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Multi-resolution habitat models of the Puerto Rican Nightjar *Antrostromus noctitherus*

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Summary

The Puerto Rican Nightjar *Antrostomus noctitherus* is an endemic Caprimulgid found in dry coastal and lower montane forests of south-western Puerto Rico. Information on the species (e.g. abundance, nesting biology) has been mostly restricted to forest reserves (i.e. Guánica Forest and Susúa Forest) with limited information available from private lands. We collected stand-level vegetation structure and geographical information from forest reserves and private lands to model habitat suitability and distribution for the Nightjar. Results of the stand-level model indicated forest type and midstorey vegetation density best predicted Nightjar habitat. Our spatial model predicted considerably more Nightjar habitat (17,819.64 ha) located outside protected areas than previously reported. Further, the model highlighted several localities of importance for the species across southern Puerto Rico, all located within private lands. We used a patch occupancy approach to assess regions identified by the landscape-level model as suitable for the Nightjar and documented the presence of the species in 32 of 55 sites, located in 12 of 18 municipalities across southern Puerto Rico. The protection and restoration of forest across the southern coast of Puerto Rico would help to ensure the long-term persistence of the Nightjar across a considerable portion of its range. Addressing habitat needs may be the single most effective mechanism to achieve recovery of the species.

Introduction

The Caribbean islands are a priority biodiversity hotspot given the high levels of endemism and rates of habitat loss (Brooks *et al.* 2002). Approximately 26% of bird species are unique to the Caribbean islands (Anadón-Irizarry *et al.* 2012). The West Indies region has undergone centuries of anthropogenic disturbance, including major loss of native vegetation, followed by secondary growth and the introduction of numerous invasive plant and animal species (Jesse 2016). Many at-risk species in the Caribbean lack reliable information on geographical distribution, often due to their rarity (Guisan and Thuiller 2005). Consequently, this may constrain conservation solutions for the avifauna of the region (Martin *et al.* 2017). Further, the rapid turnover of private lands in Puerto Rico and other Caribbean islands to uses such as urban and tourism development may threaten other ground-nesting species in the region (del Mar López et al. 2001).

Information on abundance and distribution is often lacking for Caribbean nocturnal birds, limiting the effectiveness of conservation decisions (e.g. protected area designation). This is particularly important given recently published information recognising nocturnal birds of the Caribbean as new endemics (Chesser *et al.* 2023). The population status and geographical distribution of these newly recognised endemics, Cuban Nightjar *Antrostomus cubanensis* and Hispaniolan Nightjar *Antrostomus ekmani*, have not been thoroughly assessed and are currently considered as species of conservation concern (Wege and Anadón-Irizarry 2005).

The geographical distribution of animals provides information on ecological factors that may influence species–habitat relationships (Guisan *et al.* 2017). Conservation of rare and at-risk species poses numerous challenges for practitioners, particularly when determining whether species may need intervention (e.g. habitat management) or warrant legal protections. Many conservation challenges arise from limited available information, including poorly described habitats and geographical ranges (Rutrough *et al.* 2019).

Puerto Rican Nightjar *Antrostromus noctitherus*, hereafter termed Nightjar, is a single-island endemic mostly restricted to coastal dry and lower montane forests of south-west Puerto Rico. The Nightjar is presently listed by the Puerto Rico Department of Natural and Environmental Resources (DNER) and the US Fish and Wildlife Service (USFWS) as endangered throughout its range (García *et al.* 2005, USFWS 2023). The International Union for the Conservation of Nature (IUCN) classifies the Nightjar as “Endangered” throughout its range (BirdLife International 2023). The species was once likely distributed throughout the coastal forests of Puerto Rico (Wetmore 1927). While no relict populations exist in the northern moist karst forest region of the island, Nightjar presence is known from a number of localities in coastal dry forest and lower cordillera forest of south-western Puerto Rico (Vilella and Zwank 1993).

No systematic approach to assess Nightjar distribution has been implemented on the island. Reports of new locality records have sporadically been provided by the increasing number of resident birders on the island. Moreover, a few locality records have been obtained through *The Puerto Rico breeding bird atlas* (Castro-Prieto *et al.* 2021). Habitat models are useful tools to evaluate conservation status relative to existing landscape composition and vegetation management (Rodríguez *et al.* 2007). These models are an important tool for assessing the conservation needs of the Nightjar, particularly in private land. Herein, we present multi-resolution habitat models and assessment of geographical distribution for the Nightjar.

Methods

Study area

We surveyed Nightjars during 2006–2010 within approximately 21,878.28 ha located in the dry and moist lowland forest region of southern and south-western Puerto Rico. We concentrated efforts in three main areas: Guánica Forest, Susúa Forest, and the privately owned El Convento Natural Reserve (hereafter, El Convento) (Figure 1). The DNER Forestry Division manages Guánica and Susúa Forests. El Convento is managed by Para la Naturaleza, a division of the Puerto Rico Conservation Trust (PRCT).

Guánica Forest (17°57'56"W, 66°52'44"N), a UNESCO Biosphere Reserve, is the largest reserve of the dry karst region encompassing 4,400 ha. Land use prior to protection included subsistence agriculture, grazing, and logging (Wadsworth 1950, Murphy and Lugo 1986, Molina-Colón and Lugo 2006). Guánica Forest is located in the subtropical dry forest life zone with an average annual precipitation of 762 mm and elevations ranging from sea level to 250 m (Ewel and Whitmore 1973). Forest communities include scrub forest, deciduous forest, semi-evergreen forest, and abandoned Mahogany (*Swietenia mahogani*) and Logwood (*Haematoxylum campechianum*) plantations (Figure 1). Deciduous forest is dominated by an emerging overstorey of *Bursera simaruba* and *Terminalia buceras* and midstorey species including *Coccoloba microstachya*, *Coccoloba krugii*, and *Colubrina elliptica* (Lugo *et al.* 1978, Vilella 2008).

