






Assessing occupancy and activity of two invasive carnivores in two Caribbean islands: implications for insular ecosystems

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Abstract

The introduction of exotic species is one of the major causes of the decline of global biodiversity. Tropical insular ecosystems, including many biodiversity hotspots, are particularly threatened by biological invasions. Two wild carnivores have been introduced in the Caribbean, the northern raccoon *Procyon lotor* and the small Indian mongoose *Urva auropunctata*. Understanding the spatial distribution and activity patterns of both species is crucial for conservation purposes. Here we used camera trap data to model single-season occupancy and detection of these two species on two Caribbean islands, Guadeloupe and Martinique. Our survey highlighted the broad distribution of both species on these islands, with the exception of the northern raccoon population in Martinique which appears very limited. Moreover, spatio-temporal co-occurrence with other bird and mammal species revealed that the northern raccoon and the small Indian mongoose face few or no competitors. Finally, our models show that the occupancy of both species was not influenced by any variable tested (i.e. elevation, precipitation, temperature and land cover) and that the probability to detect small Indian mongooses was influenced by land cover and camera model. These results highlight the potential of both the northern raccoon and the small Indian mongoose to have a significant impact on the native ecosystems in these hotspots of biodiversity and demonstrate the necessity to develop conservation actions towards control and limitation of these invasive carnivores.

Introduction

Ecosystem disruption through the introduction of exotic species is a major driver of the erosion of global biodiversity (Bellard, Cassey & Blackburn, 2016a; Holmes *et al.*, 2019). Insular ecosystems, often characterized by a high rate of endemism, harbour a significant part of global biodiversity (Kier *et al.*, 2009; Tershy *et al.*, 2015), and many insular regions are considered biodiversity hotspots (Myers *et al.*, 2000). Often being composed of ecologically specialized species that have evolved in isolation, these insular ecosystems are particularly threatened by the introduction of exotic predators (Banks & Dickman, 2007; Medina *et al.*, 2011; Doherty *et al.*, 2016; Bellard *et al.*, 2017; Spatz *et al.*, 2017). The Caribbean region has experienced a major decline in biodiversity as a consequence of the different waves of human colonization (Pascal *et al.*, 2007; Turvey, Brace & Weksler, 2012; Graves, 2014; Bochaton *et al.*, 2016; Turvey *et al.*, 2017; Cooke *et al.*, 2017) and the

concomitant increase of non-native species introductions (Cooke *et al.*, 2017). Notably, two wild carnivores were introduced in the Caribbean during the 17th and 19th centuries: the northern raccoon *Procyon lotor* (Linnaeus, 1758), and the small Indian mongoose *Urva auropunctata* (Hodgson, 1836) (formerly *Herpestes auropunctatus* or *Herpestes javanicus*, see Veron *et al.*, 2007; Veron & Jennings, 2017).

The northern raccoon is a meso-carnivore native to the North American continent (Lotze & Anderson, 1979). However, human activities, and particularly pet and fur trade, have led to its introduction in many regions worldwide. The species was introduced in the Caribbean during the 17th century, as well as in several regions in Europe, Iran and Japan during the late 20th century (Salgado, 2018; Louppe *et al.*, 2019). In the Caribbean, the northern raccoon has been introduced to the Bahamas (New Providence, Grand Bahama and Abaco), Saint Martin/Sint Maarten, Guadeloupe, Marie-Galante, La Désirade, Martinique (Kays *et al.*, 2009; Louppe *et al.*, 2020a), as well

as in Barbados where the population has now disappeared (Helgen *et al.*, 2008).

The small Indian mongoose is a small carnivore whose native distribution extends from Iraq to Myanmar, covering Iran, Pakistan, Northern India, Nepal and Bangladesh (Gilchrist *et al.*, 2009). However, the species was introduced into a large number of regions around the globe between the late 19th and early 20th centuries: the Caribbean archipelago, Surinam, Guyana, Croatia, Bosnia and Herzegovina, Montenegro, as well as several islands of the Mascarenes and the Japanese, Fijian and Hawaiian archipelagos (Louppe *et al.*, 2020b). These introductions were primarily conducted for the purpose of biological control, in an attempt to limit the proliferation of invasive rodents, such as the black rat *Rattus rattus* (Linnaeus, 1758) in sugar cane plantations. Occasionally, the small Indian mongoose was also introduced to eradicate venomous snakes, for instance *Bothrops lanceolatus* (Lacepède, 1789) in Martinique, *Protobothrops flavoviridis* (Hallowell, 1861) in the Japanese archipelago, or *Vipera ammodytes* (Linnaeus, 1758) on several islands of the Adriatic Sea (Berentsen, Pitt & Sugihara, 2018). Today, the species is present on more than 60 islands around the globe, almost half of which belong to the Caribbean region (Barun *et al.*, 2011; Louppe *et al.*, 2020b).

