

Indirect effects of invasive Burmese pythons on ecosystems in southern Florida

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Summary

1. Invasive predators can dramatically alter ecosystems through both direct predation and indirect effects such as trophic cascades. However, most examples of top-down effects of invasive predators in terrestrial systems stem from islands or similar low-diversity ecosystems. Snakes are an emerging guild of damaging invasive predators, but demonstration of ecosystem-level impacts of invasive snakes are limited to the single case of the brown treesnake on Guam.

2. Invasive Burmese pythons are firmly established in southern Florida and have been linked to severe (80–100%) declines of several previously common mammal species (e.g. raccoons, opossums and rabbits). Specifically, spatiotemporal patterns of mammal declines in the Everglades mirror the spread of pythons and experimental reintroductions of rabbits to areas where they had been extirpated failed due to high (77% of mortalities) rates of predation by pythons.

3. I evaluated the potential indirect effects of pythons on the nesting success of oviparous species by monitoring artificial turtle nests ($N = 183$) at 13 sites across the expanding range of the python population. I documented few mammals and low rates of nest predation (average score = 1.5 on a 1–5 scale) in the southern Everglades where pythons have been established the longest, intermediate (average score = 2.3) rates of nest predation at recently invaded sites, and very high (average score = 4.6) rates of nest predation at sites with few or no pythons. These findings represent the first documentation of potential indirect effects of pythons on non-prey species, and suggest that loss or decline of mammals is resulting in trophic cascades that threaten the Everglades ecosystem.

4. *Synthesis and applications.* My results suggest that an introduction of non-native apex predators can result in trophic cascades that alter even complex, continental ecosystems. The Burmese python invasion of South Florida shows remarkable parallels with the catastrophic case of the brown treesnake in Guam, but in some ways is even more worrisome. Documentation of both strong direct impacts on prey and potential indirect effects on Everglades' ecosystems within 15 years after being recognized as established emphasizes the need to integrate python management into restoration of the Greater Everglades Ecosystem. More broadly, non-native snakes warrant significant attention for their potential to become damaging invasive species.

Key-words: alien species, apex predators, Everglades, meso-mammals, nest predation, non-native species, reptiles, snakes, top-down effects, trophic cascades

Introduction

Biological invasions are a primary driver of the current global biodiversity crisis, causing substantial and increasing ecological and economic damage world-wide

(Pimentel, Zuniga & Morrison 2000, 2005; Clout & Williams 2009). Invasive predators can reduce or extirpate populations of native prey (Gurevitch & Padilla 2004; Caut, Angulo & Courchamp 2008) and affect non-prey species indirectly through trophic cascades and other effects (Croll *et al.* 2005; Terborgh & Estes 2010; Estes *et al.* 2011). For example, spatial patterns of abundance

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suggest that predation by exotic mongoose *Herpestes javanicus* has reduced populations of native smaller predators (lizards, snakes and frogs) on Japanese islands, apparently leading to increased abundances of insects through release from predation (Watari, Takatsuki & Miyashita 2008). Such cascading effects are difficult to predict and measure, but have the potential to extend beyond single species to affect ecosystem processes such as energy and nutrient cycling, primary production, and decomposition rates (Terborgh & Estes 2010; Estes *et al.* 2011). Generally, diversity and complexity are thought to provide resistance against invasion and impacts from alien species (McCann 2000) and most cases of damaging terrestrial invasive predators have occurred on islands or similar low diversity systems (Lockwood, Hoopes & Marchetti 2009). Thus, the potential for invasive apex predators to indirectly influence native species remains untested in most systems.

Snakes represent an emerging threat as potentially damaging invasive predators (Kraus 2009). As ectotherms, snakes are champions of energetic efficiency (Pough 1980), allowing them to attain high densities in resource-rich environments (Gragg *et al.* 2007; Willson, Todd & Winne 2011), yet persist when prey resources are low (Reed *et al.* 2012). Accidental introduction of brown treesnakes, *Boiga irregularis*, to the Pacific island of Guam resulted in extirpation of most of the island's native forest birds and contributed to declines or extirpation of native bats and lizards (Savidge 1987; Rodda & Savidge 2007; Campbell *et al.* 2012).

