

Research



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Community ecology

Mammal decline, linked to invasive Burmese python, shifts host use of vector mosquito towards reservoir hosts of a zoonotic disease

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Invasive apex predators have profound impacts on natural communities, yet the consequences of these impacts on the transmission of zoonotic pathogens are unexplored. Collapse of large- and medium-sized mammal populations in the Florida Everglades has been linked to the invasive Burmese python, *Python bivittatus* Kuhl. We used historic and current data to investigate potential impacts of these community effects on contact between the reservoir hosts (certain rodents) and vectors of Everglades virus, a zoonotic mosquito-borne pathogen that circulates in southern Florida. The percentage of blood meals taken from the primary reservoir host, the hispid cotton rat, *Sigmodon hispidus* Say and Ord, increased dramatically (422.2%) from 1979 (14.7%) to 2016 (76.8%), while blood meals from deer, raccoons and opossums decreased by 98.2%, reflecting precipitous declines in relative abundance of these larger mammals, attributed to python predation. Overall species diversity of hosts detected in *Culex cedecei* blood meals from the Everglades declined by 40.2% over the same period ($H(1979) = 1.68$, $H(2016) = 1.01$). Predictions based upon the dilution effect theory suggest that increased relative feedings upon reservoir hosts translate into increased abundance of infectious vectors, and a corresponding upsurge of Everglades virus occurrence and risk of human exposure, although this was not tested in the current study. This work constitutes the first indication that an invasive predator can increase contact between vectors and reservoirs of a human pathogen and highlights unrecognized indirect impacts of invasive predators.

1. Introduction

Natural ecosystems and their vertebrate communities are impacted by large-scale anthropogenic stressors such as habitat destruction, climate change and invasive species [1]. Such human-mediated environmental changes have been implicated as factors that may alter the prevalence of zoonotic disease and their spillover to humans [2]. For example, forest fragmentation in eastern North America has been correlated with increased prevalence of Lyme disease by reducing mammalian diversity and increasing densities of a highly competent host, the white-footed mouse, *Peromyscus leucopus* (Rafinesque) [3], leading to increased contact between the hosts and vectors. Climate change is predicted to shift geographical distributions of some infectious diseases, including many vector-borne pathogens [4]. Invasive species are important drivers of environmental change, threatening the stability of ecosystems and their associated