The current distribution of both species attests to their ability to occupy a wide range of habitats. Moreover, they are often observed in highly anthropized environments such as farmland, peri-urban and urban areas (e.g. northern raccoon: Beasley, Devault & Rhodes, 2007; Bozek, Prange & Gehrt, 2007; Prange, Gehrt & Wiggers, 2007; small Indian mongoose: Pimentel, 1955; Nellis, 1989). Contributing to their high adaptability, both species have an opportunistic although mainly carnivorous diet and feed on small vertebrates (reptiles, birds, mammals), but also bird and reptile eggs, crustaceans, insects, seeds, fruits and other vegetable items, or human waste (northern raccoons: Ikeda *et al.*, 2004; Beasley & Rhodes Jr., 2008; small Indian mongoose: Mahmood & Adil, 2017; Berentsen *et al.*, 2018). The introduction of the small Indian mongoose has been strongly correlated with the extirpation or extinction of many species of reptiles, birds and mammals worldwide (reviewed in Berentsen *et al.*, 2018). In contrast, while the northern raccoon is often considered an agricultural pest (Ikeda *et al.*, 2004; Beasley & Rhodes Jr., 2008), its influence on the native ecosystems remain poorly studied. However, the species is known to be a threat to marine turtles (Engeman, Addison & Griffin, 2016) and bird populations on several islands in its native range (Ellis *et al.*, 2007) and is thus suspected to impact bird and reptile communities in regions where it has been introduced (Hayes *et al.*, 2004; Hayes, 2006; Ourly, 2006). Finally, both species might be vectors of various pathogens, such as rabies (Everard & Everard, 1988; Arjo *et al.*, 2005; Puskas *et al.*, 2010; Beasley *et al.*, 2012; Vos *et al.*, 2012; Berentsen *et al.*, 2015; Johnson *et al.*, 2016), nematode-mediated pathologies (Beltrán-Beck, García & Gortázar, 2012) and bacterial infections (Pimentel, 1955; Everard, Green & Glosser, 1976; Miller *et al.*, 2015; Cheng *et al.*, 2018; Jaffe *et al.*, 2018; Shiokawa *et al.*, 2019).

Understanding the abiotic and biotic factors that influence the distribution of such invasive species is crucial in an effort

to maintain and protect native ecosystems. Various statistical approaches have been developed to model and predict a species' distribution with regards to environmental characteristics (Guillera-Aroita *et al.*, 2015). These approaches, such as occupancy-detection models, represent effective tools for wildlife managers and land planners in order to develop proactive measures instead of reactive decisions (e.g. Ancillotto *et al.*, 2018; Rich *et al.*, 2019). The recent development of modern wildlife monitoring technologies, such as visual and acoustic sensors (i.e. camera traps and acoustic recorders), has significantly facilitated the collection of ecological data and improved our understanding of species distribution and ecosystem interactions (Blumstein *et al.*, 2011; Aide *et al.*, 2013; Rich *et al.*, 2017; Steenweg *et al.*, 2017). Consequently, these methods are increasingly recognized as an important tool in species distribution modelling (Kéry, Guillera-Aroita & Lahoz-Monfort, 2013; Guillera-Aroita, 2017; Guillera-Aroita, Kéry & Lahoz-Monfort, 2019; Mazzamuto *et al.*, 2020).

In this study, we used camera trap data to investigate habitat occupancy of the northern raccoon and the small Indian mongoose introduced on two Caribbean islands, Guadeloupe and Martinique. Our first objective was to assess the spatio-temporal co-occurrence with potential competitors, predators, prey species, as well as humans. Our second objective was to model the occupancy and detection of the small Indian mongoose and the northern raccoon on both islands. To this end, we applied single-species occupancy-detection models using detection/non-detection data from camera trapping. The influence of various environmental biotic and abiotic predictors was investigated in order to better characterize the habitat suitability of both species on these tropical islands.

Materials and methods

Study area and camera trapping survey design

The Guadeloupe and Martinique islands have a surface area of 1628 and 1128 km², respectively, with elevations, respectively, ranging from 0 to 1467 m and from 0 to 1397 m. In Guadeloupe, we surveyed a total of 32 stations between April and May 2017, for 9 to 20 trap nights (Fig. 1). In Martinique, we surveyed 16 stations between March and May 2018, for 32 to 65 trap nights (Fig. 1). Since both volcanic islands are characterized by a very steep landscape and extensive urban areas, stations were not randomly chosen using an aerial grid. Rather, stations were set to cover the islands' high diversity of habitats and elevation gradients. Independence of the observations between stations was ensured by maintaining sufficient terrestrial distances (e.g. >2 km; home range of northern raccoon in native range was estimated between 0.02 km² (Berentsen *et al.*, 2013) and 2.44 km² (Chamberlain *et al.*, 2003); home range of the small Indian mongoose in Puerto Rico have been estimated between 0.03 and 0.2 km² (Quinn & Whisson, 2005). Each station was surveyed using one unbaited camera trap operating 24 h.day⁻¹. A set of 28 cameras were used in this study, 9 Moultrie M880 (Moultrie Feeders, Birmingham, AL, USA) and 19 Bushnell Essential E2 (Bushnell Corp.,

Overland Park, KS, USA). Cameras were positioned 20–30 cm off the ground on the side of wildlife or human trails (>0.5 m). The height was chosen corresponding to the small body size of the targeted carnivores. However, our traps were also effective to capture ground-dwelling and forest birds, as well as other mammals. Sites were chosen to ensure the uniformity of the radius of action of every camera, in order to avoid the presence of elements that may hamper detections in closed habitats. Cameras were programmed to take three pictures each time they were triggered (one picture per second), with a five-minute minimum delay between triggers.

