EFFECT OF URBAN DEVELOPMENT ON BIODIVERSITY CONSERVATION IN PUERTO RICO

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DEDICATION

To Carlos, Josefina, Paula, and to my parents Gastón & Mariela

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INTRODUCTION

Urbanization refers to the process by which rural areas are transformed to urban with an associated greater concentration of people in human settlements (Trzyna, 2005; 2007). Urban areas are growing worldwide as human population continues growing and more people choose to live in cities due to more opportunities for education, jobs, and services (Berry, 2008; Davis, 2011, Montgomery, 2008; Seto et al., 2011). Currently, half of the worlds' population lives in urban areas (Seto and Shepherd, 2009), and this trend is expected to increase in the near future, particularly in the tropics where biodiversity is greatest (Montgomery, 2008).

The increase of urban areas produces direct and indirect impacts on biodiversity. The most obvious direct impact is land cover change, a major cause of habitat loss and degradation (Elmqvist et al., 2016; McDonald et al., 2008; Wade and Theobald, 2010). Urbanization also produces indirect impacts on biodiversity including changes in water and nutrient availability, increases in abiotic stressors such as air pollution, increases in competition from non-native species, and changes in herbivory and predation rates (Pickett and Cadenasso, 2009). By 2030, about 25 percent of all endangered or critically endangered species are expected to be affected, directly or indirectly, by urban expansion (Giüneralp and Seto, 2013; McDonald et al., 2013).

Establishing protected areas is a global strategy used to stop land change and promote *in situ* biodiversity conservation (Chape et al., 2005, Beale et al., 2013). A protected area is "a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values" (Dudley, 2008). Due to their effectiveness to achieve conservation goals, protected areas have been increasing in numbers and extent, currently covering about 15% of the global land surface (UNEP-WCMC and IUCN, 2016). However, their effectiveness depends not only on their ability to stop habitat loss within their boundaries, but also in their surroundings (DeFries et al., 2005; DeFries et al., 2010; Hansen and DeFries, 2007). Surrounding lands to protected areas are attractive for agriculture or/and human settlements and development. Urban development represents a fast growing threat to protected areas in developed and developing countries (Bailey et al., 2016; Hamilton et al., 2013; Wade and Theobald, 2010). By 2030, the urban lands near protected areas are forecasted to increase substantially in almost all world regions (McDonald et al. 2008, 2009). As expanding urban areas intersect with growing protected areas, major conflicts emerge that limit protected area's conservation goals (Shahabuddin, 2009).

Puerto Rico is among the most urbanized islands in the Caribbean Archipelago (Lugo *et al*. 2012). Urban development in Puerto Rico has been described as inefficient, characterized by land consumption, and roads construction to facilitate commuting, producing a pattern of urban sprawl in 40 percent of the island (Martinuzzi et al., 2007). Thus, Puerto Rico provides an opportunity to study the effect of urban expansion on islands and on endemic species, both heavily impacted by urbanization (McKinney 2006, 2008).

The major goal of my dissertation was to understand the effect of urban development on biodiversity conservation in Puerto Rico. To accomplish this goal I: 1) described how much and what biodiversity occurs inside the network of terrestrial protected areas, 2) quantified pressure from urban development and human population around protected areas, and 3) assessed how urban development affects the distribution of anurans and reptiles along an urban-rural gradient.

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CHAPTER 1: Characterization of the Network of Protected Areas in Puerto Rico

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Abstract

Our goal was to describe how much and what biodiversity occurs inside the network of terrestrial protected areas in Puerto Rico. We conducted spatial analysis to quantify different indicators of diversity within protected areas. We found protected areas in Puerto Rico overlap the most species-rich regions in the island, encompass a diverse landscape, are dominated by core forest and include predicted habitats for 30 threatened vertebrate species analyzed here. However, when we calculated the proportion of these biodiversity features that are actually protected, we concluded that most of these features need better representation within protected areas. Besides expanding the current network of protected areas, Puerto Rico needs to continue enforcing land use plans and other available conservation tools in the island.

Introduction

Protected areas are globally known as the most adopted strategy for promoting *in situ* biodiversity conservation by preventing natural habitat conversion and reducing anthropogenic threats (Beale et al. 2013, Joppa et al. 2008, Chape et al. 2005). Hence, over the past twenty years protected areas have been increasing their coverage, currently occupying 15 percent of the global land surface and 3.4 percent of the oceans (Juffe-Bignoli et al. 2014).

Quantifying the extent of protected areas (Jenkins and Joppa 2009) represents the most used indicator to track international progress towards achieving UN Millennium Development Goals for 2020 through its Aichi Biodiversity Target 11 which seeks to protect 17 percent of terrestrial areas and 10 percent of nationally administered marine areas (http://www.cbd.int/sp/targets/). However, reporting changes in the extent of protected areas alone does not inform if protected areas are being effective in achieving conservation goals (Chape et al. 2005).

To tackle this global concern, several studies have provided more detailed assessments that quantify the ecological performance of a large network of protected areas (Butchart et al. 2015, Cantú-Salazar and Gaston 2010, Craigie et al. 2010, Gaston et al. 2008, Joppa and Pfaff 2011), as well as their ability for reducing land cover change and deforestation (Andam et al. 2008, Bruner et al. 2001). In addition, several tools have been developed to assess protected areas management effectiveness (PAME) including the Rapid Assessment and Prioritization of Protected Areas Management (RAPPAM) and the Management Effectiveness Tracking Tool (METT) (Leverington et al. 2010).

Protected areas in the insular Caribbean occupy approximately 11 to 15 percent (25,804 km^2-36,000 km^2) of the land surface (Chape et al. 2008). These protected areas have been established to safeguard one of the thirty five global biodiversity hotspots classified according to their high species richness, endemism and level of threat (Myers et al. 2000). The Caribbean is home to about 14,526 species, half of which are endemic to the region, and 912 are reported as threatened in the Red List of the International Union for Conservation of Nature (IUCN 2014). Caribbean islands are particularly vulnerable to extreme weather events, including hurricanes, tropical storms, and projected rising sea levels due to climate change, which could threaten the region's ecosystems and biodiversity. In addition, approximately 43 million people inhabit these islands (The World Bank 2015) and urban areas keep expanding in many of them (Stein et al. 2014). Due to the relatively higher vulnerability faced by species and natural ecosystems in islands in comparison to continents (Simberloff 2000), we need a clear understanding of the current performance of protected areas in promoting biodiversity conservation. This information is fundamental to identify conservation gaps and plan strategies to increase the protection of fragile ecosystems and vulnerable species in the Caribbean region.

Our goal was to describe how much and what biodiversity occurs inside the terrestrial network of protected areas in Puerto Rico. To achieve this goal we quantified the landscape diversity inside protected areas as this variable has a positive relationship with habitat diversity and niche availability for species (Diacon-Bolli et al. 2012, Kumar et al. 2006). In addition, we analyzed the configuration of the forest inside protected areas as it provides information about the quality of the forest (Turner 2005), very relevant in this study as forest represents the main habitat for most terrestrial species in Puerto Rico (Gould et al. 2007). For example, a large amount of perforations in the forest land cover (Table 1) would indicate habitat fragmentation which would affect biodiversity conservation (Krauss et al. 2010). Additionally, we calculated the proportion of high and very high species richness areas, and predicted habitats for threatened species under protection in Puerto Rico. Finally, we calculated how much of the Critical Wildlife Areas (CWAs) and Important Bird and Biodiversity Areas (IBAs) are inside the current network of protected areas. Critical Wildlife Areas represent one of the most important compendiums of species and habitats of concern generated by the Puerto Rico Department of Natural and Environmental Resources (Ventosa-Febles et al. 2005). Important Bird and Biodiversity Areas have been identified throughout the world by BirdLife International (www.birdlife.org). These areas include places of international significance for the conservation of biodiversity, particularly endangered, endemic and migratory birds. Species richness, CWAs and IBAs layers used in this study represent the most up-to-date nation-wide biodiversity maps currently available for Puerto Rico.

Our study provides an updated analysis, initially addressed by the Puerto Rico Gap Analysis Project (Gould et al. 2007), to identify key biodiversity areas inside and outside the current network of protected areas in Puerto Rico, the starting point for conservation planning at landscape level.

Methods

Study area

Puerto Rico is located in the Caribbean Archipelago, occupying a land area of approximately 8,900 km^2. The island has a tropical climate, with mean annual precipitation ranging between 500 mm and 4400 mm, and mean annual temperatures that range between

19.4°C and 29.7°C (Daly et al. 2003). The island has a complex geomorphology and soils represented by alluvial, volcanic, sedimentary, limestone and serpentine substrates and a steep topography that includes coastal plains, cliffs, hills and mountains up to 1300 meters in altitude. The simplified land cover in Puerto Rico is: 39% forest, 32% grassland, 13% woodland and shrubland, 11% urban, 3% herbaceous wetlands, 1% forested wetlands, 1% inland water, and less than 1% is natural barrens (Gould et al. 2007). Puerto Rico's terrestrial biodiversity includes at least 2780 species of plants (Proyecto Coqui 2008), and 361 native vertebrates (i.e., 277 birds, 52 reptiles, 19 amphibians, and 13 mammals) (Joglar 2005, Joglar et al. 2007).

Protected areas data

In this study we analyzed a total of 95 protected areas that represent 8.2 % (735.6 km^2) of the land surface of the island and associated cays (Gould et al. 2011). Protected areas in Puerto Rico have a mean size of 7.5 km^2 ranging from <0.1 km^2 to 114.0 km^2 (median= 2 km^2). Eighty-one protected areas are smaller than 10 km^2, and 40 of these are smaller than 1 km^2 (Figure 1). The Puerto Rico Department of Natural and Environmental Resources (DNER) manages or co-manage approximately 58% (425.7 km^2) of the protected areas, the federal government (US Forest Service and Fish and Wildlife Service) about 28% (206.5 km^2), the non-governmental organizations Para La Naturaleza approximately 13% (98.25 km^2), and others institutions about 1% (Quiñones et al. 2013).

Habitat characteristics

Landscape diversity— We quantified the diversity of the landscape inside protected areas according to: 1) vegetation cover, and 2) Ecological Life Zones (ELZs). The Holdridge Ecological Life Zones (ELZ) provides information about vegetation based on climatic, latitudinal and elevation features (Ewel and Whitmore 1973). In Puerto Rico there are six ELZ: subtropical rain forest, subtropical dry forest, subtropical wet forest, subtropical moist forest, subtropical lower montane wet forest, and subtropical lower montane rain forest (Ewel and Whitmore 1973). We used the land cover 2000 generated by the Puerto Rico Gap Analysis (Gould et al. 2007). This land cover was derived from Landsat ETM+ satellite images with a spatial resolution of 15 x 15 meters, resulting in 70 land cover classes (Gould et al. 2007). For our analysis we selected a subset of 56 vegetation classes that included all vegetation forms, and excluded those less natural and non-vegetated covers (e.g., developed, rocky cliffs). We used the Shannon Diversity Index (*H*) to calculate the landscape diversity for each landscape feature. This index takes into account both the number of species (analogous to vegetation covers or ELZs), and their relative abundances (evenness or equitability) (Nagendra 2002).

$$H = -SUM[(pi) * \ln(pi)]$$

In this equation p_i was the relative abundance (or proportion) of different vegetation cover classes or ELZs (*S*) inside each protected area. A value of *H*=0 represents the lowest landscape diversity, while values equal or greater than 1 represent a landscape with high diversity. For both landscape features, we classified the landscape diversity in five categories: very low (0≤0.29), low (0.30-0.59), intermediate (0.60-0.89), high (0.90-1.19), and very high (≥1.20).

Forest configuration— We conducted a Morphological Spatial Pattern Analysis (MSPA) to quantify the amount and configuration of the forest class inside protected areas. The MSPA classifies a raster binary image (e.g., forest vs. non-forest) into seven classes according to the arrangements of its pixels: core, bridges, islets, loops, edges, perforations and branches (Vogt et al. 2007a,b) (Table 1). We developed the raster binary image (forest vs non-forest) using a simplified version of the 2000 PRGAP land cover map that classifies the island into 8 classes (i.e., forests, woodland and shrubland, grasslands, forested wetlands, herbaceous wetlands, in-land water, natural barrens, and built-up surface) (Gould et al. 2008). For our analysis we reclassify all woody vegetation (i.e., forests, forested wetlands, woodlands and shrublands) in a new class named foreground (=2), while the other classes were reclassified as background (=1), and missing data (=0). The MSPA only describes forest pixels in the foreground.

Vertebrate diversity

Species richness— We used the predicted species richness distribution maps generated by the PRGAP for 201 species of terrestrial vertebrates (Gould et al. 2008). Predicted distributions were modeled by combining all major habitat elements considered to influence the occurrence of a species across its range and intersecting occurrence records for the species. For example, different habitat features (*eg.*, elevation, vegetation type) important for each species were identified in topographic and the land cover map at 15-m spatial resolution and then intersected with the species occurrence records defined within 24 km^2 hexagons (Gould et al. 2008). These hexagons represented the minimum mapping unit for interpreting species geographic range extent. Habitat features were extracted from the literature, while species occurrence records were derived from long-term surveys, reports and publications. All selected data used for modeling was reviewed by experts as well as final distribution maps (Gould et al. 2008). The total number of species modeled to occur in each 15-m pixel indicated the species richness. Predicted distributions maps were generated for 97 resident birds, 25 migratory birds, 47 reptiles, 18 amphibians and 14 mammals, from which 187 (93%) were native and 14 (7%) were exotics. We used natural breaks to group the geospatial layer of species richness into five categories: very low (0-16 species), low (17-34 species), intermediate (35-47 species), high (48-59 species) and very high (60-90 species). Finally, we calculated the representation of each species richness category inside protected areas, with particular interest in high and very-high species richness regions.

Predicted habitats for threatened species— Using the predicted species richness distribution maps we calculated the percentage of protection of predicted habitat for 31 threatened species: 12 birds, 9 reptiles, 7 amphibians, and 3 mammals. Twenty of these species are endemic, and 11 are non-endemic but native to Puerto Rico. Native or indigenous refers to a species that occurs naturally in an area, whose dispersal has occurred without human intervention (Manchester and Bullock 2000).

Critical Wildlife Areas (CWAs) and Important Bird and Biodiversity Areas (IBAs)—The CWAs in Puerto Rico were identified according to faunal composition and abundance, particularly endangered and/or endemic species, presence of critical habitat, and level of threat on habitats and species (Ventosa-Febles et al. 2005). The CWAs occupy approximately 1120.95 km^2 (853.13 km^2 terrestrial, 267.82 km^2 marine) of Puerto Rico's main island, associated cays and surrounding water. The IBAs have been identified in Puerto Rico according to the distribution of

55 key bird species that include: endangered, vulnerable and near threatened species as well as birds with restricted ranges, and those birds' species that aggregate in flocks (BirdLife International 2015). Puerto Rico has a total of 20 IBAs that occupy about 1971.86 km^2 of the island (1434.61 km^2 land, 537.24 km^2 marine) (Méndez-Gallardo and Salguero-Faría 2008). We calculated the proportion of terrestrial CWAs and IBAs inside protected areas.

Results

Landscape diversity

Landscape diversity indexes derived from vegetation cover classes ranged from very low (0) to very high (2.19) (mean and media=1.14), where 44 protected areas (46.3%) have a very high landscape diversity, 26 (24.7%) a high landscape diversity, 11 (10.4%) intermediate, 8 (7.6%) low, and 6 (5.7%) very low (Fig. 2). Diversity indexes based on ELZs ranged from very low (0) to intermediate (0.70) (mean= 0.09, media= 0). According to this landscape feature, most protected areas (90) have low and very low landscape diversities (Fig. 2).

Forest configuration

Forest classified as core occupied an area of 3412.96 km^2 in Puerto Rico (Figure 3). Almost 16% (543.74 km^2) of this core forest was inside protected areas (Table 2). Core forest was the most abundant class inside protected areas accounting for 91.74% of the total forest protected, while edge and perforation were the second and third most abundant classes (Table 2).

Species richness

The predicted species richness inside protected areas ranged from very low (0-16) to very high (60-90) species per 15-m pixel. Very high and high species richness regions in Puerto Rico occupied approximately 1200 km^2, and 2270 km^2, respectively. The network of protected areas captured 10.55% (126.55 km^2) of the very high and 13.19% (299.34 km^2) of the high species richness regions in the island (Fig. 4 A, B).

Threatened species, CWAs and IBAs

The total predicted habitat for 31 threatened species in Puerto Rico occupied an area of 4.85 km^2, where 1.43 km^2 (29.5%) of this area occurs inside protected area. The proportion of protection of predicted habitats for individual species ranged from 0% to 100% (mean= 47%) (Table 3). Five critically endangered species, five endangered and ten vulnerable species have ≤50% of their predicted habitat protected (Table 3). In addition, we found a negative correlation between species island-wide distribution and percentage of protection (r_s= -0.56, P <0.001). Sixty eight percent (591.9 km^2) and 41% (590.7 km^2) of the terrestrial component of CWAs and IBAs, respectively, occur in protected areas (Fig. 5).

Discussion

Eighty-two percent of the protected areas in Puerto Rico are smaller than10 km^2, an area globally considered to be too small to maintain viable populations and to reduce anthropogenic threats from outside (Cantú-Salazar and Gaston 2010). However, our results on landscape diversity indicated that the small size of protected areas in Puerto Rico is not necessarily a determinant of the biodiversity it encompasses. By contrast, according to the diversity index used here, 70% of the protected areas in Puerto Rico encompass a high and very high landscape diversity associated with an expected high diversity of habitats and species, suggesting that this index could be used as an indicator of biodiversity in small tropical islands in the Caribbean, with similar geology, ecology, and land use history.

However, we identified two main limitations from using this diversity index as an indicator of biodiversity inside protected areas. First, it is important to have a good understanding of the scale of the landscape features selected to calculate the index. For example, our results suggest high biodiversity for one landscape feature (vegetation cover) despite low landscape diversity for the other one (ELZs). An explanation for this contradictory result is the larger extent of ELZs in comparison to land cover data and the size of most protected areas in the island. Second, the assumed generality of a positive relationship between landscape diversity and species biodiversity should be locally tested, as biodiversity might depend on other attributes that differ from landscape diversity. For example, one study conducted in Japan found bird species with narrow range sizes had a highest diversity in less diverse landscapes (Katayama et al 2014).

According to our results, existing protected areas are somewhat protecting the predicted habitats for all but one threatened species modeled by PRGAP. Hence, more complex studies are needed to understand if species are being successfully protected not only in terms of their presence/absence, but also according to representation, resilience and redundancy (Redford et al. 2011). We found that very high and very low species richness regions have similar levels of protection within protected areas, which indicates the importance of using a landscape approach when prioritizing new areas to protect.

In general, unprotected high species richness regions, CWAs and IBAs, occurred in lands adjacent to existing protected areas (Fig. 5), where protected areas are samples of larger regions with similar ecological characteristics such as the karst region in the north of the island. These unprotected regions would be affected by future land development, which over the previous several decades has been characterized by extensive urban sprawl (Martinuzzi et al. 2008), even in non-urban zoning districts (López-Marrero and Hermansen-Báez 2011). In general, land development in the island has been occurring in the lowlands, near roads, close to existing urban areas, and in ecological zones with the least amount of protection (Helmer 2004, Helmer et al. 2008, Keenaway and Helmer 2007). Although human population has been declining in Puerto Rico during the last decade (United States Census Bureau 2015), the need for integrating conservation in urban and other land use planning remains as new housing units, roads and other developments keep expanding in the island.

Conclusion

Protected areas in Puerto Rico have several strengths including: their location overlapping the most species-rich regions in the island and regions classified as CWAs and IBAs. Additionally, they encompass a diverse landscape, are dominated by core forest and include predicted habitats for 30 threatened vertebrate species analyzed here. However, when we calculated the proportion of these biodiversity features that are actually protected, we concluded that most of these features need better representation within the current network of protected areas.

