EXPLORING VERTEBRATE COMMUNITY RESILIENCE TO INVASIVE MAMMAL PREDATOR INVASIONS

Diana K. Guzmán-Colón, Ph.D.[1]

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Abstract - Novel species assemblages in tropical islands present ecologists with the opportunity to explore ecosystem function and faunal community resilience to invasive species. Introduced mammalian predators to islands have a disproportionately large role in species extinctions and their variation in patterns of foraging can influence the assembly of biological communities. In this article, I argue for the need for experimental studies to elucidate the role of invasive species within faunal assemblages in Puerto Rico with a focus on the introduced small Indian mongoose (*Herpestes auropunctatus*). I conducted a preliminary assessment to define best possible study sites for obtaining an understanding of mongoose influence on Puerto Rico's terrestrial vertebrate food web. Mongoose occurrence and high species richness on sites with moderate habitat modification coincide on 3% of the island's land area, and mostly located on the southwest coastal dry forest. A deeper understanding of mongoose influence on Puerto Rico's terrestrial vertebrate food web is paramount for biodiversity management and to grasp community resilience to biotic invasion.

Keywords: biotic interactions, species richness, non-native species, faunal assemblages, Herpestes auropunctatus, food web

Resumen - Los ensamblajes noveles de especies en islas tropicales proveen la oportunidad de explorar la función de estos ecosistemas y la capacidad de recuperación de comunidades bióticas frente a la presencia de especies invasoras. Los mamíferos que han sido introducidos a ecosistemas de islas asumen un rol importante en las extinciones de especies. La variación en patrones de forrajeo de dichas especies pueden influir en el ensamblaje de las comunidades bióticas presentes en las islas. En este artículo, indago sobre la necesidad de estudios experimentales para dilucidar el rol de las especies invasoras dentro de las comunidades de fauna en Puerto Rico con un enfoque específico en la mangosta de la India (*Herpestes auropunctatus*). En este artículo presento una evaluación que identifica potenciales sitios de estudios a través de un análisis de los patrones espaciales de presencia de la mangosta y la riqueza de especies en la isla. La presencia de mangostas y riqueza de especies en sitios con modificación moderada del hábitat coinciden en el 3% de la superficie terrestre de la isla, y se encuentran principalmente en el bosque seco costero del suroeste. Un entendimiento sobre la influencia de la mangosta en la red trófica de vertebrados terrestres de Puerto Rico es primordial para el manejo de la biodiversidad y comprender la resiliencia de comunidades a la invasión biótica.

Palabras clave: interacciones bióticas, riqueza de especies, especies no nativas, islas, ensamblajes de fauna, Herpestes auropunctatus, red alimentaria

[1]SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison WI 53706, USA Corresponding author: dguzmancolon@wisc.edu

Introduction

Human influences on terrestrial ecosystems are driving most of the biogeographical patterns that were once dictated by natural climate and geological change (Helmus et al., 2014). Natural changes, such as species colonization of available niches, occurred at a much slower pace than the rapid mixing of species happening since the advent of modern human travel (Crooks, 2005). The swift reshuffling of species coupled with shifting abiotic patterns due to environmental changes, has resulted in an estimated 35% increase of ecosystems that are compositionally novel (Marris, 2009). In the world of conservation ecology, scientists grapple with uncertainty regarding the potential consequences of species introductions in altering the functionality of an ecosystem while also trying to understand how and if species might be able to adapt to both climate change and species invasions. At the same time, novel species assemblages present ecologists with the opportunity to explore classic, theoretical questions regarding ecosystem function, species assemblages, community resilience, and competition, among a suite of questions that are paramount to the understanding of the intricacies of an ecosystem. In this article, I argue for the need of experimental studies regarding the role of invasive species in the contemporary faunal assemblages and present an analysis of potential study sites. As a case study, I will focus on the introduction of an introduced predator, the small Indian mongoose (*Herpestes auropunctatus*).

