



Life-history traits moderate the susceptibility of native mammals to an invasive predator

Jose R. Soto-Shoender · Daniel C. Gwinn · Adia Sovie · Robert A. McCleery

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Abstract The invasive Burmese python (*Python molurus bivittatus*) is causing declines in the numbers and diversity of native mammals in the Greater Everglades Ecosystem (GEE). However, limited evidence suggests that some species may be less susceptible to pythons than others. This difference in susceptibility may be a function of different life-history traits. We analysed incidence data with a multi-species hierarchical occupancy model to evaluate the influence of pythons on native mammals and

examine the association between python's influence on species occurrence and life-history traits. We also used our traits-based model to predict the effects of pythons on occupancy probabilities of five mammalian species of conservation or management concern known to occur in the GEE but not detected in our study. Ten of 18 observed mammals showed significant negative effects from pythons, while one responded positively. We found that three of the six species traits evaluated (mass, fecundity, and habitat breadth) moderated the negative effects of pythons on mammal occurrence and were, thus, useful for predicting species responses. Our results suggest larger, fecund and/or species with wide habitat

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J. R. Soto-Shoender (✉) · A. Sovie · R. A. McCleery
Department of Wildlife Ecology and Conservation,
University of Florida, 110 Newins-Ziegler Hall,
Gainesville, FL 32611, USA
e-mail: soto.jroberto@usac.edu.gt

A. Sovie
University of Kentucky Natural Resources and
Environmental Science Program, Agricultural Science
Building N-212A, Lexington, KY 40508, USA

J. R. Soto-Shoender
Facultad de Ciencias Químicas y Farmacia, Universidad
de San Carlos de Guatemala, Ciudad Universitaria, Zona
12, Ciudad de Guatemala, Guatemala

D. C. Gwinn
Biometric Research, 7 Harbour Road, South Fremantle,
WA 6162, Australia

D. C. Gwinn
School of Biological Sciences, The University of Western
Australia, M004, 35 Stirling Highway, Perth,
WA 6009, Australia

breadths were less susceptible to increasing relative densities of pythons. Our results also suggest a positive and neutral associations between rodents and relative python density, likely due to wide habitat breadths, high fecundity rates, and the reduction of mammalian predators in areas with higher relative python densities. These trait relationships predicted a negative response of all five unobserved species of management concern included in our analysis. Our study provides a broader understanding of wildlife community vulnerability to invasive predators and demonstrates how trait-based models can be used to elucidate generalizable patterns and generate predictions for rare and/or undetected species.

Keywords Bayesian hierarchical occupancy model · Burmese python · Greater everglades ecosystem · Invasive species · Life-history traits · Mammals

Introduction

Biological invasions are a major threat to global biodiversity and ecosystem function (Simberloff et al. 2013). Invasive species are commonly responsible for native species declines, habitat alterations, trophic cascades, and changes to community composition (Ehrenfeld 2011; Simberloff et al. 2013). While much of the research on invasive species focuses on developing comprehensive understandings of the invasion process and its control (Mack et al. 2000; Lockwood et al. 2007; Della Venezia et al. 2018), there is less research aimed at predicting the potential effects of new and continued invasions (Ricciardi et al. 2013; Shackelford et al. 2013; Simberloff 2014). This knowledge gap limits our ability to plan, prioritize, and mitigate, the often deleterious impacts of invasive species.

One promising approach to predicting communities' responses to invasive species are models that incorporate species life-history traits (Okes et al. 2008). The use of species traits can allow for more generalizable and robust predictions of community changes than traditional species-based approaches (Nock et al. 2016). Additionally, the use of species traits provides a mechanistic understanding of how species and communities respond to changing environments (Verberk et al. 2013; Nock et al. 2016). This

approach has been used to predict the response of wildlife to climate change (Maclean and Beissinger 2017), habitat alterations (Okes et al. 2008), and invasive plants (Ceradini and Chalfoun 2017). Accordingly, a traits-based approach is well suited to predict and understand the response of species and communities to invasive predators that have decimated a number of the planet's vertebrate communities (Doherty et al. 2016).

One invasive predator reshaping native wildlife in North America is the Burmese python (*Python molurus bivittatus*), a large snake native to Southeast Asia. Since the late 1970's (Meshaka et al. 2000; Dove et al. 2011), the python population in south Florida has expanded northward throughout the Greater Everglades Ecosystem (GEE) (Holbrook and Chesnes 2011; Willson 2017). These invasive predators have devastated mid-sized mammals (McCleery et al. 2015; Sovie et al. 2016; Reichert et al. 2017); however, some anecdotal evidence suggests that smaller rodents may persist or increase in areas with pythons (Dorcas et al. 2012; Hoyer et al. 2017). Python-induced changes in the mammal community have had cascading effects on ecosystem function and disease prevalence (Willson 2017; Hoyer et al. 2017). Still, we lack an ability to predict these responses because we do not have an understanding of what makes some species and groups of mammals more vulnerable to pythons than others.

Here we investigate the potential relationships between mammal species traits and species susceptibility to invasive Burmese pythons in the GEE. Specifically, we analysed a large data set of mammal detections in the GEE with a multi-species occupancy model that integrates multiple data types (i.e. survey methods) into a single unified analysis to increase detection opportunities across species. The model estimates patterns in species occurrence probabilities, incorporates the influence of species traits on patterns in occupancy, and accounts for incomplete detection, inherent in many sampling methods. We apply this model to (1) determine if some mammals are more or less susceptible to the python invasion, (2) determine what life-history traits influence susceptibility, and (3) predict the response of mammals of conservation or management concern not detected in the study.

Material and methods

Mammal surveys

We surveyed mammals with three sampling methods at 114 30-m × 30-m sites across the GEE (Fig. 1) from November to April 2014 (for details see Sovie et al. 2016; Reichert et al. 2017). We randomly selected the order that sites were sampled, with the exception of sites with access issues. Each site was sampled with three sampling methods selected to increase detection opportunities across the species of the mammal assemblage of GEE (Isaac et al. 2020). At each site 2 observers conducted systematic faecal pellet counts (Schmidt et al. 2011) and setup two camera traps (Bushnell HD Trophy Cam, Overland Park, KS, USA) in areas with high visibility. Additionally, we deployed 2 short-focused cameras inside of buckets baited with bird seed that were specifically designed to detect rodent species (McCleery et al. 2014). We deployed all cameras for 7–14 days

straight, resulting in 7–14, 24-h sampling occasions (10 am–10 am) per survey period for each camera. Additionally, we conducted scat searches on the first and last day of the camera trap surveys at each site.

