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Habitat suitability models indicate the White-breasted Thrasher *Ramphocinclus brachyurus* occupies all suitable habitat in Saint Lucia

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Summary

Habitat suitability models can guide species conservation by identifying correlates of occurrence and predicting where species are likely to occur. We created habitat suitability models for the White-breasted Thrasher *Ramphocinclus brachyurus*, a narrowly distributed endangered songbird that occupies dry forest in Saint Lucia and Martinique. Eighty-five percent of the global population inhabits two ranges in Saint Lucia, both of which are largely unprotected and threatened by development. We developed three habitat suitability models using Maxent techniques and published occupancy datasets collected from the species' two Saint Lucian ranges, and used abiotic, land cover, and predator distribution predictors. We built one model with occupancy data from both ranges, and two others with occupancy data specific to each range. The best full-range model included 11 predictors; high suitability was associated with close proximity to Saint Lucia fer-de-lance *Bothrops caribbeaus* range, moderately low precipitation, and areas near streams. Our assessment of suitable sites island-wide was more restricted than results from a recent model that considered older land cover data and omitted predator distributions. All sites identified in our full-range model as highly suitable were in or adjacent to the species' current designated range. The model trained on southern range occurrences predicted zero suitable habitat in the northern range, where the population is much smaller. In contrast, the model trained on northern range occurrences identified areas of moderate suitability within the southern range and patches of moderately suitable habitat in the western part of the island, where no White-breasted Thrashers currently occur. We interpret these results as suggesting that White-breasted Thrashers currently occupy virtually all suitable habitat on the island, that birds in the northern range occupy marginal habitat, or that an important correlate of suitability is missing from the model. Our results suggest that habitat management should focus on currently occupied areas.

Introduction

The White-breasted Thrasher *Ramphocinclus brachyurus* is an endangered songbird endemic to the Caribbean islands of Saint Lucia and Martinique (BirdLife International 2015) and current population estimates put the species at around 2,000 individuals range wide (Temple 2005, Young *et al.* 2010). Once more common, White-breasted Thrasher range and population size are thought to have declined significantly by the early 20th century (Bond 1928, Felix *et al.* 2014). Currently, the species exists in three populations within its two-island extent; this extremely small and fragmented range is the justification for the IUCN Red List designation of the species as 'Endangered' (BirdLife International 2015). The Mandelé population, which is by far the largest extant population containing ~80% of all individuals, was not discovered until the mid-1990s (John 1995). It is speculated that forest regeneration in the previous 40 years in Mandelé led to a range shift into the area (Donald Anthony, Saint Lucia Forestry Department, ret., cited in Felix *et al.* 2014). Species in the Caribbean islands are, in general, threatened by habitat loss and fragmentation with almost 90% of primary vegetation in the Caribbean already cleared (Mittermeier *et al.* 1999). What remains continues to be threatened by the expansion of agriculture, urban and rural development, and tourism (Young *et al.* 2010). Tourism, in particular, constitutes a large part of the Caribbean economy, especially impacting coastal regions, and it is expected to increase in the coming decades (Christ *et al.* 2003, SIA 2007, Wege *et al.* 2009, UNWTO 2014). This is true in Saint Lucia, where development of a tourist resort began in 2005 within the stronghold of the White-breasted Thrasher distribution, and to date, 16% of the species' habitat within Saint Lucia has been destroyed (Felix *et al.* 2014; Figure S1 in the online supplementary material). Further habitat loss associated with the resort construction is predicted to result in White-breasted Thrasher population decline and increased risk of extinction (Mortensen and Reed 2016). This recent and proposed future habitat loss, coupled with low levels of habitat protection (only 4% of its range is protected; Young *et al.* 2010) and depredation by introduced mammals (Felix *et al.* 2014, BirdLife International 2015), helped motivate a recent conservation plan for the Saint Lucian subspecies (Felix *et al.* 2014).

Habitat suitability modelling can be valuable for conservation planning (Guisan and Zimmermann 2000, Elith *et al.* 2006, Miller 2010). For example, suitability models are used to identify actual distributions of species, a goal when selecting or prioritising key sites for protection or management (e.g. Araújo and Williams 2000). They also are used to identify potentially suitable sites for species introduction or for habitat restoration (e.g. Pearce and Lindenmayer 1998). Suitability modeling is also used to detect environmental correlates of species occurrence and to guide survey efforts in poorly known landscapes (e.g. Guisan *et al.* 2006). White *et al.* (2012) built the first habitat suitability model for the Saint Lucia White-breasted Thrasher with these goals in mind. They found that habitat suitability was associated with river presence, distance to coast, distance to main roads, building density, mean annual temperature, temperature seasonality, and total annual precipitation, though the direction of the relationships was not specified. Their habitat suitability map predicted high suitability in only one of the species' two Saint Lucian ranges (Mandelé, the species' current stronghold). Furthermore, their model identified several other regions of Saint Lucia as highly suitable, including large areas on the west and south-east coasts of the island, outside the species' current range (White *et al.* 2012). However, the authors acknowledge that some of these predictions, particularly the identification of large tracts of potentially suitable land on the west coast, should be treated with caution due to problems with data extrapolation and older data coverage for some environmental variables used to build the model. Consequently, one of the projects identified in the recent Saint Lucia White-breasted Thrasher conservation plan is to create an updated habitat suitability model that can be used to help identify areas of potentially highly suitable habitat to bring under active management (Felix *et al.* 2014).