An emerging yet pervasive issue caused in part by species invasions is the replacement of functionally diverse species by generalists ones, a process commonly known as biotic homogenization (Clavel et al., 2010). Species richness ensures adequate ecosystem functioning that provides invaluable services, such as harvestable biomass, decomposition, nutrient cycling, and pollination. Therefore, understanding species community dynamics should be a priority for conservation, especially on insular ecosystems which often serve as refuges and contain high levels of endemism, but that are highly vulnerable to climate, land-use change, and species invasions.

Ecological theory predicts that local (α) biodiversity should steadily increase at a regional scale as either new specialist or generalists species colonize these areas (Pyšek & Richardson, 2010). In this scenario, one should expect that specialists or generalists, in a moderately modified habitat, have similar fitness and can coexist regionally. However, the biodiversity among localities (β) may become homogenized following the total loss or replacement of native species (Kortz & Magurran, 2019). The consequences of these dynamics in a landscape are the establishment of novel species assemblages, which could result in a net loss of functional roles among the community and the services they provide. For example, in a case of introductions via exotic pet trade, local colonization events immediately translate into greater species richness, whereas the extinction of declining species happens over a much longer timescale. Therefore, the scenario presented above requires information on the direct and indirect effects of species interactions, with special interest in the role of invasive species in novel faunal assemblages.

Puerto Rico is a prime example of how novel plant species assemblages, dominated by non-native tree species, have provided critical habitat for native forest bird species which in turn have contributed to the dispersal of native trees (Abelleira-Martínez, 2010). However, a similar understanding of vertebrate co-existence with an invasive predator like the mongoose remains unclear.

Puerto Rico vertebrates and species richness

Puerto Rico has an estimated 26,410 species of organisms, with animals representing 43% of the total species (Joglar, 2005). Researchers have recorded over 500 vertebrate species, including terrestrial, terrestrial aquatic and marine organisms (Gould et al., 2008). Of these, about 436 are terrestrial vertebrate species and this number has further increased with introduction of species by humans introductions (Lugo et al., 2012).

Species in Puerto Rico are widespread, yet with significant spatial patterns: there are coastal or montane species, species restricted to dry or wet environments, and species restricted to particular islands in the archipelago, thus highlighting the importance of the diversity of habitats on the island (Gould et al., 2008). For example, results from the latest Puerto Rico GAP analysis on α diversity and β showed different patterns (Figure 1); specifically, mountain forested habitats tended to be more species rich (higher α diversity), but coastal regions (an area with greater heterogeneity of habitats) appear to have higher β diversity (Gould et al., 2008).

