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Original Research Article

Conservation planning for island nations: Using a network analysis model to find novel opportunities for landscape connectivity in Puerto Rico

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ABSTRACT

Oceanic islands are important habitats for many endemic species. Global conservation assessments, however, are too coarse to characterize areas of high human influence or landscape connectivity at a resolution that is useful for conservation planning on most islands. Our goal was to identify landscape elements that are essential for the maintenance of structural connectivity among natural habitat patches on islands. Using the Caribbean island of Puerto Rico as a case study, our specific objectives were to: (1) develop a map of the human footprint, and (2) characterize the connectivity of patches exhibiting low human modification that structurally connect the island's ecological network. We used the human footprint as a measure of impediments to connectivity among Puerto Rico's natural areas using network analysis. We found that more than half of Puerto Rico's current land surface had a low human footprint (56%), but that coastal areas were highly affected by human use (82%). Puerto Rico possesses a compact network of natural areas, with a few patches in the interior mountains critical to structural connectivity. The number of isolated patches is very high; more than 60% of the patches were 2000 m or more apart. Identifying sites that are key hubs to connectivity on islands and ensuring they remain undeveloped is one strategy to balance land use and conservation, and to facilitate the persistence of endemic species. We show here how to improve general conservation assessment methods to be more relevant for islands. There is potential to support an interconnected network of natural areas that promotes landscape connectivity in Puerto Rico among non-coastal habitats, because the human activities are concentrated along the coast whereas the interior mountain range has a relatively low human footprint.

1. Introduction

Mitigating the effect of human influence on ecological landscapes has become a global conservation issue (Ellis and Ramankutty, 2008). Less than a quarter of the Earth's terrestrial surface remains "wild" and 20% has been classified as semi-natural (Ellis and Ramankutty, 2008). For island nations, limited size, isolation, and high demand for natural resources all contribute to high vulnerability to human modification (Mimura et al., 2007; Vitousek et al., 1997; Wong et al., 2005).

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Although occupying only 5% of the global land area, islands are priorities for conservation because of their high levels of endemism, the small population sizes of many island species, and diverse functional traits found among many island species (Borges et al., 2018; Kier et al., 2009). Thus, it is important to identify areas of high conservation value within islands given their significance for global biodiversity and vulnerability to anthropogenic modification. Understanding the current extent, intensity and spatial pattern of human activities, which typically degrade the conservation value of patches to varying degrees, is key to this process.

Human footprint maps, *i.e.*, standardized efforts that synthesize multiple anthropogenic threats to biodiversity, have been developed at regional (González-Abraham et al., 2015; Leu et al., 2008; Tapia-Armijos et al., 2017; Woolmer et al., 2008) and global scales (Geldmann et al., 2014; Sanderson et al., 2002). Unfortunately, however, the resolution of these maps is in most cases too coarse to capture patterns of the human footprint within islands, and there are few examples of human footprint maps developed specifically for islands. The question is how to derive human footprint maps at a scale suitable for conservation planning and management on islands.

In addition to mapping the human footprint, characterizing landscape connectivity is important for conservation planning to identify barriers to the movement of organisms or processes among habitat patches (Taylor et al., 1993; Crooks and Sanjayan, 2006; Dobson et al., 1999; Margules and Pressey, 2000; Mitchell et al., 2013). In particular, measures of connectivity based on graph-theory, such as network models, provide a strong framework for evaluating multiple aspects of habitat connectivity (Pascual et al., 2007; Urban and Keitt, 2001), ranging from simple patch and landscape structural indices to more complex spatially explicit metapopulations (Calabrese and Fagan, 2004; Rojas et al., 2016; Rozenfeld et al., 2008). There are few connectivity assessments of islands (but see Zhang and Wang, 2006), and it is unclear if islands have landscape patterns that either uniquely foster or hinder connectivity.

Ecological networks, defined here as a set of spatially linked patches that are relatively uninfluenced by humans, have been the focus of conservation actions around the world aimed at increasing landscape connectivity to conserve biodiversity and other ecosystem functions (Biondi et al., 2012; Damschen et al., 2019; Hermoso et al., 2018). Network topology, the physical configuration of patches connected by links in a network, is an emergent property which stems from features such as the total network area, patch quality, patch density, and permeability of the matrix (Opdam et al., 2006). Network topology can help to predict the spread of information and disease, vulnerability to disturbance, and stability of a system (Albert and Barabási, 2002; Gastner and Newman, 2006; Melian and Bascompte, 2002). Network analysis has revealed overlooked patterns of resource partitioning for certain species (Araújo et al., 2008), helped disentangle the effects of habitat loss and fragmentation across multiple scales (Dilts et al., 2016), and helped to identify the spatial decision-making patterns of loggers in the Amazon basin (Walker et al., 2013). Conservation plans for islands could benefit from network analysis for efficient characterization of landscape connectivity. Further, network analysis can easily incorporate more information as it become available for a given species or a process of interest (Dale and Fortin, 2010; Rayfield et al., 2011; Urban et al., 2009).

The goal of this study was to identify those landscape elements that are essential for the maintenance of structural connectivity within a matrix of anthropogenic threats, to serve as resource for landscape conservation planning. Specifically, we aimed to 1) map the human footprint at a scale relevant to management (*i.e.* 30-m resolution), and 2) characterize the connectivity of patches with low human modification that structurally connect the island's ecological network. We used Puerto Rico, an island territory of the United States located in the Greater Antilles archipelago, as a case study.

2. Methods

2.1. Study area

Puerto Rico is an 8,900 km^2 island territory of the USA, one of more than thirty island nations or territories located in the Caribbean (Fig. 1). With a population of 3,725,789, Puerto Rico is densely settled (~438 persons/km^2) (United States Census Bureau, 2010), although it has seen a rapid population decline since 2005 (around 20% of the total population, Makoff and Setser, 2017; Meléndez and Hinojosa, 2017)

Altitude ranges from sea level to 1300 m, annual temperatures range from 19.4 °C to 29.7 °C, and precipitation ranges from 701 mm to 4,598 m (Daly et al., 2003). The island features diverse geology and topography, which is expressed as three major physiographic regions: coastal and interior plains, hills and central range, and the Luquillo mountain range (Fig. 1). Land cover in Puerto Rico is dominated by forests (39%) and grasslands (32%) with 11% of the area classified as urban with a high level of urban sprawl, the rest is composed of a mix of cultivated land, scrub/shrub, wetlands and shoreline (Gould et al., 2008; Wang et al., 2016). Protected areas occupy 16% of the total land surface (Caribbean Landscape Conservation Cooperative, 2016). The island supports about 3,100 plant species (more than 250 endemics and up to 300 naturalized exotics) and 378 terrestrial vertebrate species (14 endemic bird species, 15 endemic amphibians, 70 endemic reptiles)(R. Joglar, 2005; R. L. Joglar et al., 2007; Miller and Lugo, 2009).

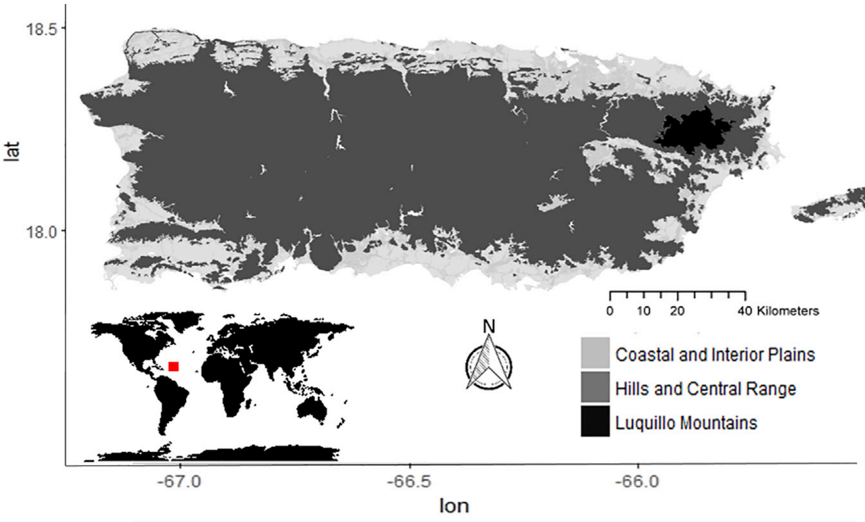

Fig. 1. Puerto Rico, one of more than thirty island nations or territories located in the Caribbean (red square), has three major physiographic regions: Coastal and Interior plains, Hills and central mountain range and the Luquillo Mountains. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2. *Human footprint model*

2.2.1. *Datasets*

We selected ten spatial datasets to create a map the human footprint, within the broad categories of land use, human access, and electrical infrastructure (Table 1).