Capture histories were created at each station for all identifiable species using the package « camtrapR » v1.1 (Niedballa *et al.*, 2016) implemented in the R software (R Development Core Team, 2019). Species detection (« 1 ») and non-detection (« 0 ») with a 60 min buffer time period between detections of the same species, were extracted for each trap night (i.e. 24 h period) at each station. For occupancy and detection modelling, this dataset was concatenated into detection histories (for each target species) with a resolution of 24 h, resulting in matrices attributing detection (« 1 »), non-detection (« 0 ») and camera disfunction (« NA ») values for each 24-h period. In addition, we selected equal number of trap nights for every sites, respectively, in Guadeloupe and Martinique, in order to uniformize sampling effort. Therefore, occupancy and detection modelling were set using data from a 9-night trap sessions in Guadeloupe, and data from a 32-night trap sessions in Martinique.

Analyses of species co-occurrence and activity patterns

The spatial co-occurrence of the northern raccoon and the small Indian mongoose with humans and potential competitors, predators or mammalian prey species was investigated. We used capture histories recorded at each site for domestic cats (*Felis catus* Linnaeus, 1758), domestic dogs (*Canis familiaris* Linnaeus, 1758), birds (we considered all bird species as one parameter), rodents (we considered all rodent species as one parameter), the common opossum (*Didelphis marsupialis* Linnaeus, 1753; present in Martinique and absent in Guadeloupe) and humans (Table 1). Co-occurrence was assessed using the combinatorial approach developed by Veech, 2013 incorporated in the R package « cooccur » v1.0 (Griffith, Veech & Marsh, 2016). This approach determines the probability that the observed frequency of co-occurrence of two species is less than, greater than, or not different from the expected frequency if the two species were distributed independently from one another among a set of sites. In addition, temporal activity and overlap were investigated using the kernel density estimates of diel activity from Meredith & Ridout, (2018) incorporated in the R package « camtrapR » v1.1 (Niedballa *et al.*, 2016).

Model covariates

We hypothesized that target species occupancy could be influenced by variation in elevation, land cover, annual mean temperature and precipitation. These parameters, widely used in

occupancy and detection models, allow to adequately depict the high diversity of habitats in these tropical islands.

Elevation data were obtained from the BD ALTI® dataset from the *Institut national de l'information géographique et forestière* (IGN, France) with a 250-m resolution. Land cover data were obtained from the CORINE Land Cover 2018 dataset downloadable from the Copernicus website (<https://land.copernicus.eu>). Annual mean temperature and precipitation data (averaged for the period 1970–2000) were obtained from the WorldClim 2.0 database (Fick & Hijmans, 2017) with a 30 s-arc resolution (~1 km²). Elevation, temperature and precipitation datasets were continuous rasters, and land cover was a categorical polygon shape file transformed into raster format. Land cover data were collapsed into 3 levels of categories: agricultural areas, natural sparsely vegetated areas and broad-leaved forest (urban areas were not sampled; Table 2). All datasets were aggregated into a 250-meter resolution.

Collinearity of the four variables was tested using the R package « virtualspecies » v1.5 (Leroy *et al.*, 2016). As elevation and temperature were correlated ($R^2 > 0.5$), we only retained elevation, considering that elevation would be more appropriate to portray habitat preferences of mammals. Environmental data for each station was extracted from the rasters (Table S1). Three stations fell outside of the raster extent due to the applied resolution (see legend in Table S1). Hence, values of the closest pixels were attributed. In addition, several land cover values extracted from raster dataset did not correspond to field observations made during trapping campaigns (see legend in Table S1). In such cases, land cover types identified in the field were attributed.

Our modelling approach also accounted for heterogeneity in target species detection probability. Detection probability may reflect variation in relative abundance, behaviour, as well as various factors related to sampling errors, such as the size of the field of view or the sensitivity of the camera. The field of view and sensitivity of the camera may vary between models and brand of cameras. In this study, we used two models of cameras (see above). Therefore, we hypothesized that camera model would influence detection probability. In addition, we included land cover data in our detection models. As previously mentioned, cameras were set on opposite sides of animal and human trails. These trails represent favoured crossing points for animals, and notably for terrestrial mammal species, particularly in environments with dense vegetations. Conversely, more open environments, with less dense vegetation, constrain animal movements less. Animal pathways are thus less easily identifiable. Therefore, we included this parameter in our detection models. We hypothesized that probability of detection would be higher in natural vegetated areas (broad-leaved forests and sparsely vegetated areas) rather than in agricultural areas.

Modelling approach

To evaluate the influence of environmental variables on the distribution of northern raccoons and small Indian mongooses in Guadeloupe and Martinique, we used single season –

Table 1 Names and descriptions of variables used in the models

Variable	Description	Source
Co-occurrence analyses		
Raccoon	Detections of northern raccoons	This survey camera traps data
Mongoose	Detections of small Indian mongooses	This survey camera traps data
Birds	Combined detections of all bird species	This survey camera traps data
Cat	Detections of domestic cats	This survey camera traps data
Dog	Detections of domestic dogs	This survey camera traps data
Human	Detections of humans	This survey camera traps data
Opossum	Detections of common opossums	This survey camera traps data
Rodents	Combined detections of all rodent species	This survey camera traps data
Occupancy and detection models		
Land cover	Land cover categories as described in Table 1	CORINE Land Cover 2018
Elevation	Elevation with 250 meter resolution	BD ALTI® - IGN France
Precipitation	Annual mean precipitation with 30 arc-second resolution	Worldclim version 2
Camera model	Model of the cameras used in this study	