The goals of this study were twofold. Our first goal was to create a habitat suitability model for the Saint Lucia White-breasted Thrasher using updated land cover data. Recent work on habitat suitability modelling suggests that including biotic factors such as predators or competitors as predictor variables can improve predictive power, robustness, and precision of models (Martin 2001, Araújo and Luoto 2007, Heikkinen *et al.* 2006, Godsoe and Harmon 2012, Gonzalez-Salazar *et al.* 2013, Araújo *et al.* 2014). In Saint Lucia, introduced mammalian predators important to the White-breasted Thrasher include the southern opossum *Didephis marsupialis*, small Asian mongoose *Herpestes javanicus*, and black rat *Rattus rattus* (Felix *et al.* 2014). Consequently, we included range data for one native and three introduced predators in our model development. Our second goal was to determine whether correlates of habitat suitability differed between the species' two Saint Lucian ranges. In contrast to our full-range model, which included training and test data from throughout the species' range, in the partial-range models, the presence points of one range were used as training data and the presence points of the other range used as test data. Because the two Saint Lucian White-breasted Thrasher populations appear to occupy somewhat different habitats (Temple 2005, Mortensen 2009, Young *et al.* 2010), we expected to see a different suite of influential predictors between the models. A more thorough understanding of habitat suitability will be useful to resource managers to identify the most suitable areas for land protection and restoration (Felix *et al.*, 2014).

Methods

Study species, study area, and species occurrence data

The White-breasted Thrasher is an endangered, non-migratory, cooperatively breeding songbird (Temple 2005). The species is territorial, and family groups consist of two breeders and 0-4 non-breeding helpers (Temple *et al.* 2006, 2009, Mortensen 2009). The species is a habitat specialist; it is found only in coastal deciduous seasonal forest on the Caravelle Peninsula in Martinique (14°44′N, 60°93′W; Gros-Desormeaux *et al.* 2014) and in two areas in Saint Lucia, the Mandelé and Iyanola ranges (13°53′N, 60°53′W and 13°59′N, 60°53′W, respectively; BirdLife International 2015) (Figure 1). These inhabited areas are not large; in Iyanola, where there are 100–200 birds (Felix *et al.* 2014), White-breasted Thrashers are found in riparian forest primarily in the steep ravines that separate scrub habitat on ridge tops, and consequently they occupy only 62–126 ha (3.6–7.4%) of the 1,700 ha Iyanola range (Temple 2005). In Mandelé where there are an estimated 1,200–2,100 White-breasted Thrashers (Felix *et al.* 2014), birds are found in both ravines and hillsides (Temple 2005, Young *et al.* 2010), occupying 450 ha (66%) of the 680 ha range (Felix *et al.* 2014). The fine-scale habitat associations of the White-breasted Thrasher in the Saint Lucia Mandelé range were characterised by Temple (2005). Within deciduous seasonal forest, the birds are found in areas with a tall intact canopy, high tree density, and abundant leaf litter. Occupied areas also have a high density of invertebrate prey and high incidence of the tree bwa gyiué *Myrcia citrifolia*, which is used by White-breasted Thrashers for food (berries) and as a nesting substrate (Temple 2005).

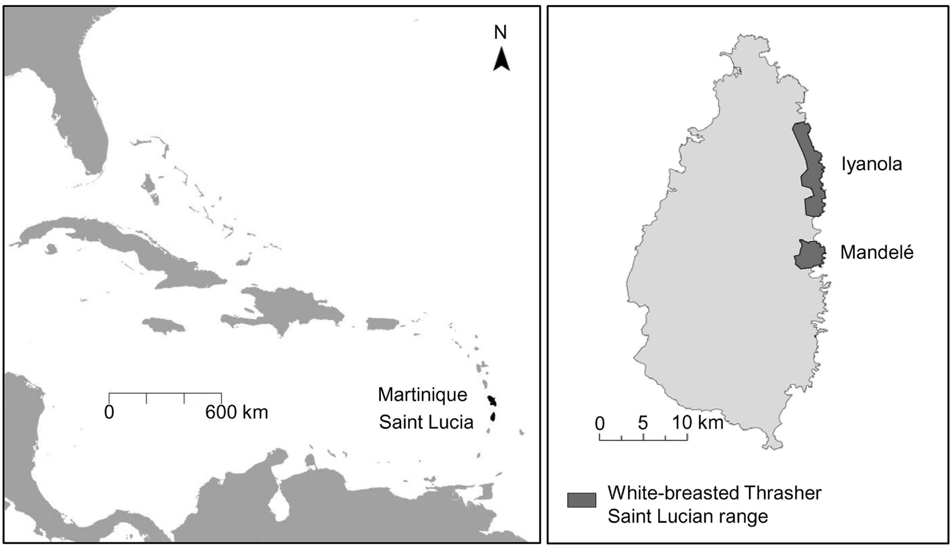

Figure 1. The White-breasted Thrasher is restricted to the Caribbean islands of Martinique and Saint Lucia. In Saint Lucia, enlarged on right, the species is present in two populations (Mandelé and Iyanola) on the east coast of the island. Range boundaries in Saint Lucia are from Temple (2005).