Susúa Forest (18°4'55"W, 66°54'19"N) comprises 1,311.49 ha (Figure 1). The reserve is located in the subtropical moist forest life zone with an average annual precipitation of 1,413 mm and elevations ranging from 80 m to 473 m. Susúa Forest is characterised by rugged topography, with ridges and slopes covered with xeric scrub similar to Guánica Forest and canopy heights ranging from 1 m to 6 m. Valleys are dominated by taller moist forest and riparian forest with trees up to 15 m in height (Kepler and Kepler 1973, Silander *et al.* 1986). Susúa Forest similarly experienced historical deforestation and disturbance from agriculture and logging. Mountain ridges and slopes are dominated by *Coccoloba microstachya*, *Machonia portoricensis*, *Ouratea litoralis*, and *Elaeodendron xylocarpum*. Riparian forest canopies are dominated by *Neolaugeria resinosa*, *Rondeletia inermis*, *Garcinia hessii*, and *Pimenta racemosa*.

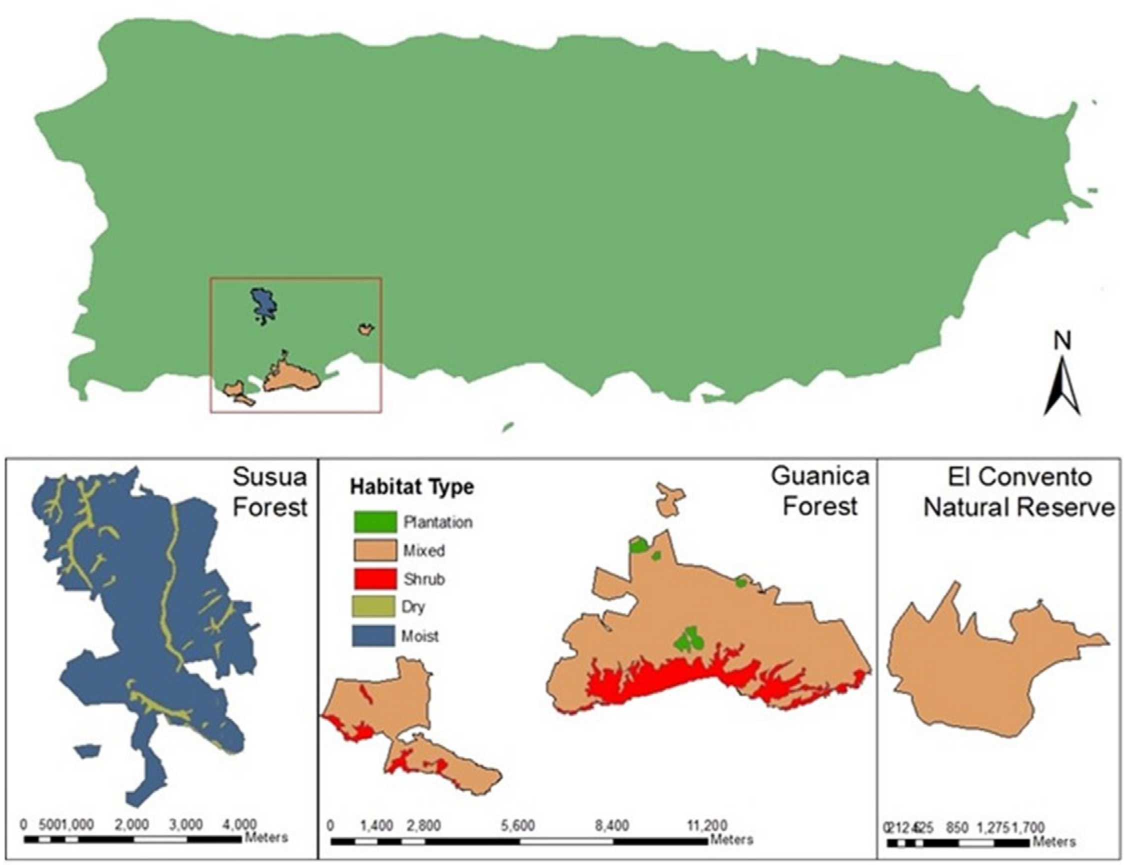

Figure 1. Map of Puerto Rico indicating the locations of study sites used for development of the Nightjar stand-level habitat model.

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El Convento (18 °2’30”N, 66 °44’44”W) is located in the municipalities of Guayanilla and Peñuelas within the dry karst region of the island’s south-west. Topography is mostly hilly with elevations ranging from sea level to 250 m and annual rainfall between 600 mm and 1,100 mm (Figure 1). In contrast to Guánica and Susúa, the region where El Convento is located includes deep karst canyons with underground rivers. Vegetation in the canyons is dominated by subtropical moist forest within the surrounding dry forest uplands (Cintrón and Beck 1977).

Dominant land use at El Convento was agriculture and grazing prior to acquisition by the PRCT. Stands of recovering secondary forest include many tree species found in Guánica Forest (Vilella and Zwank 1987). Vegetation types at El Convento include dwarf subtropical dry forest, semi-open-spiny scrubland, and semi-deciduous dry forest. Dwarf subtropical dry forest is dominated by *Pictetia aculeata*, *Bourreria succulenta*, and *Croton discolor*. The semi-open-spiny scrubland is dominated by *Ricinus communis*, *Sesbania bispinosa*, and *Prosopis juliflora*, while semi-deciduous dry forest canopies are dominated by *Guaiacum officinale*, *Comocladia dodonaea*, and *Bursera simaruba* (Cintrón and Beck 1977).

Stand-level habitat model

We collected data on the presence–absence of Nightjars, vegetation structure, and geographical characteristics within occupied range. Nightjar presence–absence was assessed using points randomly arranged along transects (González 2010). Number of transects was dictated by the availability of trails and footpaths. Points were placed every 200 m and georeferenced using a Trimble Geo-Explorer III GPS receiver. We used a game caller (Johnny Stewart Deluxe Long Range Caller Model 612-LR) for playbacks of singing Nightjars. We arrived at the survey point during crepuscular hours and, after waiting for five minutes, used playback recordings of a singing Nightjar for one minute, followed by listening for two minutes. Each survey was repeated after 20 minutes, and the presence or absence of Nightjars recorded. Surveys were conducted during clear nights at dawn and dusk for 30–45 minutes during the breeding seasons (January–June).