Table 2 Land cover categories used in this study

Categories	CORINE Land Cover description	CORINE Land Cover code
Agri	Non irrigated arable land	211
	Fruit trees and berry plantations	222
	Pastures, meadows and other permanent grasslands under agricultural use	231
	Complex cultivation patterns	242
	Land principally occupied by agriculture, with significant areas of natural vegetation	243
Sparse	Natural grasslands	321
	Moors and heathland	322
	Sclerophyllous vegetation	323
	Transitional woodland shrub	324
	Sparsely vegetated areas	333
Forests	Broad-leaved forest	311
	Inland marshes	411

single-species occupancy-detection models. As only two detections of raccoons on two different stations were made in Martinique, raccoon occupancy-detection in Martinique was not modelled.

Models were designed using the R package « unmarked » v0.13-0 (Fiske & Chandler, 2011). Site-base occupancy (ψ) was modelled as a function of elevation, land cover and precipitation. Probability of detection (p) was modelled as a function of camera model and land cover. All possible combinations of covariates (without interactions) were investigated using the R package « MuMIn » v1.43.6 (Barton, 2019). Models were ranked using the Akaike information criterion (AICc; Burnham & Anderson, 2002), and models with $\Delta\text{AICc} < 2$ were considered valid competing models. Competing models allowed to identify a sub-global model, including all variables of competing models. Sub-global model fitness was verified estimating the goodness-of-fit (MacKenzie & Bailey, 2004) and the mean dispersion parameter \hat{c} using 10000 parametric bootstraps (Burnham & Anderson, 2002). New competing models were then selected from QAICc values ($\Delta\text{QAICc} < 2$) adjusted using the \hat{c} parameter. Competing

models with non-informative parameters were not considered in further analyses (Arnold, 2010).

Results

Camera trapping survey results

Trapping surveys provided a total of 1008 trap nights in Guadeloupe and 817 trap nights in Martinique, resulting in, respectively, 1225 and 1029 identified captures (151 and 134 unidentified captures). We obtained, respectively, in Guadeloupe and Martinique, 113 and 2 captures of northern raccoons, and 280 and 207 captures of small Indian mongoose.

For modelling purposes, we used a subset of our trapping surveys. The 9 nights of trap sessions in Guadeloupe provided, respectively, for the northern raccoon and the small Indian mongoose, 35 and 163 captures, resulting in 29 and 55 detections in model matrices. The 32 nights of trap sessions in Martinique provided, respectively, for the northern raccoon and the small Indian mongoose, 2 and 207 captures, resulting in 2 and 98 detections in model matrices (Fig. 1).

Species co-occurrence

In Guadeloupe, the northern raccoon co-occurred with birds (including all bird species captured by camera traps) and the domestic cat more than expected by random (Table 3). However, while raccoon and cats presented a clear nocturnal activity pattern, with diel activity overlapping greatly (overlap density estimates $D_{hat} = 0.89$), birds identified in our data presented a diurnal activity and raccoon and bird activity overlapped little ($D_{hat} = 0.24$; Fig. 2). Small Indian mongooses also positively spatially co-occurred with birds in Guadeloupe, as well as with rodents (Table 3). Temporal activities of small Indian mongooses and birds were clearly diurnal and overlapped greatly ($D_{hat} = 0.91$). Conversely, rodents appeared strictly nocturnal and daily activity of mongooses and rodents overlapped little ($D_{hat} = 0.14$; Fig. 2).

In Martinique, small Indian mongooses spatially positively co-occurred with the common opossum. However, activity overlapped little ($D_{hat} = 0.14$) as the opossum showed a clear nocturnal activity.

Occupancy and detection models

The northern raccoon in Guadeloupe

In Guadeloupe, naïve occupancy of the northern raccoon was 0.31 (Fig. S1).

No model was better than the null model (i.e. within a delta QAIC < 2; Fig. 3), showing that none of the variables tested had a significant influence on the occupancy and detection of the northern raccoon in Guadeloupe (Table 4).