Besides expanding the current network of protected areas, biodiversity conservation inside protected areas can be enhanced through continued enforcement and promotion of the use of existing conservation mechanisms, including implementation of an island-wide land use plan (Junta de Planificación 2014), better communication of actions required to mitigate land development (e.g., land acquisition and transference to the Department of Natural and Environmental Resources), and an improved designation of critical habitats under the Endangered Species Act. Better interagency collaboration can enhance conservation. In the case of El Yunque National Forest, better collaboration in planning and enforcement of conservation regulations in the lands surrounding the largest protected area in Puerto Rico would improve conservation of biodiversity and ecosystem services both within and outside the national forest. Studies show that promoting forested coverage beyond the administrative boundary of a protected area contributes to increase the effective size of this protected area, and its capacity to conserve viable populations, species richness and ecosystem services (DeFries et al. 2005, Hansen and DeFries 2007, Hull et al. 2011, Zaccarelli et al. 2008).

Finally, keep establishing government programs that support biodiversity conservation in private lands, such as the US Forest Service Forest Stewardship Program (USDA-FS 2014) and the US Fish and Wildlife Service Partners for Wildlife (USFWS 2014) which assist and incentivize private landowners to manage part of their land for conservation. Even in urbanized landscapes, encouraging wildlife-friendly gardens and infrastructure (e.g., plants, luminary) represents an opportunity for education and for involving citizens in biodiversity conservation (Dearborn and Kark 2009, Goddard et al. 2010).

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Tables

Table 1. MSPA classes, description and explanation about the potential contribution of each class in conservation planning (Vogt pers. comm).

Forest class	Description	Relevance for conservation planning
Core	Forest pixels whose distance to non-forest pixels is greater that the given edge width (1 pixel= 15 m)	Focus class for biodiversity conservation, least fragmented.
Bridge	Set of contiguous non-core forest pixels that connect at least two different cores	Structural connectors or corridors that could potentially be used by some species to move across the landscape
Edge	Outer core boundary	Some species prefer to dwell in the foreground/background interface.
Perforation	Similar to edges, but corresponding to the inner boundary of the core area	Perforations inside core habitat are sign of fragmentation.
Loop	Similar to bridges but connecting with the same core area	Informs about connectivity.
Islet	Isolated forest patches that are too small to contain core pixels	May be the result of forest loss, but may also be important as stepping stones between cores. Focus class for restoration.
Branch	Pixels that do not correspond to any of the previous six categories	May be the result of a bridge or corridor getting interrupted, or if it continues growing it may provide connectivity. Focus class for restoration.

Table 2. MSPA indicating the extent (km^2) of forest classes inside protected areas, relative abundances (%) and the proportion of protection for each class.

	Inside protected areas		Island-wide		
Forest class	Area (km^2)	Relative abundance (%)	Area (km^2)	Relative abundance (%)	In protected areas (%)
Core	543.74	91.74	3412.96	72.25	**15.93**
Edge	22.11	3.73	569.46	12.06	**3.88**
Perforation	14.44	2.44	276.98	5.86	**5.21**
Branch	4.32	0.73	182.00	3.85	**2.37**
Loop	3.96	0.67	100.77	2.13	**3.93**
Bridge	2.82	0.48	115.50	2.45	**2.44**
Islet	1.32	0.22	65.92	1.40	**2.00**
Total	**592.71**	**100**	**4723.58**	**100**	**35.78**

Table 3. Percentage of predicted habitat protected for 31 threatened species in Puerto Rico. V= Vulnerable, CE= Critically Endangered, and E= Endangered.

Species name	**Group**	**Island-wide species habitat area (m^2)**	**Protected habitat (%)**	**US Endangered Species Act**	**Distribution class and Conservation Status**
Eleutherodactylus cooki (Grant 1932)	A	9000	0	Threatened	Endemic, V
Eleutherodactylus eneidae (Rivero 1959)	A	31275	64	Not Listed	Endemic, CE
Eleutherodactylus jasperi (Drewry and Jones 1976)	A	6075	22	Threatened	Endemic, CE
Eleutherodactylus locustus (Schmidt 1920)	A	1350	83	Not Listed	Endemic, V
Eleutherodactylus portoricensis (Schmidt 1927)	A	21825	61	Not Listed	Endemic, V
Eleutherodactylus richmondi (Stejneger 1904)	A	37575	54	Not Listed	Endemic, V
Peltophyrne lemur (Cope 1868)	A	3600	69	Threatened	Endemic, CE
Accipiter striatus venator (Wetmore 1914)	B	63675	45	Endangered	Native, CE
Agelaius xanthomus (Sclater 1862)	B	981225	25	Endangered	Endemic, E
Amazona vittata (Boddaert 1783)	B	5625	24	Endangered	Endemic, CE
Anas bahamensis (Linnaeus 1758)	B	78300	58	Not Listed	Native, V
Buteo platypterus brunnescens (Danforth and Smyth 1935)	B	221850	25	Endangered	Endemic, CE
Caprimulgus noctitherus (Wetmore 1919)	B	158850	24	Endangered	Endemic, E
Dendrocygna arborea (Linnaeus 1758)	B	178425	50	Endangered	Native, CE
Fulica caribaea (Ridgway 1884)	B	24975	26	Not Listed	Native, V
Oxyura jamaicensis (Gmelin 1789)	B	115875	49	Not Listed	Native, V
Patagioenas inornata (Vigors 1827)	B	390600	24	Endangered	Native, E
Pelecanus occidentalis (Linnaeus 1766)	B	645075	38	Endangered	Native, E
Setophaga angelae (Kepler and Parkes 1972)	B	66600	40	Not Listed	Endemic, V
Erophylla sezekorni (Gundlach 1861)	M	144900	31	Not Listed	Native, V
Brachyphylla cavernarum (Gray 1834)	M	73125	34	Not Listed	Native, V
Monophyllus redmani portoricensis (Miller 1900)	M	164925	34	Not Listed	Endemic, V
Chilabothrus inornatus (Reinhardt 1843)	R	882225	17	Endangered	Endemic, V
Chilabothrus monensis granti (Stull 1933)	R	8775	77	Endangered	Native, CE
Chilabothrus monensis monensis (Zenneck 1898)	R	900	100	Endangered	Endemic, V
Ctenonotus cooki (Grant 1931)	R	52875	44	Not Listed	Endemic, E
Ctenonotus poncensis (Stejneger 1904)	R	167850	30	Not Listed	Endemic, V
Cyclura cornuta stejnegeri (Barbour and Noble 1916)	R	900	100	Threatened	Endemic, E
Mabuya mabouya sloanei (Daudin 1803)	R	303975	25	Not Listed	Native, V
Sphaerodactylus micropithecus (Schwartz 1977)	R	450	100	Endangered	Endemic, CE
Xiphosurus roosevelti (Grant 1931)	R	14625	86	Endangered	Endemic, CE

Figures

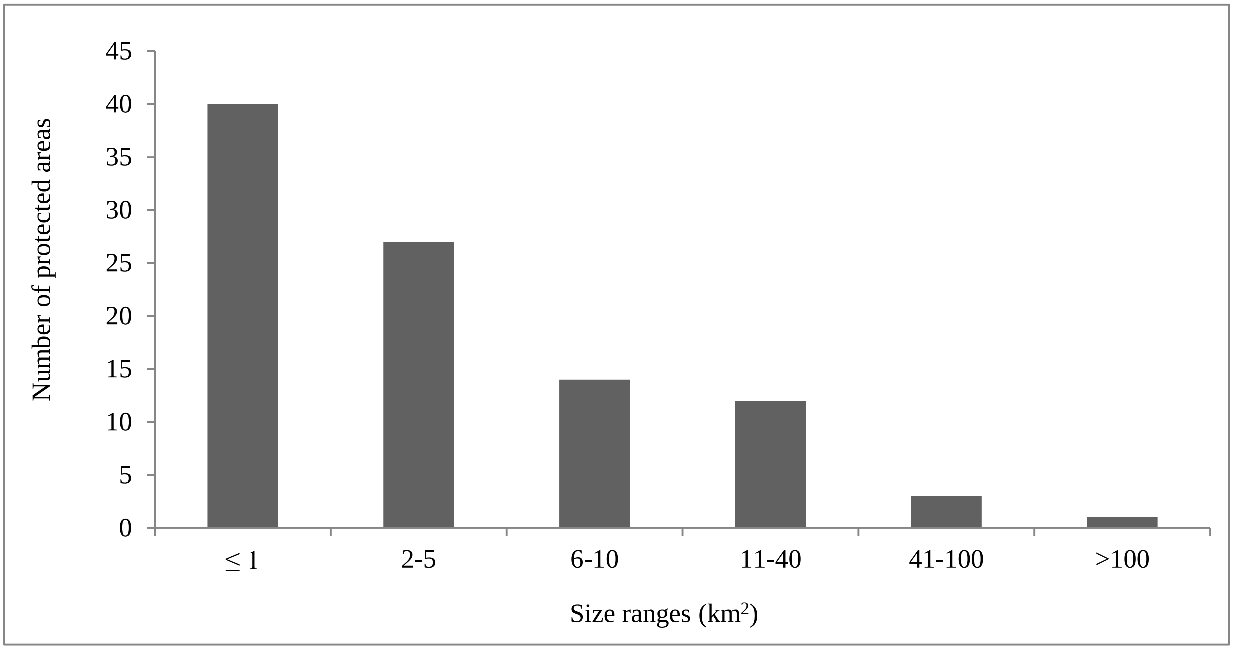


Figure 1. Size-frequency distribution of protected areas in Puerto Rico.

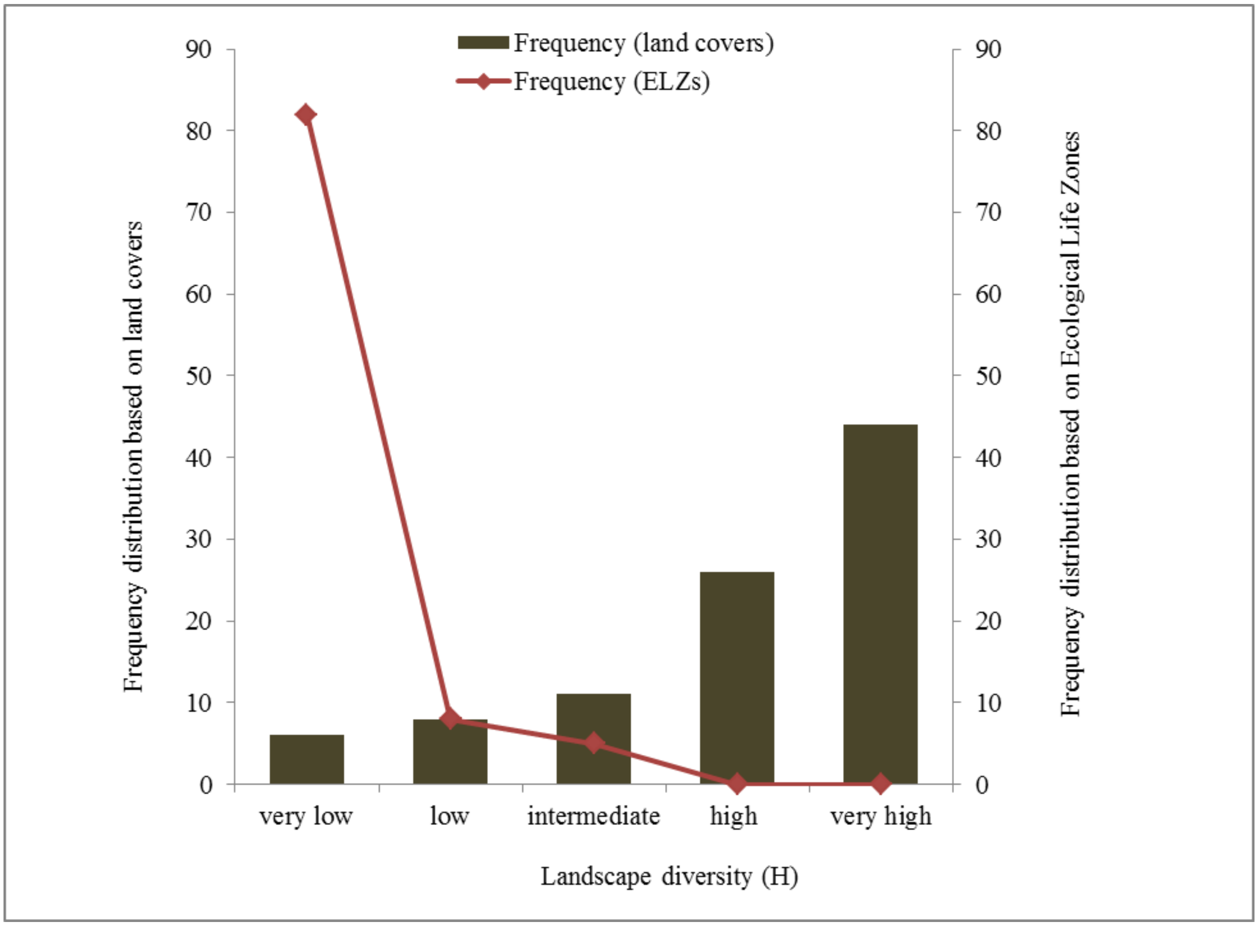


Figure 2. Frequency distribution of protected areas according to their landscape diversity.

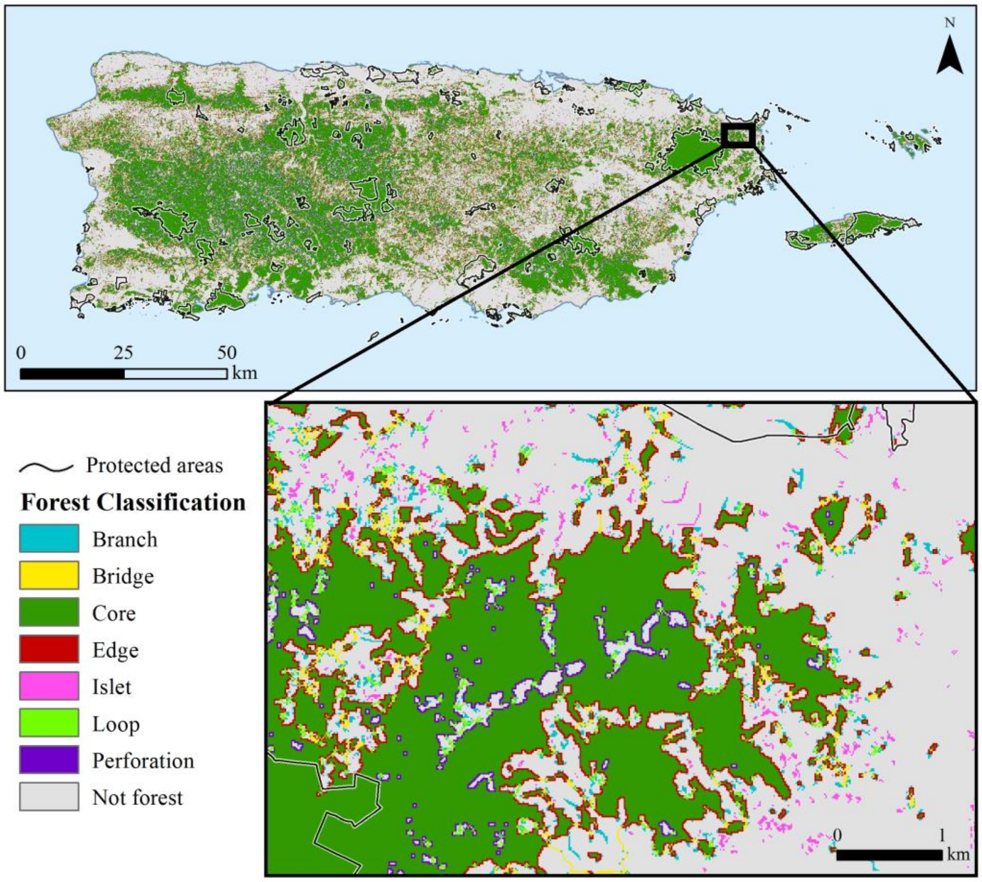
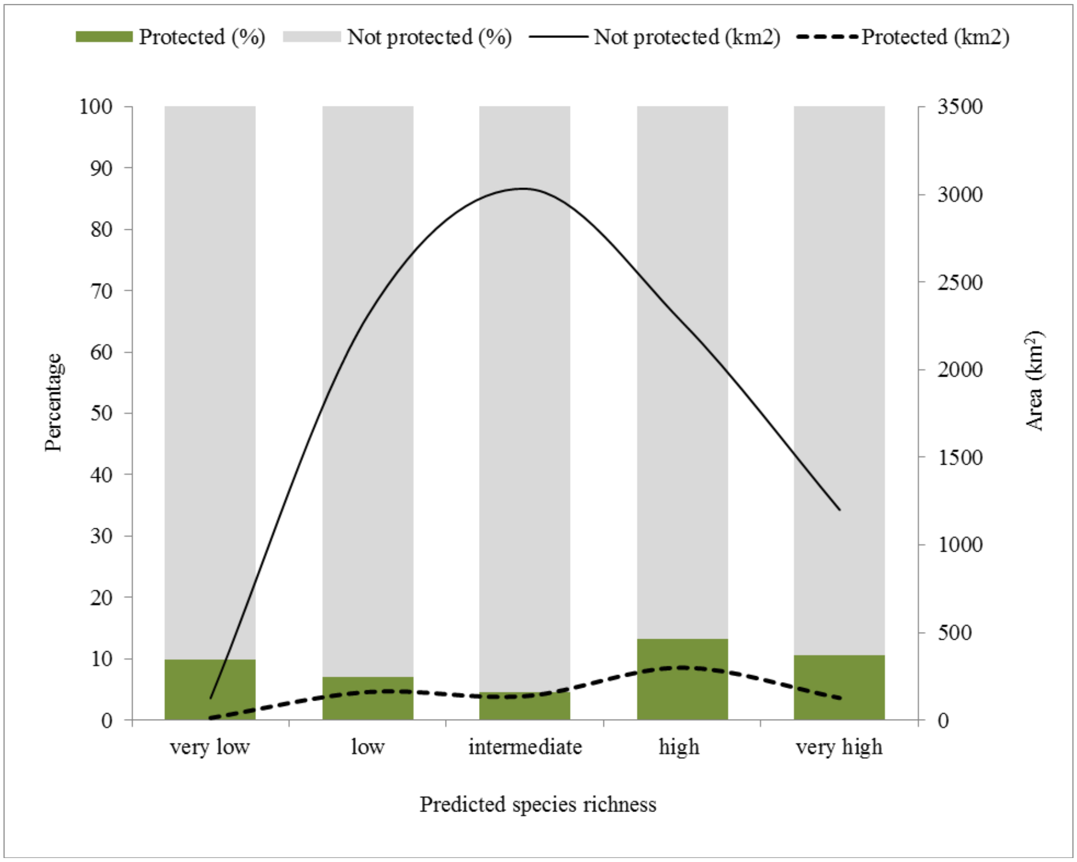


Figure 3. Morphological Spatial Pattern Analysis of the forest in Puerto Rico, and an enlarged sub-region in the northeast to show detailed interpretation of forest classes.

