

# Declining human population but increasing residential development around protected areas in Puerto Rico



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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.

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## 1. 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., 2013; 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 and 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 et al., 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,

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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% (Mackun and Wilson, 2011). 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 et al., 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.

## 2. Methodology

### 2.1. Study area, and recent population and housing changes

Puerto Rico occupies 8937 km<sup>2</sup>, 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 (USDA, 2017), 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, 2015; 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).

### 2.2. Protected areas data

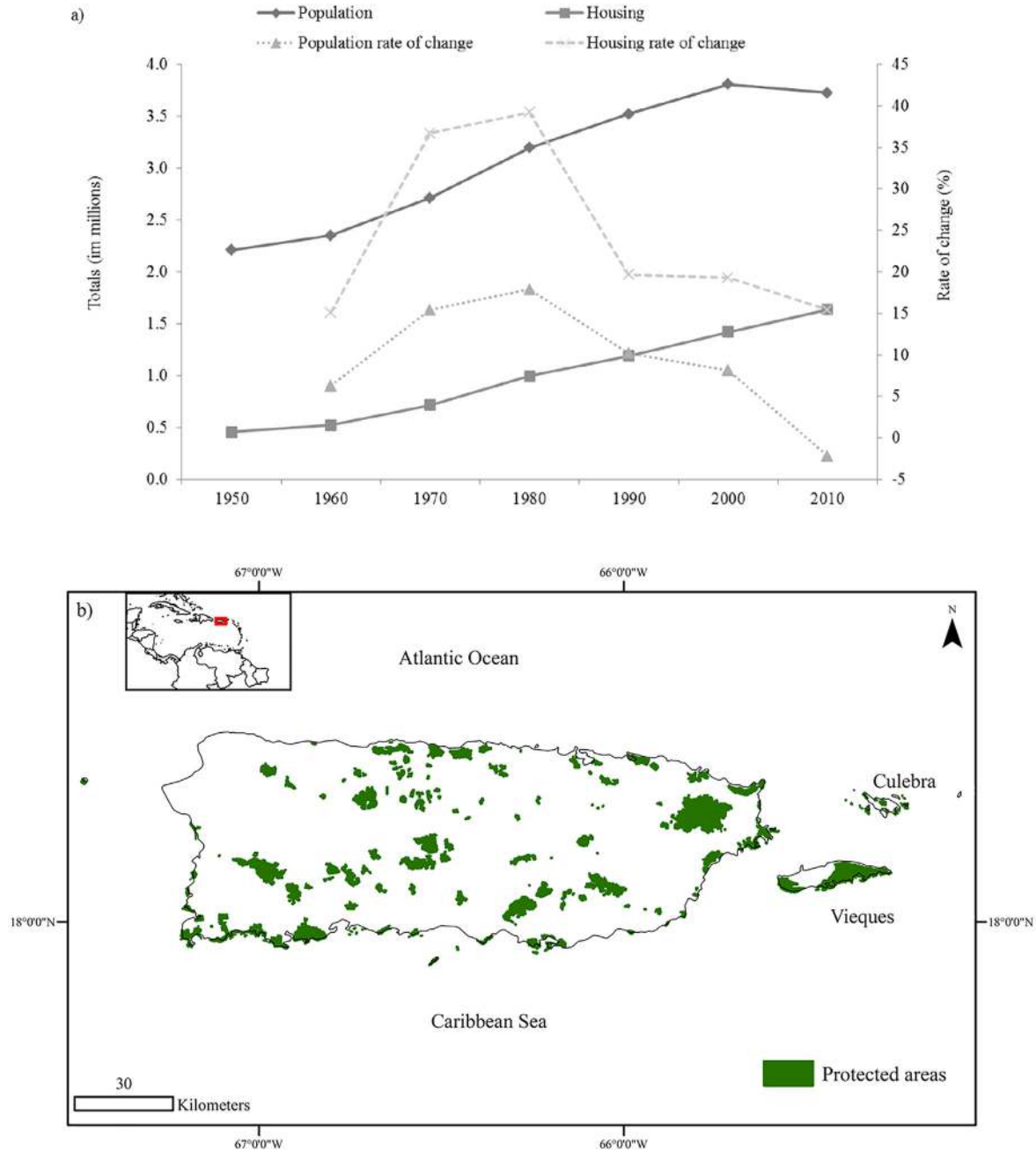
The island has a large network of protected areas and we focused our analysis on those terrestrial protected areas ( $n = 124$ ), which as of September 2015 occupied 8% (709 km<sup>2</sup>) of the land surface (Fig. 1b), and excluded marine protected areas, protected areas that are cays or islets, and 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<sup>2</sup> to 115 km<sup>2</sup> (mean = 6 km<sup>2</sup>) 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<sup>2</sup>) of the protected areas occur in the interior mountains and hills, and 29% (209 km<sup>2</sup>) in the coastal plains.