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We used published Saint Lucia White-breasted Thrasher presence data in our habitat suitability models. We combined data that had been collected across several studies: data from the Iyanola range were collected in 2003 (Temple 2005) and 2006 (Young *et al.* 2010) (n = 45 presence points total), and data from the Mandelé range were collected in 2006–2009 (White *et al.* 2012; n = 67 presence points). We counted a sighting in any year as a presence point. M. Morton (Durrell Wildlife Conservation Trust, pers. comm.) provided coordinates of the Mandelé range presence points; Iyanola presence data were digitised from survey maps into ArcMAP10 (ESRI 2014). Spatial bias in sampling can occur when a species is not sampled across the full range of environmental conditions in which it is found (Phillips *et al.* 2009), and it is known to lead to inaccuracies in presence-based models (Stolar and Nielsen 2015). The sampling designs used by Temple (2005), Young *et al.* (2010), and White *et al.* (2012) covered the entirety of the Iyanola and Mandelé ranges, so sampling bias for this species is not a concern in our study.

Predictor variables

We chose environmental predictor variables expected to influence White-breasted Thrasher distribution (Temple 2005, White *et al.* 2012) and that also could be acquired for all of Saint Lucia. The predictors we used included temperature and precipitation metrics, measures of topography, human density as an estimate of development extent, and land cover data (see Table 1 for data sources). The land cover data divide the island into 16 classes, namely: deciduous seasonal forest, deciduous seasonal forest and grassland, mixed farming with deciduous seasonal forest, semi-evergreen seasonal forest, mixed farming with semi-evergreen seasonal forest, lower montane rainforest, mixed farming with lower montane forest, montane rainforest, elfin shrublands, fumarole

Table 1. Predictor variables for habitat suitability modeling for the Saint Lucia White-breasted Thrasher.

Predictor	Source[a]
Aspect: Aspect of pixel, calculated from slope (degrees)	1
Slope: Slope of pixel, calculated from elevation (degrees)	1
Distance to stream: Distance from pixel to nearest stream (m)	2
Elevation: Elevation above sea level (m)	1
Flow accumulation: Accumulation of water at each pixel, calculated from elevation	1
Human population density (people/9 ha)	1
Land cover: Type of land cover (2009)	3
Mean diurnal temperature range (max T – min T) (°C)	4
Isothermality (Mean diurnal temperature range / temperature annual range) *100 (°C)	4
Temperature seasonality (SD * 100) (°C)	4
Annual temperature (max of warmest month – min of coldest month) (°C)	4
Annual precipitation (mm)	4
Annual precipitation seasonality (coefficient of variation)	4
Precipitation of coldest quarter (mm)	4
Saint Lucia Fer-de-lance range: Distance to range boundary (m)	5
Rattus range: Distance to nearest sighting (m)	6
Small Asian Mongoose range: Distance to nearest sighting (m)	6
Southern Opossum range: Distance to nearest sighting (m)	6

[a]1: Saint Lucia Integrated National GeoNode, sling.gosl.gov.lc, accessed 1 March 2013
2: provided by M. Morton, Durrell Wildlife Conservation Trust, pers. comm. – data were from a 1982 DOS topological map (www.worldcat.org/title/saint-lucia-tourist-map-scale-150000/oclc/12343945) that was digitized by the Saint Lucia Mapping Ministry of Physical Development
3: R. Graveson, Lesser Antilles botanical consultant, & R. Rock, Saint Lucia Forestry Department, pers. comm
4: WorldClim Global Climate Data, worldclim.org, accessed 1 March 2013
5: R. Devaux, St. Lucia Research Institute, K. Breach, Imperial College London, and M. Morton, pers. comm
6: Clarke (2009)