The Burmese python, *Python molurus bivittatus*, a native of southern Asia and among the largest snakes in the world, is now firmly established over a large area of southern Florida, including all of Everglades National Park (ENP) (Dorcas & Willson 2011). Since recognition as a reproducing population in 2000 (Meshaka, Loftus & Steiner 2000; Snow *et al.* 2007), both the number of pythons found and their geographical range have expanded considerably. Pythons consume a wide range of vertebrate prey (principally mammals, large birds and their eggs, and American alligators) and have recently been linked to severe declines in several species of once-common mammals in ENP (Dorcas *et al.* 2012; McCleery *et al.* 2015). Spatiotemporal patterns of mammal-relative abundances are consistent with pythons as the cause of 85–100% declines in raccoons *Procyon lotor*, Virginia opossums *Didelphis virginiana*, bobcats *Lynx rufus*, rabbits *Sylvilagus palustris* and *Sylvilagus floridanus*, gray foxes *Urocyon cinereoargenteus*, and white-tailed deer *Odocoileus virginianus* (Dorcas *et al.* 2012). Recently, McCleery *et al.* (2015) directly linked mammal declines to python predation by monitoring the fate of marsh rabbits, *S. palustris*, translocated to regions of ENP where rabbits had not been seen in years, as well as to a control site at the periphery of the python invasion. Translocations failed to re-establish marsh rabbit populations in ENP and predation by pythons accounted for 77% of rabbit

mortality in ENP, whereas mammals were the primary predators (accounting for 68% of mortality) at the control site. Mammal declines linked to pythons are likely to have substantial indirect impacts on food webs and ecosystem function (Terborgh & Estes 2010) in southern Florida, but the nature and extent of these impacts remain unknown.

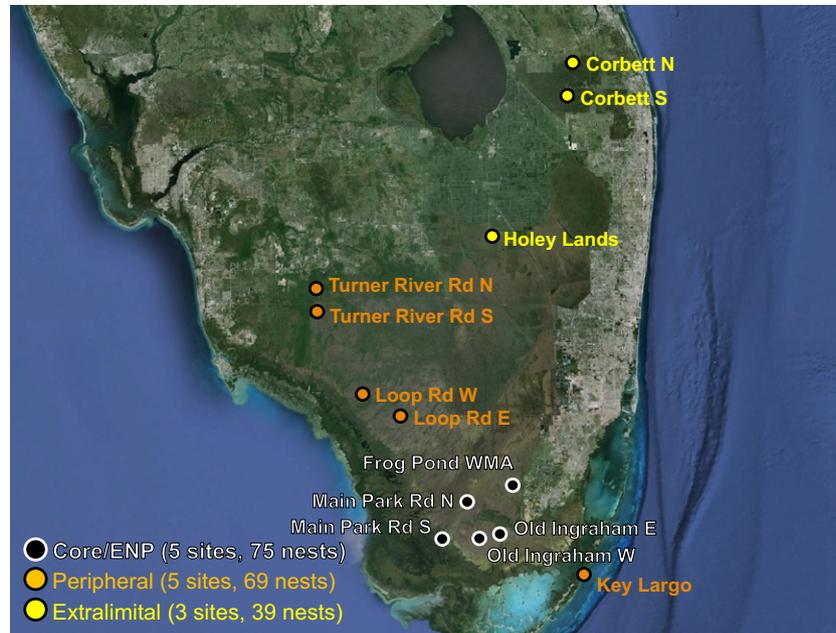
In this study, I provide the first evaluation of indirect effects of invasive pythons on southern Florida ecosystems. Specifically, I investigated whether predation rates on artificial turtle nests vary spatially in relation to the severity of python-associated declines of mammals. Turtles are a ubiquitous and vital part of many ecosystems, including those of the Everglades (Congdon, Greene & Gibbons 1986; Ernst & Lovich 2009). Raccoons, opossums and foxes are well known predators of reptile nests, and predation rates on turtle nests can often exceed 90% (Ernst & Lovich 2009). I tested the predictions that nest predation rates would be lowest in the southern part of ENP where pythons have been established the longest and mammals are now rare, moderately high in peripheral areas where mammal declines are less severe, and high in areas where pythons are not yet known to be established.