Mammalian life-history traits

We evaluated the potential influence of six species traits to moderate the vulnerability of mammals to pythons. The specific traits were chosen based on our a priori belief that they may influence predation rates and prey population resilience. For example, predation rates can be influenced by prey encounter rates, python gape limitation and habitat co-occurrence, while population resilience can be influenced by prey fecundity rates and generalist versus specialist life-history strategies. We considered the continuous variables of average adult mass (M), home range size (HR), and average annual fecundity (F), as well as the binary variables indicating if the species is aquatic (AQ) and/or arboreal (AB) and if it has a high habitat

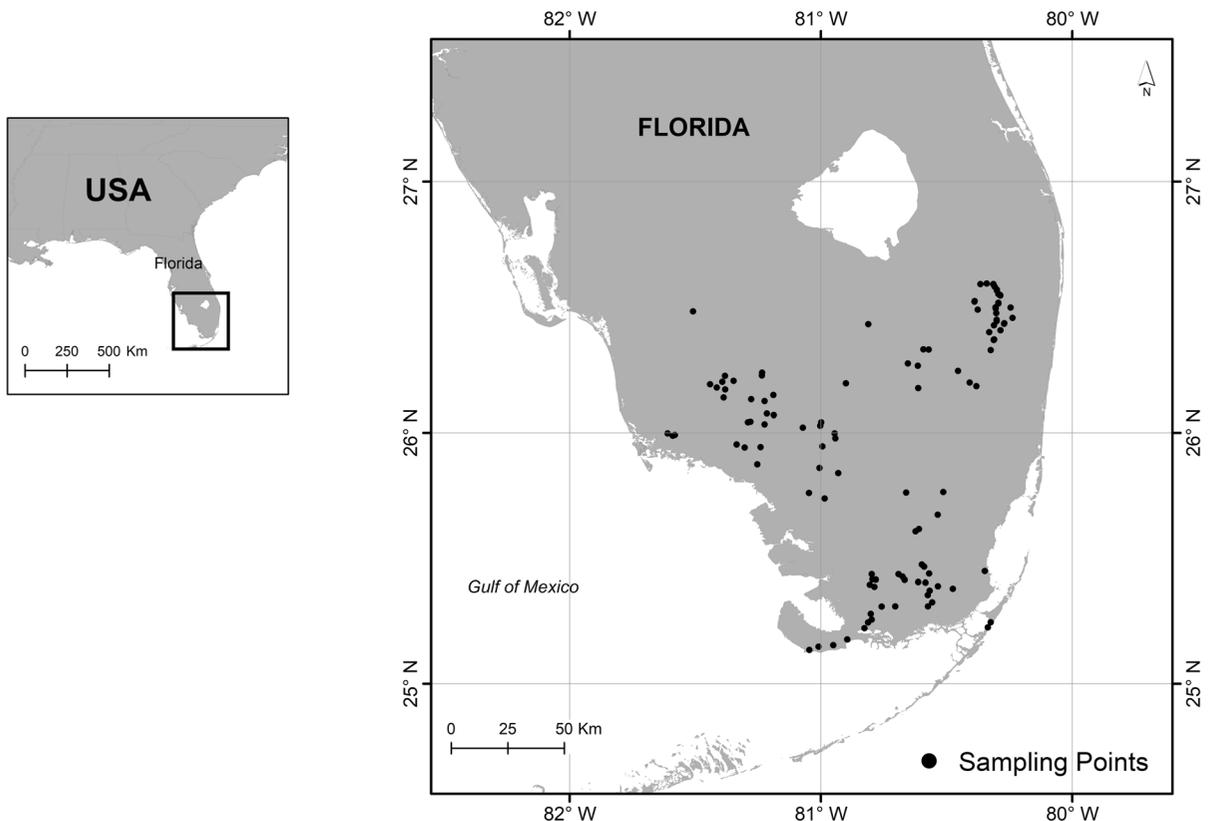


Fig. 1 Map of study area depicting sampling sites distributed across the Greater Everglades Ecosystem

breadth (*HB*) in our analysis (Table 1). We quantified habitat breadth (1 = species uses more than one broad habitat layer; 0 = species uses only one broad habitat layer), aquatic associations (species association to aquatic habitats 1 = aquatic; 0 = terrestrial) and arboreal associations (0 = very little to no use; 1 = intermediate to constant use) as binary variables. We predicted that larger home-range sizes and stronger associations with aquatic habitats would increase a mammal's susceptibility to pythons by increasing encounters with the predator (Greene 1986; Dove et al.

2011; Barker and Barker 2008), while an arboreal behaviour would decrease susceptibility by reducing encounters rates (Rahman et al. 2014). We also predicted that larger mass would reduce susceptibility to pythons because larger prey are, theoretically, less susceptible to predation once encountered by a predator (Greene 1986). Furthermore, pythons are gape limited (Shine 1991) and smaller pythons may not be able to consume large prey. Lastly, we predicted that higher fecundity rates and greater habitat breadth may reduce mammals' susceptibility to pythons by

Table 1 Life-history traits used in the multi-species Bayesian hierarchical occupancy modelling procedure

Species	Scientific name	Mass (gm.)	Home range (km ²)	Fecundity	Habitat breadth	Aquatic	Arboreal
Observed species							
Big Cypress fox squirrel	<i>Sciurus niger avicennia</i>	1100	0.23	5.00	1	0	1
Black rat	<i>Rattus rattus</i>	143	0.002	22.09	1	1	1
Bobcat	<i>Lynx rufus</i>	6374	31.5	3.05	0	0	0
Cotton mouse	<i>Peromyscus gossypinus</i>	28	0.003	14.8	1	0	1
Cotton rat	<i>Sigmodon hispidus</i>	111	0.002	10.6	1	1	0
Coyote	<i>Canis latrans</i>	11,989	19	6.32	0	0	0
Eastern gray squirrel	<i>Sciurus carolinensis</i>	545	0.009	5.82	1	0	1
Florida black bear	<i>Ursus americanus</i>	110,500	31.2	1.71	0	0	0
Florida panther	<i>Puma concolor coryi</i>	53,954	131	2.04	0	0	0
Marsh rabbit	<i>Sylvilagus palustris</i>	1355	0.03	17.64	0	1	0
Nine-banded armadillo	<i>Dasypus novemcinctus</i>	3949	0.04	3.84	1	0	0
Raccoon	<i>Procyon lotor</i>	6374	4.63	3.04	1	1	1
Rice rat	<i>Oryzomys palustris</i>	53	0.003	21.65	1	1	0
River otter	<i>Lontra canadensis</i>	8087	14.2	3.32	1	1	0
Round-tailed muskrat	<i>Neofiber alleni</i>	265	4 × 10 ⁻⁵	10.49	1	1	1
Striped skunk	<i>Mephitis mephitis</i>	2400	2.33	11.38	0	0	0
Virginia opossum	<i>Didelphis virginiana</i>	2442	0.58	17.24	1	0	1
White-tailed deer	<i>Odocoileus virginianus</i>	75,901	2	1.99	0	0	0
Unobserved species							
Everglades mink	<i>Neovison vison evergladensis</i>	1600	7.5	4	0	1	0
Feral hog	<i>Sus scrofa</i>	84,472	1.18	6.78	0	0	0
Gray fox	<i>Urocyon cinereoargenteus</i>	3834	1.83	3.71	0	0	0
Red fox	<i>Vulpes vulpes</i>	4820	3.5	4.59	0	0	0
Key Largo woodrat	<i>Neotoma floridana smalli</i>	249	0.002	4	0	0	1

Life-history traits: Mass = average adult body mass; Home range = average home range size in km²; Fecundity = average litter size x litters per year. The following were modeled as binary covariates: Habitat breadth = indicating whether species used one or more habitat layers (1 = species uses more than one habitat layer; 0 = species uses only one habitat layer); Aquatic = species association to aquatic habitats (1 = aquatic; 0 = terrestrial); Arboreal = species use of the canopy (0 = very little to no use; 1 = intermediate to constant use). Data obtained from Pantheria (Jones et al. 2009), Brown (1997), and IUCN species accounts

allowing them to be resilient to higher predation pressure and disturbance (Hoyer et al. 2017; Raubenhaimer and Simpson 2003; Swihart et al. 2003; Layman et al. 2007).