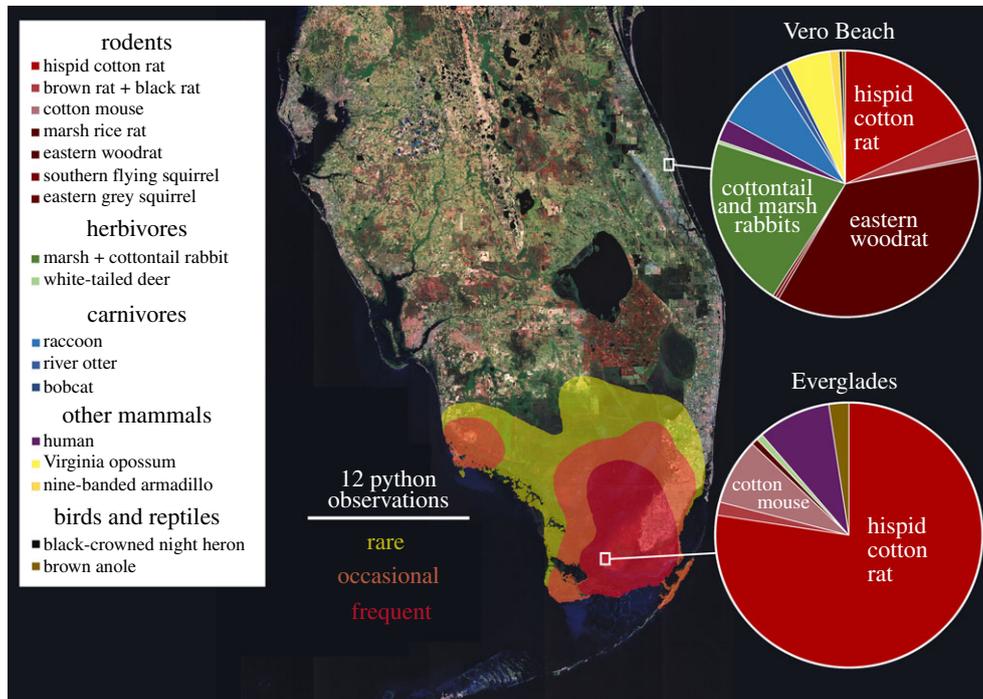


Figure 1. Blood meal host diversity of *Culex cedecei* and distribution of Burmese python [11] in Florida, 2016.

native biota [5,6]. Introductions of non-native species, particularly predators, have led to the decline of numerous species and, in the worst cases, extirpation or extinction [7]. Another important ramification of invasive species is their disruption of natural communities and ecological processes—indirect effects that cascade across trophic levels [7].

Transmission of zoonotic pathogens is mediated by the structure and composition of vertebrate communities [8]. Diverse vertebrate communities may provide an ecological service by reducing the risk of spillover of zoonotic pathogens to humans through a dilution effect, whereby an abundance of noncompetent hosts mitigate disease risk by decreasing vector contact with pathogen reservoirs [8]. However, since several members of the vertebrate community may serve as competent hosts, community composition may be a better predictor of disease prevalence rather than simple richness [9]. Disturbances that shift the community towards relatively greater densities of reservoir host species should increase contact between vectors and reservoir hosts [10], increasing overall pathogen prevalence [9]. Invasive apex predators are disturbances that profoundly alter vertebrate communities [7] and while the direct impacts of invasive predators (e.g. predation of native species) are well documented, comparatively little is known about how invasive predators affect the transmission of zoonotic pathogens.

The Burmese python, *Python bivittatus* Kuhl, is an invasive apex predator that has established in southern Florida (figure 1) and has been incriminated in large-scale mammal declines [11,12]. We investigated whether the python-attributed impacts on the mammal community of southern Florida have impacted contact between the reservoir hosts and vectors of a zoonotic vector-borne pathogen. Everglades virus (EVEV), subtype II of the Venezuelan equine encephalitis complex, is a mosquito-borne zoonotic *Alphavirus* endemic to Florida that causes occasional nonfatal neurological disease in humans [13,14]. The hispid cotton rat, *Sigmodon hispidus* Say and Ord, and the cotton mouse, *Peromyscus gossypinus* (Le Conte), are reservoir hosts of EVEV [15–17]

and the mosquito *Culex cedecei* Stone and Hair is the sole enzootic vector [16,18]. Field studies from southern Florida during the late 1970s demonstrated that *Cx. cedecei* feeds predominantly (88–90%) upon mammals, acquiring about half of blood meals from rodents in the Everglades [18], the remainder (46%) being derived from medium-sized (northern raccoon, *Procyon lotor* (Linnaeus), Virginia opossum, *Didelphis virginiana* Kerr) and large-sized mammals (white-tailed deer, *Odocoileus virginianus* (Zimmermann)). During the 1970s and thereafter, these medium- and large-sized mammals were common in the Everglades National Park [12]. However, by the early 2000s, raccoon, opossum and deer experienced massive declines (87.5–99.3% reductions) in the Everglades National Park linked to the proliferation of the Burmese python, while rodent populations have remained stable or even slightly increased [11,12]. These changes in host abundance may have profound effects on host use, given dramatic differences in size (deer versus rat) and circadian patterns of activity of the hosts as well as vectors, resulting in unequal exposure to bites. Other than host abundance these factors are not likely to have changed between past [18] and present studies. Comparing host use of the EVEV vector *Cx. cedecei* prior to python invasion [18] with current host use patterns provides the opportunity to investigate how an invasive apex predator may alter host–vector contact, a key interaction driving pathogen transmission.