Vegetation sampling sites were randomly selected from locations established for Nightjar surveys (González 2010). We used a random numbers table to select direction and distance (≤75 m) from survey points. Location coordinates were georeferenced at the plot centre and elevation recorded using a Thommen© altimeter to the nearest metre. We sampled a total of 232 points along 28 routes at Guánica Forest, Susúa Forest, and El Convento. Of these, 113 points were on mixed habitat, 16 on plantation habitat, 9 on shrub, 52 on dry, and 42 on moist habitat. Nightjars were found in all five habitat types.

Overstorey was all vegetation over 2 m tall and 5 cm or greater diameter at breast height (DBH). Forest type, canopy height, and canopy closure were estimated from the plot centre. Height (m) of the tallest tree was recorded using a clinometer and canopy closure estimated using a spherical densiometer. Midstorey and understorey vegetation (vegetation <2 m tall) was sampled within a 50-m diameter plot. Tree DBH (cm) and visual obscurity (%) were estimated at 5 m and 25 m from the plot centre. Visual obscurity classes (0–0.5 m, 0.5–1.0 m, 1.0–1.5 m, and 1.5–2.0 m) were estimated using a Nudds’ board (Nudds 1977). Ground cover was sampled at the plot centre with leaf litter sampled within a 30-cm diameter circle and dry weight obtained for each sample.

We used Generalised Linear Mixed Models (GLMMs) (SAS 2008) to determine whether the number and presence–absence of Nightjars observed in Guánica Forest, Susúa Forest, and El Convento were related to geographical and vegetation variables. Nightjar data included count and binary response variables, while random variables comprised study site and trails. We used a GLMM with Poisson distribution and log-link function for the count responses, and a binomial distribution with a logit-link function for presence-absence data. Model selection was conducted using Akaike’s Information Criterion (AIC) in a stepwise algorithm using forward and backward directions (Burnham and Anderson 2002, Klavitter *et al.* 2003). We used approximately 70% (n = 162) of the data for model development and the remaining 30% (n = 70) for model validation.

The Poisson model was used to determine the probability a survey point was classified as occupied by 0–3 Nightjars given habitat characteristics within 75 m of the survey point. The binomial model determined the probability of classifying a point as occupied given habitat characteristics within 75 m of the survey point. We conducted all statistical analyses using SAS version 9.2 (SAS 2008).

Landscape habitat model

We developed vector-based GIS land cover types for Guánica Forest, Susúa Forest, and El Convento using ArcGIS 9.2 (ESRI 2006). Habitat coverages were generated by digitising polygons using 2004 georeferenced aerial imagery, digital topographical maps, ground truthing, existing habitat maps, and ancillary data from available digital coverages (Lugo *et al.* 1978, Gould *et al.* 2008). We classified associations based on vegetation and geological characteristics. Also, we updated the Guánica Forest habitat map developed by Lugo *et al.* (1978) and modified the Puerto Rico Gap Analysis of land cover into concise classes (Gould *et al.* 2008).

Published information on Nightjar habitat relationships was used to develop variables of importance for the landscape habitat model including vegetation type, geology, physiography, land use, and ecological life zone (Kepler and Kepler 1973, Vilella and Zwank 1993, Vilella 1995, 2008). We selected seven corresponding spatial databases from the Puerto Rico Gap Analysis comprising land cover type, landscape units, physiography, topography, urban and rural land use, developed areas, and ecological life zones (Table 1). Each GIS layer was classified into a scale of suitability: 3 = most suitable (high); 2 = moderately suitable (moderate); 1 = marginally suitable (low). We used Arc GIS 9.2 Spatial Analyst to generate model results.

Additionally, we reclassified land cover classes using weighted values assigned in decreasing order of magnitude. The weighted linear combination (WLC) modelling approach is one of the most widely used GIS-based decision rules for deriving composite maps. This modelling approach has been applied in land use and suitability, site selection, and resource evaluation decisions (Herzfeld and Merriam 1995, Malczewski 2000). Hence, land cover classes were multiplied by 10^6, landscape units by 10^5, physiographical classes by 10^4, topographical classes by 10^3, land use classes by 10^2, development classes by 10, and ecological life zone classes by 1. Each reclassified layer was combined using Spatial Analyst, assigned a unique output value to each unique combination of input values,

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Table 1. Land cover variables selected from the Puerto Rico Gap Analysis Project (Gould *et al.* 2008) and Nightjar suitability classification level. Each GIS layer was classified as; 3 = most suitable (high), 2 = moderately suitable (moderate), and 1 = marginally suitable (low).

Digital coverage	Variable	Level
Land cover type	Mature secondary lowland dry limestone semi-deciduous forest	3
	Mature secondary lowland dry non-calcareous semi-deciduous forest	3
	Mature secondary lowland dry limestone evergreen forest	3
	Young secondary dry	3
	Moist serpentine semi-deciduous forest	3
	Young secondary lowland dry non-calcareous semi-deciduous forest	2
	Young secondary lowland dry limestone semi-deciduous forest	2
	Mature secondary dry and moist serpentine semi-deciduous forest	1
Landscape units	Subtropical dry limestone/plain and subtropical dry and moist ultramaphic/ ridge	3
	Subtropical dry limestone/ridge, and subtropical dry and moist ultramaphic/ plain	2
	Subtropical dry limestone/upper slope	2
	Subtropical dry and moist ultramaphic/upper slope	2
	Subtropical dry and ultramaphic/lower slope	1
Physiography	Hills	3
	Mountains	2
	Plains	1
Topography	Plain	3
	Slope bottom	3
	Flat summit	3
	Side slope	2
	Plateau	1
	Upper slope	1
Urban and rural land use	Rural low-density	3
	Rural high-density	1
Developed areas	Non-built areas	3
Ecological life zones	Subtropical dry and lowland moist	2
	Subtropical wet	1

and a new raster dataset generated. Outputs were listed in decreasing order among all land cover layers and classes. This final classification was then categorised into habitat suitability classes as the final output of the model.

Nightjar geographical distribution

Finally, we conducted a rapid assessment of Nightjar geographical distribution on sites predicted by the landscape habitat model. We randomly selected survey points within areas identified by the landscape model as Nightjar habitat. We noted whether survey points were located within areas identified as DNER conservation priority sites or predicted Nightjar habitat by the Puerto Rico Gap Analysis Project (García *et al.* 2005, Gould *et al.* 2008).