We obtained most trait data for the 18 observed and 5 unobserved species studied (Table 1) from the Pantheria database (Jones et al. 2009). Unobserved species were augmented to the observed species data by adding 5 all-zero detection histories (see Dorazio and Royle 2005, Dorazio et al. 2006, Royle et al. 2007) When trait data was missing for a species, we referred to a regional mammal field guide (Brown 1997), the species accounts of the IUCN List of Threatened Species (<https://www.iucnredlist.org/>), or other pertinent literature. As a measure of fecundity, we multiplied average litter size by number of litters per year obtained from Jones et al. (2009).

Python density estimates

We obtained the most comprehensive measure of relative python density for the time period before 2014, when mammal surveys were conducted. At each survey site, we extracted relative python density estimates (pythons km⁻²) generated by the Reaction–Diffusion model of Bonneau et al. (2016). This model combined distance to the assumed python invasion epicentre and 15 years of opportunistic presence-only python data to estimate variation in relative python density throughout south Florida. While these model predictions were an imperfect representation of the density of python, perfect information does not exist and the predictions appear to correspond well with anecdotal observations and perceptions of spatial variation in python abundance across the region.

Visual obstruction index

We used averaged Robel pole (Robel et al. 1970) measurements as a covariate describing visual obstruction in our model of camera and faecal count detection probability. This covariate is a common measure used to quantify the potential for vegetation to obstruct the view of camera traps (Soto-Shoender et al. 2018). Measurements were taken at 5 points per survey site. The first point was located at the centre of the site and the following four measurements were taken from four cardinal directions at 10-m away from

the centre. A mean visual obstruction index per survey site was obtained by averaging the measurements across the 5 points.

Modelling framework

We used a Bayesian hierarchical formulation of a multi-species occupancy model (e.g. Royle and Kery 2007) to evaluate the influence of species traits on the species-specific responses of mammals to python densities (Brown et al. 2014). There are several key advantages of this modeling approach for our purpose. Firstly, the occupancy modeling approach allows for the explicit estimation of detection probability, providing a means to overcome the problematic assumption of perfect and constant detection (MacKenzie et al. 2018). Secondly, the explicit modeling of the detection process allows us to integrate multiple sampling methods into a single unified analysis, increasing detection opportunities across a variety of mammal species and environmental conditions, and thus increasing the resolution of our analysis (Isaac et al. 2020). Lastly, we structured our model with several hierarchical layers that allow for the separation of community-level processes from species-level processes (Gelman et al. 2004). The advantage of modeling this community-level layer, in our context, is the potential for increased precision of species-level parameters due to sharing of information across species (often referred to as “borrowing power”, Gelman et al. 2004) and a decrease in the probability of spurious results for species with sparse data due to the natural model regularization that occurs for random effects (often referred to as “Bayesian shrinkage”, Link and Saur 1996; Saur and Link 2002; Gelman et al. 2004). In addition to improved parameter estimates, the community-level layer provides a natural framework to evaluate the interaction between species traits and environmental characters on the distribution of species, increasing the transferability of our results from observed mammal species to unobserved mammal species (Yates et al. 2018; Regos et al. 2019).

Model structure

We modeled species occurrence as a latent binary random effect that is distributed as, $z_{ij} \sim \text{Bernoulli}(\psi_{ij})$, where the parameter ψ_{ij} is the

probability of occurrence for species i at location j . When the parameter $z_{ij} = 1$, species i occurred at site j , and when $z_{ij} = 0$, it did not. The detection of the species was then modeled as the result of multiple binomial draws for each of the three sampling methods employed in our study as, $y_{ijm} \sim \text{Binomial}(p_{ijm}z_{ij}, k_m)$, where our data, y_{ijm} is the sum of detections of species i at site j with sampling method m and can range between zero and the number of replicate samples collected with sampling method m (i.e. k_m). The parameter p_{ijm} is the detection probability of species i at site j with sampling method m that is conditional on the species being present (i.e. $z_{ij} = 1$). The term $p_{ijm}z_{ij}$ represents the unconditional detection probability and is the explicit link between the occurrence state sub-model and the detection sub-model because $p_{ijm}z_{ij}$ takes the value of zero if the species is not present and the value of p_{ijm} when the species is present.

We incorporated the single covariate, python density, into our occurrence sub-model with a logit link as:

$$\text{logit}(\psi_{ij}) = b0_i + b1_i D_j \tag{1}$$

where β_0_i is the species-specific intercept, which represents the mean of the logit-scale species-specific occurrence probability across sites. The parameter β_1_i is a slope parameter representing the effect of modeled python density (D_j) on the occurrence probability of species i , where negative values indicate that the species' occurrence decreases as python density increases and a positive value indicates that species' occurrence increases as python density increases.

To account for the fact that differences in vegetation density and body size may influence species-specific detection probabilities across sites (O'Connell et al. 2006), we incorporated covariates for visual obstruction at sites (VO_j) and body mass of species (M_i) into the detection sub-model for camera trapping. To increase the transferability of rodent trap detection probabilities to the smaller unobserved species (i.e. Key Largo woodrat, *Neotoma floridana smalli*), we included a binary covariate indicating when the average adult mass was less than 250 g (M'_i). We incorporated these covariates into the detection sub-models with a logit link as:

$$\text{logit}(p_{ijm=1}) = \gamma 0_i + \gamma 1 VO_j + \gamma 2 M_i \text{ (m = 1, indicating camera trapping surveys)} \tag{2}$$

$$\text{logit}(p_{ijm=2}) = \varphi 0_i + \varphi 1 VO_j \text{ (m = 2, indicating scat surveys)} \tag{3}$$

$$\text{logit}(p_{ijm=3}) = \eta 0_i + \eta 1 M_i \text{ (m = 3, indicating rodent surveys)} \tag{4}$$

where $\gamma 0_i$, $\varphi 0_i$, and $\eta 0_i$ represent the species-specific intercept for each sampling method (i.e. average species-specific detection probability with each sampling method) and $\gamma 1 - \gamma 2$, $\varphi 1$, and $\eta 1$ represents the influence of covariates on the respective detection probability per method.

We modeled the community hierarchical layer by either specifying the species-level parameters as random effects or the result of fixed-effect covariate relationships. Specifically, we modeled the intercepts of the occurrence sub-model ($\beta 0_i$) and detection sub-models (i.e. $\gamma 0_i$, $\varphi 0_i$, and $\eta 0_i$) as random effects drawn from community-level hyper distributions ($\theta_i \sim \text{Normal}(\mu, \sigma)$), where θ_i represents any of the species-level parameters previously listed (i.e. $\beta 0_i, \gamma 0_i, \varphi 0_i$, and $\eta 0_i$) and μ and σ are hyperparameters that represent the community mean and standard deviation of the species-level parameters. This structure allows for mean occurrence to vary among species and mean detection probability to vary among species and sampling methods. We specified the effects of visual obstruction and body mass on detection as fixed effects that are shared among species.