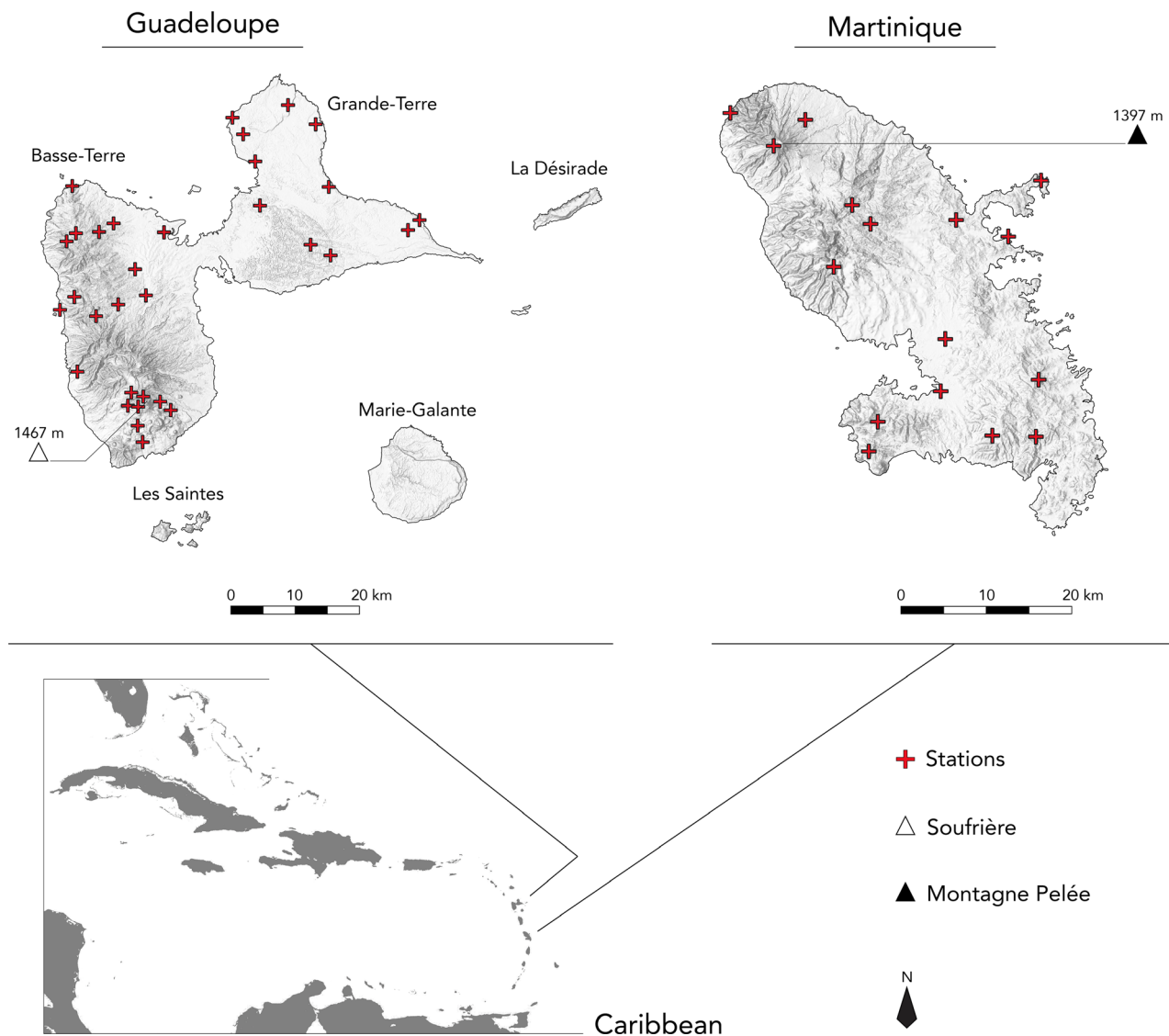
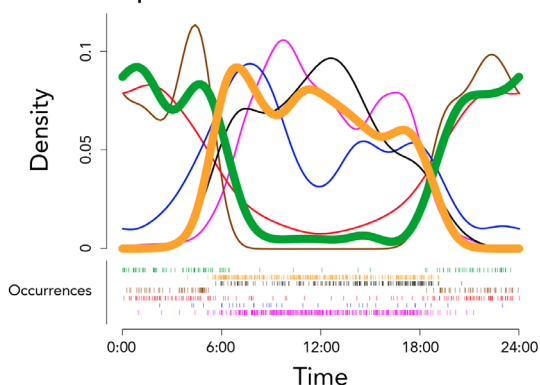


Figure 1 Camera trap locations in Guadeloupe and Martinique.

Table 3 Positive co-occurrence probabilities of the northern raccoon and the small Indian mongoose with birds and other mammal species in Guadeloupe and Martinique

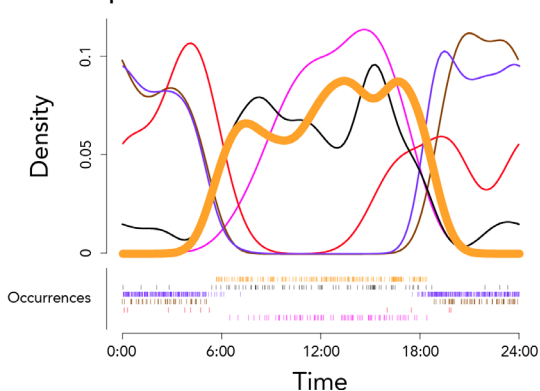
			Obs. cooccur.	Prob. cooccur.	Exp. cooccur.	P_{less}	$P_{greater}$
Guadeloupe							
Northern raccoon	/	Birds	12	0.177	6.7	1	0.001
Northern raccoon	/	Domestic cat	12	0.229	8.7	0.996	0.028
Small Indian mongoose	/	Birds	15	0.306	11.6	0.998	0.02
Small Indian mongoose	/	Rodents	11	0.198	7.5	1	0.006
Martinique							
Small Indian mongoose	/	Common opossum	9	0.48	7.2	1	0.044

Guadeloupe



Overlap	raccoon	mongoose	birds	rodents	cat	dog
raccoon						
mongoose	0.24					
birds	0.24	0.91				
rodents	0.86	0.14	0.15			
cat	0.89	0.30	0.31	0.81		
dog	0.39	0.81	0.75	0.30	0.45	
human	0.18	0.86	0.84	0.11	0.27	0.72

Martinique



Overlap	mongoose	birds	opossum	rodents	cat
mongoose					
birds	0.84				
opossum	0.14	0.19			
rodents	0.10	0.17	0.88		
cat	0.33	0.38	0.68	0.67	
human	0.81	0.74	0.08	0.06	0.23

Figure 2 Activity patterns of mammal species detected during the survey.

