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Reintroduction or natural colonisation? Using cost-distance analysis to inform decisions about Rodrigues Island Fody and Warbler reintroductions.

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Abstract

When making decisions about reintroducing a species, practitioners need to consider whether the release site contains habitat suitable for those species, whether past extinction drivers have been remedied and whether reintroduction is the best option for the species to recolonise the release site. These concerns are captured within two paradigms; the habitat and metapopulation paradigms. We use cost-distance analysis to assess the need for reintroduction of two bird species, Rodrigues Fody and Rodrigues Warbler, to Anse Quito reserve on Rodrigues Island, testing hypotheses based on these underlying paradigms. Given a lack of detailed field studies of dispersal across the landscape on either species we rely on expert judgement. Our results show that experts believe Rodrigues Fody will naturally colonise Anse Quito but that Rodrigues Warbler may not, at least within a time frame of 10 years. This information and treatment of expert judgement allows greater justification in reintroduction planning. Our method shows one way to assist in reintroduction decision making in poorly studied systems.

Introduction

The ability of animals to move across landscapes affects nearly all components of their life-history (Singleton et al., 2002; Prugh et al., 2008; Benitez-Lopez et al., 2010; Aben et al., 2012). When the ability to move through the landscape is reduced, this can lead to conservation concerns for threatened species. Increasing fragmentation and loss of habitats at the landscape scale, for example, is cited as one of the biggest threats to species survival (Prugh et al., 2008; Benitez-Lopez et al., 2010; Ewers et al., 2010). Heterogeneous species distributions can arise in fragmented landscapes, and patches may be vacant because they are poor quality, or they may be suitable yet unoccupied due to stochastic processes (Hanski, 1999; Armstrong, 2005; Prugh et al., 2008).

Understanding why a species is absent from a landscape fragment is a common problem in reintroduction biology (Armstrong, 2005; Osbourne & Seddon, 2012; IUCN, 2013). If fragment isolation is the major reason for a species absence, then reintroduction is often proposed (Komdeur, 1994; Osbourne & Seddon, 2012). Current reintroduction guidelines advise full consideration of alternative solutions that may achieve the same benefit as reintroduction but at lower cost and risk, such as waiting for natural re-colonisation to occur (IUCN, 2013). Reintroduction into an unoccupied fragment should only be considered if it is suitable (Osbourne & Seddon, 2012; Bennett et al., 2013).

The distinction between landscape fragments being unoccupied because they are either isolated or of poor quality for a particular species is captured by two ecological paradigms; the metapopulation paradigm and the habitat paradigm (Hanski, 1999; Armstrong, 2005; Davies-Mostert et al., 2009). The metapopulation paradigm explains species distribution over the landscape by fragment area, isolation and intrinsic population rates (Hanski, 1999). In metapopulation biology, a landscape fragment is more likely to be colonised and persist if it is

larger and closer to other colonised fragments (Hanski, 1999; Prugh et al., 2008). When landscapes become increasingly fragmented, then local extinctions may simply re-occur following any re-colonization via stochastic processes, despite a given fragment being suitable. A suggested solution to this for managing threatened species is a ‘managed metapopulation’ whereby a series of small, isolated subpopulations are managed as a single population by translocating individuals between them to buffer against stochastic elements (for example African wild dogs, *Lycaon pictus*; Davies-Mostert et al, 2009).

In contrast, the habitat paradigm explains species’ distributions as being solely the result of fragment quality (Hanski, 1999; Armstrong, 2005). A species will remain present if the fragment is suitable (Hanski, 1999; Singleton et al., 2002; Osbourne & Seddon, 2012). The implicit assumption is that distributions are not affected by stochastic processes or connectivity (Armstrong 2005). Although often considered in isolation, both paradigms will always operate together, and both should be considered in management planning (Armstrong, 2005).

Cost distance analysis provides one way to evaluate how difficult a move to an unoccupied landscape fragment is, and relates to both paradigms by considering both isolation and suitability within and between fragments (Singleton et al., 2002; Adriaensen et al., 2003; Beier et al., 2009; Richard & Armstrong, 2010; Aben et al., 2012). This method calculates a cumulative cost to move between a source and a destination, where the land cover types at each site and between them is important, as well as the distance moved to reach the destination. The analysis requires assigning resistance values to land cover types, according to its facilitating/hindering effects on the movement process (Adriaensen et al., 2003), but defining these values for poorly studied species is difficult (Yamada et al., 2003; Beier et al., 2008; Beier et al., 2009; Richard & Armstrong, 2010). One option is to study dispersal through land cover types for a given species (Beier et al., 2008; Dreiezen et al., 2007; Richard & Armstrong,