### 2.3. 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 et al., 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.

### 2.4. 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



**Fig. 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).

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<sup>2</sup>,

people/km<sup>2</sup>) 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).

### 3. Results

#### 3.1. 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. 2). 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<sup>2</sup> in 2000 to 176 housing units/km<sup>2</sup> in 2010 (Fig. 3).

From 2000 to 2010, 28,868 fewer people lived within 1 km of the protected areas (Fig. 2). 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<sup>2</sup> in 2000 to 363 people/km<sup>2</sup> in 2010 (Fig. 3).

#### 3.2. 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 to 1824 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

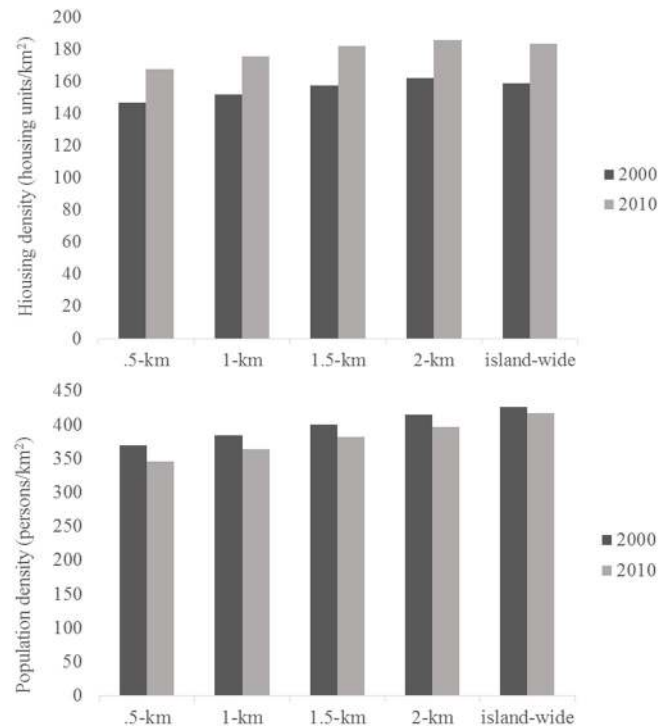


Fig. 3. Housing density, and population density within buffer zones around the entire network of protected areas, and island-wide.

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 Martín 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).

### 4. Discussion

#### 4.1. 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, 2010). 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 are a consequence of urban sprawl (Martinuzzi et al., 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).

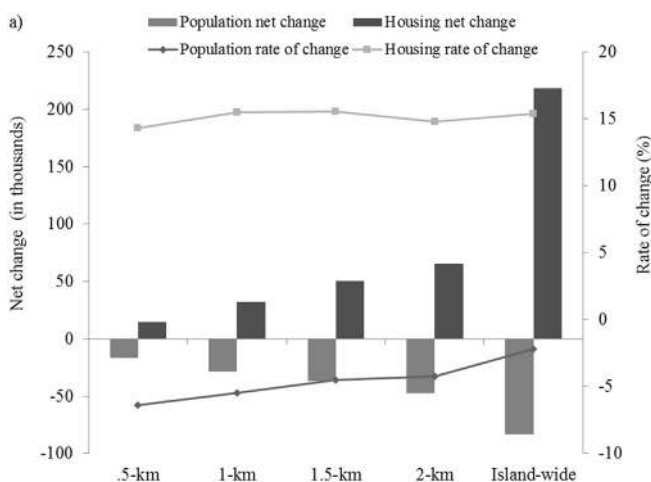


Fig. 2. Population and housing net change, and rates of change within buffer zones around the entire network of protected areas and island-wide, between 2000 and 2010.