A)



B)

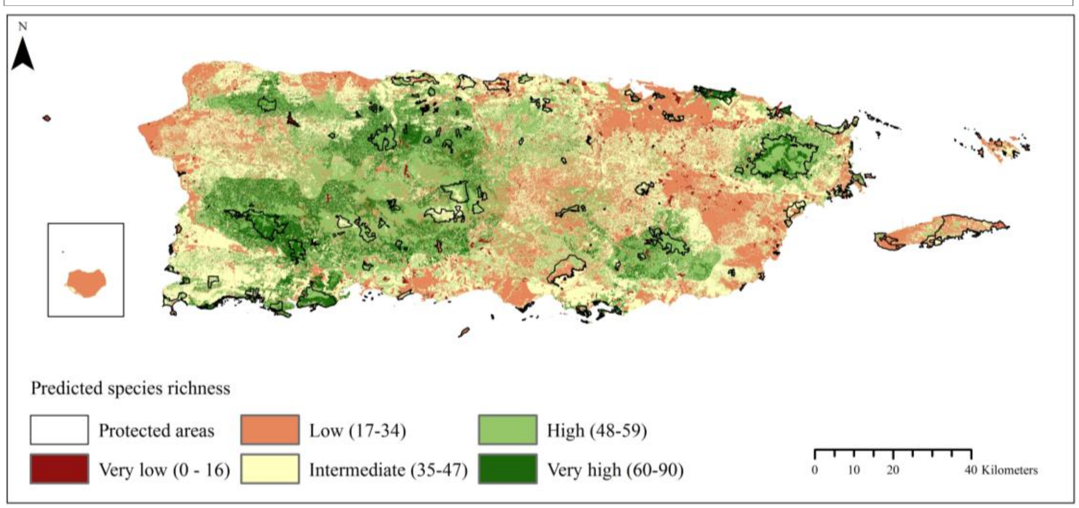


Figure 4. A) Extent of protection for each species richness class, and B) map of the predicted species richness in Puerto Rico.

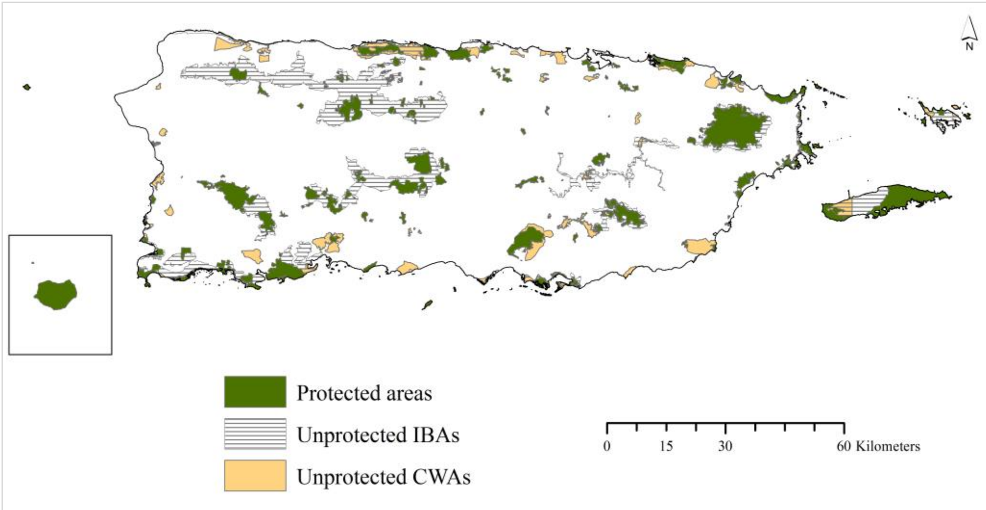


Figure 5. Map of Puerto Rico showing the unprotected Critical Wildlife Areas, and Important Bird and Biodiversity Areas.

CHAPTER 2: Declining human population, but increasing residential development around protected areas in Puerto Rico.

Castro-Prieto, J., Martinuzzi, S., Radeloff, V. C., Helmers, D. P., Quiñones, M., & Gould, W. A. (2017). Declining human population but increasing residential development around protected areas in Puerto Rico. ***Biological Conservation 209,*** **473–481**.

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Abstract

Increasing residential development around protected areas is a major threat for protected areas worldwide, and human population growth is often the most important cause. However, population is decreasing in many regions as a result of socio-economic changes, and it is unclear how residential development around protected areas is affected in these situations. We investigated whether decreasing human population alleviates pressures from residential development around protected areas, using Puerto Rico - an island with declining population – as a case study. We calculated population and housing changes from the 2000 to 2010 census around 124 protected areas, using buffers of different sizes. We found that the number of houses around protected areas continued to increase while population declined both around protected areas and island-wide. A total of 32,300 new houses were constructed within only 1 km from protected areas, while population declined by 28,868 within the same area. At the same time, 90% of protected areas showed increases in housing in the surrounding lands, 47% showed population declines, and 40% showed population increases, revealing strong spatial variations. Our results highlight that residential development remains an important component of lands surrounding protected areas in Puerto Rico, but the spatial variations in population and housing changes indicate that management actions in response to housing effects may need to be individually targeted. More broadly, our findings reinforce the awareness that residential development effects on protected areas are most likely widespread and common in many socioeconomic and demographic settings.

Key words: human- population, island, protected areas, Puerto Rico, residential development.

Introduction

Establishing protected areas is a widespread conservation strategy, designed to reduce habitat loss due to land use, and to stem biodiversity loss across the world. However, many protected areas fail to achieve these goals due to unmanaged or ineffective management of land use on adjacent lands (DeFries et al., 2005). Lands around protected areas are important to ensure connectivity and species movement, and when land use intensity is low in these lands they contribute to the effective size of the protected area (Hansen and DeFries, 2007). Habitat loss and degradation around protected areas, on the other hand, increase the isolation of a protected area and the magnitude of human effects (Barber et al., 2011; Mcdonald et al., 2009), ultimately altering the conservation value of the protected area (Wood et al., 2015). Understanding land use and human population changes around protected areas is therefore key for protected area management and biodiversity conservation in general (DeFries et al., 2007; Joppa et al., 2009).

The process of urban expansion and residential development accompanied by human population growth near protected areas throughout the world represent a growing pressure (Güneralp et al., 2015; Pejchar et al., 2015; Spear et al., 2013). Indeed, population growth is the most important driver of land development, together with an increase of per capita Growth Domestic Product (Güneralp and Seto, 2013; Seto et al., 2011; Wade and Theobald, 2010) that promote amenity migration and the development of second homes near protected areas in highly-developed countries (Hansen et al., 2002; Leroux and Kerr, 2013). By 2030, urban areas and residential developments are predicted to expand around most protected areas in some regions in Europe (Brambilla & Ronchi, 2016), and in Asia (Mcdonald et al., 2008), while from 1940 to 2030 1 million new housing units are projected to be constructed within 1-km from protected areas boundaries in the conterminous United States (Radeloff et al., 2010). Residential development is also expanding in many Pacific and Caribbean Islands (Stein, Carr, Liknes, & Comas, 2014).

However, while total human population is expected to expand in the next decades, many places of the world are projected to see declines in population, with unclear effects on land change, protected areas and biodiversity conservation. For example, between 2015 and 2050, human population is projected to decrease in 48 countries across the world including in regions with the highest population densities such as China and Europe (e.g., Spain, Greece, Germany, Portugal (United Nations, 2015a). Decline in fertility, aging populations, and outmigration are among the most important drivers of populations decline in these countries. Similarly, several islands in the Caribbean (e.g., Cuba, Jamaica, Puerto Rico) are projected to undergo population decline during the same period (United Nations, 2015a). Further, regions within countries are also exhibiting population declines despite net population increases at the national level. For example, the state of Michigan in the United States showed a recent population decline of 0.6% of its population over the last census decade (2000-2010) losing 54,804 people even though the US population increased by 9.7% (US Census Bureau, 2016). Domestic outmigration due to economic crisis and unemployment explained population decline in this state (Farley, 2010), but the potential consequences of these population declines on protected areas is unknown, adding uncertainty to management planning.

Understanding changes in residential development around protected areas in places with population declines can help in anticipating potential opportunities for conservation and restoration, as well as to better understand the link between changes in population, housing, and protected areas. Questions on whether decreasing human population alleviates pressures from residential development around protected areas, or whether housing expansion is a widespread problem, are critical considering the high urbanization rates globally (United Nations, 2015b) and future prospects for population declines in some countries and regions (United Nations, 2015a). However, our knowledge on these topics is limited.

Our goal was to understand how residential development around protected areas has changed in response to the recent human population decline, using Puerto Rico as a test case. The island of Puerto Rico, in the Caribbean, supports a high human population density, is rich in endemic species (Gould et al., 2008) and is considered a biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). It has seen an abrupt population decline over the last decade as a result of outmigration due to an economic crisis and aging population. Specifically, our objectives were: 1) to quantify total change in housing and population around the protected areas network and compare these changes with the island as a whole, and 2) assess variability by analyzing spatial patterns of housing and population change around individual protected areas across the island.

Methods

Study area, and recent population and housing changes

Puerto Rico occupies 8,937 km^2, supports 3.7 million people, and is one of the most urbanized islands in the Caribbean Archipelago (Lugo et al., 2012a). It includes three inhabited islands: the main island (with 99.7% of the population), Vieques and Culebra (with 0.3% of the population), as well as several non-inhabited islands, islets, and cays. Puerto Rico is a mountainous island with 55% forest cover (Forest Inventory and Analysis National Program, 2014), heavily urbanized coastal areas, and relatively low-density development in the uplands (Helmer et al., 2008; Kennaway and Helmer, 2007; Parés-Ramos et al., 2008). The island is part of the Caribbean Islands Global Biodiversity Hotspot (Birdlife International, 2010), it supports different forest types (subtropical dry, moist, wet, and rain forests), as well as many endemic and endangered species.

The population of Puerto Rico decreased by ~83,000 people, or 2%, from the year 2000 (pop. 3,808,610) to 2010 (pop. 3,725,789). During that time period there were 218,472 new housing units built, representing an overall growth in new housing of 15%, or 9% growth of new occupied housing (115,206), and 66% growth of new vacant housing (103,264) (US Census Bureau 2015; Fig. 1a). The main cause of the population decline was the economic crisis beginning in the mid-2000s with a local debt crisis and worsening with the 2008 recession. These events caused rapid outmigration of Puerto Ricans to the mainland United States (Pew Research

Center, 2014; Abel and Deitz, 2014). As a result, Puerto Rico was placed among the top 10 countries with the biggest population decline rate in 2014 (Statista, 2016), and this depopulation trend is projected to continue thru 2050 (US Census Bureau, 2016). Nevertheless, residential development in Puerto Rico continued to rise, as it has done for the past 60 years, always exceeding population growth (Fig. 1a). Housing projections for 2030 suggest that the number of houses in the island will continue to increase (Stein et al., 2014).

Protected areas data

The island has a large network of protected areas and we focused our analysis on those terrestrial protected areas (n=124), which as of September 2015 occupied 8% (709 km^2) of the land surface (Fig. 1b), and excluded marine protected areas, protected areas that are cays or islets, and marine extensions of coastal protected areas (Caribbean Landscape Conservation Cooperative, 2015). Terrestrial protected areas in Puerto Rico are typically small, range from less than 1 km^2 to 115 km^2 (mean= 6 km^2) and include public and privately-owned land (e.g., State Forests and Natural Reserves, US Forest Service National Forest, US Fish and Wildlife Service Refuges, NGOs). About 71% (500 km^2) of the protected areas occur in the interior mountains and hills, and 29% (209 km^2) in the coastal plains.

Census data

To evaluate changes in population and housing units we used population and housing data for the years 2000 and 2010 from the US Census at the level of census block, which is the smallest census unit (US Census Bureau, 2015). A housing unit is a living quarter in which the occupant or occupants live separately from any other individuals in the building and have direct access to their living quarters from outside the building or through a common hall, and includes permanent residences, seasonal houses and vacant units (US Census Bureau, 2015). Thus, apartments and multifamily units in a single structure are counted as multiple housing units. A major challenge for direct comparisons of census datasets from different years is the potential changes in the number and boundaries of the census blocks between years (Logan, Xu, & Stults, 2014). In Puerto Rico there were ~55,000 census blocks in 2000 but ~76,000 census blocks in 2010. To overcome this limitation we used an algorithm to allocate 2000 housing and population data to 2010 blocks and adjust those blocks for the protected area's boundaries (Radeloff et al., 2010; (Syphard et al., 2009) using the 2000-2010 census blocks and Block Relationship File provided by the US Census Bureau, and our protected areas layer.

Analysis

To quantify changes in people and housing units around protected areas, we used buffers of different sizes around protected areas. Measuring changes in land use/land cover at different distances to protected areas is a common approach to quantify the strength of the interactions between protected areas and external pressures in surrounding lands (Hamilton et al., 2013; Leroux and Kerr, 2013; Ye et al., 2015). Land use activities at shorter distances are expected to have a larger effect on protected areas than if the same activity occurs further away (Mcdonald et al., 2009). For the purpose of this study we used distances of 0.5, 1, 1.5 and 2 km of the boundary of the protected areas, which were large enough to include multiple census blocks, representing 8%, 15%, 23%, and 31% of the island's land surface, respectively. We decided our buffers based on the size of the island and to align with previous research for comparison of results (Radeloff et al., 2010). For each protected area and buffer zone, we extracted the number of housing units and population in 2000 and 2010 from the census based on the proportion of the census block that was embedded in the buffer. For example, if half of the census block laid within the buffer zone, so half of the population in that census block was counted for the analysis, based on the assumption that population and housing are evenly distributed within census blocks as in Radeloff et al. (2010). We did not evaluate changes in population and houses within the limits of protected areas because population and housing are expected to occur at very low densities inside protected areas in Puerto Rico.

For objective one, i.e., quantify changes in housing and population around the entire network of protected areas, we summarized the total housing and population in 2000 and 2010 for each buffer around the entire protected area network, and reported the changes in total numbers of people and houses, rates of change relative to 2000 conditions (i.e., % change), as well as changes in densities (i.e., housing/km^2, people/km^2) between the two years. We also compared these values with the results for the entire island.

For objective two, i.e., changes in housing and population around individual protected areas, we calculated changes in the total number of people and houses, rates of change relative to 2000 conditions, as well as changes in densities around each protected area, and created maps depicting the changes at the level of individual protected area for the entire island. Analysis at the level of individual protected areas allowed us to assess spatial patterns of population and housing changes around the island, and to identify the number of individual protected areas that experienced increase, decrease, or no change in surrounding population and/or housing. Although we reported changes around protected areas using different buffer sizes, we focused some of our result based on the 1-km buffer distance, which is somewhere in the middle ground of our buffer sizes. Residential development at this buffer size has shown to affect biodiversity inside protected areas (Wood et al., 2015). Furthermore, the 1-km buffer zone is relevant because we can make comparisons with other studies linking land use change within this distance to protected areas (Maiorano et al., 2008; Radeloff et al. 2010, Wilson et al., 2015).

Results

Housing and population around the entire network of protected areas

From 2000 to 2010, 32,300 new houses were constructed within 1 km of the protected areas (Fig.2a). By 2010, there were 240,504 housing units (old and new) within 1 km of the protected areas, accounting for 15% of all houses in the island. The rate of housing growth within 1 km (16%) was quite similar among buffers and the island at large (15%, Fig.2). As a result, housing density within 1 km increased from 152 housing units/km^2 in 2000 to 176 housing units/km^2 in 2010 (Fig. 3a).

From 2000 to 2010, 28,868 fewer people lived within 1 km of the protected areas (Fig. 2b). Overall, 497,558 people lived within 1 km of the protected areas, accounting for 13% of the total population in the island by 2010. Rates of population decline within buffers ranged from -6% to -4%, but all exceeded the island-wide rate (-2%). The highest rate of population decline occurred within 0.5 km (-6%), where the population decreased from 259,542 in 2000 to 243,066 in 2010. Population density within 1 km decreased from 385 people/km^2 in 2000 to 363 people/km^2 in 2010 (Fig. 3b).

Housing and population around individual protected areas

When examining individual protected areas, we found considerable variation in terms of housing and population change within 1 km of each individual protected area (Fig. 4). Of the 124 terrestrial protected areas, 58 had fewer people within 1 km of their boundaries between 2000 and 2010 (11 to 5739 fewer people, or 3% to 41% decline), 50 protected areas had more people (i.e., 11 to 868 more people, or 3% to 279% growth); and 16 exhibited minimal change ranging from -10 to 10 people (-2% to 2%). On the other hand, 112 of the 124 protected areas showed increases in housing numbers within 1 km of the boundaries between 2000 and 2010, i.e., 11 to1,824 new housing (3% to 310% growth), while only 4 protected areas had -11 to -55 fewer houses (-3% to -36% decline), and 8 protected areas exhibited minimal change of -10 to 10 units (-2% to 2%) (Fig. 4). Population and housing changes within other buffer zones around individual protected areas are shown in the Appendix 1, but the trends were consistent.

In general, the highest increases in population and housing occurred within 1 km of the boundaries of the protected areas located in the eastern part of the island (e.g., El Yunque National Forest), central-east (e.g., Carite State Forest, Sistema de Cuevas y Cavernas de Aguas Buenas Natural Reserve), and north of the island (e.g., Laguna Tortuguero Natural Reserve, Caño Tiburones Natural Reserve) (Fig. 4, Appendix 1). The highest declines in population around protected areas occurred in the municipality of San Juan, Puerto Rico's capital city (e.g., Caño Martin Peña Natural Reserve, Nuevo Milenio Urban Forest) and in the east of the island (e.g., Medio Mundo y Daguao Natural Area), however, housing units increased around these protected areas like around protected areas with no change in population around them (e.g., Cabo Rojo National Wildlife Refuge) (Fig.4, Appendix 1).

Discussion

Housing and population around the entire network of protected areas

Our most important finding was that high rates of residential development remain to be an important threat to protected areas in Puerto Rico despite the overall population decline in the island, and around the entire network of protected areas. However, we found residential development around protected areas is similar to the general rate for the island, contradicting other studies that found a disproportional residential growth near protected areas (Brambilla and Ronchi, 2016; Radeloff et al. 2010; Wade and Theobald, 2009). In general, and considering the small size of Puerto Rico, it is likely that some of the new housing developments that we observed around protected areas is a consequence of urban sprawl (Martinuzzi, Gould, & Ramos González, 2007). For example, we found there were almost two-and-a-half times more housing units within 1 km of Puerto Rico's protected areas than around all US National Parks in the conterminous U.S. by the census year 2000 (208,204 vs. 85,000 housing units, respectively) (Radeloff et al. 2010).

Housing and population around individual protected areas

We found considerable spatial variation of population and housing change among individual protected areas. For example, almost half of the protected areas witnessed a decrease in population in their vicinity, while the other half witnessed a population increase as showed in other studies (Hansen et al., 2002; Wittemyer et al., 2008), and contradicting global findings that showed no evidence of disproportional population growth near protected areas (Joppa et al., 2009). These different results suggest that actual population changes around individual protected areas were masked by the overall population decline when analyzing all protected areas as a group, and that the large drop in population near a few protected areas located in the metropolitan area (e.g., Caño Martin Peña Natural Reserve, Nuevo Milenio Urban Forest) were likely the main contributors for the overall decline. Similarly, we found spatial variation of housing change among individual protected areas. Although housing units increased around most protected areas, the rates of increase showed considerable variations. For example, about 60% of the protected areas witnessed an increase in housing in their vicinity at higher rates than around protected areas when analyzed altogether and for the island at large. For example, housing units growth by 90% (1154 new houses) around Bosque Tropical Palmas del Mar Conservation Easement, and by 74% (104 new houses) around Vieques National Wildlife Refuge.

Our analysis was not designed to identify the causes and mechanisms of increasing housing development around protected areas in the island; however, there are likely several factors at play. For example, economic factors in Puerto Rico promote new residential developments in the island. Tax-related benefits, warm weather conditions throughout the year, and tropical beaches, are some of the factors that make Puerto Rico an ideal retirement destination for US citizens. For example, government Act 22 (Individual Investors Act) exempts residents from taxes on dividends, which is highly attractive for foreign investors during a phase of declining property prices in the island. Despite families and individuals continued out-migration, the government of Puerto Rico continues to promote the development of new housing construction through programs like "Impulso a la Vivienda" Act 152, American Recovery and Reinvestment Act of 2009, and the USDA Rural Housing Service, and the identification of public lands for affordable housing development to low and moderate income households are a priority in the Puerto Rico State Housing Plan for fiscal years 2014-2018 (Estudios Tecnicos Inc, 2014).