2.2.2. *Variable scoring for human footprint*

We assigned a score from 0 to 1 to each variable, representing irreversibility of habitat modification (Table 2). A score of 0 indicates no documented modification and a score of 1 indicates severe human modification and irreversibility. For example, the conversion of a forest patch to pasturelands alters species composition and soil attributes, however, some ecosystem functionality is retained or is restorable (Shimamoto et al., 2018). Therefore, pasturelands were assigned a lower human modification score than urbanized areas, but a higher score than forests (González-Abraham et al., 2015). Our scores were based on published studies relevant to Puerto Rico and followed the scoring system used in other studies (Etter et al., 2011; González-Abraham et al., 2015; Sanderson et al., 2002; Theobald, 2013; Woolmer et al., 2008)

2.2.2.1. Land cover. We simplified the 13-class land cover classification scheme to five classes (Table 2): Mixed primary and secondary forests, wetlands, scrub, shrubs and shoreline, grasslands, and cultivated lands (pastures and agriculture). We eliminated: “Open Water” and “Natural Barrens” (represented <0.4% of the island’s area or 3,576 ha). The latter included Rocky cliffs and shelves, Gravel beaches and stony shoreline, Fine to coarse sandy beaches, mixed sand and gravel beaches, Salt and mudflats, and they were included in the “shore” category.

Puerto Rico’s landscape has experienced rapid land cover change during the 20th century (Helmer, 2004). The landscape underwent a 64% reduction in agricultural lands between 1977 and 1992 and these areas mostly reverted to mixed secondary forests. Some of the former agricultural land has converted to pasture (48,000 ha) or urban/developed lands (~7,300 ha) (Helmer, 2004). While some pasturelands have also reverted back to secondary forest in the past decades (a total of 64,000ha)(Helmer, 2004). We did not assign specific values to protected areas because we also wanted to capture human modification within their boundaries.

Grassland cover represents a mix of active or abandoned pastures that are is actively maintained by intentional fire and grazing. Other land covers influenced by humans include shrub and scrublands, which have been recently abandoned or are described as marginally active and semi-active pastures. Wetlands are a natural land cover on the island, but when they are not flooded, they are used for grazing or hay cultivation, and some wetlands develop on disturbed saline swamplands. Most shore land is subject to artificial maintenance and periodically flooded (Gould et al., 2008).

2.2.2.2. Dams. Dams can prevent the migration of riverine species (e.g. shrimp), between freshwater and saltwater (Holmquist et al., 2008; Ligon et al., 1995; March et al., 2003). In Puerto Rico’s freshwater ecosystems, even low-head structures on inland streams were found to decrease connectivity for aquatic species (Cooney and Kwak, 2013). To characterize both downstream and upstream effects, we assigned scores at two levels: at the dam site and at the watershed level. We

Table 1
Variables, data sources and spatial resolution or scale of data used in the creation of the human footprint index for Puerto Rico.

Category	Variable	Source	Spatial resolution or scale of data
Land Use	Land cover:	NOAA's Coastal Change Analysis program. High-Resolution Land Cover Classification scheme	30 m grid
	Dams	US Army Corps of Engineers National Inventory of Dams. (2013).	Point vector layer
	Watersheds	United States Geological Survey Watershed Boundary Dataset. 2014	Generally developed at 1:24,000/ 1:12,000 scale
	Mines (Open)	Mineral Resources Data System (MRDS): U.S. Geological Survey Digital Data. 2005	Point vector layer
Access			
Electrical Power Infrastructure	Roads	USA: Census –Tiger/Line Files. 2010	1:100000
	Railways	Puerto Rico Transportation and Roads Authority	Line vector layer
		Puerto Rico Planning Board	Point vector layer

Table 2
Impervious surfaces and reservoir volume density scores of human modification for each variable used in the analysis.

Variable	Class	Score
Land cover	Mixed Forests	0
	Wetlands	0.1
	Scrub/Shrub/Shore	0.3
	Grasslands and Herbaceous	0.5
	Cultivated/Pastures, Hay	0.6
Developed land	Impervious	1
	Open developed spaces	0.7
Dams (Volume of water/land area)		
	$\geq$ 310409 m^3/km^2	0.3
	14239–310409 m3/km2	0.2
	< 14239 m3/km2	0.1

defined large dams as either a) $\geq$15 m high from the lowest foundation to the crest, spillway discharge of >2000 m^3, or b) having a reservoir volume of >1000 000 m^3; Clarke 2000). We defined the zone of influence of each dam to be a circle with a diameter equal to the dam's crest length plus 100 m to account for any spatial inaccuracies of the data, following Woolmer et al. (2008). All dam locations were assigned the highest modification score of 1. To assess the influence of large dams at the watershed level, we calculated the reservoir volume (m^3) per area (km^2) for each watershed influenced by a dam, and using the distribution of values for volume/area, we assigned a human modification score for entire watersheds designating the top 75% of volume/km^2 as 0.5, the median volume/km^2 as 0.3, and the lowest 25% received a score of 1, following the approach developed by WWF-Canada (2003) and implemented by Woolmer et al. (2008). Watersheds without dams were given a score of 0 (Table 2).

2.2.2.3. Impervious surfaces. Urban development has especially long-lasting ecological consequences (Blair, 2004; Hansen et al., 2005). We used land cover data to identify impervious surfaces and open developed spaces (Table 2). Open-developed spaces have a mixture of constructed materials, and managed vegetation such as parks or gardens.

2.2.2.4. Roads and railways. Compared to Australia (11 km/km^2) or Netherlands (331 km/km^2), Puerto Rico's road network is very dense (301 km/km^2). Roads fragment landscapes affecting wildlife demography and water quality, promote spread of invasive species, and limit accessibility to natural areas (Fahrig and Rytwinski, 2009; Forman and Alexander, 1998). In tropical dry forests, roads alter sediment production and run-off. Even when a relatively small percentage of the land in dry forests are disturbed, there's an increase in run-off and sediment delivery to into coastal waters (Ramos-Scharrón & Thomaz, 2017).

We divided the roads into primary (highways, expressways) and secondary (local) roads. We set the maximum human modification score for primary roads at 1, and a maximum score for secondary roads at 0.8, and assigned incrementally lower modification scores with increasing distance from roads, out to 1000 m (Table 3). Similarly, we assigned a modification score that declined with distance from railways, out to 500 m, following Woolmer et al. (2008). The basis for the buffer values follow a "road-effect zone" based on common ecological effects extending different distances from a road (Forman and Alexander, 1998). Given that we could not find specific studies on effect zones for roads in PR, we assumed that there are road effect even at >500m as previous studies have demonstrated that roads lead to contagious development (Ibisch et al., 2016). While the linear decay rate followed the methodology established in the re-scaled Global Human Footprint analysis by Woolmer et al., (2008). We believe that we were able to capture road density influence when two road buffer zones overlap within a pixel, these scores are not additive, using Theobald, 2013 fuzzy algebraic sum we aimed to reduce errors due to partial dependence between layers (i.e., road buffers) that can coincide in the same pixel.

Table 3
Human modification scores for each infrastructure variable used in the analysis.

Variable	0–10 m	11–90 m	91–500 m	501–1000 m
Roads				
Primary	1	0.8	0.6	0.4
Secondary	0.8	0.6	0.4	0.2
Railways	0.6	0.4	0	0
Mines				
Active	0.5	0.3	0.1	0
Inactive	0.3	0.1	0	0
Electrical Power				
Power Stations	1	0.6	0.2	0.1
Substations	0.3	0.2	0.1	0

2.2.2.5. Mines. Sand extraction is common in Puerto Rico (Orris and Carbonaro, 1992; Rodriguez, 2017). We distinguished active from inactive mines assigned scores following the same decay function used for roads, with a score of 0.5 for active mines and a maximum score of 0.3 for inactive mines (Table 3).

Power Plants and Electrical substations.

We divided Puerto Rico's electrical power infrastructure into two categories: main power plants (score of 1) and electrical substations (0.3) (Table 3), with a distance decay function with distance. Although transmission line data was available, the majority of the electric lines ran parallel to the roads, thus we decided to exclude these from the analysis.