To evaluate model predictions, we surveyed 55 sites (130 m radius plots) for Nightjar presence across southern Puerto Rico during April–May 2009. Points were georeferenced using a GPS receiver and each site visited to determine vegetative status and access. Points were surveyed three times during dawn and dusk hours on clear nights to reduce the influence of weather on calling males (Kepler and Kepler 1973, Mills 1986). Finally, we used a patch occupancy approach (single-species, single-season) in the program PRESENCE version 2.2 (Hines 2006) to assess Nightjar presence on points randomly selected within predicted habitat. We used the three sampling occasions at each of the 55 sites to model Nightjar detection probability and estimate occupancy for the surveyed area. To meet model assumptions of population closure we restricted sampling to 23 days during the height of the breeding season (Vilella 1995). Model assumptions included: (1) the species of interest is identified correctly (no false detections); (2) constant occupancy over survey season; (3) constant occupancy probability across sites; (4) detection probability was constant for all sites and surveys; (5) detection histories at each location were independent (MacKenzie *et al.* 2006).

Results

Stand-level habitat model

Nightjars were found in all habitat types (Table 2). At Guánica Forest, unmanaged plantations represented 1.7% (62.7 ha), mixed forest 81.4% (3084.1 ha), and shrub 16.9% (643.78 ha). Susúa Forest included 91.3% (1193.68 ha) moist forest and 8.7% (113.72 ha) dry forest. El Convento consisted of 37.5 ha of mixed forest. Leaf litter biomass in moist forest averaged 35.7 ± 21.2 g (range 0.84–106.3 g) and was 20% higher where Nightjars were present. At sites where we detected at least two individuals, canopy closure was 3% greater ($\bar{x}$ = 79.49 ± 18.1%) and canopy height averaged 9.8 ± 4.0 m (range 4–28.6 m). Leaf litter biomass in dry forest averaged 33.33 ± 25.23 g (range 0.84–95.13 g) and was the highest of all the habitats sampled. Canopy closure in dry forest averaged 76.96 ± 11.59% (range 48.53–97.06%) and height averaged 9.4 ± 4.78 m (range 4.71–28.56 m).

We located Nightjars in plantation forest at elevation ranging from 72 m to 160 m. Leaf litter biomass in unmanaged plantations averaged 44.17 ± 23.03 g (range 9.95–74.94 g). Canopy height averaged 6.88 ± 13.66 m (range 6.88–13.66 m), and canopy closure ranged from 2.94% to 98.52%. Visual obscurity in plantation forest was 44.38% (0–0.5 m), 47.18% (0.5–1.0 m), 46.16% (1.0–1.5 m), and 40.56% (1.5–2.0 m). Lastly, Nightjars were detected in shrub habitat at elevations ranging from 31 m to 45 m. Leaf litter biomass averaged 23.73 ± 11.59 g (range 11.83–34.99 g), canopy height averaged 7.96 ± 5.18 m (range 4–13.82 m), and canopy closure ranged from 5.88% to 91.18%.

Three of 10 variables significantly differed between sites with and without Nightjars, including canopy closure ($F_{1,\ 158}$ = 4.06, P = 0.046), 1.5–2.0 m visual obscurity ($F_{1,\ 158}$ = 4.95, P = 0.027), and habitat type ($F_{4,\ 155}$ = 5.42, P = 0.0004). The best model (AIC = 194.32) correctly classified 81.4% of sites where Nightjars were present, including habitat type ($F_{4,\ 154}$ = 6.19, P <0.0001) and 1.5–2.0 m visual obscurity ($F_{1,\ 154}$ = 45.76, P = 0.017). Furthermore,

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Table 2. Habitat characteristics, mean, standard deviation (SD), and range, at plots sampled for Nightjar presence–absence in Guánica Forest, Susúa Forest, and El Convento, Puerto Rico.

Habitat characteristics	Absent			Present		
	Mean	SD	Range	Mean	SD	Range
Elevation (m)	160.8	123.9	0–470	139.8	93.5	20–419
Leaf litter (g dry weight)	28.4	24.7	0–84	35.7	21.2	0.84–106.3
Diameter at breast height (cm)	10.37	5.35	5–36.5	9.64	4.89	5–31.3
Canopy closure (%)	74.6	24.3	0–100	76.6	17.5	3–100
Canopy height (m)	10.8	5.3	4.4–28.2	9.8	4.0	4–28.6
Visual obscurity 0–0.5 (%)	54.4	24.6	7.7–100	47.7	23.6	2.33–100
Visual obscurity 0.5–1.0 (%)	39.4	22.6	0–100	47.8	23	0–95
Visual obscurity 1.0–1.5 (%)	37.7	23.3	66.7–74.7	39.7	22.6	0–95
Visual obscurity 1.5–2.0 (%)	40	25	0–93	43	25.6	3–95

covariate coefficients indicated Nightjar presence was 2.35 units greater in plantation forest than shrub, while mixed forest was 0.99 units lesser than plantation forest. We found no difference in Nightjar presence between mixed and shrub habitat. Further, three of 10 variables differed between sites regarding Nightjar abundance per area, including canopy closure ($F_{1,\ 158}$ = 2.69, P = 0.087), 1.5–2.0 m visual obscurity ($F_{1,\ 158}$ = 3.66, P = 0.057), and habitat type ($F_{4,\ 155}$ = 4.38, P = 0.002). The best model (AIC = 420.86) included habitat type ($F_{4,\ 153}$ = 6.03, P = 0.0002), canopy closure ($F_{1,\ 153}$ = 2.04, P = 0.1557), and canopy height ($F_{1,\ 153}$ = 4.18, P = 0.0426) and correctly classified 55.7% of the observed Nightjar abundance.

Landscape habitat model

Model results estimated 21,878.28 ha of suitable Nightjar habitat were distributed across southern Puerto Rico, representing approximately 2.4% of the total area of the island (Figure 2).