We evaluated the influence of species traits on mammal response to pythons by modeling the species-level python effects on species occupancy ($\beta 1_i$) as a function of a linear combination of species life-history trait covariates. This is equivalent to modeling occurrence probability as a function of environmental character (i.e. relative python density), species traits (life-history characteristics), and the interaction between the two (Brown et al. 2014; Hui et al. 2015). The species traits were incorporated into the model as fixed effects as:

$$b1_i = \zeta 0 + \zeta 1 M_i + \zeta 2 F_i + \zeta 3 HR_i + \zeta 4 A Q_i + \zeta 6 AB_i + \zeta 7 HB_i \tag{5}$$

where ζ_0 represents the intercept (i.e. the average python effect across species) and $\zeta_1 - \zeta_7$ represent the influence of the trait on the response of the mammal species to pythons (where M_i = mass; F_i = fecundity; HR_i = home range; AQ_i = association to aquatic habitats; AB_i = arboreality; and HB_i = habitat breadth).

Model fit evaluation

We used a Bayesian p-value to evaluate model fit of the full model for each species (Kery 2010). The Bayesian p-value is a posterior-predictive check that provides a measure of over or under dispersion of the data relative to the model. We perform the model fit procedure by simulating data directly from the model for each Markov Chain Monte Carlo iteration. We then calculate a Pearson residual to measure the discrepancy between the data (simulated and observed) and the model expectation. The Pearson residual was calculated as, $[(o-e)/\sigma^2]$, where o is either the observed or simulated number of detections, e is the expected value (i.e. $e = k_m p_{ijm}$), and σ^2 is the variance of e [i.e. $\sigma^2 = k_m p_{ijm}(1-p_{ijm})$]. The simulated data are considered “perfect” because they are generated directly from the model and, thus, the resultant Pearson residual represents the fit of the model when all model assumptions are perfectly met (Kery 2010). We then obtained a fit metric that is equal to one when the Pearson residual was greater for the observed data than the simulated data and is equal to zero, otherwise. The Bayesian p-value was then calculated as the mean of the posterior sample of the fit metric for each species, where values between 0.05 and 0.95 indicate adequate fit and a mean of 0.5 indicates perfect model fit.

Model selection

To prevent model overfitting, we employed a Bayesian model reduction procedure called Stochastic Search Variable Selection (SSVS, George and McCullock 1993). The use of the SSVS method to produce models with desirable predictive properties was first introduced by George and McCullock (1993) but has been thoroughly discussed in more recent ecological literature (O’Hara and Sillanpää 2009; Tenan et al. 2014; Hooten and Hobbs 2015). The SSVS method invokes

parameter shrinkage by using a hierarchical structure for the covariate effects that is conditional on a random-effect inclusion parameter (i.e. w_c). Each covariate is multiplied by its associated inclusion parameter (e.g. $w_1 \zeta_1$ *mass*), which is a latent Bernoulli variable with uninformative prior probabilities equal to 0.5 ($w_i \sim \text{Bernoulli}(0.5)$, equal probability of covariate being included or excluded in the model). The posterior probability of this parameter is interpreted as the probability that a covariate is included in the optimal predictive model. Barbieri and Berger (2004) demonstrated that a single model that includes covariates with inclusion probabilities ≥ 0.5 will have optimal predictive properties; however, the full model, including all covariates and inclusion parameters will produce model averaged posterior distributions and model predictions. Thus, we evaluated support for the species trait covariates with both the inclusion probabilities and summaries of the model averaged posterior distributions. We considered a covariate ‘important’ when its inclusion probability ≥ 0.5 , and when the model averaged 95% Bayesian credible intervals did not overlap zero (but may be bounded by zero).

Priors and model specifications

We applied uninformative student t-distributions as priors for logit-scale parameters (i.e., covariate parameters used in the occupancy, detection, and life-history trait models) with $\sigma = 1.57$ and $\nu = 7.763$ as per Gelman (2007) such that back-transformed values assigned equal probability for all values between zero and one. We applied mildly informative half student t-distributions as priors on all variance hyperparameters with $\sigma = 1.8$ and $\nu = 2$. These priors were used to stabilize the MCMC procedure while having negligible influence on the shape of the posterior distributions. We fit our models using software JAGS (Plummer 2003) and R (R Development Core Team 2011). We ran two parallel chains with 100,000 iterations, after a burn-in of 50,000 iterations and a thinning rate of 10. We assessed convergence using the Gelman-Rubin diagnostic where an estimate > 1.1 indicates low convergence rates between chains (Brooks and Gelman 1998).

Results

We detected 18 species, 12 with camera traps, seven with scat surveys, and four with rodent traps (Table 2). Average occupancy probabilities ranged from 0.01 (coyote [*Canis latrans*]) to 0.49 (white-tailed deer [*Odocoileus virginianus*], Fig. 2a). Occupancy probabilities for four species were > 0.30 (white-tailed deer, raccoon [*Procyon lotor*], marsh rabbit [*Sylvilagus palustris*], and Virginia opossum [*Didelphis virginiana*]), while all other values were < 0.20 (Fig. 2a). Model parameters converged satisfactorily (all GR statistics < 1.1 ; range = 1.00–1.01) and the Bayesian p-values indicated adequate model fit for all observed species (range = 0.23–0.61; Table 2).

Detection probabilities varied considerably among species and sampling methods (Fig. 3). Camera traps yielded the highest detection rates for the greatest

number of species and was the least variable among species. For example, the lowest detection probability was 0.01 for striped skunk (*Mephitis mephitis*), while the highest was 0.1 for raccoon (Fig. 3a). Alternatively, detection probabilities with scat surveys was limited to a few species and was highly variable between species ranging from 0.02 (striped skunk) to 0.47 (marsh rabbit, Fig. 3c). Rodent traps yielded detection rates $> 50\%$ for 4 rodent species but none of the other mammals in the study (Fig. 3b). We did not detect any relationship between visual obstruction and detection with camera traps, nor did we detect any relationship between the average adult body mass and camera detection (all parameter 95% credible intervals included zero and parameter inclusion probabilities were < 0.5). Alternatively, detection with rodent traps was significantly higher for species with lower adult

Table 2 Summary of sampling sites and model fit per species

Species	Number of sites detected			Bayesian <i>p</i> -value
	Camera	Rodent traps	Scat surveys	
Observed species				
Big Cypress fox squirrel	1	0	0	0.49
Black rat	0	8	0	0.61
Bobcat	8	0	0	0.39
Cotton mouse	0	16	0	0.52
Cotton rat	0	12	0	0.58
Coyote	1	0	0	0.44
Eastern gray squirrel	2	0	0	0.37
Florida black bear	2	0	0	0.24
Florida panther	0	0	1	0.29
Marsh rabbit	22	0	30	0.49
Nine-banded armadillo	1	0	0	0.24
Raccoon	32	0	3	0.49
Rice rat	0	22	0	0.45
River otter	1	0	0	0.23
Round-tailed muskrat	0	0	1	0.23
Striped skunk	1	0	1	0.33
Virginia opossum	14	0	1	0.46
White-tailed deer	33	0	14	0.35
Unobserved species				
Everglades mink	0	0	0	0.29
Feral hog	0	0	0	0.23
Gray fox	0	0	0	0.29
Red fox	0	0	0	0.28
Key Largo woodrat	0	0	0	0.01