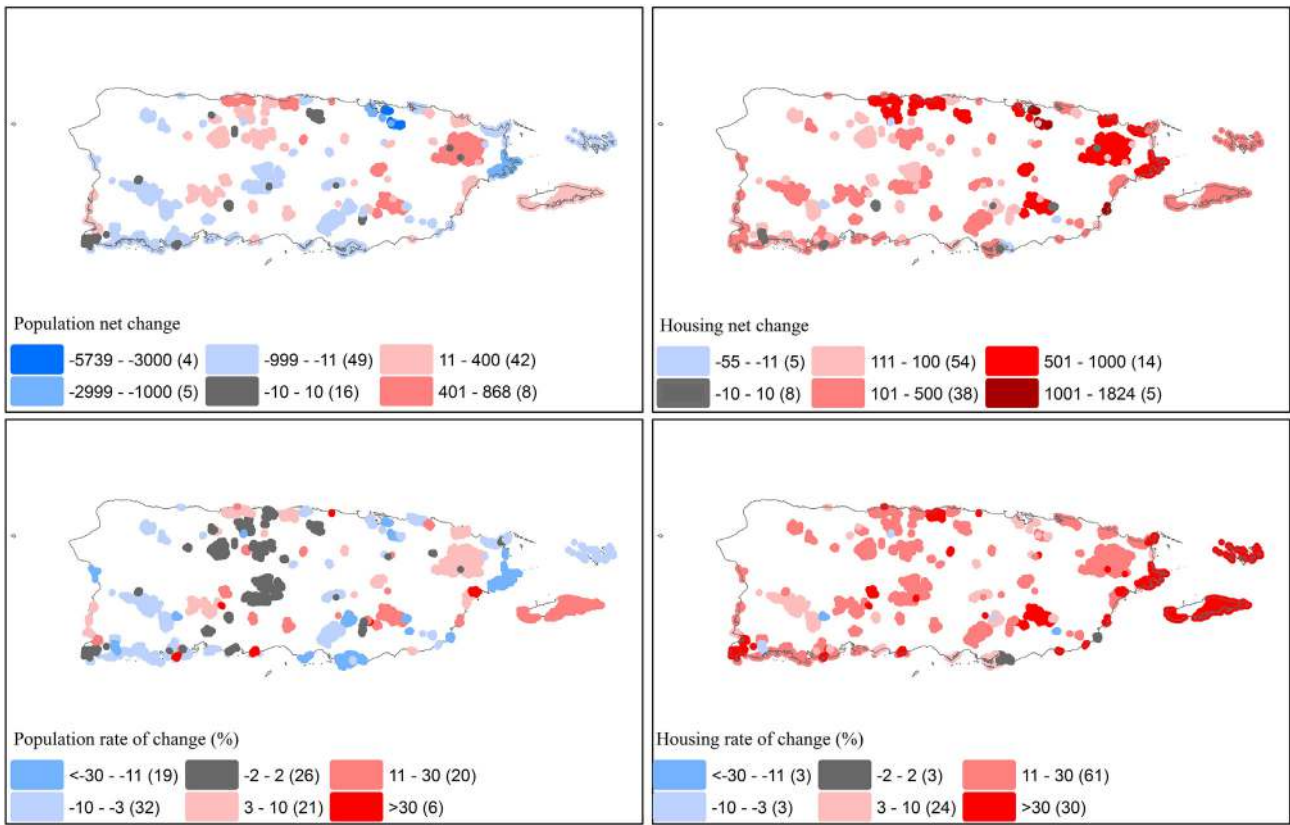


Fig. 4. Spatial patterns of housing and population changes within 1 km of individual protected areas. The number of protected areas in each class is shown between parenthesis.

#### 4.2. 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 Martín 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).

#### 4.3. 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 et al., 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 et al., 2013; Morse et al., 2014). For example, nonnative flora contributes to 32% (1032 species) of the total flora in Puerto Rico and the US Virgin Islands (Rojas-Sandoval and 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 (*Todux 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 et al., 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.

#### 4.4. 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 analyze yearly data so we were unable to detect yearly changes in housing that could have happened as a consequence of massive outmigration that occurred in the middle of the analyzed time period (D'Veira 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 and Gould, 2007), but in our case this limitation was quite reduced because of the small size of census blocks in Puerto Rico.