2.3. Human footprint calculation

We used a "fuzzy algebraic sum" to calculate the human footprint in Puerto Rico (Bonham-Carter, 1992; Theobald, 2013), and to address the issue of non-independence among variables. The overall value of human modification H_i at each cell i is calculated as:

$$H_i = 1 - \prod_{j=1}^{k} (1 - h_j)$$

where h_j is the human modification score of each layer ($j = 1 \dots k$), with values ranging from zero to one.

2.3.1. Level of agreement between the global HF and our final HF model

Lastly, we compared the 1 km^2 resolution global human footprint map developed by Sanderson et al., (2002) with our HF map by calculating a Kappa statistic as a degree of agreement of scores between the two maps. This analysis was based on a sample of 1,669 random points with a minimum distance of one km (a total of 8.7% of the Global HF map of the island).

2.4. Network datasets

2.4.1. Landscape representation patches

We characterized structural connectivity using attributes from both patches (habitat area and human modification score) and links (see section 3.1.2 below for description). We considered patches with >25 ha area and with a human footprint ranging from 0 to 0.3 as high quality. We selected the patch size based on the average home range sizes of IUCN red-listed species and species of concern from the Puerto Rico GAP analysis (Gould et al., 2008) (Table 4). We used Core Mapper within Gnarly Landscape Utilities in ArcGIS 10.3 (http://www.circuitscape.org/gnarly-landscape-utilities; accessed 30 March 2018) to calculate the average habitat value within a 25-ha circular moving window. The resulting habitat patch layer contained 352 patches with a total area of 3,121 km^2 (35% of the total land surface; protected areas represented 16% of the area of these patches).

2.4.1.1. Links by resistance distance. We used the HF map layer as a cost surface to model pair-wise connectivity between all patches. This layer represents landscape resistance to movement from 0 (no resistance) to 1 (maximum resistance). We used Circuitscape to create the cost surface layer using an eight neighbor rule (McRae et al., 2008).

2.4.2. Network construction

We converted the set of connected patches and their pair-wise resistance values into an adjacency matrix, in which connections present between two patches represented the total resistance distance between zero and one. The network was constructed and analyzed using the "igraph" package in R (Csardi and Nepusz, 2006). Finally, we removed links between patches with >0.6 resistance distance.

Table 4
Several native species average home range (ha) and maximum daily movement recorded in literature.

Species	Average home range (ha)	Maximum daily movement (m)	Reference
Yellow shouldered blackbird (*Angelaius xanthomus*)	256	10,000	Post, 1981; Post, 2020
Puerto Rican Amazon (*Amazona vittata*)	22	2,058	Lindsay et al., 1991; Snyder et al., 1987
Puerto Rican Nightjar (*Anthrostomus noctitherus*)	5.2	360	Vilella, 1995; Vilella , 2010
Puerto Rican Boa (*Epicrates inornatus*)	11	26	Puente-Rolón and Bird-Picó, 2004; Wunderle et al., 2004
Various frog species *Eleuctherodactylus spp.*	0.0005	5	Woolbright, 1985; Ovaska, 1992

2.4.2.1. Links by euclidian distance. We built five additional adjacency matrices to construct networks with various dispersal distance thresholds for hypothetical species (from 300 to 2600 m, in 600m steps). We selected the specific distances based on home range sizes of five species prioritized on the IUCN red list and Puerto Rico GAP analysis (Gould et al., 2008) (Table 4). Centroid-to-centroid Euclidian distances between habitat patches were calculated using SDM toolbox GIS extension for ArcGIS 10.3 (www.sdmtoolbox.org/data/sdmtoolbox/; accessed April 15, 2018).

2.4.3. Network analysis

2.4.3.1. Network parameters. We quantified several route-specific properties of network connectivity, including flux, redundancy, and vulnerability (Rayfield et al., 2011) as well as network resilience (Table 5). Within the island's network, "components" refer to subsets of patches that are structurally connected to each other, but are disconnected from other subsets in the network. For this study, the network metrics dealing with "distance" refer to the number of links or paths needed to reach any two patches in the network. Redundancy refers to the presence of multiple or alternate potential movement routes among habitat patches. Route vulnerability captures the stability of the network, and the degree to which the landscape structure funnels movement.

2.4.3.2. Network topology. We evaluated network topology by comparing the actual network in Puerto Rico to a null model derived from 10,000 networks with the same number of patches and links that were randomly arranged (see Table 5 for metrics). We fitted the connectivity distribution and the clustering coefficient distribution of each network to a power law (M. Newman, 2005). This processing was done using package "igraph" in R.

2.4.3.3. Assessing network resilience. We wanted to investigate how the connectivity of the network changed as patches were removed to reveal the network's robustness to patch loss. Thus, we quantified the effects of patch removal following the principles of percolation theory (Stauffer and Aharony, 1994). In particular, we assessed the fraction of patches that could be removed before the largest component disintegrated into smaller components (*i.e.*, network contained 50% or less of its original patches, or reached zero components (Franceschet, 2012; M. E. J. Newman, 2010; Stauffer, 1987). We progressively removed patches using three strategies: 1) in decreasing order from most connected to least connected, 2) random, and 3) in decreasing order of patch area size.

3. Results

3.1. Human footprint in Puerto Rico

Our human footprint map for Puerto Rico provides a spatially detailed view of current human influences on the island (Fig. 2). More than half of the island's area (56%) has very low or low human footprint (HF class < 0.3) and highest HF areas (> 0.5) are concentrated around main roads, cities, and coastal areas.

While most of Puerto Rico has a very low and low human footprint (55% of the area), there were far more patches in the highest HF class than the lowest class (16,787 versus 4,344 for in the lowest HF class), indicating fragmentation in areas where human activities are concentrated (Table 6).

3.1.1. Local HF index comparison with global HF
Our HF map and the 1 km resolution Global HF developed by Sanderson et al. (2002) were spatially distinct (unweighted Kappa Index of 0.21 (CI $=$ 0.19–0.23; SE $=$ 0.007) on a scale of -1 to 1, with 1 indicating perfect agreement, 0 indicating what would be expected by chance and a negative value indicating disagreement. In our visual assessment, the influence of roads and dense urban areas were well represented in the Global HF, but it overlooked the heterogeneity of human influence that

Table 5
Topological network-level measures (Adapted from Rayfield et al., 2011 and references within; Minor and Urban, 2008).

Connectivity Property	Metrics	Definition	Ecological Relevance
Route-specific flux	Degree Distribution	Probability distribution of patch degrees (connections) over the entire network. P(k)	Distribution of potential source and sink habitat patches.
	Network order (Number of Patches *N*)	Total number of patches within network	Number of habitat patches in the habitat network
	Network size (Number of Connections *k*)	Total number of links within network	Number of pairs of directly connected habitat patches
	Number of components	Total number of groups of structurally connected patches and links	Number of distinct, unconnected groups of habitat patches. Spatially isolated components
	Average shortest path length (characteristic path length)	Average length of the shortest path connecting patch pairs. Implies efficiency of movement within a network. This metric requires discovering all possible paths between patches *i* and *j*, and then finding the shortest path length (l_{ij}). Note that length refers to the number of links or paths between any two patches.	When short (<6 steps; Travers & Milgram, 1969), all patches tend to be easily reachable. Could imply a patchy landscape rather than a hierarchical organization.
	Diameter (component level) and size of largest component (network level)	Measures the greatest distance of a path between any pair of patches in the network. Can be interpreted as the easiness of an organism to functionally reach all other patches in the network.	Indicates the compactness of a component, short diameter implies fast movement through the network.
Route Redundancy	Clustering Coefficient	Measures the average fraction of the patch's neighbors that are also neighbors with each other.	A high clustering coefficient can facilitate dispersal among patches and more resilient to patch removal
Route Vulnerability	Connectivity Correlation	Measures the relationship between average connections of a focal patch relative to the average number of connections of its neighbors	High values can indicate a presence of sub-networks. Sub-networks (compartmentalization) tend to reduce the spread of a surging disturbance
Resilience	Iterative removal of patches based on three percolation strategies: random, area, degree	Number of patches whose removal disconnects the largest component of the network	Simulates the overall connectivity of the network and relative importance of habitat patches when they are destroyed

was apparent at a finer scale. Overall, the Global HF underestimates the amount of the most natural areas and overestimates the amount of human modification (Fig. 3).