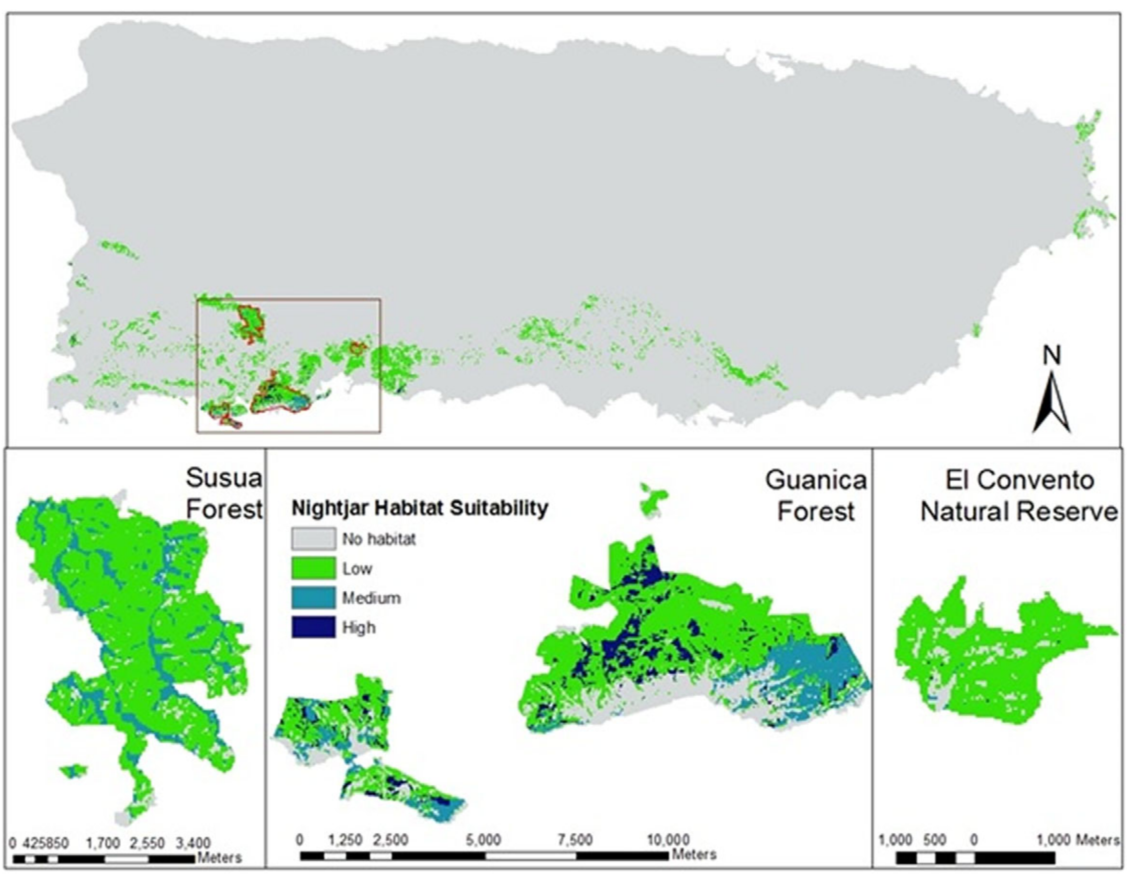

Figure 2. Distribution of predicted suitability of Nightjar habitat across Puerto Rico. Inset illustrates predicted Nightjar habitat within sites selected for development of the stand-level habitat model.

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Moreover, 4,058.64 ha were located within protected areas. Our results indicated 655.11 ha of high-quality Nightjar habitat of which 54.7% was found within protected areas. Medium-quality habitat included 978.21 ha, 68.5% of which was located within protected areas. Lastly, low-quality habitat included 20,244.96 ha and 18.6% occurred in protected areas.

Guánica Forest represented 65.4% (2,652.84 ha) of suitable Nightjar habitat on the island. Of the predicted habitat within protected areas, Guánica Forest included 56% (367.02 ha) of high-quality habitat, 49% (478.08 ha) of medium-quality habitat, and only 9% (1,807.74 ha) of low-quality habitat. Model results indicated 1,099.71 ha of suitable habitat were available in Susúa Forest, representing 27.1% of Nightjar habitat in protected areas. Susúa Forest included no high-quality Nightjar habitat but did include 20% (195.48 ha) of medium-quality habitat and 4.5% (904.23 ha) of the low-quality habitat found in protected areas. At El Convento 198.1 ha of suitable Nightjar habitat was available, representing 4.9% of Nightjar habitat within protected areas. Of these, 0.068% (0.45 ha) were classified as high-quality habitat, 0.1% (1 ha) as medium-quality habitat, and 1% (196.7 ha) as low-quality habitat.

We surveyed sites across 18 municipalities of southern Puerto Rico at locations of predicted Nightjar habitat (Table 3). Survey points were located outside protected areas and sites previously reported to harbour Nightjars (Kepler and Kepler 1973, Villella and Zwank 1993, Delannoy 2005). These included a wide diversity of landscapes including relatively undisturbed dry forest areas, regenerating forest, and areas greatly modified by agriculture or urban development. Some survey points were also located in areas of moist forest or riparian forest.

We detected Nightjars in 32 of 55 survey points at sites identified by the model as Nightjar habitat, encompassing 12 of 18 municipalities across southern Puerto Rico (Figure 3). Nightjars were generally absent at sites located on highly disturbed areas or areas that did not represent suitable habitat such as riparian forest (Villella and Zwank 1993). Conversely, Nightjars were most commonly detected within areas of secondary or mature forest, regardless of land use in the surrounding areas (e.g. grazing, agriculture, or low-density housing).

We detected Nightjars in 18 of 55 plots for a naïve occupancy estimate of 0.33 ± 0.06 (Table 4). Thus, 33% of survey points were occupied by Nightjars. Nightjar detection probability was 1.0. We considered two simple models, both assumed occupancy probability was constant for all plots (ψ(.)) and detection probability was either constant (p(.)) or varied by survey (p(s)). Estimates of Nightjar occupancy and associated standard errors were similar regardless of the detection probability model structure.

Discussion

The results of the stand-level model indicated that vegetation structure adequately assessed Nightjar habitat. Vilella (2008) reported that leaf litter biomass, midstorey stem density, and canopy closure best predicted Nightjar nesting habitat. Our results indicated that habitat type and 1.5–2.0 m visual obscurity (40%) with a semi-closed midstorey best predicted Nightjar presence. Sites where Nightjars were absent were generally in shrub habitat, riparian habitat, or steep slopes. Vegetation structure has been reported to be a primary factor determining habitat use (Rotenberry 1985). Our results indicated that habitat type and midstorey vegetation influenced patterns of Nightjar presence at the stand level.