2010, Stevenson-Holt et al, 2014), yet this takes substantial effort that may be beyond the capacity or priority of some programs (Yamada et al., 2003; Richard & Armstrong, 2010; Aben et al., 2012). This predicament is a common scenario faced by threatened species managers and often results in urgent decisions being made by experts unilaterally, using poorly clarified assumptions, and at most implicitly accounting for uncertainty in knowledge. A far better approach is using formal tools to obtain expert knowledge, considering the known limitations of such knowledge, and then using expert knowledge to solve management decisions (Burgman et al., 2011; Runge et al., 2011; Martin et al., 2012). Crucially, explicit exposure of assumptions and full treatment of uncertainty in knowledge provides the necessary detail for others to engage with and improve, or support, the management decisions being made.

This study aimed to investigate whether Rodrigues Fody (*Foudia falvicans*; hereafter Fody) and/or Rodrigues Warbler (*Acrocephalus rodericanus*; hereafter Warbler) will naturally recolonise 34ha Anse Quitar reserve on Rodrigues Island, or whether reintroduction might be needed. Managers would like both bird species to become established at the reserve as part of the site's restoration. The suitability of Anse Quitar, and ability of Fody and Warbler to reach it, are only a component of the broader recovery objectives managers have. We therefore developed two broad hypotheses based on the metapopulation and habitat paradigms and the manager's decision support needs. If range expansion of both species is mediated by selection of species-specific suitable habitat and the Anse Quitar reserve does not contain this, then colonization will not occur either naturally or by reintroduction (H1, habitat paradigm). Under H1 we would not suggest considering reintroduction without further habitat restoration. Alternatively, the landscape at Anse Quitar reserve may contain species-specific suitable habitat but no longer be accessible as a result of unsuitable land cover types in the connecting landscape. Natural re-colonisation is unlikely until the connecting landscape becomes suitable for each species (H2, metapopulation paradigm). Under H2 we would suggest reintroduction

if it best met the broader set of management objectives. Such a reintroduction could speed up an eventual natural colonisation or be a desired component of a managed metapopulation.

Methods

Study Area

Rodrigues island (19°4'S, 63°3'E) is a 108km² volcanic island in the Indian Ocean. Rodrigues was once completely forested but became highly degraded following human colonisation, with much of its native forest destroyed, replaced by agriculture and invasive exotics (Impey et al., 2002; Showler & Jones, 2002). The island is characterized by a central ridge with a high-point of 398m. Most remnant vegetation is located on this central high ridge and in forested valleys leading to the coast on either side (Showler & Jones, 2002; Norfolk, 2010; Steward, 2010). The forest is a mix of approximately 65 native and exotic species including vacoas (*Pandanus* spp), mango (*Mangifera indica*), jamrosa (*Syzygium jambos*), guava (*Psidium* species) and tecoma (*Tabebuia pallida*) (Steward, 2010). Three other forest types are also present and distinguishable from mixed forest, these are Eucalyptus stands (*Eucalyptus tereticornis* and *Eucalyptus grandis*), coastal casuarina (*Casuarina equisetifolia*) and acacia (*Leucaena leucocephala*) (Steward, 2010). Heterogenous smallholder croplands interspersed with small and patchy residential areas comprise the non-forest landscape of the island's interior, with grassland pasture more common towards the coast. The Anse Quitor restoration project is situated in a valley near the coast in the southwest of the island. It appears isolated from the current range of both Fody and Warbler. Active restoration through removal of exotic plant species and replanting native species has been ongoing since 1996.

A landscape map created from aerial imagery was adapted to reflect categories relevant to the study species and used to map differing cost or resistance to travel across the landscape (Figure 1). Full details are available in the Supplementary Information.

Study Species

Both the Fody and the Warbler are small insectivorous passerines that represent the only remaining endemic bird species on Rodrigues island (Impey et al., 2002; Sinclair & Langrand, 2003; Showler et al., 2002). They are currently listed as Near Threatened under the IUCN Red List criteria (Birdlife International, 2013a,b). Both species live in forest habitat on the elevated central ridge and radiating valleys. They are territorial pair breeders throughout most of the year, with small territory sizes (Impey et al., 2002; Showler et al., 2002). Historical records indicate both birds were once common throughout the island (Impey et al., 2002; Showler et al., 2002). The Fody population declined dramatically to an estimated 10 individuals by 1968 (Impey et al., 2002), but has shown a substantial recovery since that time, with an estimated 803 pairs reported in 2010 (Norfolk, 2010). Similarly, the Warbler population declined to an estimated 8 individuals in 1979, but has since increased, with an estimated 3,100 - 3,900 individuals recorded in 2010 (Showler et al., 2002; Steward, 2010; Birdlife International, 2013 a,b). This rapid population increase in both species is possibly an unintended result of afforestation for water-catchment management, and a shift from timber to coal fuel usage (Impey et al., 2002; Birdlife International, 2013 a,b).