Materials and methods

To examine the effects of python-associated mammal declines on nest predation pressure, I monitored artificial turtle nests between May and July 2013 (nesting season for many freshwater turtles in the region). Artificial nests differ from natural turtle nests, and thus the results of this study should conservatively be considered as an indicator of the general strength of predation pressure by mammals, rather than as a quantitative index of turtle nest survival in nature. I constructed nests at 13 sites spanning the spatial gradient of the python invasion and corresponding with areas where mammal declines have been documented (Fig. 1; Dorcas & Willson 2011; Dorcas *et al.* 2012). I grouped sites into three treatments: (i) 'Core' areas where pythons have been established for the longest period of time [Main Park Rd and Old Ingraham Hwy in ENP; Frog Pond Wildlife Management Area (WMA)]; (ii) 'Peripheral' areas where pythons have been documented more recently [Loop Rd and Turner River Rd in Big Cypress National Preserve (BICY), Crocodile Lake National Wildlife Refuge on Key Largo]; (iii) 'Extralimital' areas where breeding python populations had not yet been confirmed (J.W. Corbett WMA, Holey Lands WMA). The mean distance among sites within treatment areas was 17.1 km for Core sites, 69.6 km for Peripheral sites and 53.0 km for Extralimital sites. Sites were selected to represent habitats suitable for turtle nesting; all nest locations were within 5 m of standing water and featured sparse vegetation and well-drained soil. Following these criteria, all sites were located in open or edge habitats along canals, ponds, and other relatively permanent water bodies. In many cases, sites had evidence of natural turtle nests and turtles were observed nesting in the vicinity of the artificial nests on multiple occasions.

I constructed artificial turtle nests by digging small holes (c. 15-cm deep and 10-cm wide) in which I buried four quail eggs (Marchand *et al.* 2002; Foley, Price & Dorcas 2012). At each site, I constructed four to five nest clusters, each consisting of three

Fig. 1. Study sites used to evaluate the effects of python-associated mammal declines on nesting success of freshwater turtles. Sites were grouped into three categories in relation to their location along the spatial extent of the python invasion of southern Florida: 'Core' sites where pythons have been established for the longest period of time (Main Park Rd and Old Ingraham Hwy in ENP; Frog Pond WMA); 'Peripheral' sites areas where pythons have been documented more recently (Big Cypress NP, Key Largo); 'Extralimital' areas where established python populations have not yet been confirmed (Corbett WMA, Holey Lands WMA). Each site contained four to five clusters of three artificial turtle nests monitored by a game camera. [Colour figure can be viewed at wileyonlinelibrary.com]



nests spaced 1 m apart. I monitored each cluster with a motion-sensitive wildlife camera (Model M880; Moultrie Feeders, Calera, AL, USA) placed to capture still photographs of animals visiting the nests throughout the day and night. Clusters were spaced at least 1 km apart to maintain independence. After backfilling nests with soil, I poured 500 mL of turtle-scented water on each nest, simulating a female turtle's habit of urinating on the nest site to ease excavation (Ernst & Lovich 2009). Water was scented by maintaining large female Florida softshell turtles *Apalone ferox* in approximately 19 L of water for 5 days. At all times during nest construction I wore latex gloves to reduce imparting human scent on the nest site.

I visited each site every other day for 14 days. During each visit I downloaded camera files and scored predation of each nest on a 1–5 scale: (1) no disturbance to nest at all; (2) disturbance to nest, but eggs not exposed; (3) disturbance to nest with eggs exposed; (4) some, but not all eggs eaten or missing; (5) all eggs eaten or missing. For each date, I averaged predation scores within each nest cluster (three nests) and then averaged cluster averages to obtain a grand average predation score for each site. For all analyses, I considered the site (four to five nest clusters) as the statistical unit, with a total replication of five core sites (75 nests), five peripheral sites (69 nests) and three extralimital sites (39 nests). One camera was stolen at an extralimital site.