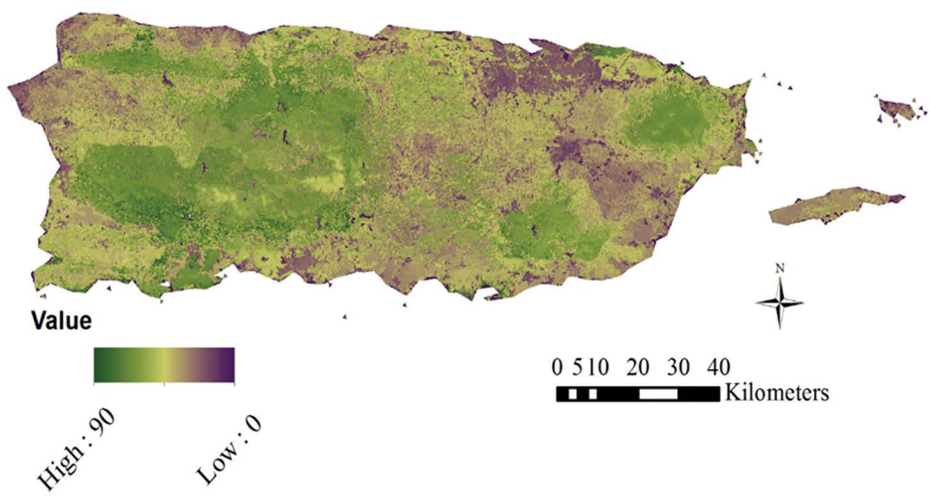

Figure 1. Map using the sum of all predicted species distribution data from 202 terrestrial vertebrate species. The dataset displays species richness values calculated as part of the Puerto Rico Gap Analysis project (PRGAP) and modelled using the 2000 Puerto Rico land cover map at a spatial resolution of 15 by 15 meters. Species richness is the total number of species that are predicted to potentially occur within an area. Represented in this map are the following major taxa: eighteen amphibians, one hundred and twenty-three birds, fourteen mammals and forty-seven reptiles. Data layers acquired from public repository https://caribbeanlcc.databasin.org.

The small Indian mongoose (*Herpestes auropunctatus*)

The small Indian mongoose is a solitary opportunistic predator native to parts of the Middle East, South and Southeast Asia. Mongooses were introduced into sugarcane fields in most of the Caribbean islands during the late 1800s to early 1900s as a means of biological control for rats (*Rattus sp.*). Currently, mongooses are known to inhabit 29 islands of the West Indies where declines in the number of bird, reptile and amphibians species followed shortly after mongoose introductions (Gorman, 1975; Roy Horst et al., 2001). Mongooses use diverse habitats, from forests to open grasslands and suburban areas, although abundances differ in montane versus coastal forests (Guzman-Colon & Roloff, 2014). This species is relatively long lived with reported ages of up to 6 years (Hoagland et al., 1989), and has a high reproductive capacity, with a gestation period of 42 days and 1-4 offspring in each litter (Nowak, 1991). To date, there are no detected predators or competitors that might restrict mongoose populations in Puerto Rico. Estimated average mongoose densities on the island range from 0.19 to 9.0 mongooses/ha (Johnson et al., 2015; Quinn & Whisson, 2005), with home range sizes of 3.1-52.2 ha (Quinn & Whisson, 2005), but these numbers vary widely by study and locality. These characteristics make the mongoose a phenomenal generalist and invasive species, thus managing for mongoose control a daunting task.

In addition to being a perceived threat to native wildlife, mongooses are a reservoir of rabies, leptospirosis and other diseases (*i.e. Salmonella*) on islands of the Caribbean (Benavidez et al., 2019; Everard & Everard, 1992; Miller et al., 2014). Although the International Union for Conservation of Nature (IUCN) classifies the mongoose as one of the top 100 worst invasive species, some researchers have suggested that the mongoose has become naturalized to Puerto Rico and should be considered part of the faunal composition of the island (Lugo et al., 2012). While we ignore the importance of mongoose introduction relative to other potential causes of declines of native species in the Caribbean (Waltington-Linares, 2007), it is plausible that mongooses are key members of contemporary faunal assemblages. Under this assumption, several questions arise for conservation, such as, what are the consequences of intense species control, when should funding be directed towards intervention and how to design integrated pest management programs.

Removal of mongooses has been a central part of conservation programs in many islands. In Puerto Rico, mongoose population control programs consist of seasonal individual removal on sites where the endangered Puerto Rican parrot (*Amazona vittata*) inhabits (F. Cano, personal communication, May 2011). Live box traps are the most common method of mongoose control employed (Barun et al., 2011). While most of the mongoose studies in Puerto Rico have focused on gathering information for management, for example, trap location, bait flavor and toxicity (Berentsen et al., 2018; Guzman-Colón et al., 2019), few studies have quantified the effects of mongoose introduction to a seemingly naïve (to predators) insular community of native and endemic species, including species' responses or adaptations to mongoose presence. Because of the scarcity of data on species interactions with this introduced predator, a deep understanding of predator food web and predation risks in the Caribbean is needed to understand the current role of mongooses in the faunal community of Puerto Rico.