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

| Protected area               | 0.5-km |     |         |     | 1-km   |     |         |     | 1.5-km |     |         |     | 2-km   |     |         |     |
|------------------------------|--------|-----|---------|-----|--------|-----|---------|-----|--------|-----|---------|-----|--------|-----|---------|-----|
|                              | HU     |     | POP     |     | HU     |     | POP     |     | HU     |     | POP     |     | HU     |     | POP     |     |
|                              | Net    | %   | Net     | %   | Net    | %   | Net     | %   | Net    | %   | Net     | %   | Net    | %   | Net     | %   |
|                              | change |     | change  |     | change |     | change  |     | change |     | change  |     | change |     | change  |     |
| Río 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 Robleada 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  |



(continued)

| Protected area                                    | 0.5-km     |     |            |     | 1-km       |    |            |     | 1.5-km     |    |            |     | 2-km       |    |            |     |
|---|------------|-----|------------|-----|------------|----|------------|-----|------------|----|------------|-----|------------|----|------------|-----|
|   | HU         |     | POP        |     | HU         |    | POP        |     | HU         |    | POP        |     | HU         |    | POP        |     |
|   | Net change | %   | Net change | %   | Net change | %  | Net change | %   | Net change | %  | Net change | %   | Net change | %  | Net change | %   |
|   |            |     |            |     |            |    |            |     |            |    |            |     |            |    |            |     |
| 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 Espíritu 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 Moulrier 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.

## References

- Abel, J., Deitz, R., 2014. The causes and consequences of Puerto Rico's declining population, Federal Reserve Bank of New York. Current Issues in Economics and Finance. <http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150444>.
- Araújo, M.B., Williams, P.H., 2000. Selecting areas for species persistence using occurrence data. *Biol. Conserv.* 96:331–345. [http://dx.doi.org/10.1016/S0006-3207\(00\)00074-4](http://dx.doi.org/10.1016/S0006-3207(00)00074-4).
- Araújo, M.B., Williams, P.H., Fuller, R.J., 2008. Dynamics of extinction and the selection of nature reserves. *Hung. Q.* 49:1971–1980. <http://dx.doi.org/10.1098/rspb.2002.2121>.
- Barber, J.R., Burdett, C.L., Reed, S.E., Warner, K.A., Formichella, C., Crooks, K.R., Theobald, D.M., Fristrup, K.M., 2011. Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. *Landsc. Ecol.* 26:1281–1295. <http://dx.doi.org/10.1007/s10980-011-9646-7>.
- Birdlife International, 2010. Critical ecosystem partnership fund. *Ecosystem Profile: The Caribbean Islands Biodiversity Hotspot*.
- Bradbury, M., Peterson, M.N., Liu, J., 2014. Long-term dynamics of house hold size and their environmental implications. *Popul. Environ.* 36:73–84. <http://dx.doi.org/10.1007/s11111-014-0203-6>.