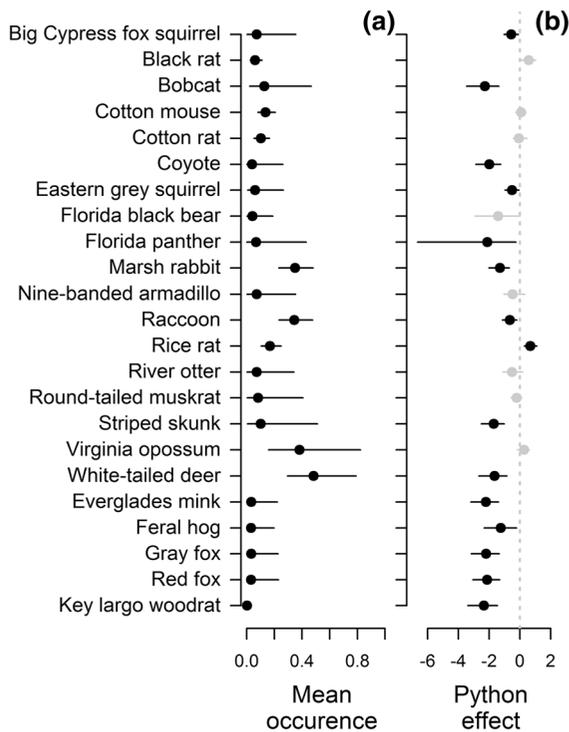


Fig. 2 **a** Average species-specific occupancy probabilities and their 95% Bayesian credible intervals across the study site obtained from mammal surveys in the Greater Everglades Ecosystem (November to April 2014); **b** Effect of relative python density on species-specific occupancy probability. The black dots and bars indicate that the python effect estimate is statistically different than zero

mass (i.e. < 250 g, $\eta_1 = 6.95$, 95% CI = [5.72, 8.32], $w = 1.00$).

Python density had a negative and relevant (i.e. 95% CI did not include 0) association with the occupancy estimates for 10 species (Fig. 2b). Some of the most common species such as white-tailed deer, marsh rabbit and bobcat (*lynx rufus*) showed the strongest responses to increasing relative python densities, all declining from occurrences of > 0.40 in areas with reduced relative densities to < 0.05 in areas with greater relative densities of pythons (Fig. 4). Of the other common species, raccoons declined but still occurred > 0.10 in the areas of highest relative python density and Virginia opossums did not respond to the gradient of relative python density (Fig. 2b). Like Virginia opossums, rodent species appeared less susceptible to pythons. We found that black rats (*Rattus rattus*), cotton mice (*Peromyscus gossypinus*) and cotton rats (*Sigmodon*

hispidus) were not influenced by the relative density of pythons and that rice rats increased with the relative density of pythons (Fig. 2b, Fig. 4). Examining six mammal traits we found that three (mass, fecundity, and habitat breadth; Table 3; Fig. 5) influenced the effect of pythons on mammal occurrence probability, with model inclusion probabilities > 0.5 (Table 3). Our results suggest species that were larger, use more habitats and/or had high reproductive rates were less susceptible to increasing python densities. Finally, for mammals of conservation or management concern that went undetected in the study (i.e. Everglades mink, feral hog (*Sus scrofa*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*) and Key largo woodrat), our results suggest they all have the potential for negative associations with relative python density (Fig. 2b).

Discussion

There is little doubt that the mammal communities of the GEE are being reshaped and degraded by invasive Burmese pythons. Like previous work we have found sharp reductions in the occurrence of common meso-mammals across a gradient of relative python density (Dorcas et al. 2012; Sovie et al. 2016; Reichert et al. 2017). However, we also found some mammal species appeared unaltered by the prevalence of pythons, and at least one rodent appeared to increase with the increasing relative density of pythons. Additionally, we showed how the variability in mammals' response to the gradient of relative python density can be explained by mammalian traits. Specifically, we found increased mass, habitat breadth, and fecundity all corresponded with decreased susceptibility to invasive pythons. Through the evaluation of traits, we are able to suggest mechanistic explanations for species declines (Reichert et al. 2017) and predicted the response of undetected species, in an effort to focus future conservation and management efforts.

We found that highly fecund species that can use multiple habitats (i.e. black rats, Virginia opossums) appeared most resilient, while specialized species with reduced reproductive capacity [i.e. bobcat, Everglades mink (*Neovison vison evergladensis*)] appeared vulnerable to invasive pythons. Fecundity is considered an adaptive trait to high mortality (Read and Harvey 1989) and our results suggest it had strong association