vegetation, herbaceous swamp, freshwater swamp forest, mangrove, intensive farming, built-up areas, and areas under construction. We also included distribution data of four known White-breasted Thrasher predators – the Saint Lucia fer-de-lance *Bothrops caribbeaus*, southern opossum, small Asian mongoose, and black rat. Brown rat *R. norvegicus* sightings were included with those of the black rat because reported sightings did not always distinguish the two. In addition, although the brown rat is not a documented White-breasted Thrasher predator, its omnivorous and opportunistic diet on other islands suggests that it would eat a bird or its eggs if given the opportunity (e.g. Drever and Harestad 1998, Major *et al.* 2007). None of the mammalian predators are native to Saint Lucia. The Saint Lucia fer-de-lance is a native endemic with a proposed conservation status under IUCN standards as globally and nationally 'Endangered' (M. Morton, Durrell Wildlife Conservation Trust pers. comm.). Saint Lucia fer-de-lance distribution, which was an α-hull estimated from sighting and bite locations across the island (years = 2000–2009; Breach 2009) and opportunistic sightings during a 2009 Saint Lucia Parrot *Amazona versicolor* survey (Morton *et al.* 2011), was provided to us as a shapefile (M. Morton, K. Breach, R. Devaux pers. comm.; affiliations in Table 1). The mammal coverages were created in ArcMap10 by importing the map of sightings as a PDF, rubber-sheeting that map over a map of Saint Lucia containing the other environmental layers, and then digitising the sightings. The data included surveys at *ad hoc* locations (Clarke 2009; no data have been published from systematic surveys for introduced mammalian predators). For each predator, we created a distribution contour map in ArcMAP10 by calculating distances between each pixel and the closest predator sighting (for mammals; Clarke 2009) or range boundary (for Saint Lucia fer-de-lance; Breach 2009). We used ENMTools (Warren *et al.* 2008, 2010) to test for multicollinearity between predictor variables, especially between related climate factors; one of each pair of variables was excluded if $r > 0.85$, resulting in a final set of 18 predictor variables (see Table 1 for list of variables used and data sources). When collinearity was an issue, we selected the more general variable of a pair (e.g. annual rainfall rather than rainfall in a particular month).

Using ArcMAP10, we projected predictor variables into NAD 1983 UTM Zone 20N. We interpolated the predictor variable layers to 300 x 300 m grid cells to maintain some of the detail available in the land use coverage. This spatial scale was a compromise between the coarser-scale environmental data (e.g. rainfall) and fine-scale data (e.g. land cover). After interpolation, several data layers contained a few gaps in data coverage; we filled in these gaps by manually interpolating values of neighbouring pixels in the ASCII file.

Modeling approach

We used Maxent version 3.3.3k (Phillips *et al.* 2006) to develop the set of White-breasted Thrasher suitability models. Maxent performs favourably against other modeling methods (Elith *et al.* 2006, Hernandez *et al.* 2006), its results are robust to small sample sizes (Guisan *et al.* 2007), and it can incorporate categorical environmental variables such as land cover type. Although Maxent can incorporate many different functions, we restricted the models to linear functions to minimise overfitting. Maxent calculates the probability distribution for a species that maximises entropy, or is the most uniform given the set of constraints imposed by the species presence data and environmental conditions of the study area. Thus, the average values of each environmental variable across the presence locations are considered to be the highest quality, and these values are extrapolated over the rest of the area to determine suitability of each pixel. Habitat suitability values generated by Maxent range from 0 to 1, where 1 is the most suitable and 0 is the least suitable habitat. In addition, all models were created with clamping, which limits extrapolation above or below variable extremes that can lead to predictions of very high habitat suitability (Phillips *et al.* 2006).

We created three sets of models to predict island-wide habitat suitability for the White-breasted Thrasher. In the first model (hereafter, 'full range'), we divided the individual presence records from the Iyanola and Mandelé ranges into training data (89 records) and test data (65 records).

In the other two models (hereafter 'Mandelé-trained' or 'Iyanola-trained'), the presence points of one range were used as training data, and the presence points of the other range were used as test data. Duplicate records per cell were counted as one record. We used 6,671 points to determine the Maxent distribution (i.e. background and presence points), as the Maxent default of 10,000 points is more than occurs in Saint Lucia at our sampling scale. In each of the three sets of models, we modelled habitat suitability using the 18 predictor variables (Table 1). We also modelled suitability omitting the White-breasted Thrasher mammalian predators from the predictor variable set as an additional evaluation of their relative importance in the model.

For each of the three sets of suitability models, we used a backwards stepwise method to remove the least important predictor variable identified by Maxent from each model (Phillips *et al.* 2006, Phillips and Dudik 2008) until one predictor remained. We chose the best model from the full range model and each of the partial range models using AIC_c calculated in ENMTools, and we used ΔAIC_c of 2.0 as our criterion for choosing the top model (Akaike 1973, Warren and Seifert 2011). For nested models, if $\Delta AIC_c < 2$, the simpler model was chosen (Arnold 2010).

Model evaluation

We used AUC value (area under the curve of the receiver operating characteristic plot [ROC]) retrieved from test data to assess predictive performance of our top model in each set (Fielding and Bell 1997). To further validate the best model from each set, we built models from 99 sets of points randomly selected from across the island and compared the area under the ROC curve (AUC) of these random models to the AUC of the predictive models (Raes and ter Steege 2007). The same numbers of points used to create the habitat suitability models were used to create the random models. The AUC of the predictive model was considered significant if it was more extreme than 95% of the AUC distributions of the null (random) models; that is, the relationship between where the species had been found and the environmental values at those locations was significantly stronger than expected by chance (Raes and ter Steege 2007).

