3). Hydroperiod had only a weak, but significant linear relationship with site-level species richness ($\beta_{\text{python-hydroperiod}}^{\alpha\text{-diversity}} = 0.0004$, CRI = 8.0×10^{-5} , 7.6×10^{-4}). Neither hydroperiod nor water depth had significant effects on community dissimilarity measures.

Habitat

Mean habitat-specific species richness derived from the posterior distribution ($\alpha\text{-diversity}_{\text{habitat}}$) closely resembled that of the observed data ($\alpha\text{-diversity}_{\text{habitat}}^{\text{obs}}$). 'Briefly flooded woodland and hammocks' had the greatest total number of species ($\alpha\text{-diversity}_{\text{BFWH}}^{\text{obs}} = 9$, $\alpha\text{-diversity}_{\text{BFWH}} = 12.02$) followed by 'freshwater marsh-prairie' ($\alpha\text{-diversity}_{\text{FWM}}^{\text{obs}} = 8$, $\alpha\text{-diversity}_{\text{FWM}} = 10.49$), 'scrub and forested swamps'

Table 2 Summary of mean model coefficients for individual species-level relationships between occurrence and model covariates, including python density per square km ('pyth'), distance to urbanization ('urban'), hydroperiod ('hydro'), mean water depth ('depth') and habitat types ('hab1', 'hab2', 'hab3' and 'hab4').

Species	pyth	urban	pyth*urban	hydro	depth	hab1	hab2	hab3	hab4
Nine-banded armadillo	(-1.89)	-0.90	-0.42	-0.30	-0.33	-0.74	-2.27	(-2.84)	(-2.90)
Florida black bear	(-2.05)	-0.51	-0.81	-0.29	-0.31	-0.25	-2.28	(-2.91)	(-2.99)
Bobcat	(-2.55)	-0.32	-0.93	-0.47	-0.37	-0.89	-2.32	(-2.37)	-1.88
White-tailed deer	(-1.82)	0.64	0.35	-0.77	-0.05	-0.37	-2.55	(-2.93)	0.47
Big Cypress fox squirrel	(-1.85)	0.07	-1.17	-0.28	-0.29	-1.71	-2.26	(-2.82)	-1.55
Virginia opossum	(-1.52)	-0.54	-1.29	-0.57	-0.74	0.65	-1.86	(-2.87)	-2.29
Marsh rabbit	(-2.55)	(-0.98)	-0.64	-0.06	0.15	-0.86	(-2.81)	-1.88	-1.16
Raccoon	(-2.03)	(-1.58)	-0.87	-0.15	-0.28	-1.87	-1.29	(-2.81)	-1.16
Eastern grey squirrel	(-1.95)	-0.47	-0.87	-0.25	-0.31	-0.07	-2.30	(-2.90)	(-2.98)
Striped skunk	(-2.10)	-0.09	-1.11	-0.27	-0.27	-0.92	-2.30	(-2.42)	(-3.00)
Coyote	-1.38	-0.90	-1.26	-0.27	-0.28	-1.71	-2.37	(-2.88)	(-2.87)
River Otter	(-1.98)	-0.77	-0.52	0.19	-0.19	-1.69	-2.26	-2.23	(-2.98)
Florida panther	(-1.90)	0.30	-1.46	-0.24	-0.26	-1.80	-2.27	(-2.39)	-2.85
Round-tailed muskrat	(-1.91)	-0.39	-0.88	0.17	-0.28	-1.68	-2.27	(-2.83)	-1.66

Notation: '(') indicates a significant effect.

Habitat effects were modelled as binary covariates, where *hab1* = 'briefly flooded woodlands and hammocks', *hab2* = 'coastal', *hab3* = 'freshwater marsh-prairie' and *hab4* = 'scrub and forested swamp'. See Table S1 in Supporting Information for habitat types classified for each site. Species: nine-banded armadillo (*Dasyus novemcinctus*), Florida black bear (*Ursus americanus floridanus*), bobcat (*Lynx rufus*), white-tailed deer (*Odocoileus virginianus*), Big Cypress fox squirrel (*Sciurus niger avicennia*), Virginia opossum (*Didelphis virginiana*), marsh rabbit (*Sylvilagus palustris*), raccoon (*Procyon lotor*), Eastern grey squirrel (*Sciurus carolinensis*), Striped skunk (*Mephitis mephitis*), coyote (*Canis latrans*), North American river otter (*Lontra canadensis*), Florida panther (*Puma concolor coryi*) and round-tailed muskrat (*Neofiber alleni*).