- Brambilla, M., Ronchi, S., 2016. The park-view effect: residential development is higher at the boundaries of protected areas. *Sci. Total Environ.* 569–570:1402–1407. <http://dx.doi.org/10.1016/j.scitotenv.2016.06.223>.
- Caribbean Landscape Conservation Cooperative., September, 2015. *Puerto Rico Protected Areas Database [version of September, 2015]. GIS data, San Juan, PR*.
- D'Vera, Cohn, Pattern, E., Lopez, M.H., 2014. Puerto Rican Population Declines on Island, Grows on U.S. Mainland. <http://dx.doi.org/10.1017/CBO9781107415324.004>.
- DeFries, R., Hansen, A., Newton, A., Hansen, M., 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecol. Appl.* 15, 19–26.
- DeFries, R., Hansen, A., Turner, B.L., Reid, R., Liu, J., 2007. Land use change around protected areas: management to balance human needs and ecological function. *Ecol. Appl.* 17, 1031–1038.
- Estudios Tecnicos Inc, 2014. *Puerto Rico State Housing Plan Fiscal Years 2014–2018 (ANNEX CC Government of Puerto Rico)*.
- Farley, R., 2010. *Michigan's Demographic Outlook: Implications for the University of Michigan (Report 10-699)*.
- Friesen, L.E., Eagles, P.F.J., Mackay, R.J., 1995. Effects of residential development on forest-dwelling Neotropical Migrant Songbirds (Efectos del desarrollo urbano sobre los bosques habitados por aves neotropicales migratorias). *Conserv. Biol.* 9:1408–1414. <http://dx.doi.org/10.1046/j.1523-1739.1995.09061408.x>.
- Gould, W., Alarcón, C., Fevold, B., Jiménez, M., Martinuzzi, S., Potts, G., Quiñones, M., Solórzano, M., Ventosa, E., 2008. *The Puerto Rico Gap Analysis Project. Volume 1: land cover, vertebrate species distributions, and land stewardship. Gen. Tech. Rep. 165 IITF-GTR-39*.
- Güneralp, B., Seto, K.C., 2013. Futures of global urban expansion: uncertainties and implications for biodiversity conservation. *Environ. Res. Lett.* 8:14025. <http://dx.doi.org/10.1088/1748-9326/8/1/014025>.
- Güneralp, B., McDonald, R.I., Fragkias, M., Goodness, J., Marcotullio, P.J., Seto, K.C., 2013. Urbanization forecasts, effects on land use, biodiversity, and ecosystem services. In *Urbanization, biodiversity and ecosystem services: Challenges and opportunities*. In: Elmqvist, T., et al. (Eds.), *Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities: A Global Assessment*. Springer. [http://dx.doi.org/10.1007/978-94-007-7088-1\\_22](http://dx.doi.org/10.1007/978-94-007-7088-1_22).
- Hamilton, C.M., Martinuzzi, S., Plantinga, A.J., Radeloff, V.C., Lewis, D.J., Thogmartin, W.E., Heglund, P.J., Pidgeon, A.M., 2013. Current and future land use around a nationwide protected area network. *PLoS One* 8, e55737. <http://dx.doi.org/10.1371/journal.pone.0055737>.
- Hansen, A., DeFries, R., 2007. *Ecological mechanisms linking protected areas to surrounding lands. Ecol. Appl.* 17, 974–988.
- Hansen, A.J., Rasker, R., Maxwell, B., Rotella, J.J., Johnson, J.D., Parmenter, A.W., Langner, U., Cohen, W.B., Lawrence, R.L., Kraska, M.P.V., 2002. Ecological causes and consequences of demographic change in the New West. *Bioscience* 52:151. [http://dx.doi.org/10.1641/0006-3568\(2002\)052\[0151:ECACOD\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2002)052[0151:ECACOD]2.0.CO;2).