The small Indian mongoose in Guadeloupe

In Guadeloupe, naïve occupancy of the small Indian mongoose was 0.66 (Fig. S1).

We considered one model to be competitive (i.e. within a $\Delta\text{QAIC}_c < 2$; Table 4). This model suggested that none of the environmental variables tested influenced the occupancy of the small Indian mongoose in Guadeloupe. However, this model suggested that the detection of mongooses in Guadeloupe was influenced by camera model, with Moultrie cameras showing higher probabilities of detection ($\beta = -2.276$, $\text{SE} = 0.424$; Fig. 3).

The small Indian mongoose in Martinique

In Martinique, naïve occupancy of the small Indian mongoose was 0.63 (Fig. S1).

We considered one model to be competitive (i.e. within a $\Delta\text{QAIC}_c < 2$; Table 4). This model suggested that none of the environmental variables tested influenced the occupancy of the small Indian mongoose in Martinique. However, this model suggested that the detection of mongooses in Martinique was positively influenced by land cover, with higher probability of detection in broad-leaved forest habitat: ($\beta = 3.321$, $\text{SE} = 0.680$; Fig. 3).

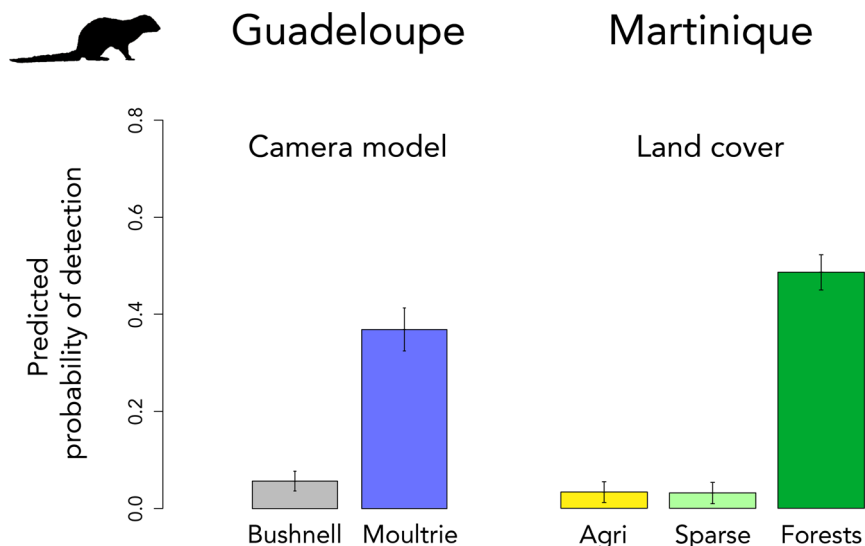


Figure 3 Selected model predictions of small Indian mongoose in Guadeloupe and Martinique (predicted covariate effects with standard errors when all other covariates are held constant at their mean). Camera models: Bushnell: Bushnell Essential E2 (Bushnell Corp., Overland Park, KS, USA); Moultrie: Moultrie M880 (Moultrie Feeders, Birmingham, AL, USA).

Table 4 Occupancy - detection models for the northern raccoon and the small Indian mongoose in Guadeloupe and Martinique

Model	QAICc	Δ QAICc	Weight	logLik	d.f.
Northern raccoon in Guadeloupe					
$\psi(\cdot), p(\cdot)$	55.3	.	0.59	-50.64	2
$\psi(\cdot), p(\text{camera model})$	57.7	2.34	0.18	-50.34	3
$\psi(\text{elevation}), p(\cdot)$	57.7	2.38	0.18	-50.39	3
$\psi(\text{elevation}), p(\text{camera model})$	60.2	4.93	0.05	-50.1	4
Small Indian mongoose in Guadeloupe					
$\psi(\cdot), p(\text{camera model})$	179.2	.	0.99	-117.93	3
$\psi(\cdot), p(\cdot)$	191.6	12.42	0.01	-128.387	2
Small Indian mongoose in Martinique					
$\psi(\cdot), p(\text{land cover})$	339.2	.	1	-163.77	4
$\psi(\cdot), p(\cdot)$	420.4	81.19	0	-207.73	2

Competitive models are highlighted in bold characters.

Mean dispersion parameters (\hat{c}) obtained using MacKenzie and Bailey's goodness-of-fit test for sub-global models were: $\hat{c}_{\text{northern raccoon in Guadeloupe}} = 2.09$; $\hat{c}_{\text{small Indian mongoose in Guadeloupe}} = 1.39$; $\hat{c}_{\text{small Indian mongoose in Martinique}} = 0.94$.

The competing models selected from QAICc values adjusted with the \hat{c} parameter from sub-global models are presented in the Table 4.