3.1.2. *Spatial patterns of anthropogenic impacts*

The three main physiographic regions of the island differ in the degree of human impact experienced (Fig. 4). Puerto Rico has higher human footprint scores in the coastal and plain areas than in the interior mountains. In total, 82% of the coastal region fell within medium to high HF classes.

3.2. *Puerto Rico ecological network*

3.2.1. *Network topology*

We used Puerto Rico's human footprint model to define a landscape ecological network. A total of 152 patches and 481 links were present, organized in a theoretical scale-free network ($R^2 = 0.95$). Such networks are distinguished by having a few highly connected patches ('hubs') and many patches with few connections (Barabási and Albert, 1999). We found that PR's network contained 33 densely connected groups ($Q = 0.47$; Newman 2006) ranging 1 to 42 patches ($x = 4$). The network had one major hub (Area = 73 km^2) in the central northwest of the island between the municipalities of Arecibo and Utuado (18.343511, −66.749858) which had the most links (31 or 6%).

3.2.2. *Network parameters*

We compared network parameters between PR ecological network and a simulated random network (Table 7) and found several differences. The clustering coefficient for the PR network was threefold that of the random network, and the connectivity correlation was positive in PR's network but negative in the random network. These characteristics imply that there are tight clusters and a few patches with a disproportionate number of connections, specifically in the central northwestern Karst region of the island.

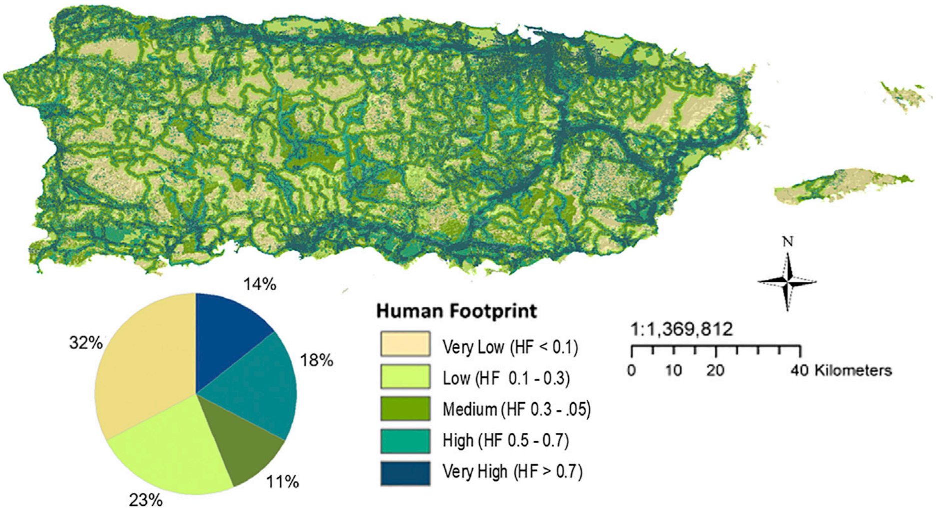

Fig. 2. The human footprint in Puerto Rico. The highest human footprint scores (blue colors) are near main roads, coastal areas, and densely populated municipalities. The areas in beige represent the lowest values of human footprint. High and very high categories covered 32% of the island, while the two lowest categories covered 55%. The totals do not add to 100% due to rounding. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 6
Total number of patches and their proportion in the island of Puerto Rico per human footprint category.

Value	Numbers of Patches	Proportion in landscape
Low (0–0.3)	4,344	**0.55**
Med (>0.3–0.7)	15,271	0.13
High (>0.7–1)	**16,787**	0.32

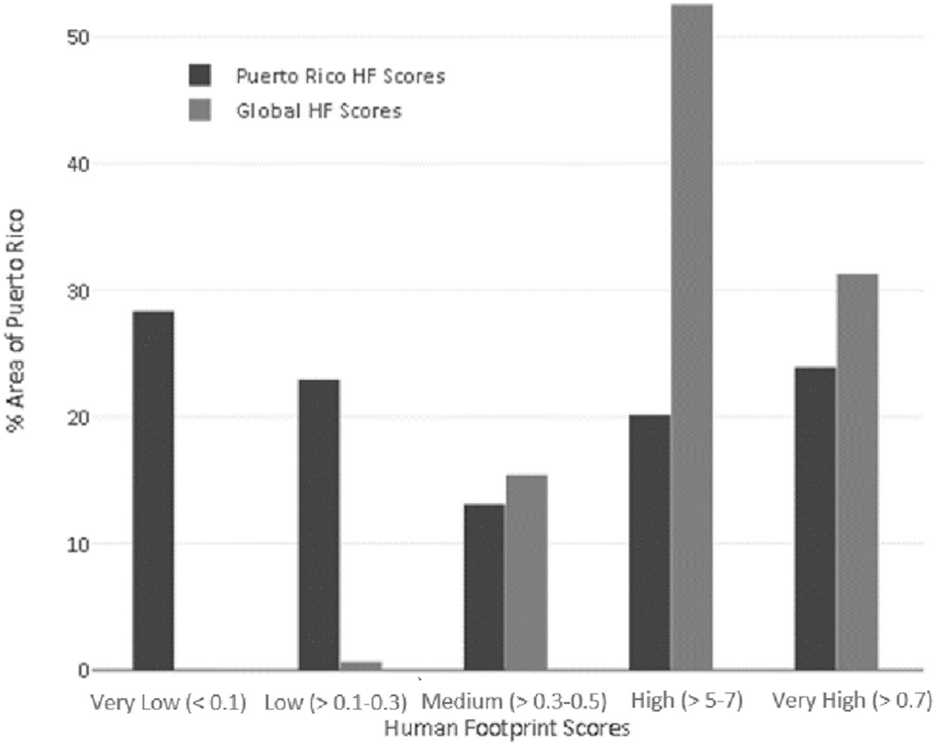

Fig. 3. Human footprint scores based on our model (black columns) compared to the global HF model (gray columns).

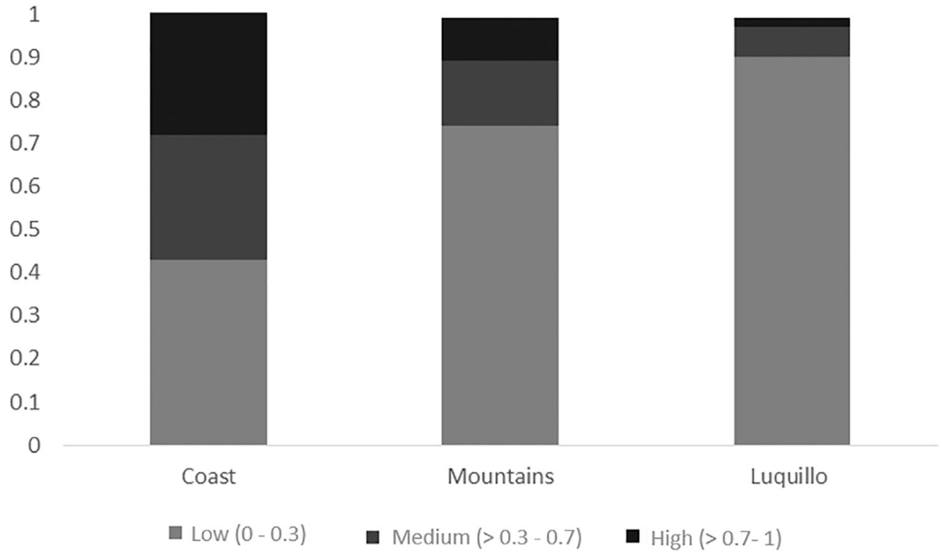

Fig. 4. Proportion of land with low, medium, and high human impact according to our HF model, within the three broad physiographic regions in Puerto Rico: Coast, Central Mountains, and Luquillo mountains.

The values for number of components, size of the largest component, and diameter, along with clustering coefficient and connectivity correlation suggest that the PR network is more compact than random, however, the average shortest path length was larger in the PR network. Thus, the random network had a higher number of short paths between patches. Since size of the largest component is related to the diameter, a better way to compare size of the network is to calculate the ratio of the size to diameter for the largest component. Both networks had the same ratio of 0.5. The random network's average shortest path length was shorter (<2.5) even though it had the largest component, compared to PR network's average shortest path length, which was relatively short (3.4). Both numbers are characteristic of a highly compact network in which hypothetical individuals would potentially interact with others through a path of <3 links even though patches were spread over a large area.