Our model identified habitat type, canopy closure, and canopy height as the parameters that best predicted Nightjar abundance. Plantation and mixed forest provided the closed canopy forest conditions most favoured by nesting Nightjars (Vilella 1995). Only three of 10 variables explained Nightjar use of sampled sites, indicating some variables may not have been appropriate to assess habitat suitability. Identifying the applicable ecological variables is vital to accurately assess species–habitat relationships (Whittingham *et al.* 2003). In the case of the Nightjar, further research may help to better understand the functional relationships between habitat conditions and abundance patterns (Rushton *et al.* 1997). Nevertheless, model results provided new knowledge on Nightjar–habitat relationships that may be useful to implement habitat conservation measures. These results complemented previous studies on nest habitat relationships (Vilella 2008), and together they could provide additional tools with which to assess Nightjar habitat at the stand level. Further, model predictions may assist future habitat management practices and recovery objectives (Diaz 1983).

Habitat conservation is a critical component of endangered species conservation (Kerr and Deguise 2004). Our landscape model predicted a 30% greater amount of Nightjar habitat than estimated by the Puerto Rico Gap Analysis Project. Gould *et al.* (2008) estimated Nightjar habitat included approximately 15,411 ha, mostly restricted to the south-western region of the island. Our model extended the location of predicted habitat further east along the southern coast of Puerto Rico, and to the north-west of the island from Mayaguez to Cabo Rojo (Figure 3).

Landscape model results generally agreed with our patch occupancy estimates. More than 65% of the predicted habitat was estimated to occur within the region encompassed by the municipalities of Guánica, Sabana Grande, Yauco, Guayanilla, Peñuelas, and Ponce in southern Puerto Rico. This region includes large areas of continuous closed-canopy forest, all under private ownership. Outside this region, predicted habitat was characterised by small forest fragments across the southern and south-eastern coast of the island. Vilella and Zwank (1993) estimated that approximately 4,583 ha (47% of total habitat) of Nightjar habitat occurred on private lands. Results of our landscape model indicated Nightjar habitat on private lands was 74.3% greater than previously reported.

Contrary to previous reports, our habitat model estimated most (81.4%) Nightjar habitat (17,809 ha) was actually found in private lands (Figure 2). While no information is available on the total number of Nightjars in private lands, our results suggest the vast majority of the global population of the species may actually reside outside protected areas. This total likely exceeds the number of individuals (i.e. 315) reported to occur in private lands by Vilella and Zwank (1993). Furthermore, these results emphasise the importance habitat conservation on private lands may play in the conservation and desired recovery of the Nightjar (Kerr and Deguise 2004). Private lands may play a critical role in conservation (Norton 2000, Ciuzio *et al.* 2013). Protecting Nightjar habitat will rely on conservation programmes available for private lands in Puerto Rico (McCormack 2004, García *et al.* 2005).

Our study provided the first opportunity to assess Nightjar habitat suitability at landscape scales. Landscape models are a useful tool to measure the extent and distribution of habitat and can be used as an index to assess the conservation priorities of different regions along a species' geographical range. These models also serve as monitoring tools to evaluate future changes in habitat. Our model confirmed that Guánica Forest remains the most important protected area for the Nightjar while highlighting the fact that 45.3% of

Table 3. Location of points used to assess Nightjar geographical distribution across southern Puerto Rico, April–May 2009.