(α -diversity_{SFS}^{obs} = 7, α -diversity_{SFS} = 10.35), 'coastal' (α -diversity_{coastal}^{obs} = 2, α -diversity_{coastal} = 4.6) and 'disturbed' (α -diversity_{disturbed}^{obs} = 8, α -diversity_{disturbed} = 3.4).

Species detection

Detection of mammals in the GEE varied considerably among species (Table 1). For example, there was greater than 75% probability of detecting white-tailed deer, raccoon and marsh rabbit in at least one of the survey days ($n = 14$ total consecutive days), but only 38–50% for nine-banded armadillo (*Dasyus novemcinctus*), fox squirrel (*Sciurus niger avicennia*), otter (*Lontra canadensis*), panther, round-tailed muskrat and striped skunk (*Mephitis mephitis*) (Table 1). We did not observe the following species that have previously been documented within the region: domestic pig (*Sus scrofa*), long-tailed weasel (*Mustela frenata*), Everglades mink (*Neovison vison evergladensis*), grey fox (*Urocyon cinereoargenteus*), or red fox (*Vulpus vulpus*) (Brown, 1997). Based on significance of model coefficients, including scat surveys significantly increased the probability of detecting several species ($\hat{\alpha}1 = 1.09$, CRI = 0.28–1.83), but vegetation structure had little to no effect on detection ($\hat{\alpha}2 = -0.14$, CRI = -0.57 to 0.18).

DISCUSSION

Patterns of mammal diversity in the GEE are seemingly paradoxical in that large conservation areas have depauperate

mammalian fauna, while urbanized areas have consistent but similar mammal communities. Urban areas may buffer the impact of pythons on species loss and community change. One potential explanation for this pattern is that pythons are detected and removed at higher rates near urban areas, allowing mammals to persist in these locations. Alternatively, the interaction between python density and distance to urbanization may be a result of the robust population of generalist mammals (e.g. marsh rabbit, raccoon, white-tailed deer, bobcat and coyote) that were more resilient to python impacts in urbanized areas. Generalist mammals often have higher rates of survival and fecundity in urbanized environments (Rodewald & Gehrt, 2014), but even elevated demographic rates may not explain the ability of some species to persist in urbanized areas with pythons (McCleery *et al.*, 2015). Understanding how other mammal communities and species are persisting in urban areas in the face of the ongoing python invasion may be critical to understanding how mammals can persist or be reintroduced throughout the GEE.

Our rigorous assessment of mammals throughout the GEE provides strong evidence that despite variation due to habitat, the current distribution of mammals in the GEE can be best explained by the long-term presence of invasive Burmese pythons and, to a lesser extent, the distance to urbanization. We were able to untangle the complex drivers of faunal distribution and found that, at some scales, factors historically known to influence mammal communities (urbanization, hydrology, vegetation communities) were also relevant to