We further explored how the number of connections for each patch were distributed compared to a simulated random network. We found that PR's network displayed a skewed distribution (skewness = 1.07; Fig. 6), indicating a complex network, and supporting our finding for a scale-free network in which there are relatively few, but very well connected patches (M. E. J. Newman, 2003).

Finally, we examined connectivity correlation of the PR network, by calculating the mean patch degree of neighbors connected to a patch of k connections (Fig. 7). For our simulated random network, there was no relationship between number of patch connections and the mean number of connections of a patch's neighbors, and all patches in the random network were accessible. In contrast, PR's network had a positive relationship ($r = 0.29$) in which patches with the greatest number of connections tended to have neighbors with more connections.

3.2.3. *Distance thresholds and patch area*

Most patches within the PR network were connected. Unconstrained by distance, only 15% of the patches were completely isolated ($k = 0$), all them in the coastal region. However, when accounting for dispersal threshold distances, 98% of patches were isolated from other patches at a maximum dispersal distance of 1000 m. Even at 2000 m, 60% were still isolated from each other (Fig. 8a). The number of components decreased as the threshold distance increased (Fig. 8b). Both the percent of isolated patches and the number of components decreased as dispersal threshold distance was increased.

3.2.4. *Network robustness*

We calculated the robustness of the PR network using three patch removal strategies. First, we quantified the effects of progressively removing the most highly connected patches, second, we removed patches randomly, and third, we progressively removed the largest patches. In the first case, when 32 (of 152, or 21%) highly connected patches were removed, 50% of all connections were lost. Under random removal of patches, 49% of patches needed to be removed to reach that threshold. When removing patches by size (area), we found that 42% of the patches in the network needed to be removed to reach the threshold.

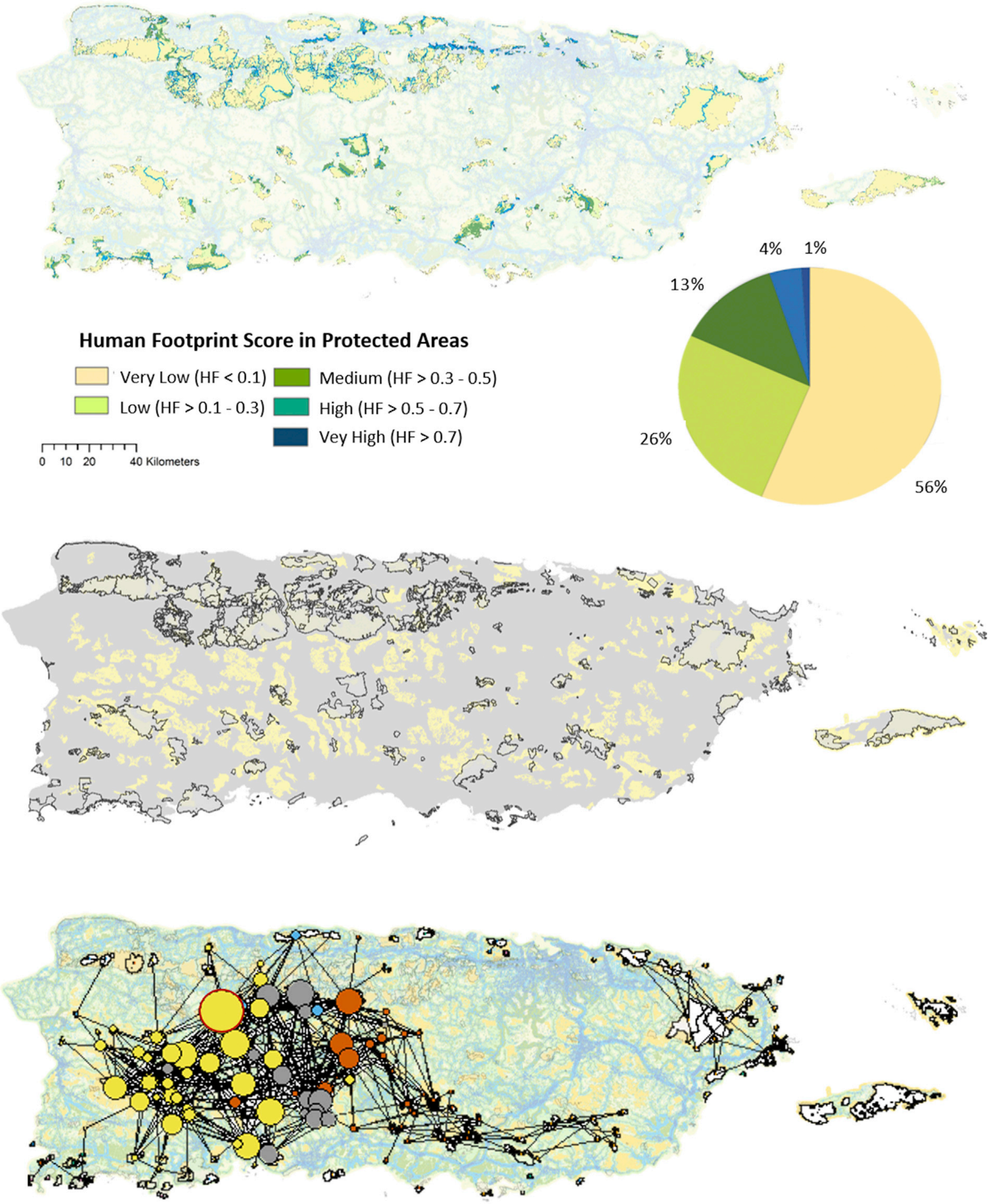

Fig. 5. Protected areas in Puerto Rico and their Human Footprint Scores (Top). Low and Very Low human modified areas accounted for 82% (1, 129.96 km^2 out of a total of 1, 378 km^2). Medium to Very High modified areas covered 18% of protected areas (248 km^2). Patches with a very low score and >25 ha (0.25 km^2) outside of protected areas (center) are scattered though the central mountainous regions and almost non-existent in coastal areas. The Puerto Rico ecological areas network (bottom). Patch size represents number of connections and patch color represents the components to which each patch belongs. The patch with the most connections, the hub, was identified as part of the Karst region in the island (delineated in red). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 7
Graph diagnostic metrics for assessing connectivity of networks.

	Puerto Rico Network	Random Network
Number of components	33	24
Size of largest component	112	129
Diameter	5.55	6
Average shortest path length	3.27	2.73
Clustering coefficient	0.25	0.09
Connectivity correlation	0.29	−0.07

4. Discussion

Our goals were to develop a human footprint map and characterize the ecological network of Puerto Rico. We found that global analysis did not capture Puerto Rico's heterogeneity, and underestimated natural areas. Our findings highlight the potential of using network analysis to reveal the spatial context and connectivity among natural habitat patches, and the need for island-specific characterization of the human footprint, rather than relying on products developed at the global scale. Further, our network model showed that Puerto Rico possesses a robust network characterized by a concentration of potential habitat patches with high connectivity values in the western mountainous region of the island. However, coastal areas are fragmented and disconnected from the main network, a cause for concern regarding conservation of littoral ecosystem processes.

4.1. Patterns of the human footprint

The spatial analysis of Puerto Rico's HF showed clear gradients in human-caused pressures among Puerto Rico's three physiographic regions. The most obvious pattern was the strong difference between the coastal and central mountain regions in terms of number and isolation of patches. Developed areas sprawled from main roads, and impervious surfaces are increasingly encroaching on the protected areas (Castro et al., 2016). Our observations agree with other studies that have shown a positive relationship between roads, human density and conversion to urban cover (e.g. Estes et al., 2012; Freitas et al., 2010; Hawbaker et al., 2005).

In coastal areas, fragmentation was high and the few areas with low human footprint score were isolated. Unfortunately, in addition to direct anthropogenic pressures, the coastal areas are also the most vulnerable to sea level rise as a consequence of climate change (Jury, 2018; Strauss and Kulp, 2018). On the other hand, most of the connected low-HF patches were concentrated in the central mountain range region. The resulting PR network has the largest component and most important hubs in a region where a multi-sectorial effort to protect 3,900 acres of diverse ecosystems has been carried out since 1999 (Ley Núm. 182 del año 2014, 2014). The PR network identified priority areas in the western karst and mountainous region that are important for conservation and landscape connectivity, and supports the current law which requires harmonizing the protection of the natural environment, while promoting sustainable development(Ley de Bosques de Puerto Rico, 1975; Ley Orgánica del Departamento de Recursos Naturales y Ambientales, 1972).