Maxent provides several statistical tools for evaluating relative variable importance in a model (Phillips *et al.* 2006). Percent contribution is a good measure of relative variable importance when there is little multicollinearity; although we did reduce multicollinearity by dropping highly correlated variables, based on some of the variable contribution metrics from Maxent, we were still left with significant collinearity for some variables. Consequently, we evaluated variable contribution using the permutation importance and jackknife tools, using the training and test data as per Phillips (2010); direction of relationship was determined using bivariate plots. This test also evaluates the sensitivity of the full model to loss of a single variable; that is, it identifies which variables have the most information not present in other variables (Phillips *et al.* 2006).

Results

Using all of the predictor variables and occupancy data from both Saint Lucian ranges (full range), our best model for predicting habitat suitability for the White-breasted Thrasher had 11 variables, including abiotic, land-use, and predator variables (Table 2). For comparison purposes, the best model that excluded mammalian predator variables from the onset had $\Delta AIC_c = 155$ and AUC = 0.979 (Figure S2, Table S1). The top suitability model had a higher AUC score than any of the null models, indicating that White-breasted Thrasher presence locations were more strongly correlated with predictor variable values than would be expected by chance (Raes and ter Steege 2007); AUC scores of the null models that ranged from 0.367 to 0.630, and AUC of the top model was 0.978. Areas with the highest predicted suitability occurred in the current Mandelé range and in parts of the Iyanola range (Figure 2, Figure S3). Areas predicted to be of moderate or low suitability occurred south and northwest of the Mandelé range, and in small patches on the west coast of the island (Figure 2, Figure S3). Island-wide, the highest suitability value was 0.884; 114 pixels

Table 2. Variables included in the best of each of the three habitat suitability models for the White-breasted Thrasher in Saint Lucia. We report permutation importance for each model (values are compared within, not across, columns), and for each variable describe the relationship with suitability for the best model. "–" indicates a variable not in the top model.

Variable	Relationship for suitability[a]	Variable importance		
		Best full range model	Best Mandelé-trained model	Best Iyanola-trained model
Saint Lucia Fer-de-lance range	Positive association (closer is better)	57.8	14.1	47.8
Annual precipitation	Negative association (until very low rainfall)	13.5	–	–
Land Cover	Deciduous seasonal forest	7.7	0.8	28.7
Small Asian Mongoose sightings	Negative association; positive for Mandelé-trained model	6.9	19.1	0.3
Isothermality	Negative association	6.6	0.5	1.1
Human density	Negative association (higher suitability where humans absent)	3.0	–	1.7
Rattus sightings	Negative association (farther is better)	1.9	–	–
Distance to streams	Positive association (closer is better)	1.8	–	10.3
Precipitation of coldest quarter	Negative association	0.5	1.1	–
Precipitation seasonality	Positive association	0.3	9.4	0.8
Temperature seasonality	Positive association	< 0.1	0.1	–
Southern Opossum sightings	Negative for Mandelé-trained model; positive for Iyanola-trained model	–	47.4	4.9
Temperature annual range	Positive association	–	0.5	0.3
Elevation	Negative association	–	6.4	4.1
Slope	Positive association	–	0.6	–

[a]see Figure S4 for a detailed view of the relationships.

had a suitability value > 0.55 (1.71% of the pixels), and only 8 pixels (0.12%) had a predicted suitability value of ≥ 0.8. There were few pixels outside the currently designated Mandelé or Iyanola ranges identified as having high (≥ 0.8) suitability, and all pixels of moderate or higher (> 0.55) suitability occurred on the east coast (Figure S3). Table S2 shows the frequency of binned suitability values island-wide.

For our best model, the permutation evaluation using training data identified distance to Saint Lucia fer-de-lance range as the most important variable, with high suitability associated with proximity to the Saint Lucia fer-de-lance range (Table 2, Figure S4). The next most important variables based on this evaluation tool were precipitation, where habitat suitability was positively associated with moderately low precipitation, and land cover type, with higher suitability in areas with deciduous seasonal forest cover (Table 2). The jackknife evaluation provided more subtle information. This evaluation identified land cover type as the most important variable when modelled alone, followed by distance to Saint Lucia fer-de-lance range and distance to small Asian mongoose sightings. Specifically, higher habitat suitability was associated with deciduous seasonal forest cover, proximity to the Saint Lucia fer-de-lance range, and greater distance from small Asian mongoose sightings (Table 2, Figure S4). The best model was most sensitive to loss of the variable distance to the Saint Lucia fer-de-lance range, followed by distances to small Asian mongoose sightings and isothermality (Table 2). If these results are robust, they would show the same patterns in the jackknife evaluation of the test data (Phillips 2010). In the test data, the most important single-variable effect was the same as for the training data, land cover type, followed by distance to Saint Lucia fer-de-lance range and to small Asian mongoose sightings. The top variables