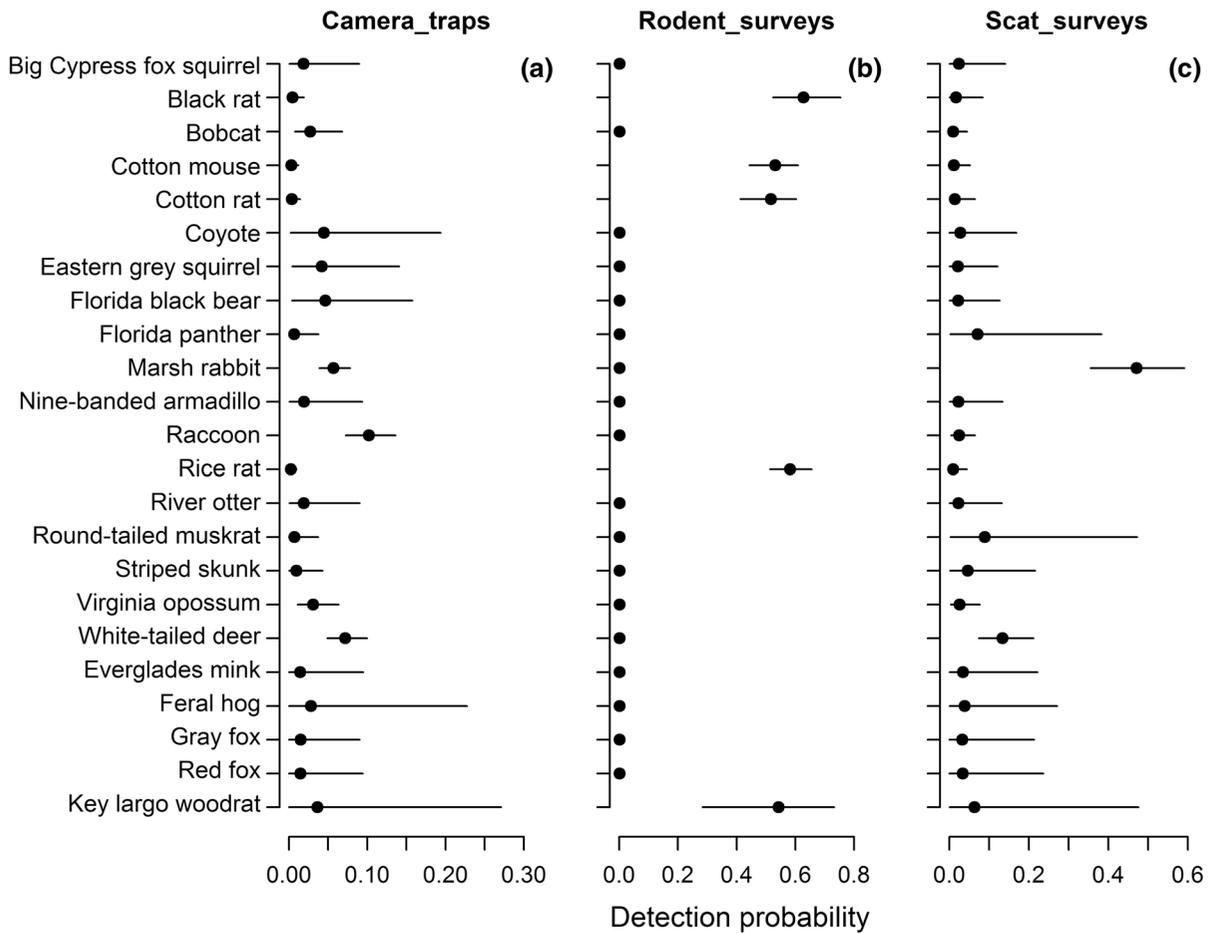


Fig. 3 Mean capture probability of each species with each sampling method

with reduced susceptibility to pythons. Rodents were the most fecund mammals in our study, some of which were capable of producing > 20 young annually (Brown 1997). Fecund rodents can breed year-round in south Florida (Brown 1997), and may be able to bolster their populations during colder periods when the risk of python predation is reduced (McCleery et al. 2015). While high fecundity enhances rodents’ resilience to predation pressures, it may also result in a stable food source for pythons in areas without other mammal species. This phenomenon is analogous to invasive brown treesnake (*Boiga irregularis*) populations, on Guam, that are sustained by rodents and lizards in areas where avifauna have been extirpated (Fritts and Rodda 1998).

Greater habitat breadth of mammals has been associated with resilience to environmental stressors (Devictor et al. 2008; Smith and Reeves 2012).

Accordingly, mammals with greater habitat breadth in our study showed a reduced response to increased relative densities of pythons. Increased habitat breadths of mammals in the GEE, a large freshwater wetland, is effectively a measure of mammals’ ability to use upland and arboreal habitats as well as aquatic ones. Many prey species alter their habitat use when faced with an increased risk of predation (Creel and Christianson 2008). Habitat generalists’ ability to use areas other than the wet environments, favored by pythons (Mutascio et al. 2018), may help them persist when python densities increase.

Pythons have the capacity to consume large-bodied species (Dorcas et al. 2012; Boback et al. 2016), and larger pythons that are not gape limited are likely to select larger prey (Shine 1991). Nonetheless, we found that larger mammals (e.g., white-tailed deer, coyote) appeared more resilient to pythons than smaller

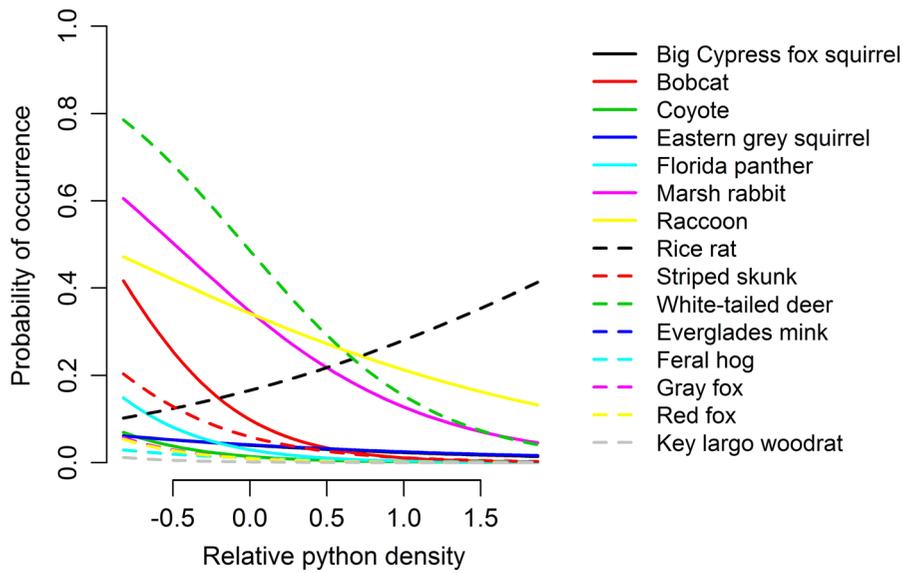


Fig. 4 Predicted species-specific occupancy probability as a function of python density, only species with relevant effects (i.e. 95% CI did not include 0) were included. Everglades mink,

feral hog, gray fox, red fox, and Key largo woodrat were not detected during survey and modelled as a function of data augmentation

Table 3 Parameter posterior summaries and model selection results for the interaction of species traits with the effect of python density

Species trait	Posterior mean	95% CI	Inclusion probability
Mass	0.293	0.000, 0.897	0.581
Habitat	1.708	1.020, 2.528	1.000
Fecundity	0.431	0.149, 0.696	0.987
Arboreal	- 0.136	- 0.799, 0.000	0.332
Aquatic	- 0.004	- 0.308, 0.246	0.141
Home range	- 0.058	- 1.060, 0.374	0.219

mammals. The increased resilience of larger mammals supports the hypothesis that an animal’s susceptibility to predation during predator encounters decreases with size (Greene 1986). However, it is also possible that pythons avoid larger prey because consuming large prey makes snakes more vulnerable to predation due to the slow digestion process (Siers et al. 2018). While large mammals were more resilient than smaller mammals, they still appeared to decrease with increasing relative densities of pythons (Dorcas et al. 2012; Reichert et al. 2017). These declines may be a function of direct predation or pythons indirectly altering the distributions of larger mammalian predators by depleting their prey species (McCleery et al. 2015).

With our model, we applied estimated relationships between mammal species traits and detections to

predict the distribution of both observed and unobserved mammal species relative to pythons. This extrapolation required two important assumptions, first, that species traits accurately predict the python effects for observed species, and, second, that these relationships are transferable to the component of the mammal community that was not observed in our samples. Several lines of evidence suggest that these assumptions were adequately met. Firstly, a comparison of the python effect estimates generated with our model to an analogous model, that specifies the species-level python effects as random effects (i.e. $\beta_{1i} \sim \text{Normal}(\mu, \sigma)$), as opposed to predicting with species traits), resulted in similar point estimates and similar conclusions (Supplementary Material Fig. S1). The Pearson correlation coefficient between the python point estimates of the models was 0.64,