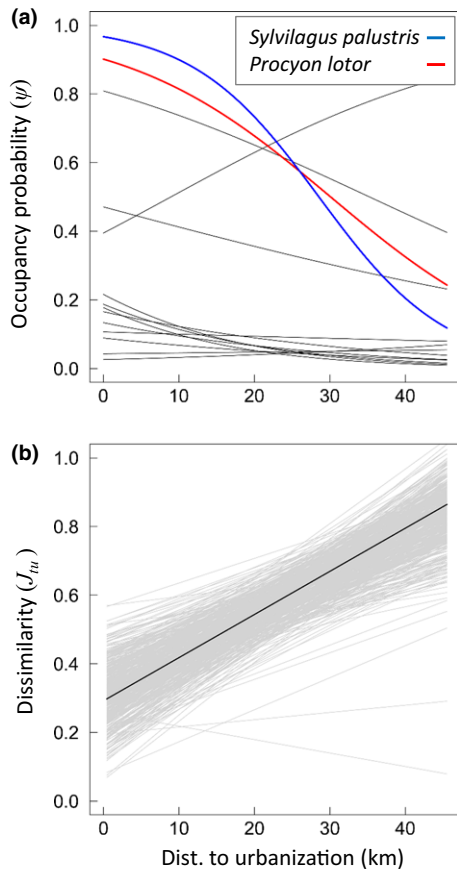


Figure 2 Effects of distance to urbanization on (a) species occupancy and (b) Jaccard dissimilarity due to species turnover. As distance to urbanization decreases, local mammal communities become more similar (homogenization due to urbanization) – dominated by a few urban-adapted species, including marsh rabbits (*Sylvilagus palustris*) and raccoons (*Procyon lotor*). [Colour figure can be viewed at wileyonlinelibrary.com]

mammals in the GEE. Yet after variation in vegetation communities, pythons made the strongest contribution to reduced distributions among mammals (Table 2). Similar to the conclusions drawn from effort-corrected data collected from road surveys (Dorcas *et al.*, 2012), mammals were scarce in the southern portion of the GEE (Fig. 1).

All mammals detected in this study, except coyotes (Figure S1), showed a negative response to longer python residence times (modelled as python density). Our results provide empirical support that pythons are associated with the local extirpation and displacement of medium- to large-sized mammals in the southern portion of the GEE (Dorcas *et al.*, 2012; McCleery *et al.*, 2015). The patterns of python-induced reductions in occurrence were particularly pronounced for species with higher probabilities of detection (e.g. deer, raccoon, and rabbits). The predicted response for species with minimal detections (fox squirrel, bear, round-tailed muskrat) may be biologically meaningful or a result of modelling species-level effects based a common distribution for all species (i.e. random species effect).

Our inferences on the negative effects of pythons on mammal distributions across the GEE rely on predicted python density from a previously developed R-D model (Bonneau *et al.*, 2016). The R-D model assumption of constant spread over a homogenous landscape is an oversimplification of the invasion process and accounting for heterogeneous landscapes, and other potential sources of variation in python movements (Hart *et al.*, 2015; Smith *et al.*, 2016) would likely result in more accurate predictions of python density. ‘Python density’ likely reflects time since invasion where ‘higher density’ is indicative of a longer residence time. Whether pythons remain in an established area after invasion is unclear, but patterns from this study indicate that mammals did not redistribute to these sites post-invasion.

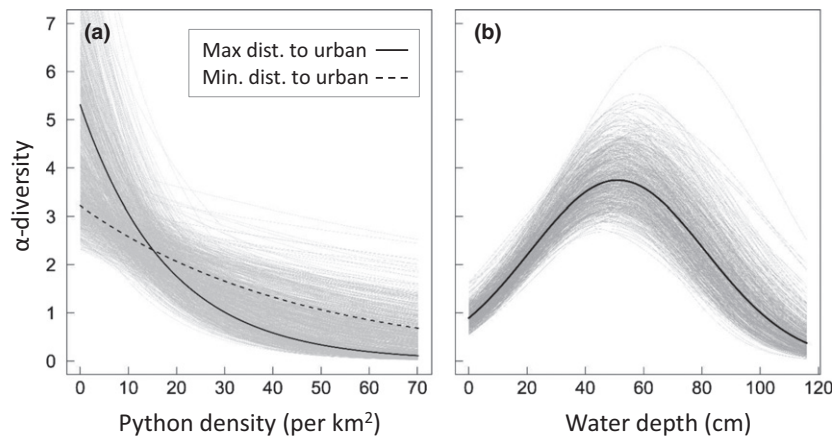


Figure 3 Predicted site-level species richness (α -diversity) across gradients of (a) python density at maximum and minimum observed distances from urbanization and (b) mean site-level water depth. Model predictions based on (a) multiple linear regression with interaction and (b) simple regression with a quadratic term using GLM with *Poisson* error distributions at the posterior means (black solid and dashed lines) and ($n = 500$) MCMC samples (grey lines) from hierarchical community model.