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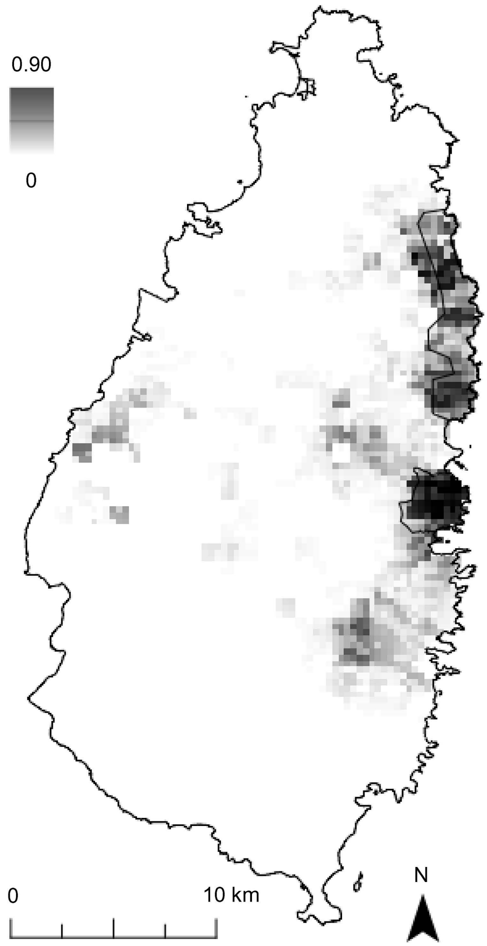

Figure 2. Predicted suitable habitat for the White-breasted Thrasher in Saint Lucia based on presence data from both the Iyanola and Mandelé ranges (full range model). Each pixel represents the predicted suitability of that site, ranging from 0 (white, low suitability) to 0.9 (black, high suitability). A colour version of this map can be found in the Supplementary Material.

that showed the most information not present in other variables were slightly different for the test data; they were distance to the Saint Lucia fer-de-lance range, land cover, and isothermality. Overall, the model evaluations showed a moderately consistent picture of the importance of land cover, distance to Saint Lucia fer-de-lance range, distance to small Asian mongoose sightings, and isothermality, although there were inconsistencies among the models, which could be related to the presence of multicollinearity (Phillips *et al.* 2006).

For the models trained on presence data from one part of the range and tested on the other, the top Mandelé-trained model included 11 variables, with the most important variable, according to the permutation evaluation, being distance to southern opossum sightings, followed by distances to small Asian mongoose sightings and to the Saint Lucia fer-de-lance range (Table 2). In contrast, the best Iyanola-trained model included 10 variables; distance to Saint Lucia fer-de-lance range and land cover were the most important variables from the permutation test (Table 2). The Iyanola-trained model performed better than the randomly built models: AUC of the top Iyanola-trained model was 0.803 and of the null models was 0.268–0.727; the AUC of the top Mandelé-trained

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model was 0.457, which is within the range of the null models (0.319–0.703). For the Mandelé-trained model without mammal data, AUC= 0.919 and ΔAIC_c = 173.72; for the Iyanola-trained model without mammal data, AUC= 0.869 and ΔAIC_c = 10.11 (Figure S2, Table S1).

Unsurprisingly, given the differences in predictor contribution to each of the top partial-range suitability models, the resulting habitat suitability maps differed substantially (Figure 3). Both models predicted high (or moderately high) habitat suitability in the range used to train the data. The model trained on Iyanola presence data predicted high (0.7) suitability throughout most of its range and moderate suitability (0.2) in almost half of the Mandelé range (Figures 3A and S5A). In contrast, the habitat suitability model that was trained on the Mandelé range predicted that almost all high-quality habitat was within its own range. Interestingly, this model classified all of the Iyanola range as unsuitable (Figures 3B and S5B).

Discussion

In Saint Lucia, the White-breasted Thrasher is currently restricted to two small areas on the east coast. The range has shifted over the past 50 years, likely due to changes in forest succession and land use (Graveson 2009, Felix *et al.* 2014). Because only 4% of the White-breasted Thrasher's current range is protected (Felix *et al.* 2014), and because there are recent (Mortensen 2009,