It has been argued that limiting human influence into areas of conservation value may be the most cost-effective and direct way of achieving global sustainability goals (Ibisch et al., 2016b). Our findings suggest that some unprotected land may be suitable for conservation or sustainable mixed uses in Puerto Rico. Currently, protected areas cover around 16% of the island (Caribbean Landscape Conservation Cooperative, 2016) however, our study found that very low and low HF areas cover 53% (Fig. 5). Identifying unprotected areas of conservation value is very important since unprotected secondary forests are the dominant forest type in the island (Chazdon et al., 2009). Secondary forests >20 years old in the island exhibit novel plant species assemblages and share some characteristics with mature forests in terms of structure, heterogeneity and complexity (Herrera-Montes and Brokaw, 2010) meaning that ecosystem function could recover in a relatively short period of time if human modification is limited. Further, second-growth forests will be critical spots for conserving evolutionary diversity for multiple species and assume a pivotal role in terms of carbon sequestration and carbon stocks (Chazdon, 2008; Edwards et al., 2017).

Global land-use trends in indicate that agricultural expansion takes place on fertile soils, while abandoned farmlands are most common on marginal areas with poor soils (Cramer et al., 2008). Abandoned farmlands present an opportunity for ecological restoration efforts on islands, but management of degraded landscapes is highly varied and the impacts of second-growth forest on biodiversity also varies substantially (Queiroz et al., 2014). Islands share similar histories of land use dynamics yet trajectories of forest regeneration over time are varied (Aide et al., 1995; Blondel and Médail, 2009; Chazdon, 2003). In the Caribbean island of St Croix for example, 40-year-old post-agricultural tropical dry forests that regenerated from former plantations shares similar structural characteristics but differs in species composition(Atkinson and Marín-Spiotta, 2015), a pattern similar to post-agricultural forests in Puerto Rico. In contrast, there is a wide range of responses to pastoral or agricultural abandonment in the Mediterranean islands (Médail, 2016). While agricultural abandonment has led to a general increase in matorral and second-growth forests on some Mediterranean islands, the relationship between successional processes, biodiversity, and land-management is still uncertain (Rühl and Pasta, 2007; Schaich et al., 2015). In

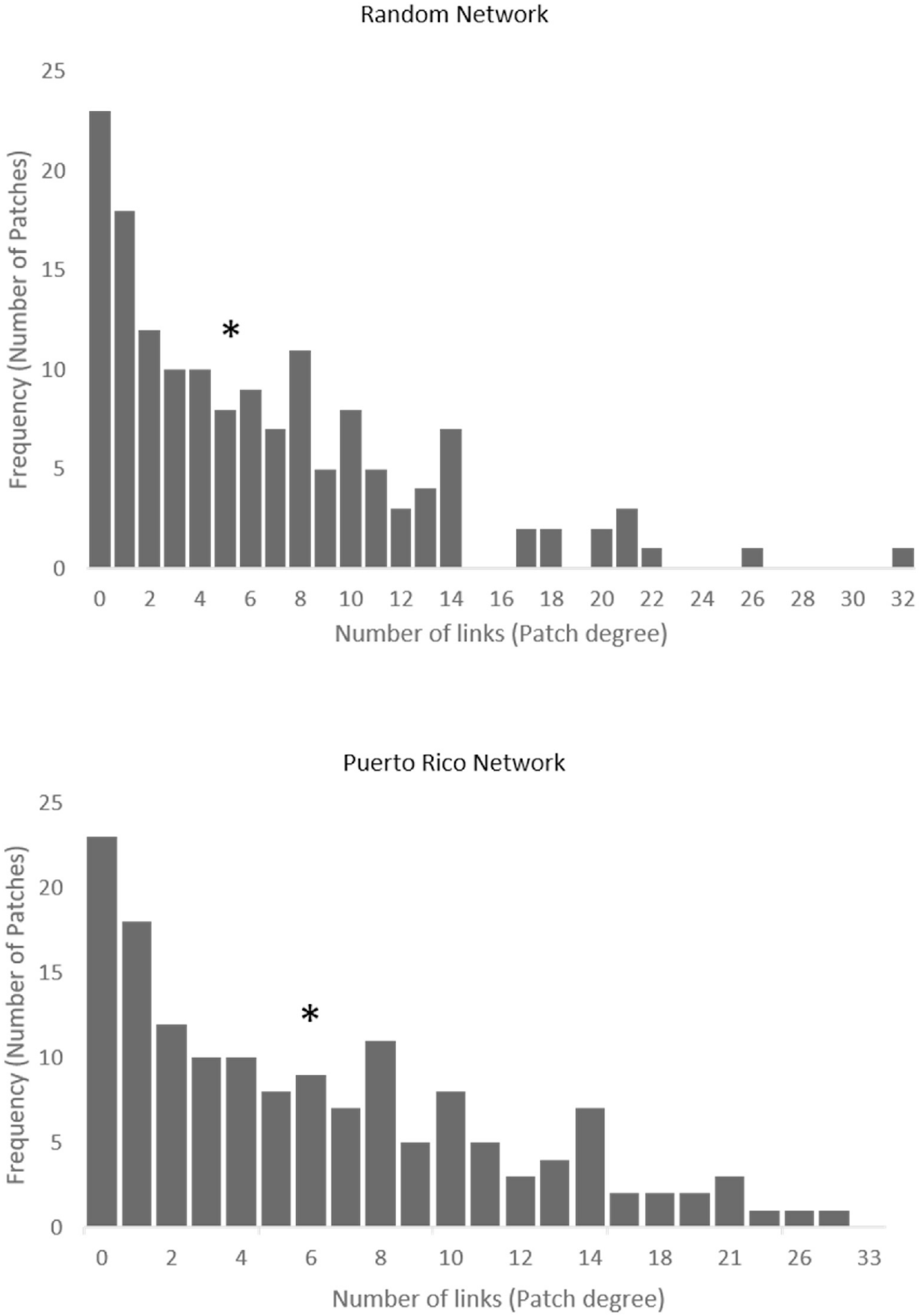

Fig. 6. Patch-degree distribution for Puerto Rico's ecological network. In this graph, there are far more patches with few a links. The distribution of patch degrees is heavily skewed to the right for both the random network (1.49) (Top), and for Puerto Rico's network (1.07) (bottom). The asterisk indicates mean patch degree.

some cases, the end of traditional agricultural land use in Mediterranean islands has led to severe soil erosion or extinction of endemic species (Médail, 2016; Petanidou et al., 2008). Although global analyses are good at capturing general trends, specific conservation problems can differ by island. In this study we have identified unprotected land areas of high conservation value.