Discussion

This study presents the first analysis of the distribution and habitat preferences for the most widespread introduced wild carnivores in the Caribbean region, the northern raccoon *Procyon lotor*, and the small Indian mongoose *Urva auropunctata*.

Occupancy and detection of both species were assessed using camera trapping data and single season – single-species models. Our results revealed that occupancy of both raccoons and mongooses in Guadeloupe and Martinique was not influenced by classic environmental descriptors such as elevation, precipitation and land cover. Alternatively, the detection probability was influenced by a diversity of predictors. Notably, land cover appeared to influence detection probability of the small Indian mongoose in Guadeloupe and Martinique. Our results suggest that both species have the potential to occupy a large

part of the available areas in Guadeloupe and Martinique, leaving little areas free of invasive predators in these islands.

Occupancy and detection of the northern raccoon

In Guadeloupe, our results appear congruent with previous studies on the habitat preferences of the northern raccoon showing high ubiquity both in its native and introduced range (Lesmeister *et al.*, 2015; Fischer *et al.*, 2016; Reichert *et al.*, 2017; Louppe *et al.*, 2019; Pease, Holzmüller & Nielsen, 2019). The raccoon was observed in 31% of our trapped sites, and in a high diversity of habitats including humid and dry broadleaf forests, sparsely vegetated areas, agricultural areas and mangroves. However, our models showed that neither land cover, elevation nor precipitation significantly influenced its distribution. These results suggest that none of the environmental variables used in this study were able to adequately depict the ecological pattern influencing the distribution of the northern raccoon in Guadeloupe.

In Martinique, only two raccoons were detected, preventing analyses of occupancy and detection for this island. The very few occurrences are congruent with the low number of observations reported by local people and local authorities (e.g. ONCFS/OFB, see <http://www.oncfs.gouv.fr/Connaitre-les-especes-ru73/Le-Raton-laveur-ar2035>; pers. obs.) and reveal strong differences in population abundance and density in comparison with Guadeloupe. These differences may reflect the introduction history and the management of the species in these islands. The northern raccoon was introduced in Guadeloupe most probably during the early 19th century from animals captured in Eastern North America (Pons *et al.*, 1999; Helgen & Wilson, 2003; Lorvelec *et al.*, 2007; Louppe *et al.*, 2020a). Surprisingly, the Guadeloupean raccoon was considered an endemic species, *Procyon minor* (Miller, 1911) (Pinchon, 1967), until very recently (Pons *et al.*, 1999). Being protected by law, popular among Guadeloupeans, and considered an emblematic species of the island, raccoon populations thrived. Conversely, the raccoon was first reported in Martinique in 1954 (Lorvelec *et al.*, 2007) and was never considered endemic. Although no specific effort has been made to limit raccoon populations in Martinique, the species did not benefit from the same protection as in Guadeloupe, possibly preventing the same proliferation. The expansion of raccoon populations in Martinique might also be slowed down by potential competitive interactions with other nocturnal mammals, such as cats and opossums. However, our data showed few camera trap detections of cats on Martinique (11 captures, while 137 captures were made in Guadeloupe). Conversely, our survey revealed that opossums were abundant in Martinique, with a detection rate comparable to that of the small Indian mongoose. Competitive pressure from the marsupial could arise from competition for resting sites or access to food resources. However, competition for food is likely limited as Carver *et al.* (2011) showed that in Virginia (USA), foraging times of raccoons and opossums were independent, suggesting a neutral association between these two species. Moreover,

although arthropods represent the main animal food resource for both species, northern raccoons might preferably feed on crayfishes and crabs when available, while the common opossum might prefer insects and carrions (Llewellyn & Uhler, 1952; McManus, 1974; Lotze & Anderson, 1979).

These results show that investigating habitat preferences of the northern raccoon in Guadeloupe and Martinique would require an increased sampling effort, with additional stations sampled and a longer time of survey. Further studies, taking into account the diversity of anthropized habitats (i.e. urban areas, roads or the type of crops) might improve our understanding of the environmental characteristics influencing the occupancy of the northern raccoon in these tropical islands. Future studies might also consider multiple methods, such as hair snares, baited camera traps, or scat detection dogs (Long *et al.*, 2007; Garcia-Alaniz, Naranjo & Mallory, 2010; Monteroso *et al.*, 2014). Using multi-scale occupancy models, data derived from multiple methods can be combined, allowing to estimate occupancy across different spatial scales (Nichols *et al.*, 2008).

Occupancy and detection of the small Indian mongoose

Similar to the results obtained for the northern raccoon in Guadeloupe, our models showed that neither land cover, elevation nor precipitation influenced occupancy of the small Indian mongoose in Guadeloupe and Martinique. In addition, the proportion of sites where at least one observation was made was very high in both islands, being higher than 60%. Detection probabilities of mongooses in Guadeloupe were influenced by camera models, but surprisingly not by land cover. Conversely, detection of the small Indian mongoose in Martinique was influenced by land cover, with, as expected, higher probabilities of detection in forests, where wildlife trails are more easily distinguishable and represent favoured crossing points for animals.