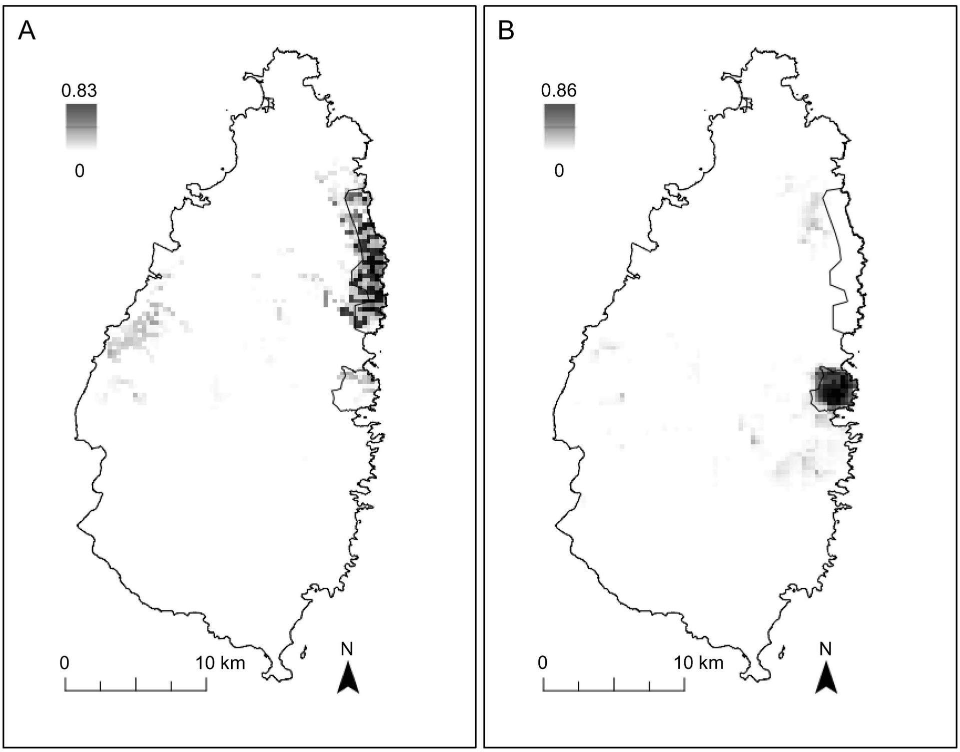

Figure 3. Habitat suitability maps for the White-breasted Thrasher in Saint Lucia. Each pixel represents the predicted suitability of that site, ranging from low (white) to high (black) suitability. (A) Iyanola-trained model: presence data from the Iyanola range were used as training data and presence data from the Mandelé range used as test data. (B) Mandelé-trained model: presence data from the Mandelé range were used as training data and presence data from the Iyanola range used as test data. Colour versions of these maps can be found in the Supplementary Material.

Young *et al.* 2010, White *et al.* 2012) and proposed habitat losses (Ernest 2005), the recovery plan for this species recommends increased land protection and habitat restoration (Felix *et al.* 2014). Determining habitat suitability is critical for planning these types of conservation measures. White *et al.* (2012) created a habitat suitability model for the White-breasted Thrasher on Saint Lucia, but the amount of high-quality habitat identified as suitable was over three times greater than that currently occupied, and much of it was in the western part of the island. Like the Iyanola range, the west coast of Saint Lucia contains secondary dry forest habitat with ongoing disturbance (Graveson 2009), and much of this is what White *et al.* (2012) identified as suitable habitat; however, all available evidence suggests that White-breasted Thrashers are absent from the area and were never there in any numbers. The only recorded White-breasted Thrasher sighting on the west coast was of a pair near the capital city of Castries in 1951 (Bond 1966, 1967), despite extensive subsequent surveys (Diamond 1973, King 1981, Babbs *et al.*, 1988, Ijsselstein 1992). There are also three collected specimens reported from the west part of the island, but the reliability of the reported collection locations is unknown, and none of the reported locations are within areas identified by any of our models as currently suitable habitat. Two of the reported specimens are from the capital city (reported in VertNet, searched 23 June 2015), but the collection locations are recorded as being '24 miles east' of Castries, which is either well into the ocean (based on reported coordinates), is a driving distance along a road, or is in error, so the specific collection site is ambiguous (cf. Roberts *et al.* 2010). There is also a specimen from the 1890s apparently collected in the south-west part of the island (reported as Fonds St. Jacques; roughly 2 km inland of Petit Piton). Recent surveys of the west coast confirmed the species' current absence (John 1995, Temple 2005).

In White *et al.*'s (2012) White-breasted Thrasher habitat suitability model, land cover was considered, but ultimately it was not included in the final suitability model because it had low explanatory power. We found a high importance of land cover in our habitat suitability assessment, which was not surprising for a habitat specialist. It is possible that land cover did not show strong relationships to White-breasted Thrasher site occupancy in White *et al.*'s (2012) model because the land cover data were almost 30 years old. White *et al.* (2012) also did not consider predators in their model. Our analysis, which predicted a much more restricted distribution for White-breasted Thrasher habitat suitability, used a much more recent land cover database and included distributional data on predators, which might affect the species' distribution.

Our full range model, which used data from the entire occupied portion of the Saint Lucia range, predicted that virtually all the most suitable habitat in Saint Lucia for the White-breasted Thrasher is found within the current range of the species, primarily in the Mandelé range. Parts of the Iyanola range were categorised as unsuitable or marginally suitable by our model, as well as by White *et al.* (2012), and this matches field observations that only a small subset of this range appears to be occupied by the species (Temple 2005). Our best model included five variables that each had > 5% contribution, and two of those were predators (Table 2). The most influential variable was Saint Lucia fer-de-lance presence (positive association), followed by annual precipitation (negative association), land cover type, in which deciduous forest was positively associated with White-breasted Thrasher presence, small Asian mongoose presence (negative association), and isothermality (negative association). In the south-eastern part of the island, south of the Mandelé range, there is an area that is identified as moderately suitable (Figure 2, Figure S3). This area once had White-breasted Thrashers, but they disappeared after human conversion of the area to agriculture and support services (Bond 1928). We suspect that the reason this area is identified as being of moderate quality is that there are still small patches of dry forest habitat mixed in with the developed areas.