2. Methods

We measured host use of *Cx. cedecei* inside and outside the introduced range of the Burmese python in Florida using PCR-based blood meal analysis and compared our results with analogous data obtained prior to the introduction and proliferation of the Burmese python in the Everglades [18]. Blood-fed *Cx. cedecei* were sampled in Everglades National Park and Vero Beach, FL using resting shelters (range 14–27 per sampling day) [19], a method targeting *Cx. cedecei* and other species that exhibit specialized resting behaviours [18]. Everglades sampling was

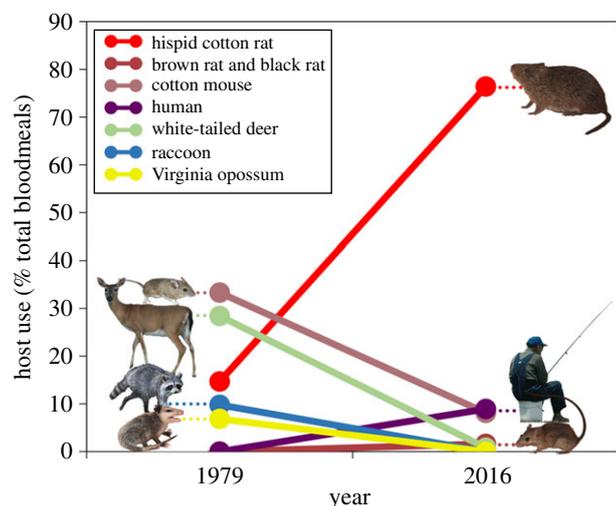


Figure 2. Shifts in host use by *Cx. cedecei* in the Everglades before [18] and after (current study) invasion by Burmese python. Animals appearing on the left decreased in relative host use between 1979 and 2016, while those on the right increased over the same period.

conducted at eight locations, all occurring on hardwood hammocks of the sawgrass prairie, the same habitat as Mahogany Hammock, site of Edman, and on average 6.3 km distant from that site (range 0.4–14.1 km). Sampling was conducted on 20 days, spread across five non-consecutive months (Dec 2015–Aug 2016) (permit no. EVER-2015-SCI-0054). In Vero Beach, FL, sampling was conducted weekly from December 2015 to November 2016. Blood meal analysis of 2015–2016 samples followed previously published PCR-based protocols [19], whereas Edman [18] used antibody-based methods for identifying vertebrate source of mosquito bloodmeals. We used the chi-squared test of independence to compare historical [18] and current distributions of (i) total host blood meals, (ii) reservoir versus non-reservoir host bloodmeals in the Everglades, and (iii) seasonal patterns of reservoir versus non-reservoir host use. We compared abundance of *Cx. cedecei* between the Everglades and Vero Beach (Feb–Aug 2016) using Poisson regression modelling [20,21]. Statistics were performed in SAS v. 9.4.

3. Results

Analysis of *Cx. cedecei* blood meals ($n = 125$) from the Everglades revealed a significant shift in taxa-specific host use between the historic [18] and current blood meal data ($X^2 = 136.4$, d.f. = 11, $p < 0.001$) (figure 2) and a significant shift towards feeding upon aggregated reservoir hosts ($X^2 = 35.0$, d.f. = 1, $p < 0.001$), i.e. cotton mouse and hispid cotton rat (figure 2), that was not related to season ($X^2 = 2.2$, d.f. = 3, $p = 0.533$). Feedings on hispid cotton rats, perhaps the most important EVEV reservoir host [17], increased from 14.7% [18] to 76.4% of overall blood meals (increase of 419.7%; figure 2). In contrast, feedings upon deer, raccoon and opossum in the Everglades decreased precipitously, from 45.1% [18] to just 0.8% of total hosts (figure 2). Shannon–Wiener diversity (H) of hosts fed upon also decreased by 40.2% between the historic ($H = 1.68$, [18]) and current studies ($H = 1.01$).