Implications for management

Management actions to mitigate threats from residential development around protected areas in tropical islands like Puerto Rico will benefit from considering the spatial variability found in our study, but also on taking into account the ecological context in islands, very different from those in continents and temperate regions of the world. Effects associated with residential development and human population near protected areas are less predictable in our study case because of the island's social and ecological context. For example, Puerto Rico like other islands in the Caribbean region have high rates of biodiversity and endemic species (Pulwarty, Nurse, & Trotz, 2010), but also a high percentage of nonnative animals and plants that are widely distributed, and many of which have become naturalized and constitute novel ecosystems (Martinuzzi, Lugo, Brandeis, & Helmer, 2013; Morse et al., 2014). For example, nonnative flora contributes to 32% (1,032 species) of the total flora in Puerto Rico and the US Virgin Islands (Rojas-Sandoval & Acevedo-Rodríguez, 2014), and some of the novel forests in these islands have contributed to the restoration of previously deforested sites (Lugo et al., 2012b). Furthermore, many native vertebrates in Puerto Rico are found at very high densities in yards and green areas within urban areas, showing that residential areas in the tropics provide suitable habitats for biodiversity (Herrera-Montes, 2014; Joglar and Longo, 2011; Lugo et al., 2012a; Lugo et al., 2012c). However, it has been demonstrated that not all native vertebrates are able to thrive in urban areas in Puerto Rico, such is the case of the endemic Puerto Rican tody (*Todus mexicanus*), and the Puerto Rican bullfinch (*Loxigilla portoricensis*) notably less abundant in developed lands of the island (Vazquez-Plass, and Wunderle, 2013).

Thus, further research is needed to better understand if the impacts associated with residential development in temperate and continental regions of the world (Friesen et al., 1995; Schindler et al., 2000; Suarez-Rubio and Lookingbill, 2016; Wood et al. 2015) can be translated to tropical islands where the scales are different as are the nature of the biota and its biodiversity. Furthermore, there is a need to bring together diverse sources of data that reflect habitat and species dynamics to better understand residential effects on species persistence, extinction rates and distribution (Araújo and Williams, 2000; Araújo et al., 2008; Yackulic et al., 2015), to more effectively aide conservation design. This kind of work has been conducted for avian communities in lands surrounding state forests in Puerto Rico (Irizarry, Collazo, & Dinsmore, 2016). Finally, it is equally important to understand how residential development alters ecosystem services provided by protected areas in tropical islands such as water supply, and climate regulation as well as whether these effects are increased or attenuated when housing units are vacant or occupied, a common scenario in regions with declining human population and expanding housing development.

Caveats of our analysis

One important caveat of our finding is the fact that we analyzed decennial census data looking at only two years (2000 and 2010), but we did not analyzed yearly data so we were unable to detect yearly changes in housing that could had happened as a consequence of massive outmigration that occurred in the middle of the analyzed time period (D'Vera et al., 2014). For example, housing could have stabilized or even decreased after this year, but we were unable to detect this with decennial census data. Yet, if that was the case, strong reduction in population could have alleviated residential growth during this period, but we failed to detect it. Another limitation of our methodology is the assumption that population and housing units are equally distributed within census blocks, which we know is unrealistic (Sleeter & Gould, 2007), but in our case this limitation was quite reduced because of the small size of census blocks in Puerto Rico.

Conclusion

We demonstrated that lands around protected areas in Puerto Rico are extremely vulnerable to development, and that residential development can continue to grow despite the human population declines. More broadly, our study provides evidence to support that human population is not always the most important predictor of human pressures on natural resources consumption and impacts on biodiversity (Bradbury et al., 2014; Liu et al., 2003). However, we emphasize the importance of considering spatial variability in this type of analysis, in order to plan effective management actions at local scales. Establishing effective buffer zones and improving land use regulations around protected areas would be fundamental strategies to stop more development near protected areas.

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Figures

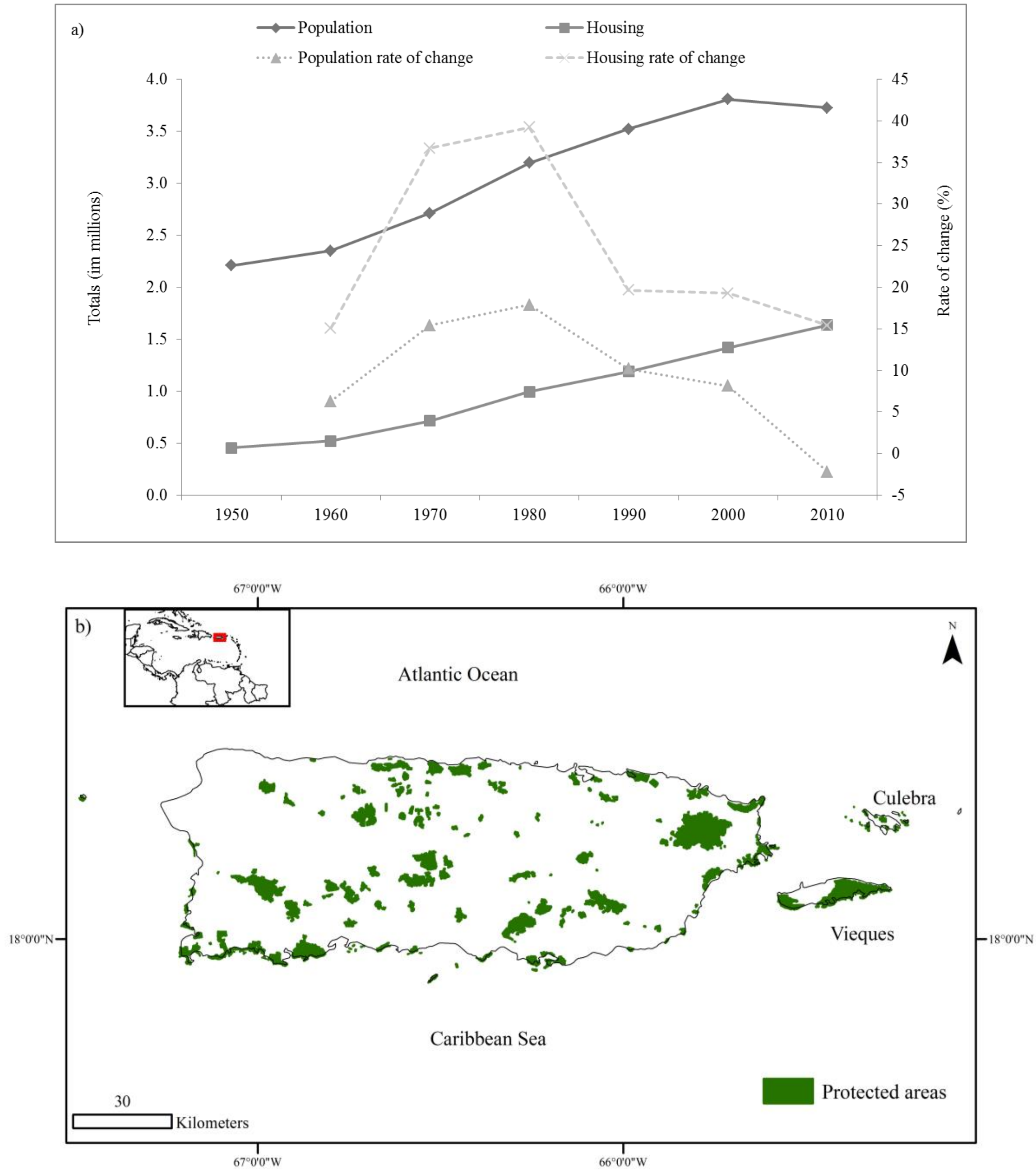

Figure 1. a) Puerto Rico's total population and housing units from 1950 to 2010, and rates of population and housing changes between decades (dotted lines). b) Study area showing protected areas in Puerto Rico (mainland, Culebra and Vieques).

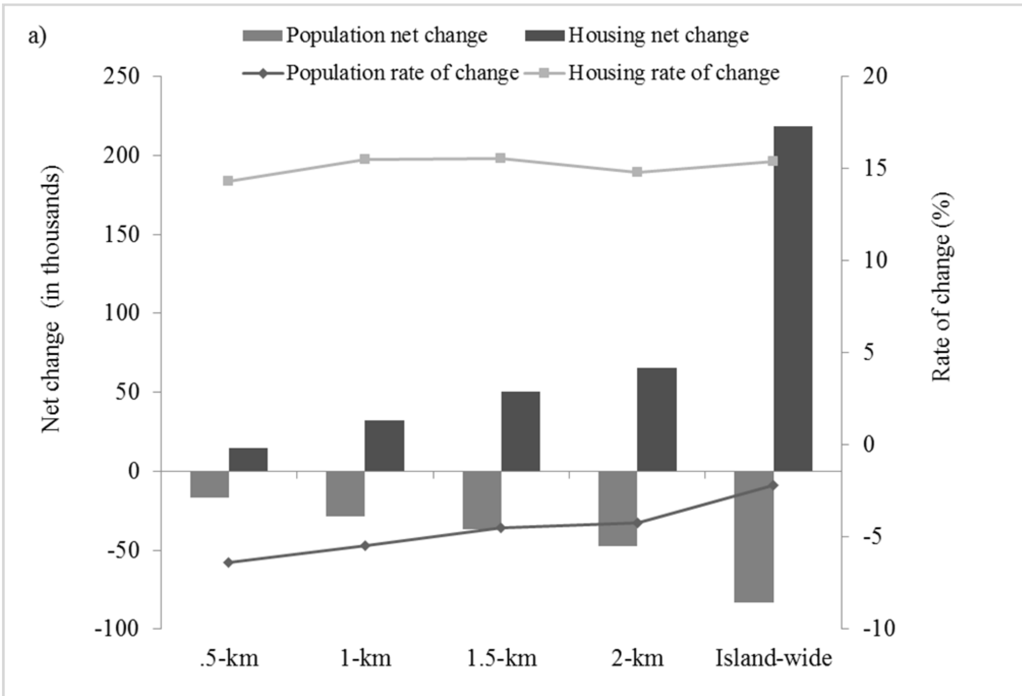

Figure 2. Population and housing net change, and rates of change within buffer zones around the entire network of protected areas and island-wide, between 2000 and 2010.

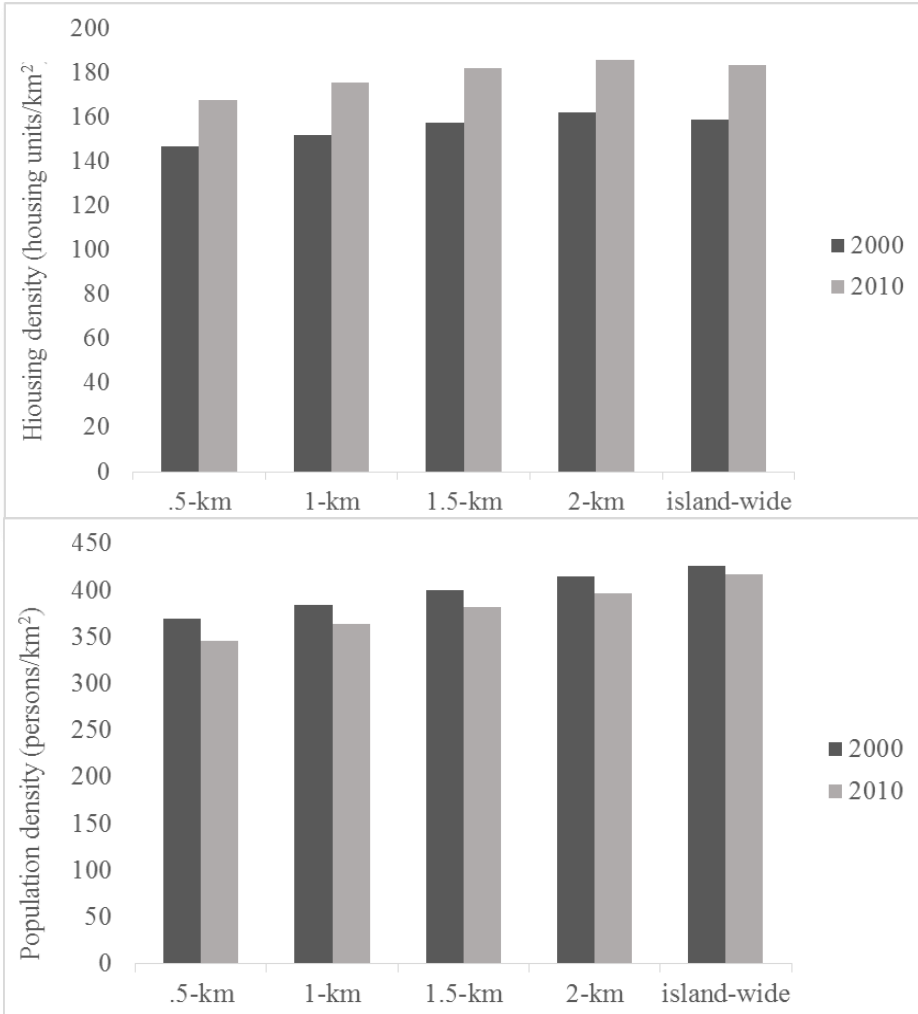

Figure 3. Housing density, and population density within buffer zones around the entire network of protected areas, and island-wide

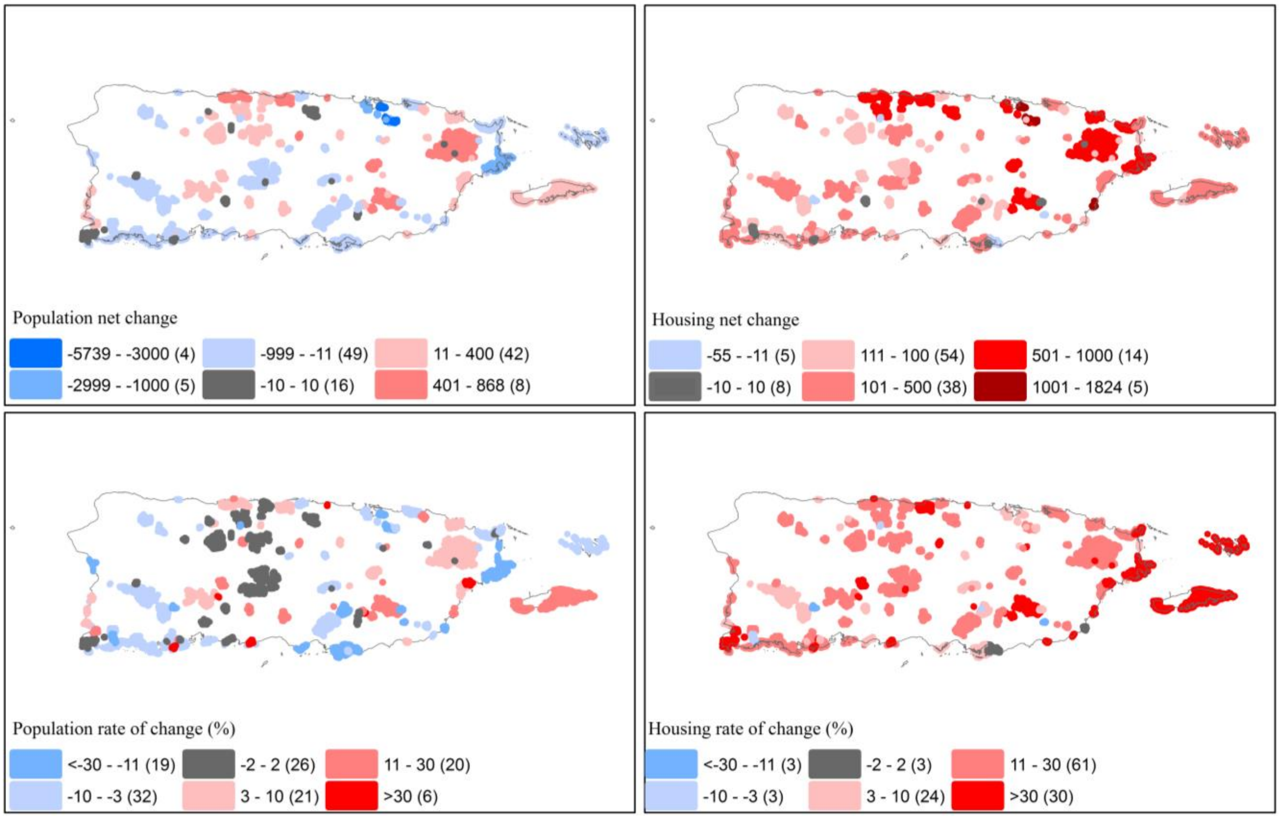

Figure 4. Spatial patterns of housing and population changes within 1 km of individual protected areas.

Appendices

Appendix 1. Housing and population net change and rate of change within buffer zones around individual protected areas.

	.5-km				1-km				1.5-km				2-km			
	HU		POP		HU		POP		HU		POP		HU		POP	
Protected area	Net Change	%	Net Change	%	Net Change	%	Net Change	%	Net Change	%	Net Change	%	Net Change	%	Net Change	%
Rio Piedras Old Acueduct	-13.1	-15	-62.0	-33	68.4	5	-1685.1	-38	707.0	9	-3840.9	-20	2292.3	16	-5135.9	-14
Pterocarpus Forest of Dorado	146.2	53	195.3	31	472.0	43	779.4	35	682.7	38	1276.9	33	781.9	22	1017.8	12
Cañón San Cristóbal NPA	66.2	8	-119.8	-5	154.7	9	-183.9	-4	329.9	11	-126.3	-1	406.2	10	-339.8	-3
Cerro Las Mesas NPA	34.4	18	-12.0	-2	59.1	10	-114.5	-7	129.7	10	-245.0	-7	169.2	9	-284.7	-6
El Convento Caves NPA	56.1	38	86.1	20	133.8	16	-57.8	-2	203.3	11	-385.4	-7	274.6	7	-1258.9	-10
Culebras NPA	17.6	21	80.2	58	60.7	45	152.2	59	113.3	46	220.5	50	57.7	16	127.2	19
El Conuco NPA	8.1	55	2.8	10	16.6	40	0.2	0	25.4	41	-0.8	-1	43.9	37	-5.4	-3
Finca Jájome NPA	16.9	19	-13.5	-5	42.3	20	-13.5	-2	88.6	23	48.7	5	131.4	21	93.2	6
Hacienda Buena Vista NPA	-10.6	-28	-22.7	-24	-16.9	-14	-36.0	-13	-31.8	-14	-82.7	-14	-5.9	-1	-81.9	-7
Jorge Sotomayor del Toro NPA	25.7	52	24.5	18	57.4	53	56.6	20	90.6	28	7.1	1	101.5	21	-128.6	-9
La Robleda NPA	5.9	6	5.7	3	47.4	19	81.7	14	91.2	20	99.7	9	90.1	14	76.8	5
Luz Martínez de Benítez NPA	16.5	8	-33.4	-6	165.4	20	52.0	2	278.1	17	54.5	1	400.0	15	-34.0	0
Marín Alto NPA	-27.5	-47	-69.7	-51	-55.2	-36	-152.2	-41	81.2	26	75.4	9	134.6	27	90.0	7
Marueño NPA	9.4	8	3.2	1	8.3	4	-6.1	-1	-19.9	-5	-110.5	-10	35.8	5	-54.8	-3
Medio Mundo y Daguao NPA	564.1	43	-1436.4	-39	817.9	31	-1830.8	-25	985.4	26	-1960.6	-19	1184.5	23	-2610.6	-19
Ojo de Agua NPA	50.5	12	-79.7	-6	197.3	30	224.7	11	313.8	27	298.6	8	549.8	33	639.0	12
Paraíso de las Lunas NPA	53.2	43	90.1	25	132.4	28	172.1	13	212.0	22	254.2	9	533.0	30	730.5	14
Pedro Marrero NPA	31.1	38	22.7	9	47.1	20	-33.0	-4	104.6	29	34.2	3	151.6	24	19.9	1
Punta Cabullones NPA	3.4	32	-1.0	-3	64.6	310	120.3	279	80.5	223	141.3	181	68.9	43	77.9	19
Punta Pozuelo NPA	-27.4	-14	-54.3	-14	0.5	0	-14.6	-5	1.3	1	-21.0	-6	-24.2	-10	-83.0	-16
Río Encantado NPA	244.9	22	196.1	6	295.6	16	71.8	1	552.4	22	518.4	7	665.6	22	611.1	7
Río Guaynabo NPA	25.0	7	-38.5	-4	43.7	5	-177.9	-7	356.5	19	151.8	3	729.5	18	402.1	4