Point	Municipality	Sector	Presence[1]	DNER priority[2]	Latitude	Longitude	No. Nightjars	Notes
0	Juana Diaz	Tijeras	1	0	18° 3’ 42.25”N	66° 29’ 4.19”W	1	Forested hills
1	Ponce	Cañas	0	0	18° 2’ 9.26”N	66° 39’ 16.52”W	0	Disturbed forest with houses
2	Guayama	Caimital	1	0	17° 59’ 18.15”N	66° 6’ 3.64”W	1	Forested area
3	Guánica	Susúa Baja	1	0	17° 59’ 29.22”N	66° 53’ 14.47”W	2	Adjacent to Guánica Forest
4	Guayanilla	Magas	1	1	18° 1’ 40.19”N	66° 46’ 3.66”W	≥3	Similar to El Convento
5	Lajas	Costa	0	0	17° 59’ 33.80”N	66° 58’ 29.21”W	0	Habitat similar to Guánica Forest
6	Coamo	Santa Catalina	0	0	18° 7’ 2.34”N	66° 23’ 29.76”W	0	No habitat
7	Peñuelas	Encarnación	1	1	17° 59’ 48.53”N	66° 42’ 14.56”W	≥3	Large forest fragment
8	San Germán	Sabana Eneas	0	0	18° 4’ 29.80”N	67° 5’ 19.18”W	0	Area dominated by moist forest
9	Sabana Grande	Tabonuco	0	1	18° 6’ 58.71”N	66° 56’ 1.45”W	0	Moist forest, no Nightjar habitat
10	San Germán	Minillas	1	0	18° 3’ 17.42”N	66° 59’ 41.31”W	2	Nightjars on hill beyond point
11	Guánica	Ciénaga	1	0	17° 59’ 37.17”N	66° 56’ 44.91”W	≥3	Hill with good forest cover
12	Coamo	Santa Catalina	1	0	18° 6’ 26.52”N	66° 23’ 16.41”W	1	One Nightjar >300 m
13	Peñuelas	Encarnación	1	1	17° 59’ 13.72”N	66° 41’ 50.74”W	1	Good forest cover
14	Guánica	Ciénaga	1	0	17° 59’ 25.91”N	66° 55’ 57.78”W	≥3	Hill with good forest cover
15	Guayanilla	Cedro	1	0	18° 1’ 55.80”N	66° 45’ 6.97”W	≥2	Within Puerto Rico Conservation Trust (PRCT) property
16	Sabana Grande	Tabonuco	0	1	18° 6’ 33.18”N	66° 55’ 52.01”W	0	Riparian forest, no habitat
17	Sabana Grande	Rincón	1	1	18° 6’ 4.32”N	66° 56’ 38.85”W	2	Houses nearby, point in a slope
18	Yabucoa	Playa	0	0	18° 3’ 56.86”N	65° 48’ 17.38”W	0	Heavily urbanised
19	Humacao	Candelero Abajo	0	0	18° 4’ 29.95”N	65° 48’ 31.14”W	0	Near the water, houses all around
20	Santa Isabel	Boca Velazquez	0	0	18° 0’ 33.29”N	66° 24’ 26.37”W	0	Grassy area, no forest
21	Lajas	Palmarejo	1	1	17° 59’ 23.88”N	67° 4’ 11.47”W	3	Good area, planned development
22	Lajas	Parguera	1	1	17° 59’ 10.14”N	67° 3’ 10.47”W	2	Good area, planned development
23	Cabo Rojo	Boquerón	1	1	18° 0’ 4.58”N	67° 10’ 55.13”W	2	Forested hill, cattle, and ATV trails
24	Cabo Rojo	Pedernales	0	0	18° 2’ 51.65”N	67° 9’ 50.52”W	0	Recovering forest
25	Cabo Rojo	Guanajibo	0	0	18° 9’ 42.29”N	67° 10’ 39.99”W	0	Regenerating forest
26	Mayaguez	Juan Alfonso	0	1	18° 11’ 1.41”N	67° 5’ 32.57”W	0	Hills with forested slopes
27	Mayaguez	Quebrada Grande	0	1	18° 10’ 50.14”N	67° 6’ 14.08”W	0	Hills with forested slopes
28	Cabo Rojo	Guanajibo	0	0	18° 7’ 23.07”N	67° 8’ 34.40”W	0	Forest fragment
29	Lajas	Llanos	1	1	17° 59’ 56.53”N	67° 6’ 29.54”W	2	Forest fragment
30	Lajas	Llanos	1	1	18° 0’ 4.20”N	67° 6’ 7.95”W	2	Forest fragment
31	Sabana Grande	Santana	1	1	18° 6’ 18.64”N	66° 57’ 25.21”W	≥3	Forested hill, many Nightjars
32	Sabana Grande	Rincón	0	1	18° 6’ 25.35”N	66° 56’ 21.25”W	0	Riparian forest habitat.
33	Ponce	Cañas	1	0	18° 2’ 43.24”N	66° 40’ 29.53”W	1	One Nightjar >300 m
34	Ponce	Cañas	1	0	18° 2’ 29.37”N	66° 40’ 39.10”W	≥3	Good forest cover
35	Juana Diaz	Rio Cañas Arriba	1	0	18° 3’ 34.89”N	66° 26’ 5.05”W	≥3	Many Nightjars, heavily forested
36	Lajas	Lajas Arriba	0	0	18° 3’ 22.21”N	67° 0’ 48.44”W	0	Moist forest, no Nightjar habitat
37	San Germán	Cain Bajo	0	0	18° 6’ 7.45”N	67° 2’ 42.81”W	0	Cleared area
38	Lajas	Costa	0	0	17° 59’ 38.31”N	67° 0’ 42.22”W	0	Similar to Guánica Forest
39	Coamo	Los Llanos	0	0	18° 2’ 48.18”N	66° 24’ 41.39”W	0	Poor access, lots of vehicle noise
40	Sabana Grande	Torre	1	0	18° 3’ 0.87”N	66° 54’ 33.50”W	2	Similar to Susúa, Nightjars far
41	Sabana Grande	Torre	1	1	18° 3’ 0.05”N	66° 54’ 49.25”W	1	Similar to Susúa, 1 Nightjar south

(*Continued*)

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Table 3. (*Continued*)

Point	Municipality	Sector	Presence[1]	DNER priority[2]	Latitude	Longitude	No. Nightjars	Notes
42	Guayanilla	Quebradas	1	1	18° 2’ 1.89”N	66° 48’ 35.89”W	≥3	Similar to Guánica
43	Lajas	Costa	1	0	17° 59’ 19.66”N	66° 59’ 30.13”W	2	Similar to Guánica
44	Ponce	Cañas	1	1	17° 58’ 36.31”N	66° 41’ 34.25”W	≥2	Good forest cover
45	Juana Diaz	Rio Cañas Arriba	1	0	18° 3’ 43.46”N	66° 27’ 15.53”W	≥3	Forested hilltop
46	Coamo	Pedro Garcia	0	0	18° 7’ 30.83”N	66° 23’ 15.72”W	0	Moist forest area
47	Santa Isabel	Jauca 2	0	1	18° 0’ 46.21”N	66° 19’ 55.54”W	0	Riparian forest
48	Salinas	Quebrada Yeguas	1	0	18° 2’ 17.42”N	66° 10’ 42.59”W	2+	Forested area, Nightjars >300 m
49	Salinas	Quebrada Yeguas	1	0	18° 2’ 39.60”N	66° 11’ 34.13”W	2+	Nightjars north of point
50	Guayama	Pozo Hondo	1	0	18° 0’ 16.16”N	66° 10’ 52.55”W	2	Similar to Parguera Hills.
51	Naguabo	Santiago y Lima	0	0	18° 11’ 0.66”N	65° 42’ 3.74”W	0	Limited vegetation cover
52	Fajardo	Cabezas	0	0	18° 21’ 20.46”N	65° 38’ 26.98”W	0	No habitat
53	Salinas	Rio Jueyes	1	1	18° 1’ 7.30”N	66° 19’ 45.19”W	2	Nightjars on hill west of point
54	Salinas	Lapa	1	1	18° 2’ 51.35”N	66° 15’ 52.38”W	3	Good habitat

[1]Status: 1 = Nightjar(s) present, 0 = absent; [2]Puerto Rico Department of Natural and Environmental Resources (DNER) Priority Conservation Area: 1 = yes, 0 =no.