- Helmer, E.H., Brandeis, T.J., Lugo, A.E., Kennaway, T., 2008. Factors influencing spatial pattern in tropical forest clearance and stand age: implications for carbon storage and species diversity. *J. Geophys. Res.* 113 G02S04. [10.1029/2007JG000568](https://doi.org/10.1029/2007JG000568).
- Herrera-Montes, A., 2014. Maintaining herpetofaunal diversity in urban landscape: implications for conservation. Thesis Dissertation San Juan, University of Puerto Rico, Rio Piedras Campus Available at: <http://search.proquest.com/naturalsciollection/docview/1652880123>. Accessed on May 2016.
- Irizarry, J.I., Collazo, J.A., Dinsmore, S.J., 2016. Occupancy dynamics in human-modified landscapes in a tropical island: implications for conservation design. *Divers. Distrib.* 22:410–421. <http://dx.doi.org/10.1111/ddi.12415>.
- Joglar, R., Longo, A., 2011. *Guía de biodiversidad urbana : especies en ciudades y bosques urbanos de Puerto Rico*. Proyecto Coquí, 2011. ISBN: 978-0-9845498-0-1.
- Joppa, L.N., Loarie, S.R., Pimm, S.L., 2009. On population growth near protected areas. *PLoS One* 4, e4279. <http://dx.doi.org/10.1371/journal.pone.0004279>.
- Kennaway, T., Helmer, E., 2007. The forest types and ages cleared for land development in Puerto Rico. *GIScience Remote Sens.* 44, 356–382.
- Leroux, S.J., Kerr, J.T., 2013. Land development in and around protected areas at the wilderness frontier. *Conserv. Biol.* 27:166–176. <http://dx.doi.org/10.1111/j.1523-1739.2012.01953.x>.
- Liu, J., Daily, G.C., Ehrlich, P.R., Luck, G.W., 2003. Effects of household dynamics on resource consumption and biodiversity. *Nature* 421:530–533. <http://dx.doi.org/10.1038/nature01359>.
- Logan, J.R., Xu, Z., Stults, B.J., 2014. Interpolating U.S. decennial census tract data from as early as 1970 to 2010: a longitudinal tract database. *Prof. Geogr.* 66:412–420. <http://dx.doi.org/10.1080/00330124.2014.905156>.
- Lugo, A.E., Carlo, T.A., Wunderle, J.M., 2012a. Natural mixing of species: novel plant-animal communities on Caribbean Islands. *Anim. Conserv.* 15:233–241. <http://dx.doi.org/10.1111/j.1469-1795.2012.00523.x>.
- Lugo, A.E., Helmer, E.H., Valentín, E.S., 2012b. Caribbean landscapes and their biodiversity. *Interciencia* 37, 705–710.
- Lugo, A.E., Martínez, O.A., Da Silva, J.F., 2012c. Aboveground biomass, wood volume, nutrient stocks and leaf litter in novel forests compared to native forests and tree plantations in Puerto Rico. *Bois Forests des Trop.* 66, 7–16.
- Maiorano, L., Faluccci, A., Boitani, L., 2008. Size-dependent resistance of protected areas to land-use change. *Proc. Biol. Sci.* 275:1297–1304. <http://dx.doi.org/10.1098/rspb.2007.1756>.
- Martinuzzi, S., Gould, W.a., Ramos González, O.M., 2007. Land development, land use, and urban sprawl in Puerto Rico integrating remote sensing and population census data. *Landsc. Urban Plan.* 79:288–297. <http://dx.doi.org/10.1016/j.landurbplan.2006.02.014>.
- Martinuzzi, S., Lugo, A.E., Brandeis, T.J., Helmer, E.H., 2013. Case study: geographic distribution and level of novelty of Puerto Rican forests. *Nov. Ecosyst. Interv. New Ecol. World Order:* 81–87. <http://dx.doi.org/10.1002/9781118354186.ch9>.
- McDonald, R.L., Forman, R.T.T., Kareiva, P., Neugarten, R., Salzer, D., Fisher, J., 2009. Urban effects, distance, and protected areas in an urbanizing world. *Landsc. Urban Plan.* 93: 63–75. <http://dx.doi.org/10.1016/j.landurbplan.2009.06.002>.
- McDonald, R.L., Kareiva, P., Forman, R.T.T., 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol. Conserv.* 141:1695–1703. <http://dx.doi.org/10.1016/j.biocon.2008.04.025>.
- Mackun, P., Wilson, S., 2011. Population distribution and change: 2000 to 2010, 2010 Census Briefs. U.S. Department of Commerce Economics and Statistics Administration U.S. Census Bureau, p. 11.
- Morse, N.B., Pellissier, P.A., Cianciola, E.N., Brereton, R.L., Sullivan, M.M., Shonka, N.K., Wheeler, T.B., McDowell, W.H., 2014. Novel ecosystems in the Anthropocene: a revision of the novel ecosystem concept for pragmatic applications. *Ecol. Soc.* 19. <http://dx.doi.org/10.5751/ES-06192-190212>.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <http://dx.doi.org/10.1038/35002501>.
- Parés-Ramos, I.K., Gould, W.A., Aide, T.M., 2008. Agricultural abandonment, suburban growth, and forest expansion in Puerto Rico between 1991 and 2000. *Ecol. Soc.* 13 (doi:1).
- Pejchar, L., Reed, S., Bixler, P., Ex, L., Mockrin, M., 2015. Consequences of residential development on biodiversity and human well-being. *Front. Ecol. Environ.* 13, 146–153.