I evaluated differences in mean nest predation score after 14 days among core, peripheral and extralimital regions using ANOVA, with site as the statistical unit and $\alpha = 0.05$. Nests in the core region suffered significant predation from crows *Corvus* sp. (see below), which have not been documented as prey of pythons (Reed & Rodda 2009; Dove *et al.* 2011). To restrict the analysis to nest predation by mammals, I excluded nest clusters ($N = 9$ clusters at three sites) where crows were the only potential nest predator captured on cameras (in most cases, crow predation could be confirmed in photos), and compared mean nest predation scores using ANOVA.

Three independent reviewers, blind to site identities and locations (treatments) reviewed all camera photos to identify

mammals and other potential nest predators (e.g. crows). The number of mammal and crow observations was totalled for each camera over the 14-day period. Observations were classified as separate observations if more than one individual was clearly identifiable or if >10 min elapsed between successive photographs. Although I did not mark or individually identify mammals, I have no reason to suspect that re-sighting rates of individual mammals differed substantially among sites and exploratory analyses using more conservative methods for enumerating mammal abundances (minimum number of individuals or presence/absence of species at each camera) did not substantially alter my conclusions about spatial variation in mammal populations.

As with nest predation, I considered the site (four to five nest clusters) as the statistical unit ($N = 5$ core sites, $N = 5$ peripheral sites and $N = 3$ extralimital sites). I evaluated differences in the mean number of mammal observations per nest cluster among core, peripheral and extralimital regions using ANOVA, with site as the statistical unit and $\alpha = 0.05$. I used linear regression to examine the relationship between the mean number of mammal observations per camera at each site with mean nest predation score, excluding nests predated by crows.

Results

I recorded a total of 520 independent mammal observations on 60 cameras monitoring 183 artificial turtle nests throughout southern Florida. A diverse array of mammal species was documented, including high observation rates of raccoons (224 observations) and Virginia opossums (109 observations), and moderate observation rates of white-tailed deer (67 observations), bobcats (47 observations), armadillos *Dasypus novemcinctus* (24 observations) and feral hogs *Sus scrofa* (20 observations). Rabbits ($N = 8$), Florida panthers *Puma concolor* ($N = 5$), domestic cats *Felis catus* ($N = 4$), coyotes *Canis latrans* ($N = 4$), black bears *Ursus americanus* ($N = 2$), river otters *Lontra*

canadensis ($N = 1$) and rodents ($N = 3$) were infrequently observed. Carnivorous mammals that are found (or were historically found) in mesic habitats of southern Florida, but were not recorded on cameras, included foxes *Vulpes vulpes* and *U. cinereoargenteus*, skunks *Mephitis mephitis* and mink *Mustela vison*.

Mean observation rates of mammals differed significantly among regions for raccoons (ANOVA; $F_{2,12} = 435.15$; $P < 0.001$), bobcats (ANOVA; $F_{2,12} = 18.00$; $P = 0.007$) and armadillos (ANOVA; $F_{2,12} = 9.23$; $P = 0.016$). Few mammals (only opossums, deer and rodents) were observed at 'Core' sites (Fig. 2). Peripheral sites had a higher incidence of mammal observations and higher diversity. The most common species observed at peripheral sites were deer, raccoons, opossums and bobcats, and two sites in the northern portion of BICY were the only sites where Florida panthers and black bears were recorded (see Table S1, Supporting Information). The only rabbit recorded at a peripheral site was on Key Largo (see Table S1). Extralimital sites had substantially higher rates of mammal observations, including very high numbers of raccoons, opossums, deer and bobcats. In most cases, each nest cluster at extralimital sites was visited by multiple mammals each night, with an average of 14.6 and 6.2 observations per camera for raccoons and opossums, respectively, over the 14-day period. Extralimital sites also had the highest incidences of rabbits, armadillos, feral hogs and coyotes. Several species of birds, especially herons and egrets (Ardeidae), crows *Corvus ossifragus* and *Corvus brachyrhynchos*, and wild turkeys *Meleagris gallopavo* were recorded. Most birds showed no clear geographical trend in observation rates. However,