Mongoose relationship with other species

Small mammals are considered one of the most detrimental biological invaders to island ecosystems (Courchamp et al., 2003). In general, introduced mammalian predators have a disproportionately large role in species extinctions and their variation in patterns of foraging specialization can influence invasibility of biological communities. The effect of predatory introductions can be influenced by properties of the local ecosystem. Some theoretical studies show that the probability of invasion success should decrease with species number and with strength of interspecific interactions (Post & Pimm, 1983; Rejmanek & Richardson, 1996). Given its diversity of environments, Puerto Rico provides an ideal scenario to explore whether there is any relationship between species diversity and resistance to mongoose invasions. In the broadest sense, are species-rich, tropical communities truly more invasion resistant than species-poor temperate communities?

A study relating the number of terrestrial vertebrate species to mongoose presence in the Caribbean found that the number of terrestrial vertebrate species appeared to be negatively correlated (-0.90) with mongoose presence (Horst et al., 2001). However, causality was not confirmed given that island size was more strongly correlated with mongoose densities (-0.98) than species richness. Yet, the general trend observed in the Caribbean was that smaller islands supported higher mongoose density but low vertebrate diversity, whereas larger islands support low mongoose densities but higher vertebrate diversity (Table 1). Perhaps the number of invasion opportunities for a mongoose increases the likelihood that the species will successfully establish, and islands with low vertebrate diversity allow mongooses to colonize empty niches.

Table 1

Average mongoose population densities on five Caribbean islands

Island	Area (km^2)	Mongoose density (No./ha)	Number of terrestrial species
St. Croix	270	6.4	197
Grenada	310	6.6	208
Trinidad	4,800	2.5	417
Puerto Rico	8,900	2.5	338
Jamaica	11,420	2.6	307

Note. No./ha-Number/hectare. Modified from Horst et al. (2001).

Despite the accumulation of independent observations for the effects of introduced mongooses upon Caribbean and Pacific islands, few attempts have been made to quantitatively describe the magnitude of the ecological impact or relationships on the island's food web. Although studies on diet are limited, stomach and fecal content analyses reveal that mongoose feed on a wide variety of mostly small vertebrates and invertebrates (71-89%), and plant material 15-29% (Pimentel, 1955; Vilella, 1998), with dietary preferences differing by habitat (Gorman, 1975). However, stomach content analysis only reveals what the predator has consumed in the few hours prior to being captured and a more holistic view of their diet is needed.

A call to explore the diet of the mongoose with isotopic analysis

Recent advances in the use of stable isotope analysis (SIA) for diet studies could allow researchers to obtain a deeper understanding and characterization of mongoose influence on our insular food web. Animal tissues contain a ratio of heavy to light isotopes of carbon (δ13C) and nitrogen (δ15N) which are partially acquired from their food sources. Because prey items are assimilated into a predator's tissue, natural variation in the isotopic signature of potential prey items can be traced into the isotopic values of the consumer to estimate dietary proportions. This technique is increasingly being used in animal studies to deduce trophic level via predictable increases in δ15N and in food resources via variations in δ13C from different organic matter sources (Karasov & Martínez del Rio, 2007). Recent SIA studies in the island of St. John's indicate that mongooses might prefer prey found close to the site of capture, thus showing geographic differences in consumption by mongoose inhabiting similar localities (deHart et al., 2016). Given this, one would recommend that population control programs target small areas, since mongoose movements appear to be exploratory in extensive areas, but their foraging behavior is limited to local sites. Interestingly, deHart et al. (2016) and Powers et al. (2020) found that consumption differed among ages, with older individuals likely relying more heavily on marine-derived nutrients. In St. John, mongooses relied heavily on brown pelican eggs (*Pelecanus occidentalis*) and consume a wide variety of herpetofauna species. Overall, mongoose diet assessed by SIA was shown to be more variable than previously quantified (Gorman, 1975; Pimentel, 1955; Vilella, 1998). The main strength of SIA is the ability to investigate the responses of individuals to determinant of survival such as food availability, competition, predation, and predation risk (Flaherty & Ben-David, 2010).