Río Maricao NPA	39.3	26	19.9	5	67.6	23	4.6	1	147.0	27	77.7	5	124.1	23	40.5	3
San Juan Park NPA	31.9	12	-65.8	-9	146.7	19	63.7	3	229.3	13	-120.8	-3	522.2	16	295.4	3
Sendra NPA	63.8	31	85.5	17	234.2	32	287.5	15	330.9	18	202.8	4	439.0	13	30.0	0
Sierra la Pandura NPA	94.9	28	11.5	1	231.3	22	-95.6	-3	351.8	19	-275.9	-5	378.9	13	-626.5	-8
Ulpiano Casal NPA	10.4	17	-1.4	-1	8.5	4	-67.9	-12	31.3	7	-138.9	-11	85.4	14	-83.2	-5
Pueblo de Adjuntas' Forest	-0.2	0	-77.2	-18	99.5	34	106.4	13	198.2	48	299.8	25	310.3	49	393.3	20
Aguirre ST	-50.5	-6	-390.9	-19	-11.3	-1	-739.8	-18	154.1	6	-758.5	-11	230.6	7	504.4	7
Boquerón SF	124.9	20	-28.3	-4	178.6	16	-101.4	-8	528.0	32	50.5	2	613.1	28	7.2	0
Cambalache SF	464.1	18	70.5	1	836.6	15	43.0	0	1653.0	20	1442.5	6	2599.4	23	3322.5	11
Carite SF	222.9	31	59.9	3	742.5	45	841.8	18	1043.6	38	1056.7	14	1239.3	35	1127.2	12
Ceiba SF	18.1	7	-66.2	-11	29.4	4	-237.7	-14	124.6	7	-336.0	-9	344.2	7	-1615.5	-17
Cerrillos SF	5.2	14	0.6	1	77.7	26	119.1	12	117.5	22	173.4	11	141.3	16	123.9	5
Guajataca SF	34.7	20	-19.4	-4	95.1	18	-84.5	-6	194.3	20	-122.5	-4	319.6	19	-134.5	-3
Guánica SF	152.7	12	-230.4	-7	297.4	13	-391.2	-7	481.6	13	-199.1	-2	631.0	12	-21.7	0
Maricao SF	79.3	10	-61.8	-3	154.2	9	-242.0	-5	399.0	12	-226.7	-3	568.0	12	-447.6	-3
Monte Choca SF	32.2	8	-116.3	-9	69.5	9	-160.1	-6	167.8	12	-77.2	-2	346.4	17	208.5	3
Monte Guilarte SF	92.0	28	52.7	5	159.9	21	81.9	4	242.4	19	20.9	1	340.4	19	109.7	2
Piñones SF	77.0	23	36.2	4	116.1	14	-77.0	-3	207.3	10	-410.0	-7	244.0	5	-1544.9	-12
Río Abajo SF	28.9	16	29.0	6	64.4	16	27.4	2	96.4	14	-4.0	0	124.3	12	-79.3	-3
Susúa SF	51.4	10	-11.3	-1	93.6	6	-183.6	-5	189.5	9	-183.2	-3	273.9	8	-402.0	-5
Toro Negro SF	143.4	30	89.2	6	212.5	23	-34.8	-1	331.2	21	-57.7	-1	527.6	23	77.2	1
Tres Picachos SF	36.6	19	0.3	0	71.9	17	-15.7	-1	87.1	11	-153.2	-7	176.0	14	-186.8	-5
de Vega SF	444.7	17	263.9	4	813.3	15	-3.5	0	1161.7	13	-400.8	-2	1686.8	14	-499.2	-1
La Olimpia SF	24.0	12	-42.9	-7	110.6	22	66.7	5	220.8	22	96.2	4	300.3	23	182.7	5
San Patricio UF	282.7	7	-682.8	-8	780.0	8	-1246.5	-6	1673.5	11	-1359.8	-4	1877.4	9	-3215.6	-7
Nuevo Milenio UF	527.1	11	-863.6	-7	1824.3	14	-1878.5	-6	3505.9	14	-3241.5	-5	5141.4	13	-7952.2	-8
Dona Ines Mendoza UF	511.1	9	-1417.3	-10	1405.5	10	-3274.5	-9	2262.6	10	-4373.9	-7	4104.3	12	-6058.8	-7
Cabo Rojo NWR	275.6	49	-12.0	-2	486.2	48	-5.9	0	604.3	45	21.1	1	727.2	48	-5.0	0
Río Camuy Caves	52.0	26	18.5	3	95.2	19	13.5	1	210.2	24	54.1	2	302.4	23	98.5	3
San Juan EC	302.8	11	-507.9	-7	960.4	11	-4951.1	-19	1929.4	9	-5616.9	-10	3979.0	12	-7372.6	-8

Culebra NWR	115.4	93	-3.2	-2	309.2	59	-27.6	-3	475.2	57	-41.1	-3	521.3	57	-45.0	-3
El Tallonal	4.7	4	-4.6	-2	34.9	11	22.3	3	74.1	9	-39.8	-2	153.1	10	-9.3	0
El Yunque NF	297.7	17	71.1	1	801.4	21	593.1	6	1247.8	20	704.7	4	1805.1	19	932.7	4
Finca A Matos	21.8	16	-16.0	-5	39.1	13	-12.9	-2	-0.9	0	-136.2	-16	21.1	2	-386.8	-18
Finca Banco Popular de PR	14.1	15	-12.7	-5	74.1	26	37.5	5	83.7	13	-82.1	-5	155.0	18	67.4	3
Finca CDK1_Guillermety	3.3	11	6.1	7	10.9	18	18.2	12	59.8	39	107.2	25	88.1	33	145.6	20
Finca CDK2_Negron	2.9	17	5.5	12	10.8	26	17.1	15	82.6	66	178.1	49	124.1	61	258.3	44
Finca Colón	6.0	47	0.7	2	12.7	47	1.6	2	25.0	47	3.1	2	35.6	47	4.5	2
Finca El Pitirre Inc. #16	0.6	12	2.1	34	2.8	28	3.3	30	2.0	33	1.5	22	2.1	35	2.0	30
Finca El Verde	1.4	42	1.5	16	6.6	20	3.3	4	31.6	30	48.8	18	62.0	32	108.0	22
Finca Hernandez Dairy	-2.2	-3	-33.1	-15	23.2	9	-40.3	-6	84.2	14	-72.0	-4	122.0	12	-67.9	-2
Finca J Gutierrez	18.3	11	-4.6	-1	20.3	9	-12.9	-2	-26.7	-3	-471.3	-23	17.6	1	-555.7	-18
Finca Jose Santiago	3.9	6	-0.5	0	23.6	7	-4.6	-1	65.5	8	10.9	1	156.4	10	52.4	1
Finca Los Frailes	6.5	95	20.7	149	12.2	27	35.1	30	46.3	48	114.7	45	136.3	38	226.5	23
Finca M Rodriguez	2.9	10	-6.5	-9	12.1	13	-4.1	-2	20.5	15	14.0	4	18.3	7	-23.2	-3
Finca Nolla	61.4	9	-96.2	-6	113.3	8	-302.5	-8	327.6	14	-160.9	-3	553.0	17	93.8	1
Finca North Investment & Properties, Inc.	8.5	15	-0.4	0	23.7	14	13.7	3	34.2	9	-17.4	-2	73.8	10	9.8	1
Finca P Hernandez	5.7	38	8.3	20	16.8	37	25.4	21	19.0	15	-3.2	-1	21.8	15	-2.5	-1
Finca San Andrés Dairy	-32.0	-19	-162.1	-32	-33.5	-6	-296.1	-18	-2.1	0	-89.6	-4	56.4	4	226.3	5
Finca Shapiro	-1.2	-4	-17.9	-24	15.5	31	10.4	9	37.9	16	-27.1	-5	83.8	19	17.6	2
Finca Sucn. Lopez	7.4	22	7.4	8	16.2	10	-11.8	-3	25.1	14	0.2	0	25.9	11	-21.8	-3
Guayama EF	24.7	36	-5.7	-3	37.0	29	-6.8	-2	51.4	23	-4.3	-1	72.2	20	-42.2	-4
University of Puerto Rico BG	174.6	6	-925.4	-15	1299.6	15	-4274.9	-19	2721.2	15	-4996.7	-11	4283.7	14	-6921.4	-10
Laguna Cartagena NWR	9.2	8	-27.4	-9	30.5	12	-46.5	-7	59.1	11	-112.3	-8	102.0	12	-139.0	-7
Manatí EF	23.3	21	16.5	5	56.9	18	34.9	4	104.9	22	91.7	7	181.9	23	187.1	9
Iris Alameda de Boquerón SWR	79.0	42	51.9	21	231.4	39	116.8	16	450.8	37	112.7	7	665.7	41	129.4	6
Lago Guajataca SWR	70.5	23	-38.5	-4	151.0	23	-65.3	-3	273.0	24	-63.0	-2	366.3	22	-75.8	-2
Lago La Plata SWR	42.0	12	7.9	1	197.5	18	118.6	4	429.0	23	519.0	9	1245.3	36	2208.4	21
Lago Luchetti SWR	-21.2	-15	-100.0	-27	-53.7	-17	-221.6	-26	-30.5	-6	-223.7	-17	-23.4	-3	-319.0	-15

Bahía de Jobos NERR	4.0	1	-253.6	-20	105.2	9	-423.5	-13	175.7	9	-461.8	-9	414.7	16	-54.2	-1
Pterocarpus Forest NR	78.6	125	187.6	116	383.0	82	869.0	76	720.0	67	1537.0	57	1172.3	51	2036.6	36
Caño La Boquilla NR	227.8	26	-237.4	-11	360.0	26	-409.6	-12	614.3	28	-321.0	-6	894.9	28	-351.5	-4
Caño Martín Peña NR	195.3	4	-1368.2	-12	1100.0	7	-5739.0	-16	2715.0	9	-7514.9	-12	2747.9	6	-12126.3	-13
Caño Tiburones NR	216.5	14	115.8	3	598.4	18	420.7	5	984.0	19	626.8	5	1222.0	17	651.9	4
Cayo Ratones NR	0.9	19	-0.1	-3	14.6	13	-6.9	-5	170.5	59	141.5	33	669.6	100	934.5	75
Cerro Las Planadas NR	26.4	7	-119.6	-11	49.0	5	-321.4	-13	84.1	7	-409.6	-12	198.8	13	-257.2	-6
Ciénaga Las Cucharillas NR	349.6	8	-1558.0	-12	551.6	6	-1549.3	-6	548.9	5	-2253.8	-7	711.6	5	-3694.4	-9
Corredor Ecológico del Noreste NR	303.7	23	-150.5	-5	627.0	18	-424.0	-6	1040.5	19	-343.8	-3	1389.9	17	-785.3	-4
Cueva del Indio NR	37.3	32	-2.6	-1	106.4	47	72.0	13	168.9	39	92.4	9	110.5	23	0.9	0
Bahías Bioluminiscentes de Vieques NR	13.7	39	14.2	21	71.4	37	66.7	17	162.2	41	64.1	7	184.6	26	-16.8	-1
Río Espíritu Santo NR	479.7	33	426.5	14	824.2	25	287.1	4	1079.8	21	-81.6	-1	1367.7	20	-217.4	-1
Belverede NR	210.2	27	-23.1	-1	325.9	30	147.8	6	536.7	30	369.2	9	1200.4	57	1373.2	30
Seven Seas NR	262.7	75	24.6	5	288.0	44	-12.4	-2	228.7	25	-172.8	-9	346.2	20	-329.7	-10
Hacienda La Esperanza NR	319.2	25	126.8	4	636.7	21	38.6	0	941.2	25	533.6	5	1491.6	30	1763.5	14
Humedal de Punta Vientos NR	125.5	83	91.8	24	171.2	57	54.8	7	222.4	37	-84.6	-5	285.4	25	-244.7	-8
Inés María Mendoza -Pta Yeguas NR	38.5	11	-3.9	0	11.9	2	-261.9	-13	35.0	3	-354.4	-13	99.5	9	-202.2	-7
La Parguera NR	76.4	14	-65.1	-8	92.4	16	-48.9	-6	200.2	24	5.0	0	353.1	25	12.5	1
Laguna de Joyuda NR	99.7	21	62.9	11	181.3	20	104.3	8	448.8	35	555.0	25	1077.0	61	1658.2	49
Laguna Tortuguero NR	448.8	35	585.4	16	982.7	31	757.9	9	1446.6	25	747.4	5	2009.2	21	465.4	2
Las Cabezas de San Juan NR	105.0	67	-4.8	-2	120.1	44	-16.1	-5	122.5	36	-36.4	-7	154.7	42	-26.6	-5
Las Piedras del Collado NR	4.3	39	1.4	4	-1.8	-3	-45.2	-26	15.9	12	-49.3	-12	60.9	21	-14.0	-2
Manglar de Punta Tuna NR	134.4	34	-102.3	-9	209.2	36	-69.1	-4	263.4	33	-30.3	-1	314.3	24	-206.5	-5
Mata de Platano FS and NR	5.7	13	-4.2	-4	17.7	7	-23.1	-4	9.7	1	-173.9	-10	75.3	6	-147.2	-4
Pantano de Cibuco NR	22.0	12	-47.9	-9	63.4	11	-104.1	-7	205.0	13	-207.1	-5	459.6	10	-868.2	-7
Punta Cucharas NR	42.2	7	329.8	13	279.5	9	-203.5	-2	439.5	8	-1159.8	-6	410.1	6	-943.8	-4
Punta Guaniquilla NR	96.2	23	45.5	13	77.5	11	23.0	4	275.2	26	110.2	11	253.9	18	40.4	3
Punta Petrona NR	40.1	11	-137.1	-12	70.8	9	-263.1	-12	110.4	9	-444.0	-13	145.1	7	-753.4	-13

Cuevas y Cavernas de Aguas Buenas NR	365.9	24	497.3	11	703.1	24	815.5	9	1439.6	30	2138.6	15	2331.6	33	3492.7	17
Bosque Pterocarpus Lagunas Mandry y Sta Teresa NR	42.3	5	-203.9	-8	219.7	12	159.7	3	406.6	19	540.5	9	781.9	26	998.0	12
Bosque Tropical Palmas del Mar CE	840.6	95	242.7	22	1154.0	90	346.1	18	1450.0	80	272.3	9	1734.5	73	319.8	7
Centro Esprìritu Santo CE	10.3	27	3.2	3	20.0	17	-0.5	0	64.2	14	-43.1	-3	132.1	13	-50.2	-2
El Rabanal CE	15.9	14	-16.3	-4	90.5	27	61.4	6	139.2	20	-17.1	-1	265.8	21	-0.1	0
El Tambor CE	78.5	15	-13.8	-1	416.2	34	446.4	11	690.8	28	469.8	6	1027.3	31	1007.1	10
Finca Don Ingenio CE	52.0	43	42.9	12	100.0	26	24.2	2	218.2	31	183.2	9	283.4	25	135.8	4
Finca Gulín CE	5.8	27	5.8	11	12.2	16	-14.8	-7	13.7	9	-41.8	-11	51.9	13	-35.2	-3
Finca Ledesma Moulier CE	-2.2	-24	-10.0	-39	23.0	39	1.2	1	57.6	36	21.7	5	67.3	35	2.3	0
Finca María Luisa CE	-8.6	-16	-29.8	-26	-9.9	-9	-53.5	-24	3.4	2	-69.2	-15	-14.0	-5	-101.3	-16
Foreman CE	12.4	73	30.1	68	46.5	46	103.7	39	105.0	48	205.1	35	114.1	26	157.1	13
Punta Ballenas NR	1.7	18	3.7	34	2.4	32	3.3	41	2.1	19	3.9	32	2.0	18	4.0	31
Siembra Tres Vidas CE	16.3	61	24.0	30	38.5	48	40.0	17	101.7	52	102.3	17	142.2	35	135.3	11
Montes Oscuros SE	59.3	28	19.5	3	140.9	16	-91.1	-4	300.3	16	-309.1	-6	591.3	18	-239.3	-3
Vieques NWR	57.3	133	51.7	75	114.3	74	73.9	25	250.2	61	115.6	14	334.4	37	58.5	3

HU= Housing, POP= population, ST= State Forest, NWR= National Wildlife Refuge, EWR= Estate Wildlife Refuge, UF= Urban Forest, SE= Scenic Easement, CE= Conservation Easement, NR= Natural Reserve, NF= National Forest, NPA= Natural Protected Area, NERR= National Estuarine Research Reserve, EC= Ecological Corridor, BG= Botanical Garden, SWR= State Wildlife Refuge.

CHAPTER 3: Herpetofauna responses to urban development in Puerto Rico

Abstract

The conversion of natural ecosystem to urban systems produces drastic environmental changes at both local and landscape scales, including habitat loss and fragmentation, known as major drivers of species extinctions worldwide. The effect of urban development on biodiversity has been well studied on temperate and continental regions of the world, however, this information is incomplete for biodiversity in tropical islands despite their importance as global biodiversity hotspots. We assessed the effect of urban development on herpetofauna (i.e., anurans and reptiles) in an urbanized tropical island, using Puerto Rico as a case study. We assessed how site and landscape-scale environmental variables, species diversity, richness, and mean abundances change along an urban-suburban gradient, and conducted General Linear Models to identify the environmental variables that best predicted species distributions along the gradient. Furthermore, we identified those species most affected by urban development and predicted it relationship with species abundances. We found similar environmental conditions, species diversity, richness and mean abundances along the gradient. Site and landscape environmental variables were important predictors of species richness, diversity, and individual abundance, while the abundances of six species (i.e., *L. albilabris, A. exsul, C. krugi, E. cochranae, B. portoricensis, and S. macrolepis*) were strongly affected by urban development. Overall, we found urban topical islands can provide habitat for native (and endemic) species by maintaining green infrastructure (e.g., yards, parks and protected areas) within the urban core.

Key words: herpetofauna, island, Puerto Rico, tropics, urban.

Introduction

The process of urbanization involves the irreversible conversion of natural habitats into towns and cities, a process known to promote habitat loss and fragmentation, and local species extinctions worldwide (Czech, Krausman, & Devers, 2000; Elmqvist, Zipperer, & Güneralp, 2016; McKinney, 2008; Seto, Güneralp, & Hutyra, 2012). The transformation of natural or semi-natural areas into urban areas, produces drastic environmental changes at both local and landscape scales known to affect species distribution, diversity and abundances (Saari et al., 2016; Shochat et al., 2010). Some of the most studied environmental changes in urban areas include higher temperatures (*i.e.*, urban heat island effect), invasive species, and pollution (e.g., noise, light), which are known to disrupt wildlife physiology, behavior, and ecology in urbanized environments (Gaston et al., 2013; Katti and Warren, 2004; Meentenmeyer et al., 2008). At the landscape scale, urbanized environments are characterized by large extensions of impervious surface, and the corresponding loss and fragmentation of available habitat for wildlife (Elmqvist et al., 2016; Güneralp & Seto, 2013; Seto et al., 2012).