Congruent with field observations and local knowledge, the small Indian mongoose appears to be able to cope with a high diversity of habitats in these tropical insular environments. Moreover, the species seems to have few potential predators and competitors, as, while the small Indian mongoose is strictly diurnal, all other carnivore species detected were nocturnal (with the exception of the domestic dog). In addition, all rodent species identified during our survey were nocturnal, demonstrating that predation pressure of the mongoose onto introduced rodents might be limited. Conversely, temporal activity of the various bird species captured in Guadeloupe and Martinique significantly matched that of the mongoose. These results confirm the potential of this species to have significant interactions with the native ecosystems in these hotspots of biodiversity.

Implications for insular ecosystems

Native ecosystems are highly vulnerable to the introduction of exotic species, particularly carnivores, which are often poorly

represented in insular habitats (Blumstein & Daniel, 2005; Bellard *et al.*, 2017; Spatz *et al.*, 2017). Having evolved with limited or even the absence of predation, insular, and especially endemic species, may be particularly threatened by such invasive predators.

Concerns about the impact of the northern raccoon on these insular environments and their economy have recently been raised. The species is known to damage agricultural productions in both native and introduced regions (Ikeda *et al.*, 2004; Beasley & Rhodes Jr., 2008). As a result, in Martinique, but even more so in Guadeloupe, attention has only focused on the assessment of the agricultural damage by the raccoon (Gourdol, 2017). However, our camera trap data highlighted that the species is also particularly present in natural habitats such as forests as well as coastal environments. These results suggest that, as observed on several islands in its native range (Ellis *et al.*, 2007; Engeman *et al.*, 2016), and as suspected for several Caribbean islands where the species has been introduced (Hayes *et al.*, 2004; Hayes, 2006; Ourly, 2006), the raccoon could be a threat to marine turtles and bird populations. Nonetheless, the influence of the northern raccoon on introduced ecosystems remains to be thoroughly assessed.

On the other hand, the negative impact of the introduction of the small Indian mongoose has been documented extensively and has been correlated to the decline of several amphibian, reptile, bird and mammal species in the Caribbean, but also in the Adriatic, Japan, and Hawaii (Barun, Simberloff & Budinski, 2010; Hedges *et al.*, 2016; Berentsen *et al.*, 2018). On Guadeloupe and Martinique, the small Indian mongoose might particularly threaten native reptile and bird species. In Guadeloupe, 36 bird species are considered near-threatened or threatened by the IUCN (IUCN France *et al.*, 2012). Among them, the forest thrush *Turdus therminieri* (Lafresnaye, 1844, Near Threatened) has been detected by our cameras in sites where mongooses were also repeatedly observed. Moreover, in Martinique, mongooses were detected in sites being in known restricted territories of endemic species, such as the Martinique lancehead *Bothrops lanceolatus* (Bonnaterre, 1790) (IUCN status: Endangered; Dewynter & Rufay, 2012), the Martinique oriole *Icterus bonana* (Linnaeus, 1766) (Vulnerable; Dewynter *et al.*, 2014), and the white-breasted thrasher *Ramphocinclus brachyurus* (Vieillot, 1818) (Endangered; BirdLife International, 2018).

Our survey also confirmed that small Indian mongooses were present in coastal environments and particularly in areas known to be sea turtle laying sites (Fig. S1). Three sea turtle species nest on the beaches of these two French islands: the leatherback sea turtle, *Dermochelys coriacea* (Vandelli, 1761) (Vulnerable), the green sea turtle, *Chelonia mydas* (Linnaeus, 1758) (Endangered), and the hawksbill sea turtle, *Eretmochelys imbricata* (Linnaeus, 1766) (Critically Endangered). These species are particularly threatened by habitat degradation, poaching and accidental catches, but also by the predation of mongooses on the turtle's eggs (Nicolaus & Nellis, 1987; Cottaz, 2015). Successful eradication of the small Indian mongoose has been conducted on the Îlet Fajou in the Guadeloupean archipelago, where sea turtle nests (Lorvelec & Pascal, 2005). Also, since 2009, conservation efforts have been

conducted in Guadeloupe and Martinique to limit the damages to turtle nests through monitoring and eradication campaigns of mongooses at laying sites during the nesting season (Biotope, 2016). However, the means implemented remain limited and the results of these efforts, although positive, remain slim and limited in time, justifying the renewal of this protection plan at least until 2022.

Conclusion

Our results highlight the capacity of the northern raccoon and the small Indian mongoose to cope with a high diversity of habitats on these two tropical islands. Our survey showed that both species occupy wide areas, with few or no potential competitors. Hence, the present study attests to the potential of both the northern raccoon and the small Indian mongoose to affect these already fragile insular ecosystems, which suggests that action directed towards the control of these species on locally identified sites of conservation interest is warranted.

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Competing interests statement

The authors declare no competing interests.

Author contributions

VL, AH and GV conceived the study. VL, SG, AH and GV designed the methodology. VL acquired the data, and VL, BP, AH and GV interpreted the results. VL wrote the first draft of the paper, and all the authors contributed to its writing.

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Supporting Information

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

Figure S1. Number of detections of both species at each station.

Table S1. Environmental data for each station. Stations gua2017-13, mar2018-4 and mar2018-t2 felt outside of the raster extent due to the applied resolution. Hence, values of the closest pixels were attributed. Land cover values did not correspond to field observations made during trapping campaigns for stations gua2017-7, gua2017-22, gua2017-24, gua2017-29, gua2017-35, gua2017-36, mar2018-15 and mar2018-18. Field observations values were attributed.