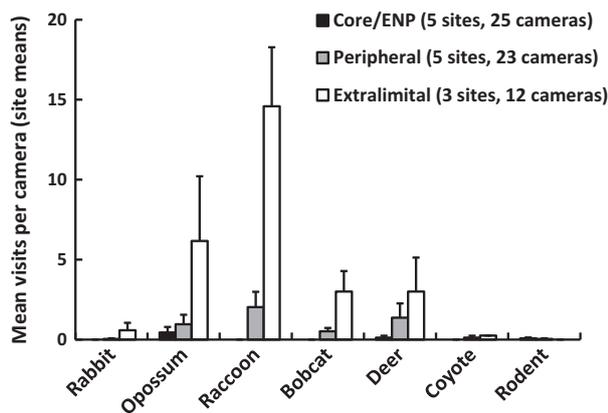


Fig. 2. Mean (± 1 SE) incidence of mammal observations on game cameras monitoring artificial turtle nests located at sites spanning the spatial extent of the python invasion of southern Florida: 'Core' sites where pythons have been established for the longest period of time (Main Park Rd and Old Ingraham Hwy in ENP; Frog Pond WMA); 'Peripheral' sites areas where pythons have been documented more recently (Big Cypress NP, Key Largo); 'Extralimital' areas where established python populations have not yet been confirmed (Corbett WMA, Holey Lands WMA). Mammals were classified as separate observations if more than one individual was clearly identifiable or if >10 min elapsed between successive photographs.

crows were observed much more frequently at core sites (mean = 7.1 observations per camera) than at peripheral (mean = 1.1 observations per camera) or extralimital sites (0 observations), and were particularly abundant along the Main Park Road in ENP (mean = 14.1 observations per camera; see Table S1; Fig. 4a).

Overall rates of nest predation increased over the 14-day period and differed significantly among regions (ANOVA; $F_{2,12} = 11.33$; $P = 0.002$). Nest predation scores were high at extralimital sites (Fig. 3a; mean = 4.6 by day 14), and moderate at both peripheral and core sites (mean = 2.3 and 2.8 respectively). Eleven of 13 nests at extralimital sites were completely predated, including all nests located in Holey Lands WMA, and all confirmed nest predators were mammals, primarily raccoons and opossums. Nest clusters along the Main Park Road in ENP were frequently predated by crows (Fig. 4b). After excluding nests predated by crows, predation rates differed even more strongly among regions (ANOVA; $F_{2,12} = 26.57$; $P < 0.001$) and were lowest at core sites (Fig. 3b; average score = 1.5), intermediate at peripheral sites (average score = 2.3) and highest at extralimital sites (average score = 4.6). At the site level, mean nest predation score (excluding predation by crows) was strongly correlated both with number of total mammal observations (Fig. 5; linear regression; $R^2 = 0.84$; $P < 0.001$) and the total number of raccoon and opossum observations (linear regression; $R^2 = 0.87$; $P < 0.001$).

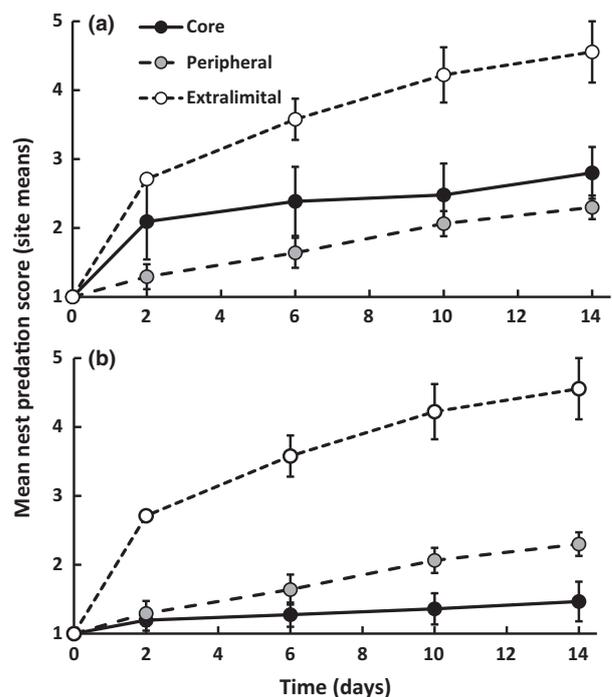


Fig. 3. (a) Mean (± 1 SE) rates of predation (scored on 1–5 scale) on artificial turtle nests located at sites spanning the spatial extent of the python invasion of southern Florida. (b) Predation rates on artificial turtle nests after excluding predation by crows by omitting nest clusters that were predated, but crows were the only potential nest predator recorded on game cameras.