Several studies around the world have assessed the effect of urban development on different taxonomic groups (Bateman and Fleming, 2012; Belaire et al., 2014; Gagné and Fahrig, 2011; Hamer and Mcdonnell, 2010; Schindler et al., 2000; Suárez-Rubio and Lookingbill, 2016; Villaseñor et al., 2014; Wood et al., 2015). In general, these studies found that urban development alters species composition, with a general impoverishment of species of greatest conservation concern and resource-specialist in urban areas (Biamonte, Sandoval, Chacón, & Barrantes, 2011; Niemelä & Kotze, 2009). Furthermore, urban areas host a higher abundance of generalist species and higher species richness, but less biodiversity because of the disproportional higher contribution of exotics (Wood et al., 2015). Other studies found that low-density urban areas can provide suitable habitats for many native species (Belaire et al., 2014; Guénard, Cardinal-De Casas, & Dunn, 2015; Villaseñor et al., 2014). A general conclusion arising from these studies is that the effect of urbanization on wildlife is difficult to generalize as it would depend on species-specific responses but also on the spatial pattern of the urban development (e.g., clustered *vs.* dispersed) (Suárez-Rubio and Lookingbill, 2016).

Although these studies have been fundamental for establishing general trends and patterns of urban wildlife, most of them have been conducted in continental and temperate regions of the world. Thus, translating these findings to other geographic regions such as tropical islands, could lead to misleading conclusions. Assessing the effect of urbanization on islands biodiversity is a major need as islands are key contributors of global biodiversity hotspots (Myers et al., 2000) and urban impacts could be detrimental on island's biodiversity characterized by a high proportion of endemic species (Island Conservation, 2017).

Puerto Rico is a subtropical island that occupies approximately 8,900 km^2 and is part of the Caribbean Islands biodiversity hotspot, in the Caribbean Region. By the 1940's agriculture abandonment for a transition to a manufacturing economy and industrialization promoted the recovery of forested lands in more than half (~55%) of the island (USDA, 2017), but it also promoted urban development particularly in the lowlands and coastal zone (Helmer, 2004; López et al., 2001; Parés-Ramos et al., 2008). From 1951 to 2000, urban cover increased from 1.7% to 11-15.4% (Gould et al., 2008; Kennaway, T. and Helmer, 2007) and half of the urban development occurred outside of the urban core, showing a high degree of urban sprawl in 40% of the island (Martinuzzi et al., 2007).

Housing development accounts for a large portion of urban development in Puerto Rico, and represents an important pressure on the most important areas for biodiversity conservation in Puerto Rico (Castro-Prieto et al., 2017). During the last census decade (2000-2010) 33,200 new housing units were constructed adjacent to protected areas for a total of 240,504 houses within 1-km from the protected areas by 2010 (Castro-Prieto et al., 2017). Understanding how biodiversity is being affected by housing development in Puerto Rico is essential to support conservation planning and mitigate impacts from this land use. The effect of housing development together with other urban effects (e.g., habitat fragmentation) have been well studied for birds in Puerto Rico (Irizarry et al., 2016; Suárez-Rubio and Thomlinson, 2009; Vázquez-Plass, E. and Wunderle, 2013), but not for anurans and reptiles, most of which (94%) are endemic species (Joglar, 2005).

Thus, the primary goal of our study was to assess the effect of urban development on the distribution of anurans and reptiles in a tropical island, using Puerto Rico, as a study case. To accomplish this goal, we: 1) calculated and compared site and landscape-scale environmental variables along the urban-suburban gradient, 2) calculated and compared species richness, diversity, mean species abundances and individual species abundances along the urban-suburban gradient, 3) assessed which environmental variables are better predictors of species richness, diversity, and individual abundances of anurans and reptiles along an urban-suburban gradients, and 4) identified and analyzed those species for which housing was a significant predictor of abundance.

Methods

Study area

The study was conducted in the northeast lowlands of Puerto Rico, and comprises the San Juan metropolitan area (SJMA) towards the suburban/rural lands in the foothills of El Yunque National Forest (Fig. 1). The study area is located within the subtropical moist forest (Ewel and Whitmore, 1973), with an annual precipitation of approximately 1800 mm, a mean temperature that ranged from 22 to 30°C, and a mean relative humidity of 89% during the study period (Herrera-Montes, 2014). Elevation ranged from 0 to 264 meters above sea level. The SJMA is one of the most extended urbanized areas in the world when compared with urban areas with similar population (Martinuzzi et al., 2007). This are is dominated by urban cover in the form of residential (i.e., housing), commercial, and industrial uses. Urban sprawl had been identified as the main pattern of urban expansion in this area (Martinuzzi et al., 2007), threatening the remaining green areas such as patches of mature and secondary forest, shrubland and grassland parcels outside protected areas.

Sites selection

A total of 30 sites were selected to represent a gradient of urbanization from SJMA to El Yunque National Forest (Herrera-Montes, 2014). Half of the 30 sites were located in urban areas, and the other half in rural areas according to the Rural-Urban Land Use Map for Puerto Rico (Martinuzzi et al., 2007). Urban areas in this map include all census blocks with a population density of at least 390 people/km^2, and surrounding census blocks that have an overall minimum density of 195 people/km^2, while rural land is all the land located outside urban areas

(Martinuzzi et al., 2007). Because most of the rural land in our study area was sub-classified as densely populated (Martinuzzi et al., 2007), we refer to rural sites as suburban sites. Urban sites had fewer species of trees (n= 65) and a larger percentage of exotic species (57%) in comparison with suburban sites (n= 76, 42%, respectively) (Herrera-Montes, 2014). Within each urban/suburban category the 15 sites were located in five different habitat types (3 sites/by each habitat type) that were identified using the Puerto Rico Land Cover Map (Gould et al., 2008): 1) mature secondary lowland forest (Mature), 2) young secondary lowland moist forest (Young), 3) lowland moist woodland and shrubland (Shrub), 4) moist grassland and pastures (Pasture), and 5) front yards (Yards) (Fig. 1, Appendix 1). Within each habitat type two major criteria were used for sites selection: 1) availability of vegetation patches with sizes >2 ha, and 2) separated from each other at least by to 2-km to minimize the effect of spatial auto-correlation among sites.

Response variable

We used as response variables individual abundances of anurans and reptiles, species richness and diversity at site scale. The information regarding species abundance and occurrence used in this study were recorded by Herrera-Montes (2014). A total of 31,754 individuals corresponding to 25 species (Table 1), including 19 reptiles and 6 anurans, were recorded during day and night surveys conducted from November 2011 to October 2012 (Herrera-Montes, 2014). Overall, species richness in this study accounted for 96% of the total species richness known for this region (Joglar, 1998; Rivero, 1998). Surveys were conducted using four different methods:

1) visual encounter surveys, 2) natural-cover surveys, 3) leaf-litter plots, and 4) active trapping. A detailed description of each methodology can be found in Herrera-Montes (2014).

Eighty-four percent (n= 21) of the total found species are endemic to Puerto Rico, or to the Caribbean (native to Puerto Rico, Dominican Republic, and/or Virgin Islands), and four species (16%) are exotics (Table 1). The two most abundant species were the Puerto Rican crested anole (*Ctenonotus cristatellus*) with 9,606 records, followed by the common coqui (*Eleutherodactylus coqui*) with 8,639 individuals, and both species were present in all sites (Table 1, Fig. 2). The two rarest species were the flat-headed blind snake (*Typhlops platycephalus*) and the Puerto Rican Galliwasp (*Dipoglossus pleei*) only present in one site, with one and two individuals, respectively (Table 1, Fig. 2).

Explanatory variables

Site-scale variables were measured in each of the 30 sites, using a 20 x 50-m plot (1000 m^2), while landscape variables were calculated within a 100-m radius buffer centered on each site using ArcGIS 10.2.2 (Fig. 1). This buffer distance was selected based on available information about species movement distances. For example, the genera *Eleutherodactylus* or "coquis" are characterized by their territorial behavior, and in general they move a few meters from their retreat sites (Woolbright, 1996). Initially, we started with a total of 15 environmental variables (8 site-scale, and 7 landscape-scale) that provided information about habitat resources, habitat complexity, and habitat loss and fragmentation (Appendix 2). Before running models we first normalized the data using *ClusterSim* in R (Walesiak & Dudek, 2009) as data were in different units and scales. Then, we examined correlations among variables altogether using *Hmisc* package in R 3.3.2, and plotted dendrograms using *varclus* function with a cutoff value of

0.3 (Spearman's *rho*; Harell and Dupont, 2017) When a variable exhibited high correlation with another (≥0.3), we removed one of them and ran a new dendrogram until none of the variables were correlated. After testing for correlations, we ended with a subset of seven non-correlated environmental variables including: minimum temperature at ground level (MinTGro), mean percentage of the relative humidity at ground level (RHGro), mean percent of herbaceous cover (Herb), foliage height diversity (Hindex), percentage of forest edge (Edge), number of housing units (Hu), and percentage of protected area (Pro) (Table 2, Appendix 2).

Statistical analyses

Environmental variables, species richness, diversity, and abundances along the urban-suburban gradient.

We used one-way ANOVA with a significance value of 0.05 to test for differences in mean environmental variables, species richness, diversity, species abundances and individual species abundances between urban and suburban sites.

Environmental predictors on diversity, species richness and individual species abundances

We used General Linear Models (GLM) to assess the effect of the environmental variables (hereafter predictors) on: a) individual species abundances, b) species richness, and c) diversity. For modeling species abundances, we eliminated those species with the lowest abundances (≤ 6 individuals), and occurring in very few sites (≤4 sites), resulting in a subset of 20 species (Table 1). We used *glmulti* package in R (version 3.1.3) (Calcagno & Mazancourt, 2010), which allows automated model selection and provides a set of *n* best models rather than a single best model. Model support was explained by the Akaike Information Criterion (AIC), where top models (i.e., most parsimonious) were those with the lowest AIC values within 2 IC units (ΔAIC<2), known to be essentially as good as the best model (Symonds & Moussalli, 2011). We used the AICc which also considered the sample size (AICc). Further, we also analyzed the AICc weight known as the relative importance of individual predictors within the top models, calculated by summing the AICc weights of each model the variable appeared in. In addition, we assessed the relationship [±] between the predictor and the response variable according to the model coefficients in the regression analysis.

Housing effect on individual species abundances

Since we were particularly interested on assessing the urban effect, we ran predictions for those species for which housing units was a statistically significant predictor in their top GLM. We ran predict function in *glmulti* by selecting the best fitted model (with the lowest AICc value) for which housing was a significant predictor. When the best model had other predictors besides housing, we ran individual predictions for each pair-wise relationship, by holding the other predictor/s constant to their mean value.

Results

Environmental variables along the urban-suburban gradient

We found the mean number of housing units and mean relative humidity in urban sites were higher than in suburban sites (F-test= 52.46, p<0.05; F-test= 3.56, p= 0.01, respectively) (Table 3). Conversely, the mean percentage of herbaceous cover was higher in suburban sites in comparison with urban sites (F-test= 0.21, p<0.05), while the mean minimum temperature (F-test= 0.66, p= 0.22), mean foliage height diversity (F-test= 1.19, p=0.37), and mean percentage of forest edge (F-test=1.51, p=0.22) were not statistically different between urban and suburban sites (Table 3). In addition, none of the surrounding lands (≤100-m) of the suburban sites overlapped a protected area, while four urban sites (i.e., UM2, UM3, US2, UYr2) were completely within or very close to a protected area.

Species richness, diversity, and abundances along the urban-suburban gradient

Overall, we found mean species richness, mean diversity and mean species abundances were not statistically different between urban and suburban sites (F-tests= 1.35, p= 0.28; F-test= 1.56, p=0.20; F-Test= 1.12, p= 0.38, respectively) (Table 3). At individual level, *L. albilabris* (F-Test= 3.48, p= 0.01), *E. brittoni* (F-Test= 5257.82, p<0.05*)*, *E. cochranae* (F-Test= 8.11, p<0.05), *C. evermanni* (F=Test= 12.22, p<0.05), *S. macrolepis* (F-Test= 240.67, p<0.05), *T. rostellatus* (F-Test= 9.57, p<0.05), and the exotic *H. mabouia* (F-Test= 3.76, p<0.05) were statistically more abundant in urban sites than in suburban sites. In the case of *E. antillensis* (F=Test= 0.11, p<0.05), *C. stratulus* (F-Test= 0.10, p<0.05), *C. gundlachi* (F-Test= 0, p<0.05), *A. caeca* (F-Test= 0.25, p<0.05), *D. pleei* (F-Test=0, p<0.05), *T. platycephalus* (F-Test= 0, p<0.05), *B. portoricensis* (F-Test= 0.18, p<0.05), *S. klauberi* (F-Test= 0.02, p<0.05), *C. inornatus* (F-Test= 0.01, p<0.05), and the exotic species *R. marina* (F-Test= 0.02, p<0.05), *I. iguana* (F-Test= 0.34, p= 0.02), and *X. vittatus* (F-Test= 0.41, p= 0.05) were statistically more abundant in suburban sites. The abundance of *C. inornatus* was the same in urban and suburban sites (F-Test= 4.37, p<0.05), while the abundances of *E. coqui* (F-Test= 0.93, p= 0.45), *C. critatellus* (F-Test= 1.55, p= 0.21), *C. krugi* (F-Test= 0.85, p= 0.38), *C. pulchellus* (F-Test= 1.50, p= 0.22), *A. exsul* (F-Test= 1.30, p= 0.31), and *M. exiguum* (F-Test= 0.48, p= 0.09) were not statistically different between urban and suburban sites.

Environmental predictors on diversity, species richness and individual species abundances

Fitted GLMs indicated that both site and landscape environmental variables were important predictors on species richness, diversity, and individual abundances (Appendix 3). At community level, only site-scale variables were significant predictors on species richness (i.e., herbaceous cover, and foliage height diversity), while none of the variables in our model were significant predictors of species diversity. Although minimum temperature was an important predictor in the best model of diversity, it was not significant. Site-scale environmental variables were the only significant predictors on the abundances of *E. antillensis*, *E. coqui*, *C. cristatellus, C. gundlachi, C. stratulus I. iguana,* and *H. mabouia* (Fig. 3). Landscape environmental variables were the only significant predictors on the abundances of *E. brittoni, L. albilabris, C. krugi*, *A. exsul*, *C. inornatus* and *M. exiguum*. Both site and landscape environmental variables were significant predictors of the abundances of *E. cochranae*, *C. pulchellus*, *S. macrolepis*, and *B. portoricensis* (Fig. 3). None of the variables in our model were significant predictors on the abundances of C. *evermanni and S. klauberi*, while for *R. marina* we did not get an estimated coefficient for any of the variables (Fig. 3).

Housing as a predictor of individual species abundances

Overall, housing was a predictor in the top models of 64% (n=14) of the response variables, including species diversity and the individual abundances of 13 species (Appendix 3). Housing was a significant predictor on the abundances of *A. exsul*, *L. albilabris*, *E. cochranae*, *C. krugi*, *S. macrolepis*, and *B. portoricensis* (Figure 3). Two of these species, *C. krugi and B. portoricensis*, exhibited a significant negative relationship with housing (Coef= -15.88, p=0.01; Coef= -1.58, p=0.01, respectively), thus their abundances was expected to decrease when the number of housing units increased within 100-m (Fig. 4). Although housing was negatively associated with the abundance of *C. krugi*, this species was not significantly less abundant in urban sites (F-test= 0.85, p= 0.38), while *B. portoricensis* exhibited a significantly higher abundance in suburban sites than in urban sites (F-Test= 0.18, p= 0.00). Further, the abundance of *B. portoricensis* was positively affected by the minimum temperature at ground level (Coef= 2.06, $p<0.05$) (Fig. 3). The three habitats with the highest abundance of *C. krugi* were: pasture within an urban site (UP2, n= 147), and mature forest within two suburban sites (SuM2, n= 127; SuM1, n= 123). The habitats with the highest abundance of *B. portoricensis* were: a mature and a young forest within suburban sites (SuM3, n=14; SuY3, n= 12, respectively), and a mature forest within an urban site (UM2, n=6).

Conversely, *A. exsul, E. cochranae, S. macrolepis and L. albilabris* exhibited a significant positive relationship with housing (Coef= 3.05, p= 0.01; Coef= 10.85, p<0.01; Coef=42.47, p<0.01; Coef=22.09, p=0.01, respectively) predicting the abundances of these species would be higher in sites with one to 55 housing units within 100-m (Fig. 4). We found the abundances of *E. cochranae* and *L. albilabris* were significantly higher in urban than in suburban sites (F-Test= 8.11, p<0.05; F-Test= 3.48, p=0.01), the abundance of *A. exsul* was not significantly higher in urban sites (F-Test= 1.30, p= 0.31). The abundance of *A. exsul* was higher in a yard within a suburban site (SuYr1, n= 22), in a yard within an urban site (UYr2, n= 19), and in a mature forest within an urban site (UM1, n= 19). The abundance of *S. macrolepis* was significantly higher in suburban sites (F-Test= 0.10, p<0.05). With the exception of *A. exsul*, for which housing was the only coefficient in the regression analysis, *E. cochranae, S. macrolepis,* and *L. albilabris* also exhibited a significant positive relationship with other variables. The abundance of *E. cochranae* was negatively associated with minimum temperature at ground level (Coef= -5.76, p<0.05), and positively associated with the percentage of relative humidity at ground level (Coef= 4.48, p= 0.02), foliage height diversity (Coef= 9.26, p<0.05), and the percentage of protected area (Coef= 4.61, p<0.05) (Fig. 3). Highest abundances of *E. cochranae* were observed for three different urban habitats: yard (UYr2, n= 55), pasture (UP2, n= 32) and young forest (UY3, n= 19). In the case of *L. albilabris*, we found the abundance of this frog was positively associated with the percentage of protected area (Fig. 3), and the habitats with highest abundance of this frog included: pasture within an urban site (UP1, n= 185), a yard within an urban site (UYr2, n= 169), and pasture within a suburban site (SuP1, n= 121). *S. macrolepis* also exhibited a positive association with foliage height diversity (Coef= 23.96, p<0.05), and a negative association with minimum temperature at ground level (Coef= -22.36, p= 0.02) (Fig. 3).

Habitats with the highest abundance of *S. macrolepis* included: a yard (UYr2, n= 277) and a shrub (US2, n= 67) in urban sites, and a young forest within a suburban site (SuY2, n=14).

In the case of *C. gundlachi, C, stratulus, C. inornatus, I. iguana,* and species diversity, housing was a predictor in their best models, but it was a weak predictor (low ∑AICcw), while for *E. antillensis* and *E. brittoni* housing was an important variable in their best models, but the coefficients were not statistically significant (Coef= -36.26, p= 0.09; Coef= 62.42, p=0.10, respectively). For *E. coqui, C. cristatellus, C. evermanni, C. pulchellus, S. klauberi, M. exiguum,* and *H. mabouia* housing was not a predictor in any of the top models for these species, neither for species richness (Appendix 3).

Discussion

Environmental variables along the urban-suburban gradient

We found urban sites in our study area differed from suburban sites in the following characteristics: 1) urban sites were within or very close to protected areas, 2) had more houses in their surroundings, 3) have a higher percentage of relative humidity, and 4) a lower percentage of herbaceous cover. Conversely, urban and suburban sites had similar values of foliage height diversity, minimum temperature, and percentage of forest edge. An interesting finding was that even though urban sites had more pressure from housing development, urban sites had forest with similar structure and complexity as forests in suburban sites, and this was because many urban sites in our study were within protected areas (e.g., San Juan Ecological Corridor, San

Patricio Commonwealth Forest) or restricted land use zones (e.g., karts region) that have been successful at halting land conversion to urban areas.