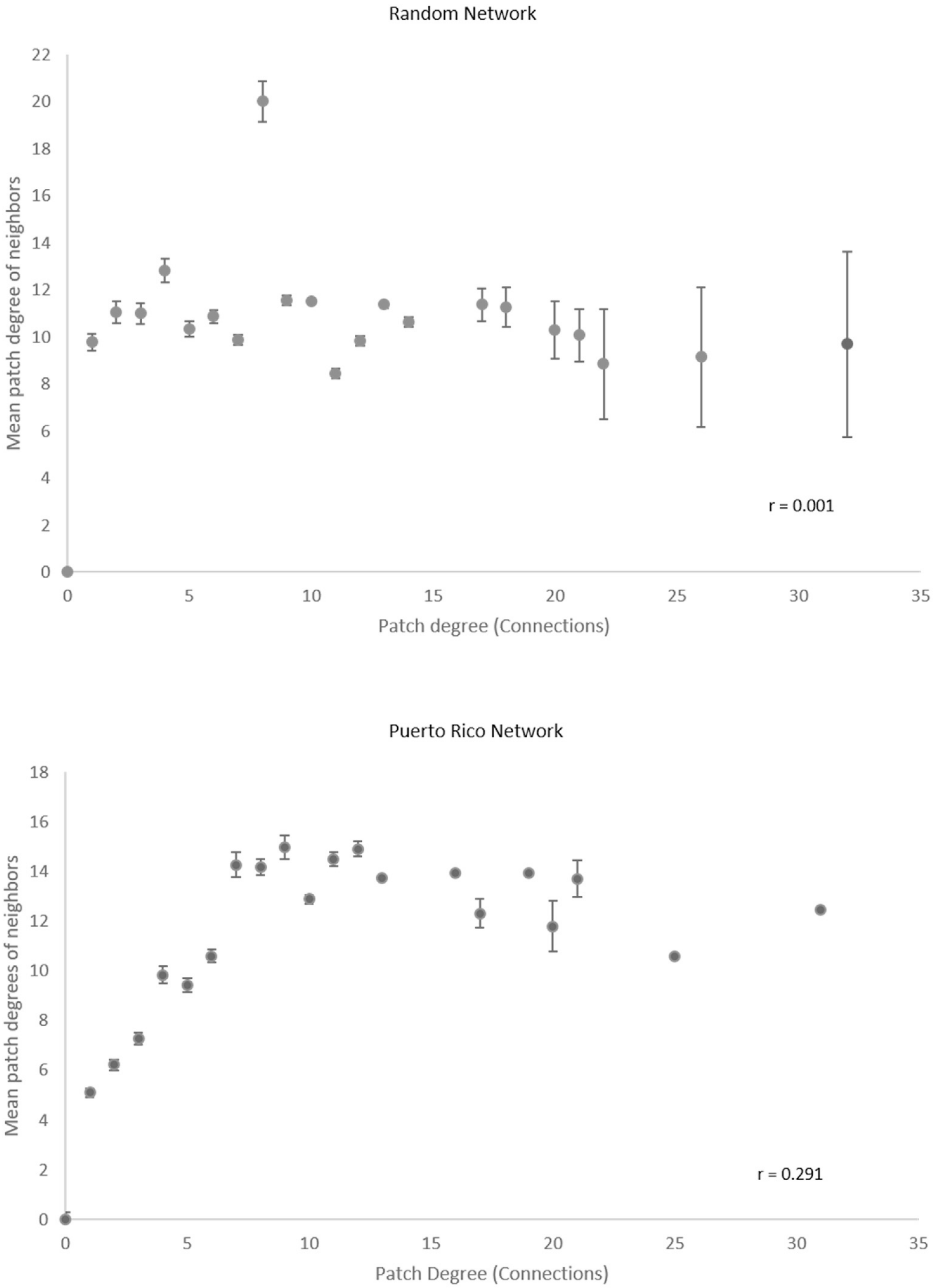

Fig. 7. Connectivity correlation for random network (top), and the Puerto Rico network (bottom). PR network had a positive relationship between mean patch degrees of neighbors and number of connections of a patch. In PR network, the higher the patch degree, the more neighbors connected to each patch. The pattern suggests that patches with a minimum of 7 or 8 connections to other patches (given our parameters) are enough to reach neighbors with the mean maximum possible of connections in the system.

For islands, balancing the trade-offs between urban development and local and global conservation goals is especially challenging. However, our characterization of human modification patterns and connectivity via network analysis provide the quantitative knowledge needed to find that balance. For example, protected area effectiveness is highly dependent on the possibility of movement through unprotected landscapes (Saura et al., 2018). That is why we included landscape context in the form of human modification scores to quantify the important areas for structural connectivity, and our approach is adaptable and hence suitable for diverse conservation goals.

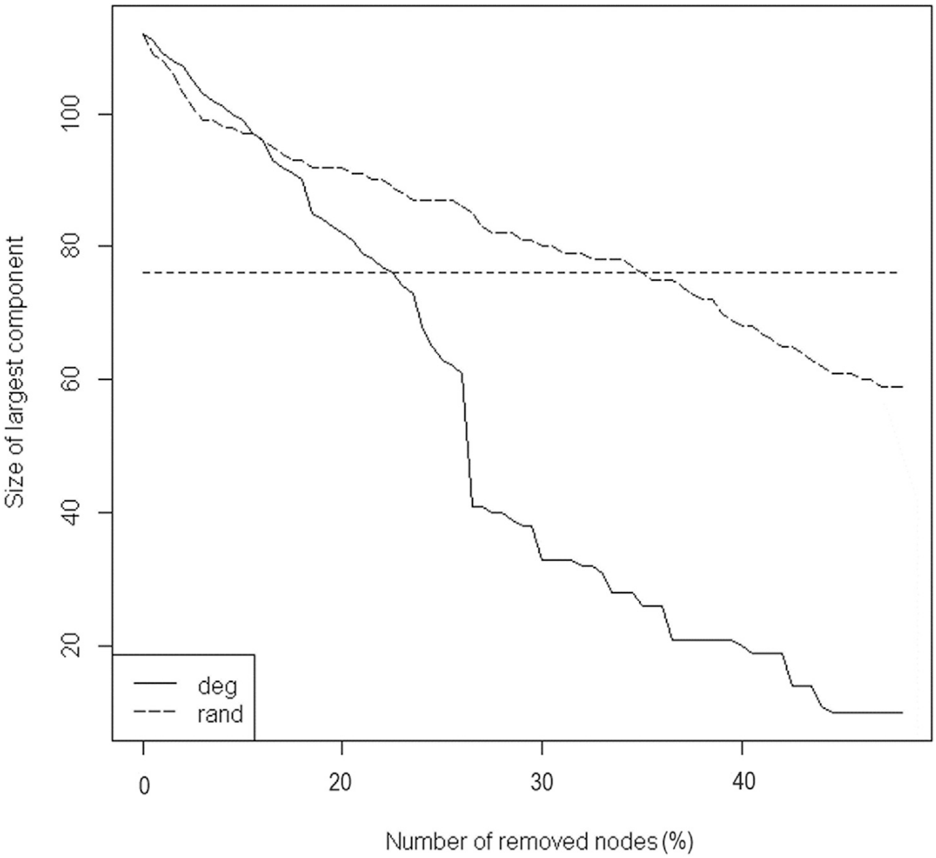

Fig. 8a. Effect of patch removal on the connectivity of the Puerto Rico ecological network. The relative size of the largest component decreases as an increasing number of patches are removed. Patches were removed according to three different percolation strategies: removal of patches with the highest number of links first (deg), random removal (rand), and by area (largest to smallest). The horizontal dashed line represents half of the total of patches in the network (n = 76).

4.2. Human footprint at the local level

Global models of the human footprint (Sanderson et al., 2002; Venter et al., 2016) are essential for understanding broad trends of human impacts in terrestrial ecosystems. However, global models are likely to be of limited use for islands as they can be incomplete. For example, most of the datasets used to build the Global HF do not consider oceanic islands which are thus excluded from global analyses. Therefore, to effectively interpret how the human footprint may influence ecological processes on oceanic islands, fine-scale island-specific data are needed. For example, our study revealed that relatively undisturbed natural areas have been underestimated by the global human footprint model, with the result that opportunities for conservation could be overlooked. Other studies have also found greater heterogeneity in fine scale models (Perkl, 2017) relative to global efforts, for example landscapes in the western United States were considered relatively undisturbed in global models but 13% of the region was covered by anthropogenic features in an analysis of fine-scale data (Leu et al., 2008). Similar to our findings for Puerto Rico, in both southern Patagonia and the Northern Appalachian Region of the USA, the global HF model underestimates the wildest areas (Inostroza et al., 2016; Woolmer et al., 2008). Overall, efforts to reassess the human footprint at greater resolution than global models are important and useful for conservation planning at the regional level.