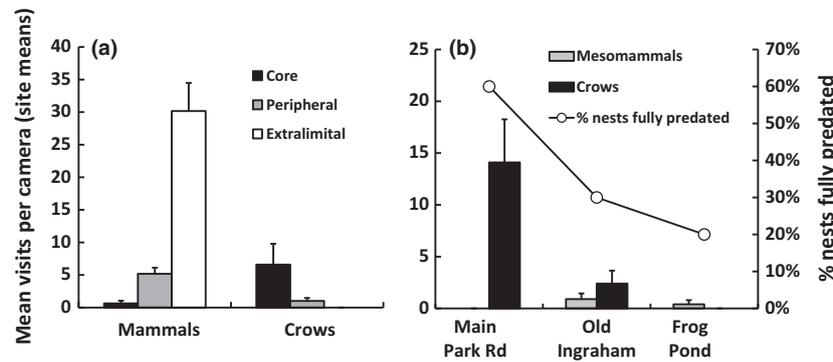


Fig. 4. Crow abundances and predation rates on simulated turtle nests in southern Florida. (a) Mean (± 1 SE) sighting rates of mammals and crows on game cameras located at sites spanning the spatial extent of the python invasion of southern Florida. (b) Mean sighting rates of mammals and crows on game cameras (bars) and % of nests fully predated (lines) at the three sites located within the core of the python's range. Note that crows were most common at Core sites, where mammals were rare, but that this pattern was driven by a very high number of crows, and high nest predation rates by crows, along the Main Park Road in ENP.

Discussion

This study demonstrates that predation pressure by mid-sized mammals is low in regions of southern Florida where pythons have been established for the longest time. Thus, the direct suppression of mammal populations (Dorcas *et al.* 2012; McCleery *et al.* 2015) by Burmese pythons has strong potential to result in indirect effects on non-prey species and trophic cascades that alter numerous aspects of ecosystem structure and function. These results highlight the potential for invasive apex predators to dramatically alter complex continental ecosystems such as the Florida Everglades.

Data from game cameras used in this study confirm that the spatial pattern of mammal abundance is inversely correlated with spatial expansion of the invasive python population in southern Florida (Dorcas *et al.* 2012). Although many of the study sites examined in the present study were in the same areas examined by Dorcas *et al.* (2012), my surveys in new locations (e.g. Holey Lands, Frog Pond WMA, Old Ingraham Hwy, Turner River Road in BICY) correspond well with the general spatial patterns reported previously. Additionally, although the present study was not intended to evaluate links between mammal declines and pythons (possible alternative hypotheses are considered in Dorcas *et al.* 2012) it does refute coyote predation as an alternative cause of mammal declines in the Everglades. Coyotes were historically absent from Florida, but have spread southward through the Florida peninsula since the 1960s (Main, Coates & Allen 2000) and have only recently been documented in ENP and the Keys (Dorcas *et al.* 2012; Greene & Gore 2013). I recorded coyotes rarely on cameras, and only at peripheral and extralimital sites. Coyotes may well affect other mammals, and their arrival could be posited as an alternative explanation for mammal declines. However, the expected spatial pattern of coyote-driven declines would be highest at the northern periphery of the current python range (i.e. where coyotes have been present for the