Species richness, diversity, and abundances along the urban-suburban gradient

The similar environmental characteristics between urban and suburban sites were also reflected in the distribution of anurans and reptiles along the urban-suburban gradient. We found species diversity, richness, and mean abundance of anurans and reptiles did not differ significantly between urban and suburban sites. This finding supports one study that found all native species of fish known for Puerto Rico occurred within a highly urbanized watershed in the SJMA, and with similar densities as in nonurban streams (Ramírez et al., 2009). However, we found the distribution of anurans and reptiles did not follow the distributions of birds along an urban-rural gradient in Puerto Rico (within the same study region), for which mean abundance, and species richness increased with the degree of urbanization, while the diversity decreased (Vázquez-Plass and Wunderle, 2013). Furthermore, our findings contradict a global meta-analysis and general knowledge that indicate urban areas have lower abundance of terrestrial animals in comparison with suburban/exurban areas (Saari et al., 2016), and a disproportionate higher abundance of synanthropic and exotic species (Shochat et al., 2010; Vázquez-Plass and Wunderle, 2013). Despite urban sites in our study had higher abundance of the exotic *H. mabouia*, the invasive species *I. iguana* and *R. marina* were more abundant in suburban sites. Furthermore, the abundance of the endangered Puerto Rican boa (*C. inornatus*) was similar between urban and suburban sites, and particularly one urban site had the highest abundance of this species.

Environmental predictors on diversity, species richness and individual species abundances

We found that site and landscape-scale environmental variables were important predictors on anurans and reptiles species diversity, richness and individual abundances. Particularly, landscape environmental variables explained the abundances of 50% (n=10) of the species (Fig. 3), indicating environmental variables at this scale are important determinants on the distribution of anurans and reptiles, like that found for birds (Irrizary et al., 2016; Suárez-Rubio and Thomlinson, 2009; Vázquez-Plass and Wunderle, 2013) and soil invertebrates (Galanes and Thomlinson, 2011) in Puerto Rico. An important limitation in our models was that we did not include other relevant landscape predictors such as forest patch size known to affect species distribution in urban landscapes in Puerto Rico (Suárez-Rubio and Thomlinson, 2009), and species interactions that also affects species distribution (Trainor et al., 2014). For example, *B. portoricensis* is an important predator on anurans and lizards in Puerto Rico (Schwartz and Henderson, 1991). Future models could be improved by including these two variables or other more specific for each individual species.

Housing as a predictor of individual species abundances

We found housing development significantly explained the abundances of *A. exsul*, *L. albilabris*, *E. cochranae*, *C. krugi*, *S. macrolepis,* and *B. portoricensis* in our study area. One of the species negatively associated with housing was the endemic lizard *C. krugi*. This species is typically associated with upland forests (USFS, 2005), and is more common in elevations above 60 meters (Rivero, 1998; Schwartz and Henderson, 1991). The site with the highest abundance of *C. krugi* (UP2) was a large patch of grass within the University of Puerto Rico Botanical Garden, which is part of the San Juan Ecological Corridor, a natural protected area in the core of San Juan. Another species that showed a negative relationship with housing was *B. portoricensis*, a snake widely distributed across Puerto Rico (Schwartz and Henderson, 1991). Despite this snake is described as a generalist in the literature (Schwartz and Henderson, 1991), we found it reached its highest abundances in forest habitats in both urban and suburban sites.

Conversely, the abundances of *L. albilabris, A. exsul, E. cochranae*, and *S. macrolepis* exhibited a positive association with housing (Fig. 3). Contrary to coqui frogs, *L. albilabris* undergoes indirect development (metamorphosis), so it requires water to reproduce using ephemeral ponds (Flores-Nieves, Logue, & Santos-Flores, 2014), but it can also take advantage of artificial structures that reserve water after heavy rains in residential areas (e.g., plant pots). Another species that was positively associated with housing was *A. exsul,* described in the literature as the most common *Ameiva* in Puerto Rico, widely distributed from sea level to 366 meters (Rivero, 1998). This species is associated with humans' habitations, parks, cities, roadsides, vacant lots, and xerophilic open areas (Schwartz and Henderson, 1991). In the case of E. *cochranae*, this is a native generalist "coqui" frog widely distributed in Puerto Rico associated with different habitats including xeric forest, humid forest, grasslands, marshes, and urban areas from sea level to 336 meters above sea level (Schwartz and Henderson, 1991). Despite *S. macrolepis* was significantly more abundant in suburban sites, this species exhibited a positive relationship with housing because of the specific characteristics of the sites. For example, UYr2 where this species had its highest abundance, is a low-density residential area for professors of the University of Puerto Rico that has many trees that produce large amounts of leaf litter (e.g., *Ficus sp.)*, thus providing optimal habitat conditions for *S. macrolepis* (Schwartz and Henderson, 1991). While US2 was a shrubland located within the University of Puerto Rico Botanical Garden. Furthermore, the abundances of *S. macrolepis*, *L. albilabris* and *E. cochranae* were higher in sites with many houses (up to 55 in our study), but also, in sites near or within protected areas or/and with high foliage height diversity.

Conclusion

Overall, we found similar environmental conditions, species diversity, richness and mean abundances along an urban-suburban gradient in Puerto Rico, despite a higher pressure from residential development in urban sites. We have two main explanations for this general conclusion. First, urban morphology in Puerto Rico, characterized by low-density constructions and sparsely populated neighborhoods (Martinuzzi *et al.*, 2007), contiguous with large patches of undeveloped public lands in protected areas such as the University of Puerto Rico Botanical Garden, Nuevo Milenio and San Patricio Commonwealth Forests, Martin Peña and Las Cucharillas Natural Reserves, and specific land use zoning such as the Karst Restricted Zone, a physiography region protected by law in Puerto Rico. Four of our urban sites (i.e., UM2, UM3, US2, UYr2) were located within any of these protected areas, thus contributing to overall high values of species diversity, richness and abundances in urban sites. Second, most species in our study were small body-sized with low mobility, and small home ranges, thus small patches of green habitats (including yards) seem to provide suitable habitats for these species.

Implications for Conservation

Our results suggest urbanized topical islands like Puerto Rico can provide habitat for endemic and endangered species, if they maintain green infrastructure in both public and private lands (i.e., yards, parcels). Our study provide evidence to support that protected areas and even small patches of unprotected forest in highly urbanized areas like the SJMA provide conservation benefits as found in other regions (Goodwin and Shriver, 2014). Furthermore, we support other finding that indicated private yards in San Juan encompassed most of the green area in dense urban areas in this city (Ramos-González, 2014). We found private yards provide habitat for endemic species in dense urban areas in the SJMA. Yards offer an extensive, unique and undervalued resource for enhancing urban biodiversity as they are important habitats in their own right, or by improving the connectivity and increasing the size of nearby urban parks (Goddard et al., 2010).

Encouraging green yards within dense urban areas, and maintaining protected areas within the urban core are vital for the conservation of urban biodiversity. Thus, tropical urbanized islands like Puerto Rico provide an opportunity to reconcile urban development and biodiversity conservation strategies.

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Tables

Table 1. List of species and their abundances during the surveyed period. Caribbean endemic includes Puerto Rico and other nearby islands (e.g., Virgin Islands). * Species not included in the General Linear Models.

Species	Common name	Distribution class	Abundance
Ctenonotus cristatellus	Puerto Rican crested anole	Endemic	9,606
Eleutherodactylus coqui	Common coqui	Endemic	8,639
Ctenonotus pulchellus	Common grass anole	Endemic	3,449
Eleutherodactylus antillensis	Red-eyed coqui	Caribbean endemic	2,858
Eleutherodactylus brittoni	Grass coqui	Endemic	1,765
Ctenonotus stratulus	Barred anole	Endemic	1,502
Leptodactylus albilabris	Caribbean white-lipped frog	Caribbean endemic	1,277
Ctenonotus krugi	Upland grass anole	Endemic	1,020
Sphaerodactylus macrolepis	Common dwarf gecko	Endemic	416
Eleutherodactylus cochranae	Whistling coqui	Caribbean endemic	217
Rhinella marina	Cane toad	Exotic	194
Ameiva exsul	Puerto Rican ground lizard	Endemic	173
Ctenonotus evermanni	Emerald anole	Endemic	146
Iguana iguana	Green iguana	Exotic	129
Sphaerodactylus klauberi	Klauber's dwarf gecko	Endemic	110
Ctenonotus gundlachi	Yellow-beard anole	Endemic	108
Borikenophis portoricensis	Puerto Rican racer	Endemic	63
Hemidactylus mabouia	Afroamerican house gecko	Exotic	48
Chilabothrus inornatus	Puerto Rican boa	Endemic	10
Magliophis exiguum	Ground snake	Caribbean endemic	7
*Xenochrophis vittatus**	Striped keelback	Exotic	6
*Typhlops rostellatus**	Puerto Rican wetland blind snake	Caribbean endemic	5
*Amphisbaena caeca**	Puerto Rican worm lizard	Caribbean endemic	3
*Dipoglossus pleei**	Puerto Rican Galliwasp	Endemic	2
*Typhlops platycephalus**	Flat-headed blind snake	Caribbean endemic	1
Total abundance			31,754

Table 2. Explanatory environmental variables used in the GLM.

Variable name	Description
Site-scale	
MinTGro	Mean minimum temperature measured throughout a year at ground level in each site
RHGro	Mean percentage of the relative humidity measured throughout a year at ground level in each site
Herb	Mean percentage of herbaceous cover in each site
Hindex	Foliage height diversity (Shannon-Weaver Diversity Index) in each site
Landscape-scale	
Edge	Percentage of forest edge within a 100-m radius buffer around each site
Hu	Number of housing units within a 100-m radius buffer around each site
Pro	Percentage of the 100-m radius buffer within a protected area

Table 3. Mean (±SE) of the environmental variables, species diversity, richness and abundances between urban and suburban sites. *Statistically significant ($p \leq 0.05$).

	Urban	**Suburban**	**F-Test**	***p-value***
MinTGro	22.27 ± 0.21	21.82 ± 0.26	0.67	*0.23*
RHGro	11.23 ± 1.28	9.84 ± 0.68	3.56	*0.01**
Herb	19.50 ± 2.93	29.33 ± 6.30	0.21	*0.00**
Hindex	1.18 ± 0.18	1.48 ± 0.17	1.19	*0.37*
Hu	16.62 ± 4.08	3.43 ± 0.56	52.46	*0.00**
Edge	7.80 ± 2.35	8.06 ± 1.91	1.51	*0.22*
Pro	24.86 ± 11.13	0.00	--	--
Diversity	1.27 ± 0.08	1.41± 0.06	1.56	*0.20*
Species richness	11.06± 0.85	12.26± 0.73	1.35	*0.29*
Abundance	43.54 ± 17.73	41.13 ± 16.73	1.12	*0.38*

Figures

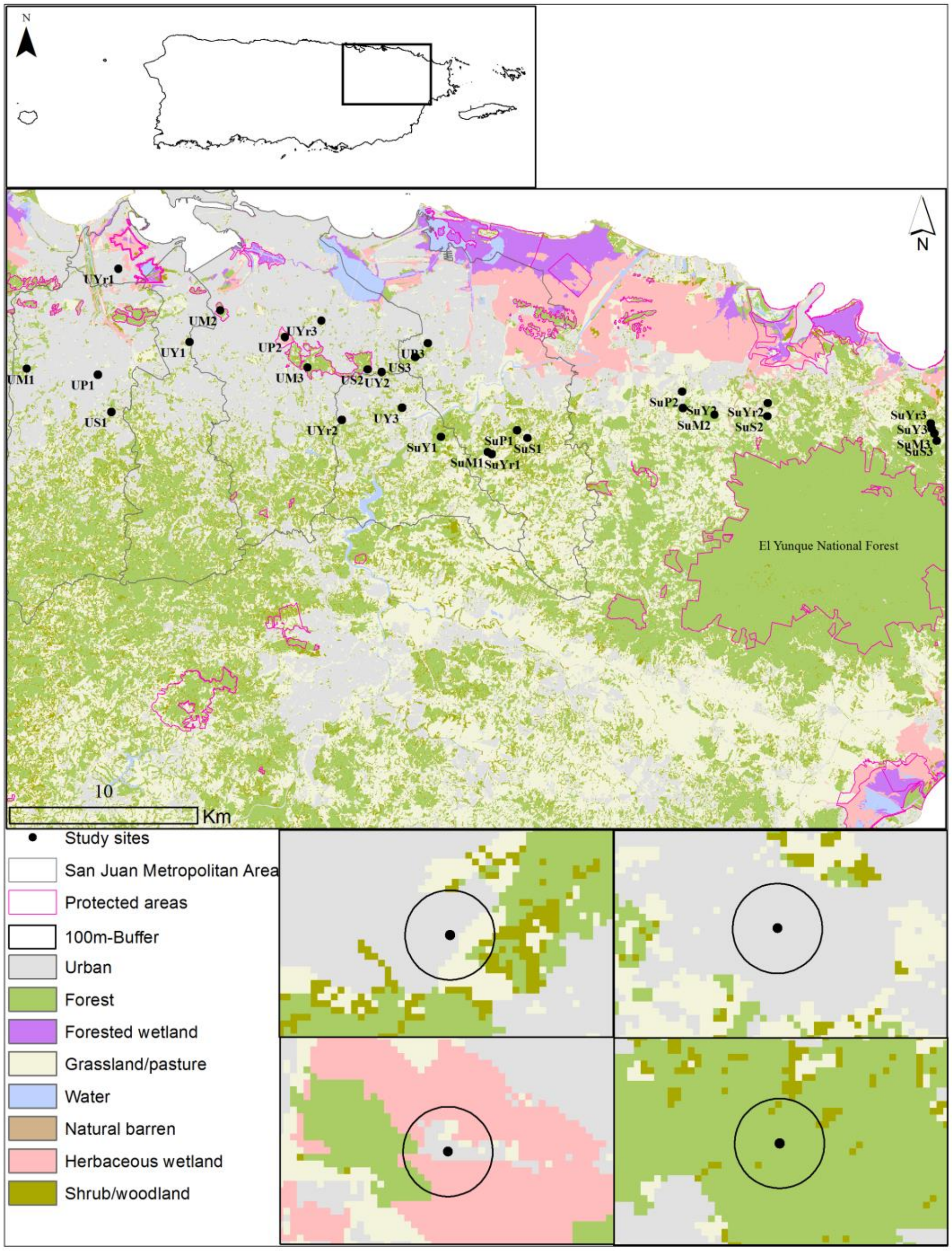

Figure 1. Study sites distributed in an urbanized landscape in the northeast lowlands of Puerto Rico. UM= urban mature forest, UY= urban young forest, US= urban shrub, UP= urban pasture, UYr= urban yard, SuM= suburban mature forest, SuY= suburban young forest, SuS= suburban shrub, SuP= suburban pasture, SuYr= suburban yard. In the right lower corner we indicated few examples of 100-m radius buffers used to measure landscape variables around each study site.

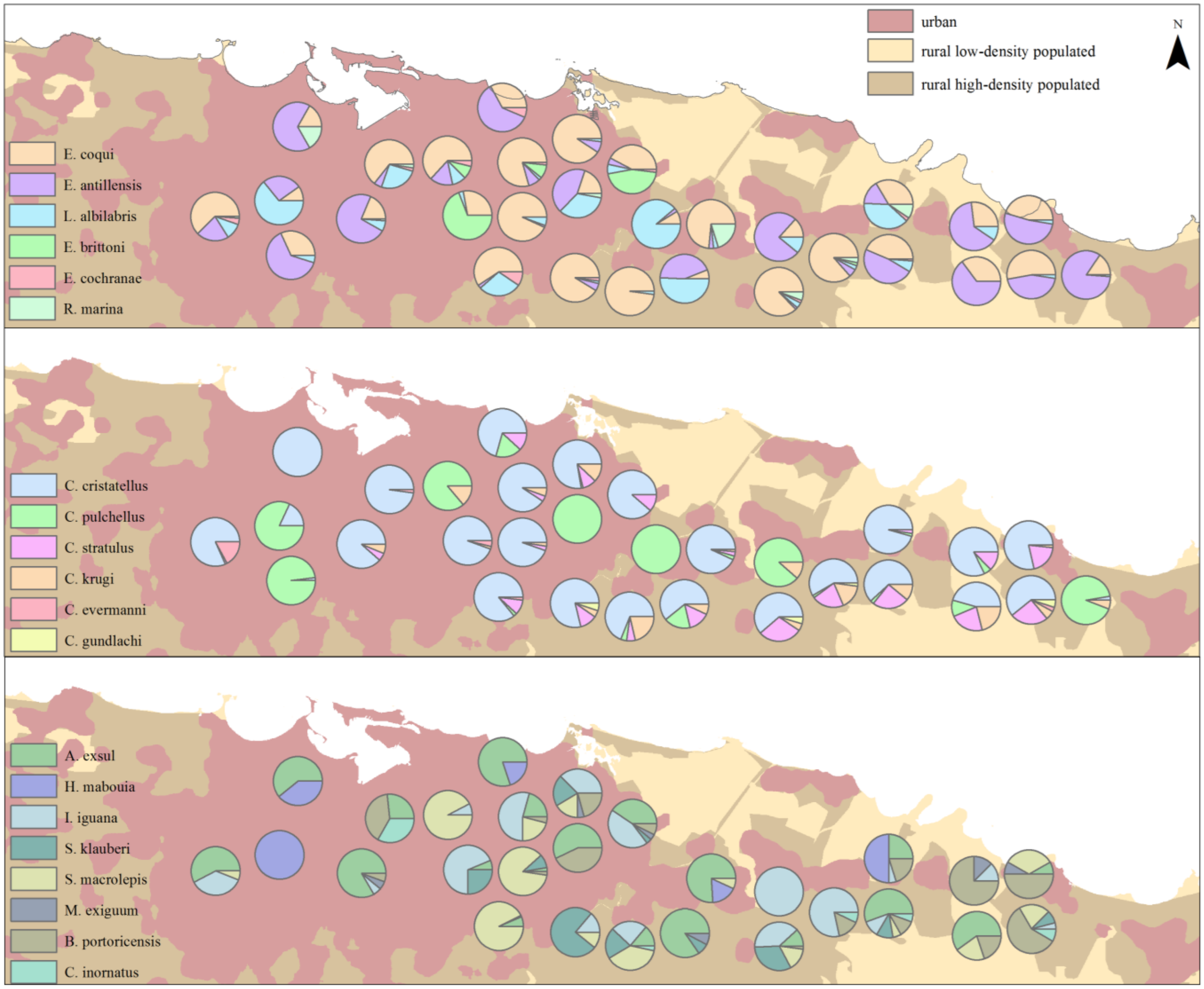

Figure 2. Species abundances in the 30 study sites overlaying the Puerto Rico Rural-Urban Land Use Map. Note in the figure below three pie charts are missing because these species were not identified in these sites.