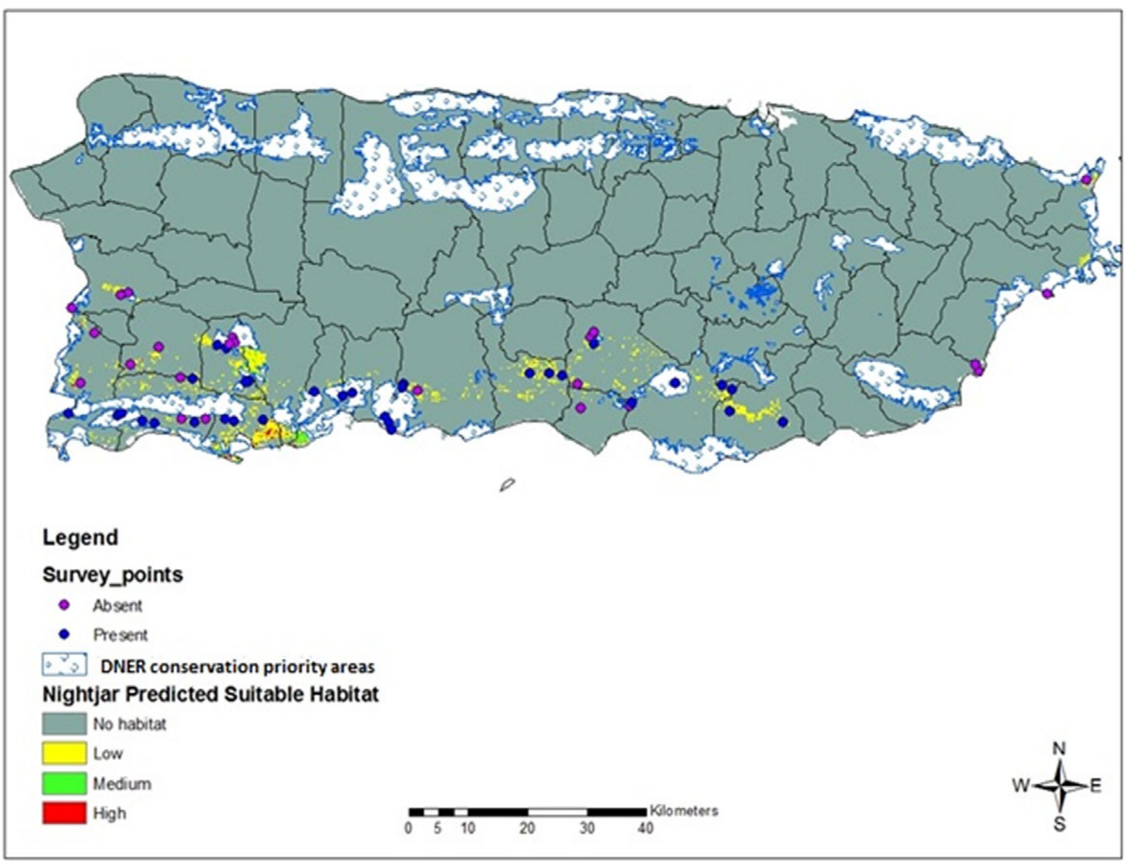

Figure 3. Map of Puerto Rico highlighting predicted Nightjar habitat, survey points used for the assessment of geographical distribution, and location of conservation priority areas identified by the Puerto Rico Department of Natural and Environmental Resources (DNER).

high-quality Nightjar habitat remains unprotected. A significant portion of this total (60%) remains under threat from proposed development projects on the periphery of Guánica Forest and housing developments near the city of Ponce (Parés-Ramos et al. 2008).

The most extensive tracts of continuous forest outside Guánica Forest are found in the region of Guayanilla-Peñuelas-Ponce (Figure 3). Protection of dry forests in this portion of the Nightjar’s range may represent the greatest conservation priority for the

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Table 4. Results of occupancy models based on Nightjar surveys across southern Puerto Rico, April–May 2009. Models are ranked based on Akaike's Information Criterion (AIC) values. Relative difference in values (ΔAIC), estimates of occupancy ($\hat{\psi}$), and standard error (SE ($\hat{\psi}$)).

Model	AIC	ΔAIC	$\hat{\psi}$	SE ($\hat{\psi}$)
ψ (.) p (.)	73.54	0	0.33	0.063
ψ (.) p (s)	77.55	4	0.33	0.063

species at present, considering the quality and extent of forest cover and virtual lack of protected areas in the region (García *et al.* 2005, Castro-Prieto *et al.* 2019). Moreover, private lands on the north-eastern boundaries of Guánica Forest and the southern limits of Susúa Forest include remaining tracts of mature dry limestone forest (Vilella and Zwank 1993). Protection of these adjacent areas as buffer zones would benefit Nightjar habitat. Buffer zones are known to mitigate the effects from surrounding land uses and help to maintain the integrity of core habitats (Wells and Brandon 1993).

Geographical range represents one of the primary elements describing the distributional component of a species' ecology (Brown *et al.* 1996). Our patch occupancy approach served as a rapid assessment of habitat model predictions and was useful in assessing Nightjar geographical distribution (Figure 3). Nightjars were absent on patches located in highly disturbed sites, riparian habitats, or densely populated areas. Incorporating these variables into future habitat modelling efforts may improve measures of predicted habitat and Nightjar occupancy. Further, sites where Nightjars were present on the first visit had detections on subsequent visits. Conversely, sites where Nightjars were absent had no further detections in any subsequent surveys. This may be related to stand-specific habitat requirements of the Nightjar as well as their documented site fidelity (Vilella 1995).

Field evaluation of the landscape model predictions yielded new Nightjar locality records at several sites on the south-central and south-eastern regions of the island. These locations were within sites identified by conservation planning efforts in Puerto Rico (Figure 3). While some of these sites were located in areas with a great degree of fragmentation, they may serve as Nightjar habitat refugia and may have restoration potential (Shafer 1995). Presently, approximately 16% of Puerto Rico is designated as protected natural areas for conservation (Castro-Prieto *et al.* 2019). Protection and restoration of forest fragments across the southern coast of Puerto Rico would help to ensure long-term persistence of the Nightjar across a considerable portion of its range (Beier and Noss 1998). Recent sightings in various municipalities of southern Puerto Rico suggest the Nightjar may be more widespread than previously reported (Vilella and Zwank 1993). However, the species remains threatened by ongoing habitat fragmentation and degradation (USFWS 2023). Therefore, protection and conservation of Nightjar habitat in private lands may be the single most effective mechanism to achieve the eventual recovery of the species.

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