- Pew Research Center, 2017. Puerto Ricans leave in record numbers for mainland U.S. Available at: <http://www.pewresearch.org>. Accessed on February 2017.
- Pulwarty, R.S., Nurse, L.A., Trotz, U.O., 2010. Caribbean islands in a changing climate. *Environ. Sci. Policy Sustain. Dev.* 52:16–27. <http://dx.doi.org/10.1080/00139157.2010.522460>.
- Radeloff, V.C., Stewart, S.I., Hawbaker, T.J., Gimmi, U., Pidgeon, A.M., Flather, C.H., Hammer, R.B., Helmers, D.P., 2010. Housing growth in and near United States protected areas limits their conservation value. *Proc. Natl. Acad. Sci. U. S. A.* 107: 940–945. <http://dx.doi.org/10.1073/pnas.0911131107>.
- Rojas-Sandoval, J., Acevedo-Rodríguez, P., 2014. Naturalization and invasion of alien plants in Puerto Rico and the Virgin Islands. *Biol. Invasions* 17:149–163. <http://dx.doi.org/10.1007/s10530-014-0712-3>.
- Schindler, D.E., Geib, S.I., Williams, M.R., 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. *Ecosystems* 3:229–237. <http://dx.doi.org/10.1007/s100210000022>.
- Seto, K.C., Fragkias, M., Gu, B., 2011. A Meta-analysis of Global Urban Land Expansion. 6. <http://dx.doi.org/10.1371/Citation>.
- Sleeter, R., Gould, M., 2007. Geographic information system software to remodel population data using dasyymmetric mapping methods. *US Geol. Surv. Tech. Methods* (11-C2).
- Spear, D., Foxcroft, L.C., Bezuidenhout, H., McGeoch, M.a., 2013. Human population density explains alien species richness in protected areas. *Biol. Conserv.* 159:137–147. <http://dx.doi.org/10.1016/j.biocon.2012.11.022>.
- Statista, 2016. The Statistics Portal. Top 20 countries with the biggest population decline by 2016 Available at: <https://www.statista.com>. Accessed on September 2016.
- Stein, S.M., Carr, M.A., Liknes, G.C., Comas, S.J., 2014. Islands on the Edge: Housing Development and Other Threats to America's Pacific and Caribbean Island Forests.
- Suarez-Rubio, M., Lookingbill, T.R., 2016. Forest birds respond to the spatial pattern of ex-urban development in the Mid-Atlantic region, USA. *PeerJ* 4, e2039. <http://dx.doi.org/10.7717/peerj.2039>.
- Syphard, A.D., Stewart, S.I., Mckee, J., Hammer, R.B., Fried, J.S., Holcomb, S., Radeloff, V.C., 2009. Assessing housing growth when census boundaries change. *Int. J. Geogr. Inf. Sci.* 23:859–876. <http://dx.doi.org/10.1080/13658810802359877>.
- United Nations, 2015a. World Population Prospects, United Nations. <http://dx.doi.org/10.1017/CBO9781107415324.004>.
- United Nations, 2015b. Department of Economic and Social Affairs. World Urbanization Prospects: The 2014 Revision (ST/ESA/SER.A/366).
- United States Department of Agriculture, 2017. Forest Inventory and Analysis Database. Forest Service Available at: <http://apps.fs.fed.us/fiadbdownloads/datamart.html>. Accessed on February 2017.
- United States Census Bureau, 2015. Population and Housing Units Estimate. Available on <https://www.census.gov/popest/>. Accessed on November 2016.
- Vazquez-Plass, E., Wunderle, J.M., 2013. Avian distribution along a gradient of urbanization in northeastern Puerto Rico. *Ecol. Bull.* 54, 141–156.
- Wade, A.A., Theobald, D.M., 2010. Residential development encroachment on U.S. protected areas. *Conserv. Biol.* 24:151–161. <http://dx.doi.org/10.1111/j.1523-1739.2009.01296.x>.
- Wilson, T.S., Sleeter, B.M., Davis, A.W., 2015. Potential future land use threats to California's protected areas. *Reg. Environ. Chang.* 15:1051–1064. <http://dx.doi.org/10.1007/s10113-014-0686-9>.
- Wittemyer, G., Elsen, P., Bean, W.T., Burton, C.O., Brashares, J.S., 2008. Growth at protected area edges. *Science* 321:123–126 80-. [10.1126/science.1158900](https://doi.org/10.1126/science.1158900).
- Wood, E.M., Pidgeon, A.M., Radeloff, V.C., Helmers, D.P., Culbert, P.D., Keuler, N.S., Flather, C.H., 2015. Long-term avian community response to housing development at the boundary of US protected areas: effect size increases with time. *J. Appl. Ecol.* n/a-n/a. [10.1111/1365-2664.12492](https://doi.org/10.1111/1365-2664.12492).
- Yackulic, C.B., Nichols, J.D., Reid, J., Der, R., 2015. To predict the niche, model colonization and extinction. *Ecology* 96, 16–23.
- Ye, X., Liu, G., Li, Z., Wang, H., Zeng, Y., 2015. Assessing local and surrounding threats to the protected area network in a biodiversity hotspot: The Hengduan Mountains of Southwest China. *PLoS One* 10:1–19. <http://dx.doi.org/10.1371/journal.pone.0138533>.