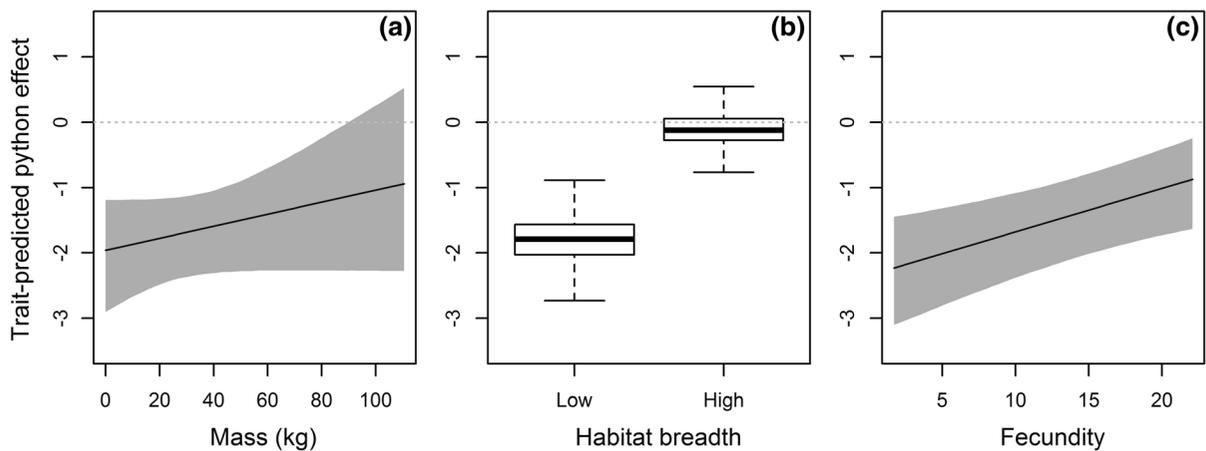


Fig. 5 Graphic depictions of the relationship between the values of mammal species traits (x-axis) and the response to pythons (y-axis, i.e. trait-predicted effect estimates for β_{1i} of Eq. 1 and 5 of the main text). A value on the y-axis of 0 indicates no relationship between mammal species occurrence and

however, when we remove the three mammal species with the greatest discrepancy between point estimates (i.e. Virginia opossum, Florida panther, coyote), the correlation coefficient increased to 0.85 (Supplementary Material Fig. S2). Furthermore, using deviance information criterion to compare the predictive performance of the models (Spiegelhalter et al. 2002) suggested that the trait-based model was the most parsimonious and thus the better model (DIC of trait-based model = 1789.92 and DIC of random-effect model = 1877.31). That the python effect estimates are transferable to the unobserved component of the mammal community is an untestable assumption, in our context. However, using trait-based approaches to enhance transferability is strongly supported in the ecological literature because these approaches account for the mechanistic processes driving species distributions (Brown et al. 2014; Yates et al. 2018; Regos et al. 2019).

By augmenting our data with undetected species, we were able to generate predictions for species that were rare or outside of the sampled area. This ability to generalize beyond observed patterns is important because it allows managers to prioritize proactive conservation actions by leveraging available data. Specifically, our finding suggests that some of the rarer (i.e. Key Largo woodrat, Everglades mink) mammals in the GEE may be particularly vulnerable to pythons. Another advantage of our trait-based approach is that

relative python density, while values less than or greater than zero indicate a predicted decline or increase in mammal occurrence with increasing relative python density, respectively. Python effect predictions were made with Eq. 5 in the main text

it can be used to fill important knowledge gaps by predicting the responses of native communities to invasive predators (Ricciardi et al. 2013; Shackelford et al. 2013; Simberloff 2014). Our study provides a preliminary understanding of how the variability in prey traits can be linked to invasive predators. We linked mass, habitat breadth and fecundity of mammals to vulnerability to invasive Burmese pythons and suggest these traits should be examined in other mammal communities invaded by non-native predators.

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Compliance with ethical standards

Conflicts of interest The authors declare they have no conflicts of interest.

Ethical approval The project was carried out with ethical approval under Research Permit EVER-2012-SCI-0038, BICY-00110, FWC_LSSC-12- 00039, University of Florida Institution Animal Care and Use Committee #201509012.

References

- Barbieri MM, Berger JO (2004) Optimal predictive model selection. *Ann Stat* 32:870–897
- Barker DG, Barker TM (2008) The distribution of the Burmese python, *Python molurus bivittatus*. *Bull Chic Herp Soc* 43:33–38
- Boback SM, Snow RW, Hsu T, Peurach SC, Dove CJ, Reed RN (2016) Supersize me: remains of three white-tailed deer (*Odocoileus virginianus*) in an invasive Burmese python (*Python molurus bivittatus*) in Florida. *Biol Invasions Recs* 5:197–203
- Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations. *J Comput Graph Stat* 7:434–455
- Brown AM, Warton DI, Andrew NR, Binns M, Cassis G, Gibb H (2014) The fourth-corner solution—using predictive models to understand how species traits interact with the environment. *Methods Ecol Evol* 5:344–352
- Brown LN (1997) A guide to the mammals of the Southeastern United States. The University of Tennessee Press, Knoxville
- Bonneau M, Johnson FA, Romagosa CM (2016) Spatially explicit control of invasive species using a reaction–diffusion model. *Ecol Model* 337:15–24
- Ceradini JP, Chalfoun AD (2017) Species’ traits help predict small mammal responses to habitat homogenization by an invasive grass. *Ecol App* 27:1451–1465
- Creel S, Christianson D (2008) Relationships between direct predation and risk effects. *Trends Ecol Evo* 23:194–201
- Della Venezia L, Samson J, Leung B (2018) The rich get richer: invasion risk across North America from the aquarium pathway under climate change. *Divers Distrib* 24:285–296
- Devictor V, Julliard R, Jiguet F (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* 117:507–514
- Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. *Proc Natl Acad Sci USA* 113:11261–11265
- Doherty TS, Dickman CR, Johnson CN, Legge SM, Ritchie EG, Woinarski JC (2017) Impacts and management of feral cats *Felis catus* in Australia. *Mammal Rev* 47:83–97
- Dorazio RM, Royle JA (2005) Estimating size and composition of biological communities by modeling the occurrence of species. *J Am Stat Assoc* 100:389–398
- Dorazio RM, Royle JA, Söderström B, Glimskär A (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854
- Dorcas ME, Pittman SE, Willson JD (2017) Burmese Pythons. In: Pitt WC, Beasley J, Witmer GW (eds) *Ecology and Management of Terrestrial Vertebrate Invasive Species in the United States*. CRC Press, Boca Raton, pp 135–162
- Dorcas ME, Willson JD, Reed RN, Snow RW, Rochford MR, Miller MA, Meshaka WE, Andreaedis PT, Mazzotti FJ, Romagosa CM, Hart KM (2012) Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proc Natl Acad Sci USA* 109:2418–2422
- Dove CJ, Snow RW, Rochford MR, Mazzotti FJ (2011) Birds consumed by the invasive Burmese python (*Python molurus bivittatus*) in Everglades National Park, Florida, USA. *Wilson J Ornithol* 123:126–131
- Ehrenfeld JG (2011) Ecosystem consequences of biological invasions. *Annu Rev Ecol Evol Syst* 41:59–80
- Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annu Rev Ecol Evol Syst* 29:113–140
- Gelman A, Carlin JB, Sterns HS, Rubin DB (2004) Bayesian data analysis. Chapman and Hall, Boca Raton
- George EI, McCollock RE (1993) Variable selection via Gibbs sampling. *J Am Stat Assoc* 88:881–889
- Greene CH (1986) Patterns of prey selection: implications of predator foraging tactics. *Am Nat* 128:824–839
- Holbrook J, Chesnes T (2011) An effect of Burmese pythons (*Python molurus bivittatus*) on mammal populations in southern Florida. *Fla sci* 74:17–24
- Hooten MB, Hobbs NT (2015) A guide to Bayesian model selection for ecologists. *Ecol Monogr* 85:3–28
- Hoyer IJ, Blosser EM, Acevedo C, Thompson AC, Reeves LE, Burkett Cadena ND (2017) Mammal decline, linked to invasive Burmese python, shifts host use of vector mosquito towards reservoir hosts of a zoonotic disease. *Biol Lett* 13:20170353
- Hui FK, Taskinen S, Pledger S, Foster SD, Warton DI (2015) Model-based approaches to unconstrained ordination. *Methods Ecol Evol* 6:399–411
- Isaac NJ, Jarzyna MA, Keil P, Dambly LI et al (2020) Data integration for large-scale models of species distributions. *Trends Ecol Evol* 35:56–67
- Jones KE, Bielby J, Cardillo M et al (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648
- Kery M (2010) Introduction to WinBUGS for Ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, Burlington
- Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol Lett* 10:937–944
- Link WA, Sauer JR (1996) Extremes in ecology: avoiding the misleading effects of sampling variation in summary analyses. *Ecology* 77:1633–1640
- Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion ecology. Blackwell Publishing, Oxford
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol App* 10:689–710
- MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2018) Occupancy estimation and modeling, 2nd edn. Elsevier, Amsterdam
- MacLean SA, Beissinger SR (2017) Species’ traits as predictors of range shifts under contemporary climate change: a review and meta-analysis. *Glob Change Biol* 23:4094–4105