A proposed systematic study

To explore the feeding ecology and trophic position of the mongoose on species-rich and species-poor areas in Puerto Rico, I examined potential sites suited to perform studies aimed at characterizing vertebrate species assemblages and species interactions mediated by prey consumption. First, I selected areas in Puerto Rico where human modification is moderate (Guzmán-Colón et al., 2020) to follow the assumption that both native and introduced species can coexist locally and have similar fitness. Within these areas, I selected sites with a two-way combination of low vs. high occurrence of species and mongooses (datasets from Gould et al. 2008;Guzman-Colon, *in prep*).

Based on this preliminary analysis, there are few places where a high probability of mongoose presence coincides with high species richness sites (3.28% of the island's land area), and that there is no difference between lower and higher mongoose presence overlapping with either lower or higher species richness sites. It is interesting to note that a higher number of species are found on the central mountainous zone and eastern rainforest of the island, while mongooses are more abundant and likely to be found near coastal and dry areas. Indeed, most of the heterogeneity of habitats are found in the coastal zones as shown in Figure 2. I suggest that future studies would be more fruitful around the areas of Cabo Rojo through Guánica (Southwest), where variability in mongoose presence and species richness are more evident.

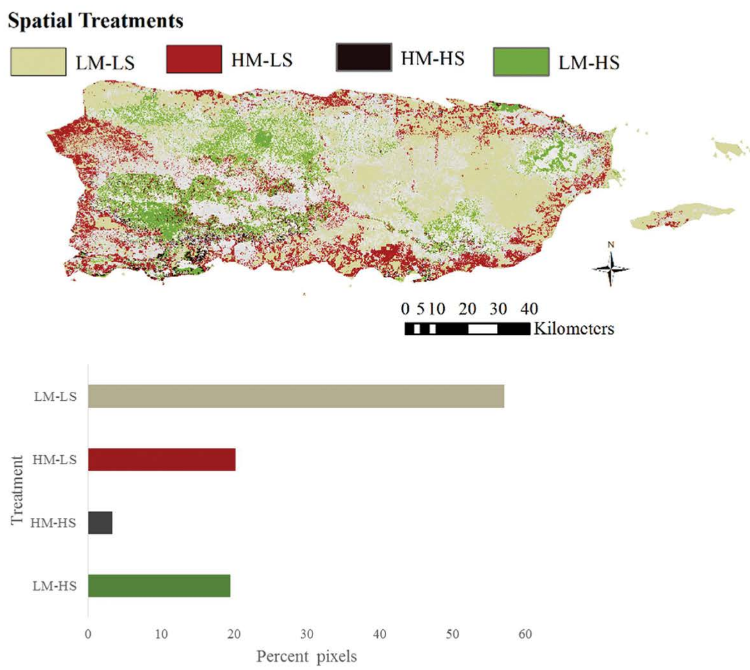

Figure 2. Map depicts sites that were identified as low mongoose presence + Low species richness (LM-LS), High mongoose presence + Low species richness (HM-LS), High mongoose presence + High species richness (HM-HS), and Low mongoose presence + High species richness (LM-HS). Bar graph shows the percent pixel represented by each spatial treatment in the model.

Concluding remarks

Mongoose presence on islands continues to be a motive for concern for conservation management. The information presented here highlights the potential to understand island terrestrial species communities through food web studies. It is important to build a baseline for a robust analysis of trophic patterns on island ecosystems. I examined potential areas where an important number of species might overlap with mongoose presence and suggested a tool (SIA) for analyzing their basic diet and biotic interactions in these areas.

Future research should consider a more comprehensive investigation of potential prey items of mongooses. The information gathered from this type of study can help target control efforts in areas relevant for the protection of endangered species. Further, it can prompt future questions about faunal biotas and community resilience to invasion in tropical systems.

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