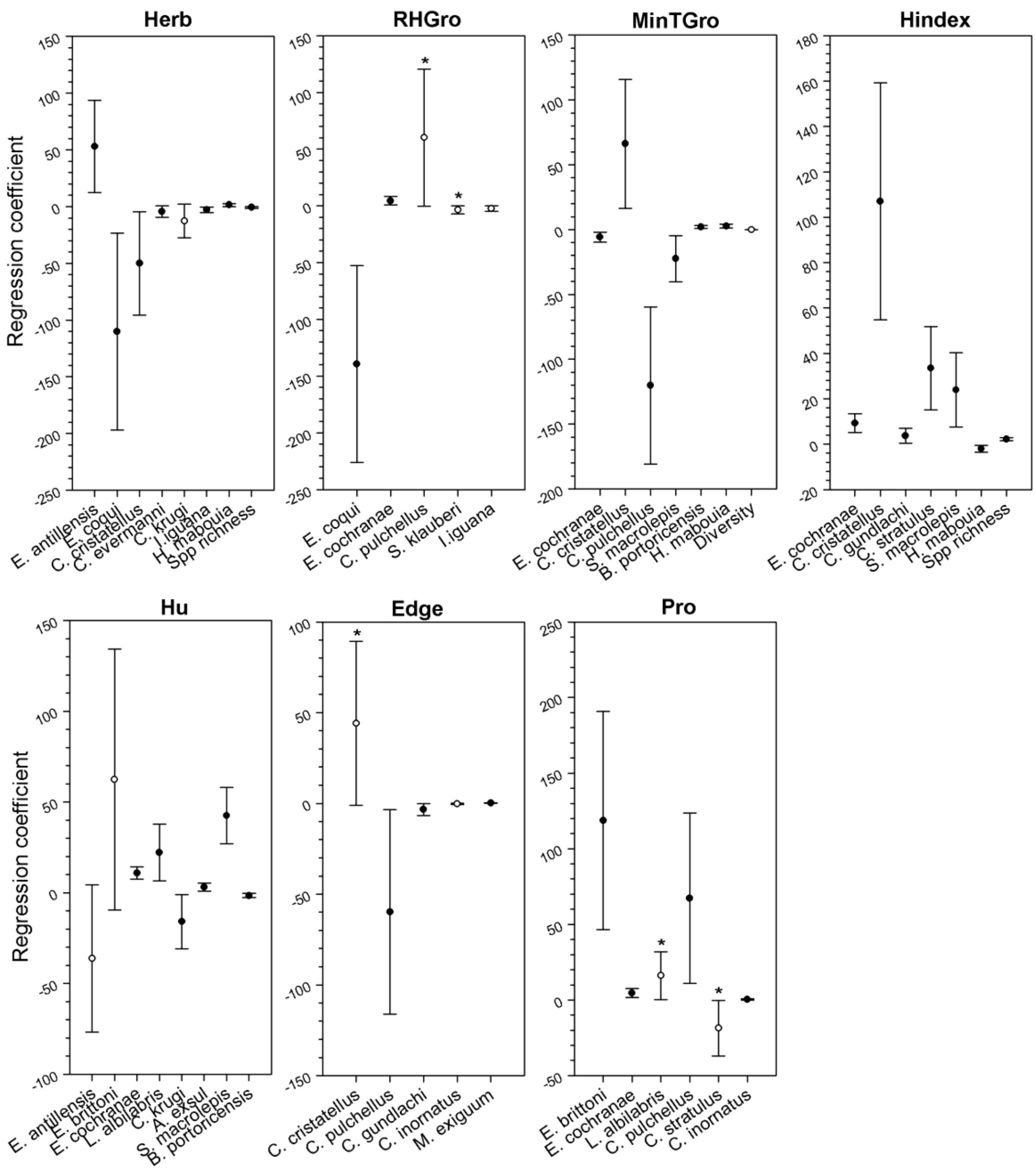

Figure 3. Estimated coefficients and 95% confidence intervals of environmental variables on the abundances of individual species. Filled circles indicate significant effects (*P<0.05*). Note differences in *y*-axis ranges. *Herb*= herbaceous cover, *RHGro*= mean relative humidity, *MinTGro*= mean minimum temperature, *Hindex*= foliage height diversity, *Hu*= housing units, *Edge*= forest edge, *Pro*= protected area.

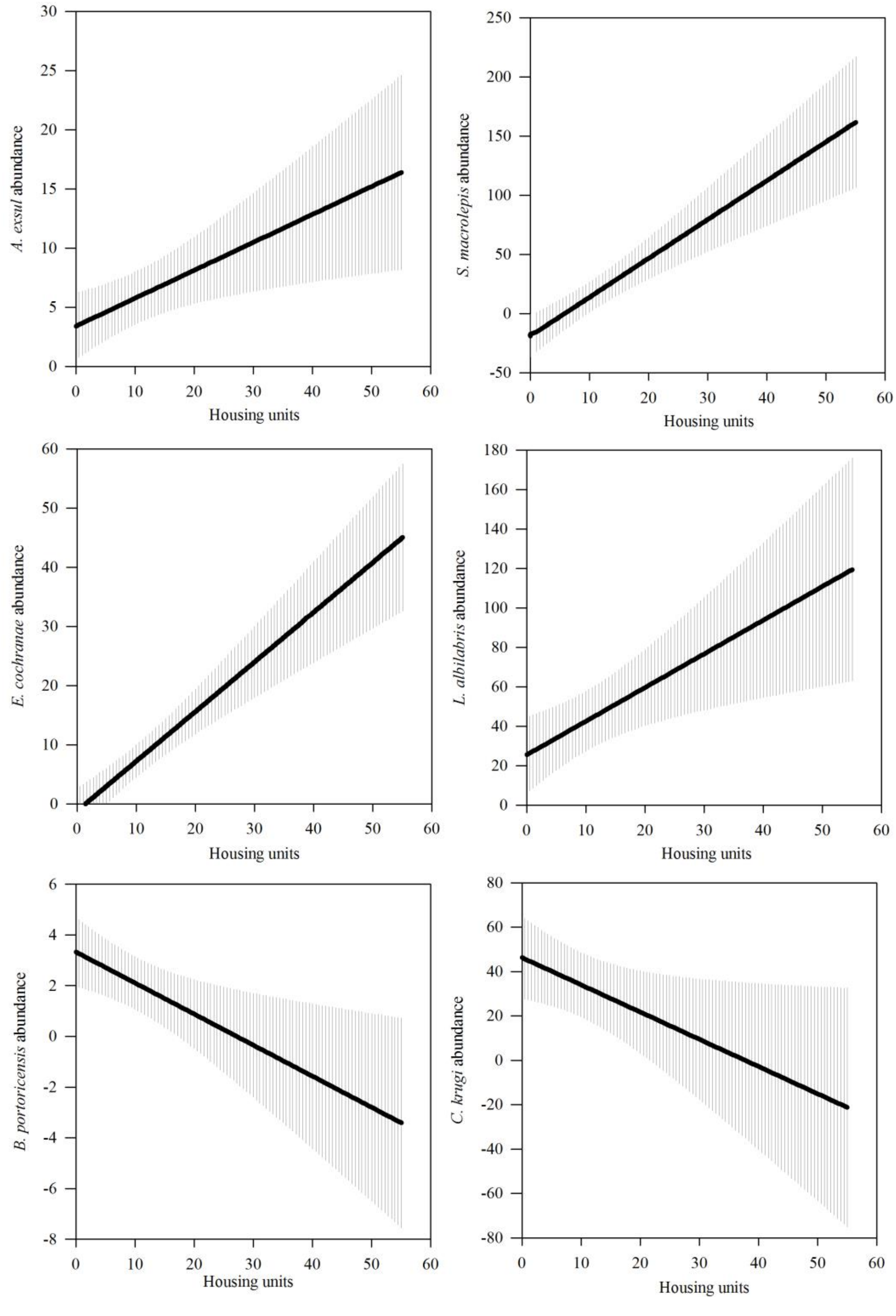

Figure 4. Prediction plots depicting correlations between housing units and individual species abundances. Margin of error at 95% of confidence.

Appendices

Appendix 1. Description and codes assigned to the study sites.

Sub area	Habitat	Code
Suburban	Mature forest	SuM1,SuM2, SuM3
Suburban	Young forest	SuY1, SuY2, SuY3
Suburban	Pasture	SuP1, SuP2, SuP3
Suburban	Shrub	SuS1, SuS2, SuS3
Suburban	Yard	SuYr1,SuYr2, SuYr3
Urban	Mature forest	UM1, UM2, UM3
Urban	Young forest	UY1, UY2, UY3
Urban	Pasture	UP1, UP2, UP3
Urban	Shrub	US1, US2, US3
Urban	Yard	UYr1, UYr2, UYr3

Appendix 2. Description of environmental variables initially considered for modeling species abundances, richness and biodiversity.

Environmental variables	Informs about	Method
Site-scale (within 1000 m^2 plot)		
Maximum, minimum, mean and standard deviation of the temperature at ground level	Microclimatic conditions	Herrera-Montes, 2014
Maximum, minimum, and mean humidity, and relative humidity at ground level	Microclimatic conditions	Herrera-Montes, 2014
Tree species richness	Forest diversity	Herrera-Montes, 2014
Stem density (for different DBH classes)	Stage of succession, and forest age (e.g., mature *vs.* young)	Herrera-Montes, 2014
Percentage of ground cover (i.e., bare, rock, litter, herbaceous, woody, artificial)	Habitat structure and complexity	Herrera-Montes, 2014
Percentage of canopy cover, and canopy height	Habitat structure and complexity	Herrera-Montes, 2014
Foliage height diversity index	Habitat structure and complexity	We used vegetation hits to calculate the Shannon-Weaver diversity index, in which hits represent species richness (Deppe & Rotenberry, 2008).
Landscape-scale (within 100-m radius buffer)		
Forest core (contiguous forest pixels), and edge (forest pixels surrounded by non-forest pixels)	Forest compactness and fragmentation (Vogt et al., 2007).	We calculated the proportion of forest core and edge using a Map of Morphological Spatial Pattern Analysis for Puerto Rico (Castro-Prieto et al., 2016).
Roads	Urbanization	We calculated roads density using the 2000 Roads Tiger Lines.
Housing units and human population	Urbanization	We used the 2010 decennial census in census blocks (US Census Bureau, 2015) to calculate the number of housing units and human population around each site, calculated as the proportion of the census block that lay within the 100-m radius buffer.
Green cover	Habitat available at landscape-scale	We calculated the percentage of forest, shrubland/woodland, grassland/pasture, herbaceous wetland, forested wetland, water, natural barren, built-up, within buffer zones using a simplified version of the Puerto Rico Land Cover Map (Gould et al., 2008). We collapsed the four vegetation classes (i.e., forest, shrubland, grassland and wetland) into one category that we named “green”.
Protected area	Habitat protected for biodiversity conservation	We calculated the percentage of the buffer that was inside a protected area using the Caribbean Landscape Conservation Cooperative Inventory of Protected Areas for Puerto Rico (CLCC, 2016).

Appendix 3. Top GLM for individual species abundances, species richness and diversity. **AICc=** Akaike Information Criterion that also considered the sample size**. ∑AICcw=** relative weight of each predictor.

Response variable	Best models (within 2 IC units)	AICc	ΔAICc	Weights	Predictor	∑AICcw
	Amphibians abundance					
E. antillensis	Herb + Hu	374.44	0.00	0.10	Herb	0.35
	Herb + Edge + Hu	374.78	0.34	0.08	Hu	0.19
	Herb	374.99	0.55	0.07	Edge	0.13
	Herb + Edge	376.19	1.75	0.04	MinTGro	0.03
	MinTGro + Herb	376.43	1.99	0.03		
E. coqui	RHGro + Herb	417.29	0.00	0.16	RHGro	0.34
	MinTGro + RHGro + Herb	418.30	1.01	0.10	Herb	0.34
	RHGro + Herb + Pro	418.85	1.57	0.07	MinTGro	0.10
					Pro	0.07
E. brittoni	Hu + Pro	408.30	0.00	0.11	Pro	0.41
	Pro	408.68	0.38	0.09	Hu	0.19
	MinTGro + Pro	408.82	0.52	0.08	MinTGro	0.12
	RHGro + Pro	409.72	1.42	0.05	RHGro	0.09
	MinTGro + Hu + Pro	410.17	1.87	0.04		
	RHGro + Hu + Pro	410.20	1.90	0.04		
E. cochranae	MinTGro + RHGro + Hindex + Hu + Pro	220.16	0.00	0.44	MinTGro	0.45
					RHGro	0.45
					Hindex	0.45
					Hu	0.45
					Pro	0.45
L. albilabris	Hu + Pro	316.89	0.00	0.11	Hu	0.24
	MinTGro + Hu + Pro	317.47	0.58	0.08	Pro	0.19
	Hu	318.38	1.49	0.05	MinTGro	0.08
R. marina	RHGro	253.43	0.00	0.06	RHGro	0.06
	Hu	253.55	0.12	0.05	Hu	0.05
	Reptiles abundances					
C. cristatellus	MinTGro + Herb + Hindex + Edge	380.39	0.00	0.17	MinTGro	0.42
	MinTGro + Herb + Hindex	381.36	0.96	0.10	Hindex	0.42
	MinTGro + Hindex	381.60	1.20	0.09	Herb	0.27
	MinTGro+ Hindex + Edge	382.34	1.95	0.06	Edge	0.23

C. evermanni	Herb	248.92	0.00	0.09	Herb	0.15
	Hindex	249.94	1.03	0.05	Hindex	0.08
	MinTGro	250.40	1.49	0.04	MinTGro	0.07
	Herb + Hindex	250.78	1.86	0.03	RHGro	0.03
	RHGro	250.78	1.87	0.03		
	MinTGro + Herb	250.91	1.99	0.03		
C. pulchellus	MinTGro + RH + Edge + Pro	397.23	0.00	0.12	MinTGro	0.34
	MinTGro + Edge + Pro	398.35	1.12	0.07	Pro	0.34
	MinTGro + Hindex + Pro	398.74	1.51	0.05	Edge	0.24
	MinTGro + Hindex + Edge + Pro	398.80	1.57	0.05	RHGro	0.17
	MinTGro + RHGro + Pro	398.86	1.64	0.05	Hindex	0.10
C. gundlachi	Hindex + Edge	222.52	0.00	0.05	Edge	0.15
	Hindex + Edge + Hu	223.40	0.87	0.03	Hindex	0.12
	MinTGro + Edge + Hu	223.43	0.90	0.03	Hu	0.10
	MinTGro + Hu	223.92	1.40	0.02	MinTGro	0.07
	MinTGro + Edge + Hu + Pro	224.01	1.49	0.02	Pro	0.04
	Hindex	224.11	1.59	0.02	Herb	0.02
	Hindex + Edge + Pro	224.35	1.83	0.02		
	Herb	224.51	1.99	0.02		
C. krugi	Herb + Hu	314.34	0.00	0.05	Herb	0.19
	Hu	314.57	0.23	0.05	Hu	0.17
	MinTGro + Hindex + Edge	314.78	0.43	0.04	MinTGro	0.17
	MinTGro + Hindex	315.15	0.81	0.04	Hindex	0.12
	MinTGro + Herb	315.26	0.91	0.04	Edge	0.09
	MinTGro + Herb + Hindex	315.26	0.91	0.04		
	Edge + Hu	315.66	1.31	0.03		
	MinTGro + Herb + Hu	315.73	1.39	0.02		
	MinTGro + Herb + Hindex + Edge	316.04	1.70	0.02		
	Herb	316.16	1.81	0.02		
	Herb + Edge + Hu	316.16	1.82	0.02		
C. stratulus	Hindex + Pro	326.85	0.00	0.07	Pro	0.39
	Herb + Hindex + Pro	326.89	0.04	0.07	Hindex	0.36
	MinTGro + Herb + Hu + Pro	327.14	0.28	0.07	Hu	0.25
	Herb + Hindex + Hu + Pro	327.32	0.47	0.06	Herb	0.24
	MinTGro + Herb + Hindex + Hu + Pro	327.68	0.82	0.05	MinTGro	0.15
	Hindex + Hu + Pro	327.79	0.93	0.05		
	MinTGro + Hindex + Hu + Pro	327.94	1.09	0.05		
	Hindex	328.24	1.38	0.04		

A. exsul	Hu	199.97	0.00	0.13	Hu	0.31
	Edge + Hu	201.41	1.44	0.07	Edge	0.06
	Hu + Pro	201.42	1.45	0.07	Pro	0.06
	Hindex + Hu	201.46	1.49	0.06	Hindex	0.06
S. klauberi	RH	226.81	0.00	0.09	RH	0.12
	Hindex	227.54	0.73	0.06	Hindex	0.06
	Herb	228.48	1.67	0.03	Herb	0.06
	RH + Herb	228.49	1.68	0.03		
S. macrolepis	MinTGro + Hindex + Hu	309.48	0.00	0.24	Pro	1.55
	MinTGro + Hindex + Hu + Pro	311.04	1.56	0.11	Hu	0.35
					Hindex	0.35
					MinTGro	0.35
B. portoricensis	MinTGro + Hu	155.85	0.00	0.25	MinTGro	0.25
					Hu	0.25
C. inornatus	Edge + Pro	85.24	0.00	0.06	Pro	0.34
	Pro	85.45	0.20	0.05	Edge	0.20
	MinTGro+Edge + Hu + Pro	85.72	0.47	0.05	Hu	0.15
	Edge + Hu + Pro	85.86	0.62	0.04	MinTGro	0.13
	MinTGro + Hu + Pro	86.37	1.12	0.03	Hindex	0.05
	Hindex + Edge + Pro	86.44	1.19	0.03		
	MinTGro + Pro	86.80	1.55	0.03		
	Hu + Pro	86.82	1.57	0.03		
	MinTGro + Edge + Hu	86.92	1.67	0.03		
	Herb + Pro	86.98	1.73	0.02		
	MinTGro + Edge + Pro	87.15	1.91	0.02		
	Hindex + Pro	87.24	1.99	0.02		
I. iguana	RHGro + Herb	204.58	0.00	0.11	Herb	0.30
	Herb	205.14	0.56	0.09	RHGro	0.16
	Herb + Hindex	205.86	1.28	0.06	Hindex	0.06
	RH + Herb + Pro	206.08	1.50	0.05	Pro	0.05
	Hu	253.55	0.12	0.05	Hu	0.05
M. exiguum	Edge	44.29	0.00	0.12	Edge	0.32
	Hindex + Edge	45.17	0.88	0.07	Hindex	0.07
	MinTGro + Edge	45.66	1.38	0.06	MinTGro	0.05
	Edge + Pro	45.90	1.61	0.05	Pro	0.05
	RH + Edge	46.09	1.80	0.05		
H. mabouia	MinTGro + Herb + Hindex	166.20	0.00	0.21	MinTGro	0.31
	MinTGro + RH + Herb + Hindex	167.35	1.15	0.12	Herb	0.31
					Hindex	0.31
					RHGro	0.11

Species richness and diversity						
Richness	Herb + Hindex	123.83	0.00	0.18	Herb	0.32
	RHGro + Herb + Hindex	124.05	0.22	0.16	Hindex	0.32
					RHGro	0.15
Diversity	MinTGro	16.73	0.00	0.07	MinTGro	0.20
	MinTGro + Hindex	16.76	0.03	0.07	Hindex	0.13
	Hu	18.05	1.33	0.04	Hindex	0.13
	MinTGro + RHGro + Hindex	18.12	1.39	0.04	Hu	0.03
	MinTGro + Hindex + Edge	18.36	1.63	0.03	RHGro	0.03
					Edge	0.03

GENERAL CONCLUSION

We found protected areas in Puerto Rico overlap the most species-rich regions in the island, encompass a diverse landscape, are dominated by core forest, and include large portions of the habitats of many threatened vertebrate species. Furthermore, protected areas in Puerto Rico have been effective in restricting urban development within their boundaries, and offer resistance to the sprawling expansion of the urban footprint across the island.

However, we found land surrounding protected areas are seek after for urban development. We found that housing construction, a major contributor of urban development in Puerto Rico, continued in the vicinity of protected areas at the same rate as the island at wide. Although the rate of housing growth is expected to decrease as a consequence of the economic crisis in the island and increasing outmigration to the United States, it is uncertain how this population decline will affect housing growth as second homes and the constructions of affordable housing for low-income families will likely increase.

Although urban areas are generally described as places with low diversity and dominated by exotic species, we found anurans and reptiles in urban areas in Puerto Rico have similar diversity, species richness and mean abundances than in rural lands. Furthermore, we found some endemic and endangered species occurred at high densities within natural ecosystems in urban sites. When we look at the individual environmental characteristics of the urban sites we found some of them were located within or very close to a protected area, or an unprotected forest with high foliage diversity, suggesting that these sites contributed to overall results when analyzing all urban sites as a group. We concluded that urban sites in Puerto Rico can maintain biodiversity if they also maintain green infrastructure within the urban core.

Since urban development is irreversible, strategies to promote biodiversity conservation in urban areas should include connecting unprotected ecosystems, including private yards, and unprotected forest patches with nearby protected areas. For example, promoting the protection of forest patches, ponds, trails and gardens in adjacent lands to a protected area contributes to increase the effective size of the protected area, and its capacity to conserve viable populations, species richness and ecosystem services.

Even in high-density urban areas within the San Juan Metropolitan Area, encouraging wildlife-friendly gardens and infrastructure (e.g., plants, luminary) represents an opportunity for education and for involving citizens in conservation that would benefit both nature and people. Minimizing and mitigating threats from urban development on biodiversity will require actions at many levels: household, and private land owners, government, NGOs and conservation groups.