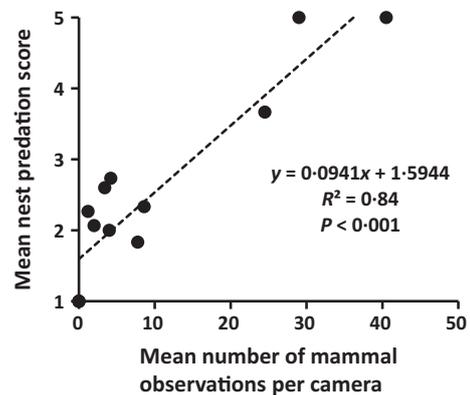


Fig. 5. Relationship between mammal abundances and predation rates on artificial turtle nests at sites ($N = 13$) spanning the spatial extent of the Burmese python invasion in southern Florida. Points represent means of four to five nest clusters (three nests monitored by a game camera) constructed at each site. Predation by crows was excluded by omitting nest clusters that were predated, but crows were the only potential nest predator recorded on game cameras.

longest time, and where I documented coyotes the most frequently). Thus, the pattern of mammal declines appears to be exactly the opposite of what would be predicted if coyotes were the causative agent.

This study represents the first documentation of potential indirect effects of introduced pythons on native non-prey species. Predation rates on artificial nests were lowest in areas where pythons have been established for at least 15 years, and where mammal abundances are greatly reduced. By nature of the progressive spread of the python population up the Florida peninsula, treatments were generally spatially clustered (although often many kilometres apart, and with the strong exception of the Key Largo site), rather than being interspersed, and I cannot completely discount the possibility that spatial variation in some factor other than the presence of pythons contributes to the strong variation in mammal abundances and nest predation

rates that I observed. However, both before–after comparisons of mammal abundances within ENP (Dorcas *et al.* 2012) and unsuccessful attempts to experimentally reintroduce rabbits in areas invaded by pythons (McCleery *et al.* 2015) strongly link python predation to mammal declines and thus, low rates of predation by mammals in the invaded region. Nesting success of freshwater turtles is often quite low, with predation by mammals being a major source of nest failure (Ernst & Lovich 2009). Thus, it is probable that pythons are having a strong positive indirect effect on turtle nesting success in southern Florida and may also be having positive indirect effects on recruitment of other small egg-laying species in the Everglades such as ground-nesting songbirds, lizards, sea turtles, and oviparous snakes. The beneficial effects on certain native species notwithstanding, my findings are troubling in underscoring the cascading effects of pythons on the Everglades food web. Likewise, not all egg-laying species stand to benefit from the python invasion; pythons have recently been recorded preying directly on eggs of larger birds such as Limpkin *Aramus guarauna* and domestic Guinea fowl *Numida meleagris* (Dove, Reed & Snow 2012). Finally, it is worth mentioning that nest predation rates at extralimital sites may be enhanced by the presence of feral pigs, which are known nest predators and were recorded at one extralimital site.

Apex predators can alter ecosystems indirectly through trophic cascades and other indirect effects (Hairston, Smith & Slobodkin 1960; Paine 1980; Estes *et al.* 2011). Removal/reintroduction studies have demonstrated that predators can exert strong indirect effects on ecosystem processes, including water and nutrient cycling (Lafferty 2004; Moore *et al.* 2007), disease dynamics (Lafferty 2004) and invasion resistance (Gruner 2004). For example, the reintroduction of wolves to Yellowstone National Park has demonstrated the key role this predator plays in driving elk browsing behaviour and controlling abundances of mammalian predators, with cascading effects on vegetation dynamics and ungulate survival respectively (Ripple *et al.* 2001; Smith, Peterson & Houston 2003; Berger, Gese & Berger 2008). This study underscores the importance of mammals as ecosystem components and suggests that loss or decline of mid-sized mammal species will result in changes to the overall Everglades ecosystem. Although turtle nesting success could be considered a minor ‘ecosystem function,’ it should caution us that other ecosystem-level changes may have already occurred or will occur in the future. These could include changes in vegetation composition or structure, nutrient dynamics, food web structure or ecosystem services. Such effects are often intricate and difficult to predict, especially in complex food webs where the possibility for compensation or redundancy of species’ roles may exist (Pace *et al.* 1999).