- McCleery RA, Zweig CL, Desa MA, Hunt R, Kitchens WM, Percival HF (2014) A novel method for camera-trapping small mammals. *Wildl Soc B* 38:887–891
- McCleery RA, Sovie A, Reed RN, Cunningham MW, Hunter ME, Hart KM (2015) Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. *Proc R Soc B*. <https://doi.org/10.1098/rspb.2015.0120>
- Meshaka WE, Loftus WF, Steiner T (2000) The herpetofauna of Everglades National Park. *Fl Sci* 63:84–102
- Mutascio HE, Pittman SE, Zollner PA, D'Acunto LE (2018) Modeling relative habitat suitability of southern Florida for invasive Burmese pythons (*Python molurus bivittatus*). *Landsc Ecol* 33:257–274
- Nock CA, Vogt RJ, Beisner BE (2016) Functional traits. In: eLS, Wiley, Chichester. <https://doi.org/10.1002/9780470015902.a0026282>
- O'Connell AF, Talancy NW, Bailey LL, Sauer JR, Cook R, Gilbert AT (2006) Estimating site occupancy and detection probability parameters for meso- and large mammals in a coastal ecosystem. *J Wildl Manage* 70:1625–1633
- O'Hara RB, Sillanpää MJ (2009) A review of Bayesian variable selection methods: what, how and which. *Bayesian Anal* 4:85–117
- Okes NC, Hocke PA, Cumming GS (2008) Habitat use and life history as predictors of bird responses to habitat change. *Conserv Biol* 22:151–162
- Plummer M (2003) JAGS: a program for analysis of bayesian graphical models using gibbs sampling. In: Leisch F, Zeileis A (eds) Proceedings of the 3rd international workshop on distributed statistical computing, Vienna, Austria
- Development Core Team R (2011) R: a language and environment for statistical computing. R Foundation for statistical computing, Vienna
- Rahman SC, Jenkins CL, Trageser SJ, Rashid SMA (2014) Radio-telemetry study of Burmese python (*Python molurus bivittatus*) and elongated tortoise (*Indotestudo elongata*) in Lawachara National Park, Bangladesh: a preliminary observation. In: Khan MAR, Ali MS, Feeroz MM, Naser MN (eds) The Festschrift of the 50th Anniversary of the IUCN Red List of Threatened Species. UCN, International Union for Conservation of Nature, Dhaka, pp 54–62
- Raubenheimer D, Simpson SJ (2003) Nutrient balancing in grasshoppers: behavioural and physiological correlates of dietary breadth. *J Exp Biol* 206:1669–1681
- Read AF, Harvey PH (1989) Life history differences among the eutherian radiations. *J Zool* 219:329–353
- Regos A, Gagne L, Alcaraz-Segura D, Honrado JP, Domínguez J (2019) Effects of species traits and environmental predictors on performance and transferability of ecological niche models. *Sci Rep* 9:4221
- Reichert BE, Sovie AR, Udell BJ, Hart KM, Borkhataria RR, Bonneau M, Reed R, McCleery R (2017) Urbanization may limit the impacts of an invasive predator on native mammal diversity. *Divers Distrib* 23:355–367
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecol Monogr* 83:263–282
- Robel RI, Briggs JN, Dayton AD, Hulbert LC (1970) Relationships between visual obstruction measurements and weight of grassland vegetation. *J Range Manage* 23:295–297
- Royle JA, Kéry M (2007) A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 88:1813–1823
- Royle JA, Dorazio RM, Link WA (2007) Analysis of multinomial models with unknown index using data augmentation. *J Comput Graph Stat* 16:67–85
- Sauer JR, Link WA (2002) Hierarchical modeling of population stability and species group attributes using Markov Chain Monte Carlo methods. *Ecology* 83:1743–1751
- Shackelford N, Hobbs RJ, Heller NE, Hallett LM, Seastedt TR (2013) Finding a middle-ground: the native/non-native debate. *Biol Conserv* 158:55–62
- Schmidt JA, McCleery RA, Schmidt PM, Silvy NJ, Lopez RR (2011) Population estimation and monitoring of an endangered lagomorph. *J Wildl Manage* 75:151–158
- Shine R (1991) Why do larger snakes eat larger prey items? *Funct Ecol* 5:493–502
- Siers SR, Yackel Adams AA, Reed RN (2018) Behavioral differences following ingestion of large meals and consequences for management of a harmful invasive snake: a field experiment. *Ecol Evol* 8:10075–10093
- Simberloff D, Martin JL, Genovesi P et al (2013) Impacts of biological invasions: what's what and the way forward. *Trends Ecol Evol* 28:58–66
- Simberloff D (2014) Biological invasions: What's worth fighting and what can be won? *Ecol Eng* 65:112–121
- Smith BD, Reeves RR (2012) River cetaceans and habitat change: generalist resilience or specialist vulnerability? *J Mar Biol* 2012:1–11
- Soto-Shoender JR, McCleery RA, Monadjem A, Gwinn DC (2018) The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. *Biol Conserv* 221:127–136
- Sovie AR, McCleery RA, Fletcher RJ, Hart KM (2016) Invasive pythons, not anthropogenic stressors, explain the distribution of a keystone species. *Biol Invasions* 18:3309–3318
- Spiegelhalter DJ, Best NG, Carlin BP, Van der Linde A (2002) Bayesian measures of model complexity and fit. *J R Statist Soc B* 64:583–639
- Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE (2003) Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Divers Distrib* 9:1–18
- Tenan S, O'Hara RB, Hendriks I, Tavecchia G (2014) Bayesian model selection: the steepest mountain to climb. *Ecol Model* 283:62–69
- Verberk WC, Van Noordwijk CGE, Hildrew AG (2013) Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshw Sci* 32:531–547
- Willson JD (2017) Indirect effects of invasive Burmese pythons on ecosystems in southern Florida. *J Appl Ecol* 54:2151–2125
- Yates KL, Bouchet PJ, Caley MJ, Mengersen K, Randin CF et al (2018) Outstanding challenges in the transferability of ecological models. *Trends Ecol Evol* 33:790–802

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