When we created models using data from one of the species' ranges and then assessed habitat suitability in the other range (i.e. partial range models), neither model performed as well as the full model, although the Iyanola region model did a better job of identifying suitable habitat in part of the Mandelé region than did the reverse application. Based on the low AUC values of the Mandelé-trained model, it appears that the combination of features associated with high suitability (i.e. White-breasted Thrasher presence) in Mandelé is not found in Iyanola. The best Mandelé model included Saint Lucia Fer-de-lance, Southern Opossum, and Small Asian Mongoose coverages. Although the final Iyanola model included the same species, the direction of the relationship was opposite for the mammal variables between the two models. White-breasted Thrashers were associated with closer distances to small Asian mongoose and farther distances from southern opossum in the Iyanola-trained model, whereas in the Mandelé-trained model they were found farther from small Asian mongoose and closer to southern opossum. The Mandelé-trained model predicted no suitable habitat within the current Iyanola range. This discrepancy between models might be due to a difference in environmental constraints between the two Saint Lucia ranges, if different environmental drivers affect the habitat suitability for the species in each area, or to the Iyanola range being generally unsuitable. The White-breasted Thrasher distribution is patchy throughout the Iyanola region, where they are primarily restricted to riparian forest near streams (Temple 2005). White-breasted Thrashers do not seem restricted by the same environmental characteristics in the Mandelé area (Temple 2005, Young *et al.* 2010). Another possibility is that an environmental factor common to both sites constrains habitat suitability but was not included in the model. For example, data were not available on several local factors thought to be important to the species, such as leaf litter depth and the presence of Bwa Gwiyé, an important food and nesting resource (Temple 2005). In lieu of these potentially important variables, other environmental qualities that differ between the sites could have been interpreted as important by the models and extrapolated across the island.

As with the full-range model, the model built on the Iyanola range identifies some habitat of moderate suitability along the west coast. These similar predictions of moderate suitability so far from the White-breasted Thrasher's current range likely reflect the habitat similarities between the two coasts, and that some important feature of habitat (used broadly to refer to more than just plant structure) is missing from our models, such as the understorey features mentioned above.

We are in the early stages of understanding which of the relationships we found are correlative and which are causative. Eventually we want to determine what limits White-breasted Thrasher population size and range (cf. O'Connor 2002). However, we can make some reasonable assertions that can be treated as hypotheses to be tested. First, we speculate that habitat availability limits the distribution of this species for two reasons: (1) the White-breasted Thrasher is a facultative cooperative breeder, which typically are limited by habitat or some habitat feature (Emlen 1982), and (2) following habitat loss in the Mandelé range in 2005–2006, family group sizes increased (Mortensen 2009), presumably due in part to displaced birds returning to previous family groups, or because of more severely limited dispersal options. We assume that habitat distribution is driven by weather, land structure, human population density, and human alterations to the landscape, so we would consider these to be secondary drivers of White-breasted Thrasher distribution. The correlations of occupancy with native and introduced predators present more complex relationships. In all three of the best models, the species was associated with areas closer to the Saint Lucia fer-de-lance range; it is possible that the Saint Lucia fer-de-lance restricts the abundance and/or local distributions of the introduced predators, or that both the White-breasted Thrasher and Saint Lucia fer-de-lance tend to live in areas that are less disturbed by humans. Overall, White-breasted Thrashers were found farther from the mammalian predators, with the exceptions of small Asian mongoose in the Iyanola-trained model and southern opossum in the Mandelé-trained model; it is possible that this positive association is driven by common habitat requirements or the birds' restricted habitat forcing them to overlap with the mammalian predators in some areas. We also note that the presumed relationships with introduced mammalian predators could have been affected by the sparsity of the mammal data, taken from point locations that were often along roads rather than from systematic surveys across the island. Consequently, greater data resolution, more extensive surveys of potential predictor variables, and experimental management actions will be needed to test these hypotheses. Finally, neither White *et al.* (2012) nor this study included understorey and related site-specific data or species detectability in the models. From Temple (2005), we know that some site specific features are associated with the presence of White-breasted Thrashers, but we do not have georeferenced data for these features island wide. Including species detectability can also improve habitat suitability models (Guillera-Arroita *et al.* 2015). Detectability is less of a problem for White-breasted Thrashers surveyed during the breeding season because they are highly territorial and have small territories (Temple 2005, Mortensen 2009).

A recent management plan for White-breasted Thrashers proposes creating reserves in the current Iyanola and Mandelé areas (Felix *et al.* 2014). Our results indicate that the currently occupied areas, particularly Mandelé, support the highest-quality habitat and should be prioritised for conservation efforts. Changes in species distributions over the past few decades suggest that some recovery can be made by allowing early successional forest to develop (Donald Anthony, St. Lucia Forestry Department, cited in Felix *et al.* 2014). Understanding the relationships between the White-breasted Thrasher and the introduced and native predators also appears to be important, and we suspect that resolution of the relationships will require more detailed distribution maps and predator abundance manipulation.

Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270915000374

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