This study revealed evidence of the potential for other species to compensate for loss of mammals. Nest predation rates by crows were highest in the region where mammals have declined the most, leading to similar

overall predation rates at ‘core’ sites and ‘peripheral’ sites. This effect, however, was strongly driven by two sites located along the Main Park Road in ENP. These sites had far higher incidences of crow observations (Fig. 4; see Table S1) than any other sites and were the only sites located along paved roads. I suspect that crow populations at this site are high because crows are subsidized by roadkill and other anthropogenic food sources provided by visitors to the national park. Whether crows along the Main Park Road were major predators on turtle nests before python proliferation is unknown. Core sites away from the Main Park Road (Old Ingraham Hwy, Frog Pond WMA) exhibited much lower rates of predation by crows and had the lowest overall nest predation rates of any sites in the study (Fig. 4; see Table S1). Thus, it is unclear to what extent other components of the Everglades food web will be able to compensate for loss of roles typically played by mammals.

The finding that python predation is already resulting in indirect effects on the Everglades food web suggests that the python invasion may be mirroring that of the brown treesnake on Guam. Snakes represent an emerging threat as invasive predators and possess a suite of physiological and life-history attributes that make them fundamentally different from other predatory vertebrates (e.g. mammalian carnivores, birds of prey; Nowak, Theimer & Schuett 2008; Reed *et al.* 2012). Most notably, snakes have extremely high assimilation efficiencies, allowing them to efficiently convert assimilated prey biomass into reproductive output and energy storage (Pough 1980; Bonnet, Bradshaw & Shine 1998; Reed *et al.* 2012). Snakes are also generally non-territorial, allowing them to attain high densities in resource-rich environments (Godley 1980; Sun *et al.* 2001), and making them more likely to be limited by prey availability than by intraspecific behavioural interactions (Reed *et al.* 2012). Introduction of brown treesnakes to Guam resulted in extirpation or suppression of most of the island’s other vertebrate species (Savidge 1987; Campbell *et al.* 2012). Removal of native vertebrates indirectly altered vegetation dynamics on Guam through reduced pollination and seed set and increased abundance of predatory arthropods through a trophic cascade (Mortensen, Dupont & Olesen 2008; Rogers *et al.* 2012). Given the potential for invasive snakes to transform invaded ecosystems and documentation of both direct and indirect effects of pythons within 15 years of their recognition as an established exotic species, any efforts aimed at preservation or restoration of the Everglades need to consider python management as a high priority.

The success of Burmese pythons and their ability to suppress or extirpate populations of native mammals is particularly surprising because, unlike Guam, the Everglades is a complex continental ecosystem with many native predators. Snakes are among the most secretive of vertebrates, and are generally infrequently encountered, even when present at high densities (Dorcas & Willson

2009). In fact, recent experimental research has shown that python detection rates during visual surveys may be less than 1%, even in habitats that are reasonably easy to search (Dorcas & Willson 2013). Taken together, the low detectability of snakes and the apparently severe impacts of the first two large-scale snake invasions highlight the importance of early action when new snake invasions are detected, even before impacts are quantified. Recent years have seen a steep increase in the number of snake invasions that warrant attention. These include: three species of large constrictors now established in Florida; boa constrictors *Boa constrictor* on the islands of Cozumel, Aruba and Puerto Rico; three species of non-native watersnakes *Nerodia* spp. in California; California kingsnakes *Lampropeltis getula* on Gran Canaria in the Canary Islands; and the Asian Wolf Snake *Lycodon capucinus* on Christmas Island (Kraus 2009; Dorcas & Willson 2011; Smith *et al.* 2012). Despite an increasing recognition of the importance of snakes as ecosystem components (Campbell *et al.* 2012; Willson & Winne 2016), how snakes interact with prey populations remains poorly understood (Gragg *et al.* 2007; Nowak, Theimer & Schuett 2008). Research on snake-prey interactions is sorely needed to understand and mitigate their impacts as invaders.

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Data accessibility

Mammal observations: available in Table S1; Nest predation data. doi: <http://dx.doi.org/10.5061/dryad.2ck58> (Willson 2016).

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Supporting Information

Details of electronic Supporting Information are provided below.

Table S1. Mammal observations recorded at 13 sites spanning the spatial extent of the Burmese python invasion in South Florida.