Culex cedecei from Vero Beach ($n = 264$) fed upon a wider diversity ($H = 1.29$) of mammal species (figure 1) than those from the Everglades ($H = 1.01$), current day. Medium- and large-sized mammals constituted 37.5% of total hosts in Vero Beach (figure 1) including rabbits (eastern cottontail, *Sylvilagus floridanus* (Bachman), and marsh rabbit, *Sylvilagus*

palustris (Bachman), 20.1% combined), white-tailed deer (0.3%), opossum (5.3%), raccoon (8.0%), armadillo (0.8%), bobcat (0.8%), and river otter *Lontra canadensis* (Schreber) (0.8%). Eastern woodrat, *Neotoma floridana* (Ord), not considered to be a reservoir host for EVEV, constituted a large percentage (36.4%) of *Cx. cedecei* bloodmeals in Vero Beach (figure 1), while hispid cotton rat constituted 18.1% of total bloodmeals.

Culex cedecei was significantly more abundant in the Everglades than Vero Beach ($X^2 = 279.05$; $p < 0.001$). On average 24.5 times more females were collected per resting shelter in the Everglades (mean = 13.6, s.d. = 17.1) compared with Vero Beach (mean = 0.56, s.d. = 0.60).

4. Discussion

Our data demonstrate that substantial shifts in the host-use patterns of *Cx. cedecei* have occurred in the Everglades and these shifts correspond with the decline of medium- and large-sized mammals attributed to the establishment and proliferation of Burmese pythons. To the best of our knowledge, this study constitutes the first indication of an invasive apex predator indirectly increasing contact between the vector and reservoir hosts of a vector-borne pathogen via restructuring of the vertebrate community. The precipitous (98.2%) decrease in bloodmeals from medium- and large-sized mammals corresponded to a dramatic increase (76.5%) in relative feedings on EVEV reservoir hosts, not a shift to feeding upon non-mammal hosts (amphibians, reptiles or birds).

Whether or not greater host species richness decreases the disease risk is a contentious issue [22,23]. Changes in the host community that increase vector feedings on reservoir hosts relative to non-reservoir hosts should increase transmission, provided that vector abundance does not decrease [9]. While our data demonstrate that *Cx. cedecei* populations in the Everglades are robust (compared with Vero Beach), comparable historic data on *Cx. cedecei* abundance in the Everglades are not available. As such we cannot make substantiated inferences regarding the total numbers of infected vectors, current day. This is an important consideration given that the abundance of infected vectors is generally agreed upon as being the most accurate/reliable metric for quantifying pathogen prevalence, and therefore disease risk [1,9].

Research on the impacts of invasive predators is generally restricted to trophic and competitive interactions. Invasive predators can drastically alter ecosystem function and ecological processes via community structure degradation [7]. An overlooked topic in invasion ecology is the potential for invasive species to alter transmission of zoonotic pathogens. The proliferation of Burmese python was first shown to coincide with declines of several diverse trophic and taxonomic mammals in south Florida, correlatively incriminating this invasive predator as the causative agent [12]. McCleery *et al.* [11] experimentally linked python predation to rabbit declines and extended this relationship to other declining mammalian species. Our results demonstrate a considerable shift in *Cx. cedecei* host use between 1979 and 2016 that reflects the decline in mammal populations attributed to python predation with a more than 400% increase in relative vector feedings on a reservoir host, a circumstance that has the potential to increase infection prevalence and disease

risk. Future studies should quantify pathogen prevalence to determine whether cascading impacts of invasive predators result in measurable increases in risk of human exposure and identify invasive predators with high probability for indirectly increasing incidence of human disease.

Ethics. Everglades National Park granted ethical approval with the permit number EVER-2015-SCI-0054.

Data accessibility. Data deposited in Dryad: <http://dx.doi.org/10.5061/dryad.mt3gr> [24].

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