4.3. Network topology and parameters

We found that the PR network follows the principle of preferential attachment, in which patches tend to connect to other patches that have an existing high level of connectivity (Barabási and Albert, 1999). Additionally, the PR system is highly compact in that within clusters, the majority of patches are connected to other patches via a path of <3 connections. Nevertheless, the high skewed patch-degree distribution and positive connectivity correlation highlights the fact that there are many patches with few or no links to other patches. In other words, there are key patches that hold the network together

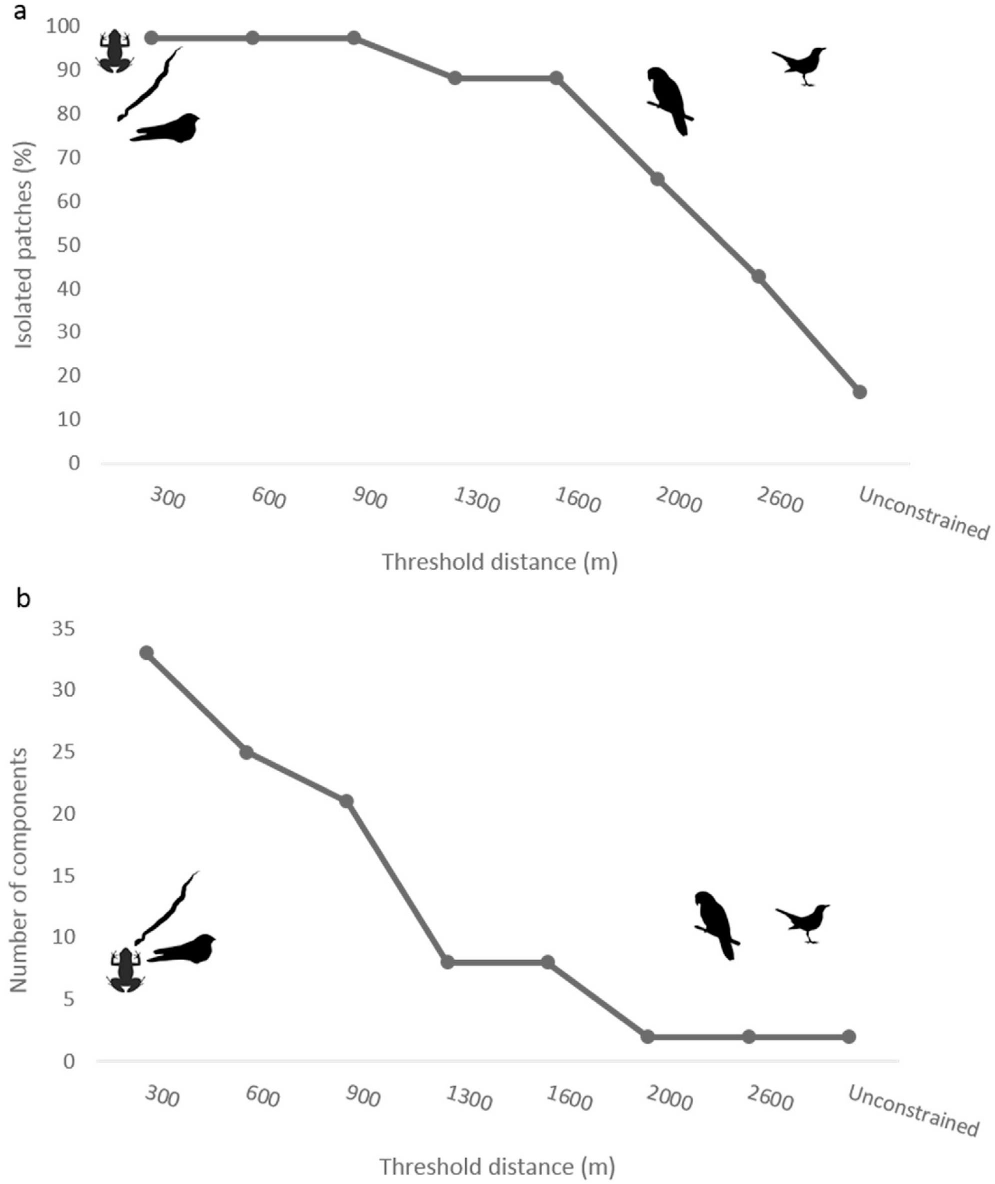

Fig. 8b. The (a) percentage of isolated patches and (b) number of components found in the PR network according to several threshold distances. Number of components included isolated patches. Five species listed in the PR-GAP analysis were used to classify threshold distances (see Table 4).

and those hubs tend to be clustered (Minor and Urban, 2008). The clustering coefficient was higher for the real PR network than for the simulated random network, indicating that there are redundant or alternative paths in the real network.

The PR network structure is attributable to the large extent of second-growth forest cover present in the western central mountain range in Puerto Rico. Prioritizing patches according to their degree of connectivity within this network can support mechanisms that promote species coexistence by facilitating colonization and promoting species' ability to survive in the aftermath of diverse disturbances (e.g. hurricanes, conversion to agriculture or pasture) (Uriarte et al., 2012). It has been shown that distance between patches influences forest recovery in Puerto Rico (Hogan et al., 2016), however in our network model, we found that only a few patches within El Yunque National Forest in the east of the island served as key hubs that provided connectivity for otherwise isolated habitat patches of the eastern coastal areas. Nevertheless, these protected areas in the east of the island are crucial for the maintenance of endemic biodiversity and for various ecosystem processes and services (Lugo, 2005), but they are in constant threat of human modification.

There are positive and negative conservation implications that emerge from a scale-free network such as the one that we found. In terms of stability or resilience, if patches were to disappear randomly, there is a high likelihood that hubs would not be affected and that overall, components would remain connected. From our analysis, it appears that the PR network could sustain a fair amount of random patch loss before overall landscape connectivity is compromised, but loss of hubs would be highly detrimental (Barabási and Bonabeau, 2003; Urban and Keitt, 2001).

4.4. Patch isolation and distance thresholds

The combination of habitat isolation, dispersal limitation and low reproduction rates of organisms exacerbates the likelihood of extinctions (Kadmon and Allouche, 2007). Our assessment of isolated patches revealed that habitat connections for species with limited dispersal ability were few and many patches were isolated. For example, there are three release sites for the captive-bred and endangered Puerto Rican parrot that differed in the degree of structural connectivity. Two of these sites, the Rio Abajo and Maricao State Forests belong to the main component of the network in the west mountainous region of the island, while the other site, El Yunque National Forest appeared isolated. Based on species dispersal distance only the parrot could reach the patches within the main the network in the western region. On the other hand, parrot dispersal is restricted on habitat patches in El Yunque that have a strong human influence in its buffer zone with only a few links connecting them to coastal habitat. These distinct spatial patterns and the fact that El Yunque is considered sub-optimal habitat for this species, are a serious consideration for the Amazon population recovery. The level of human influence in eastern Puerto Rico contribute to patch isolation and potential species movement.

4.5. Limitations

Connectivity and resistance surface models derived from naturalness indices may not contain enough information for identifying the needs of habitat specialist species. However, models of the HF are repeatable, relatively simple and further, connectivity models based on naturalness have been shown to provide a good proxy for focal species (Krosby et al., 2015). There's wide acceptance that biodiversity conservation must adopt a dynamic approach when tackling climate change, biological invasions and habitat fragmentation (Harrison et al., 2006; Willis et al., 2009). Using HF as a resistance surface for landscape connectivity models can be the first step to analyze island natural areas networks within modified landscapes and can later be complemented with analyses that focus on individual species. Further, the graph-theoric approach for connectivity presented in this study is dynamic in the sense that patch attributes are modifiable depending on the conservation objective being tested.

5. Conclusion

The main driver of biodiversity decline is human pressure on Earth's ecosystems. Island ecosystems remain disproportionally threatened by a number of anthropogenic stressors, and as a result, it is imperative to not only study the spatial arrangement of those remaining natural and semi-natural areas, but to understand the existing structural connectivity among them. The smaller geographic size of islands often means that there are many vulnerable species due to small areas of habitat, small population sizes and high endemism. Conservation and economic development goals often clash, placing unsustainable demands on resources thus leading to exploitation of natural resources and habitat modification (Graham et al., 2017). In Puerto Rico, forests in the interior mountains are subject to less human activity based on our human footprint model than coastal areas. Furthermore, patches within these forests were of utmost importance for connecting isolated coastal patches to the main network. Our analysis suggests that Puerto Rico's ecological network is likely to maintain its resilience in the face of frequent disturbances such as hurricanes, if other disturbances do not substantially alter the network. The relatively robust ecological network is in large measure attributable to agricultural abandonment and subsequent second growth forest. Other islands might exhibit a different distribution of human modification patterns given the different histories of extraction and diverse natural forces that alter their habitats (Velmurugan, 2018), however, it is plausible that an analysis of coastal habitat patches in other island nations reveal a similar pattern of patch isolation and fragmentation. We found that existing legal protections in the western mountain region of Puerto Rico were crucial for the tightly connected ecological network found and that protection of the rainforest is critical for maintaining natural areas connectivity in the eastern region. Our study provides a guide to planning and prioritizing conservation efforts based on both naturalness and importance to maintaining overall landscape connectivity, and having such analyses completed can be useful when windows of opportunity for conservation actions occur.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01075.

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