The ability of pythons to extirpate marsh rabbit populations was recently demonstrated by McCleery *et al.* (2015), but impacts of pythons across a native mammal community exhibiting such a diverse suite of functional and physiological traits are striking and possibly unprecedented in invasion ecology (Gurevitch & Padilla, 2004; Clavero *et al.*, 2009). Nonetheless, the mechanisms linking pythons to population declines among mammal species may vary. Predators (e.g. bobcats, Florida panthers) may be responding to a depletion of the prey base (McCleery *et al.*, 2015), whereas primary consumers (e.g. marsh rabbits, white-tailed deer, round-tailed muskrat) may decline from direct predation. Our work highlights the need for further investigation into patterns of co-occurrence (Pollock *et al.*, 2014) which may provide important insight for developing hypotheses about potential species interactions, including the ability for pythons to disrupt predator–prey interactions. Regardless of the mechanism, the categorically negative response of mammals may have serious implications for the health and functionality of the GEE (Forys & Allen, 2002). McCleery *et al.* (2015) suggested the loss of mammals in the GEE was likely causing a complete restructuring of the food web, declines in ecosystem function and an array of cascading ecological effects.

Effects of urbanization on mammal distributions varied by species. Site occupancy of raccoons and marsh rabbits increased around urbanized areas. Procyonids and lagomorphs have both been shown to exploit the resources around human habitation. Raccoons are known to exploit food subsidies (e.g. garbage, bird seed, pet food) and the shelter provided by anthropogenic structures (Bateman & Fleming, 2012). Rabbits can also thrive in residential areas (Adams, 1994), likely benefiting from highly productive mowed, fertilized and watered grass, and fewer predators (McIntyre, 2014; Rodewald & Gehrt, 2014). Increased presence of these two generalists did not generate an increase in overall species richness in developed areas. As predicted, we found that increasing proximity to urbanization led to more homogenized mammal communities (McKinney, 2006).

Until now, there has been little empirical evidence to understand the factors shaping declines in mammal communities throughout the GEE (Dorcas *et al.*, 2012). As predicted, the effects of hydrology and habitat type were species dependent (Table 2, Figure S1). Some mammal species rely on shallow permanently flooded wetlands (e.g. river otter, round-tailed muskrat), whereas upland mammal species such as white-tailed deer, black bears and nine-banded armadillos often avoid environments with long inundation periods (Brown, 1997). Our results indicate that the distribution of several species likely overlaps near 55 cm of water depth and that fewer species occur when water is too shallow or deep. Not surprisingly, we found that scrub and forested swamps had the highest estimates of mammal diversity. Flooded wetlands have increased availability of

food, shelter and water resources favored by an array of mammals (Brown, 1997). Alternatively, coastal environments generally had lower species richness as few mid-sized terrestrial mammals are well adapted to highly saline environments (Brown, 1997).

Decline and changes in faunal populations and communities are one of the greatest conservation challenges of our time (Ceballos *et al.*, 2015). The patterns of community change are often clear, but the drivers of these patterns can be difficult to untangle in anthropogenically altered environments (Didham *et al.*, 2005, 2007; Darling & Côté, 2008). Once the drivers of community change have been identified, it may be equally difficult to determine whether the drivers are eliminating or replacing species (Baselga, 2010). Nonetheless, we have shown that it is possible to untangle the influence of landscape drivers, which can act alone and together on different aspects of community composition. Distinguishing between these important processes of community change may be critical for determining how biological invasions alter community composition (Anderson *et al.*, 2011).

Considering predicted increases in human population growth (Smith & Rayer, 2013) coupled with the continuing spread of pythons, the prospects for maintaining a functionally diverse mammal community across the GEE is not promising. We conclude that invasive Burmese pythons represent an ecological catastrophe for mammals in southern Florida and quite possibly the entire GEE.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Individual species-level coefficients from multi-species occupancy model.

Table S1 Summary of vegetation communities and habitat types used to model medium and large-sized -mammal species occurrence in the Greater Everglades Ecosystem.

Table S2 Models used for simple and multiple regression with estimated slope coefficients.

Appendix S1 Bugs code for multispecies occupancy model.

BIOSKETCH

Brian Reichert studies the effects of multiple drivers of global change on the distribution and dynamics of wildlife populations and communities.

Author contributions: B.R., A.S., R.R., R.M. and K.H. conceived and designed the study; A.S. collected the data; B.R., A.S., B.U. and M.B. analysed the data; and B.R., A.S., B.U., R.B., K.H., M.B., R.R. and R.M. wrote the manuscript.

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