Warbler and Fody distributions were obtained in 1999 and 2010 from two survey studies for each species (Impey et al., 2002; Norfolk, 2010; Showler et al., 2002; Steward, 2010). Survey methods were similar in all studies (see Supplementary Information). Ranges for each species were bounded by known presence of birds recorded in each survey. We do not know the detection probability of either species in these previous surveys as this was not determined, and we therefore expect both sets of surveys will under-represent the true species distributions. This is the only information available to us, and is on what the experts based their judgments of dispersal ability and suitability of Anse Quitor (see below).

Expert Elicitation of Landscape Resistance Values

Without available detailed studies on dispersal and movement behaviour for either species, the resistance values (Adriaensen et al., 2003) for each of the 10 land cover classes (see Table 1 and supplementary information Table 1) was determined using expert elicitation. We asked for expert judgement on land cover preference (how likely it would be to find a given species in a given land cover type) as this was more intuitive to experts based on their working experience with each species.

We assumed that land cover preference would provide a suitable surrogate for land cover resistance and could be translated into a number representing the resistance to each species of crossing each land cover type. Our assumption is supported by the observation that expanding populations of both Fody and Warbler appear largely restricted to forest type land cover and from dispersal studies of other non-migratory and threatened island passerine species that show a greater reluctance to travel through land cover types that they do not also reside in (Richard & Armstrong 2010; Richardson 2015). All experts were aware of and agreed with this assumption.

Expert judgement was elicited from 11 experts, broadly following the recommendations of Yamada et al. (2003) and Gregory et al. (2012) using a modified Delphi approach via email. Eleven experts exceed the 3-7 recommended as sufficient for this process by Gregory et al. (2012). Experts were identified as those who had both detailed knowledge on either species in different occupied sites and detailed knowledge of the island's land cover and forest restoration. Calibration of experts was achieved by providing a summary of available evidence of land cover use by each species and through discussion over multiple rounds of visualizing the values each expert provided. During group discussions, the values were presented anonymously. The

goal of the modified Delphi approach is to better obtain the expert's true belief and allow greater robustness in behavioural aggregation between experts (for further detail of this approach see McBride et al., 2012).

Values were elicited on a three-point scale for each land cover type, including their most likely value, their highest possible and lowest possible values such that the true value would fall somewhere within the range (i.e. with 100% confidence). This approach is proven to reduce the problems of overconfidence that is frequently observed in expert opinions of uncertain system states (Burgman et al., 2011). We chose to use the three-point scale as it was easier to explain to the range of experts via email than an alternative four-point scale (where confidence is requested rather than defined). Estimates by the 11 experts were then averaged to obtain a unique set of values for each land cover type to reflect uncertainty, defined as a mean most likely value, mean lowest and mean highest bounds. For each species we then used the lowest, highest and most likely values for each land cover type to fit a beta-PERT distribution to the estimates, a distribution specifically developed for the treatment of expert-elicited information (Vose 1996). We used this to generate an empirical distribution of 1,000 sets of random values for the probability of each species' presence in each land cover type, to fully account for uncertainty.

Land cover preference scores (elicited on a scale of 0-1) were converted to resistance values by inverting them and, to allow analysis in the GIS, linearly rescaling to lie between 1 (the highest possible land cover preference and lowest resistance) and 100 (the lowest possible land cover preference and highest resistance).

Resistance Maps

A series of 1,000 GIS resistance maps were produced for each species by using the expert elicited and converted scores to attribute each 20m cell in a GIS raster map, representing the resistance to movement and so cost associated with moving across it.

Cost Distance Analysis

Cost distance analysis calculates the least relative cost required to move between two geographic locations across resistance maps (ESRI ArcGIS; Adriaensen et al., 2003; Driezen et al 2007; Stevenson-Holt et al., 2014). Travel cost is calculated by combining linear distance moved and resistance value of each cell passed through. The least cost path is determined by analysing the cost to move out of each starting cell into a neighbouring one and choosing the move that has the least cost. This is repeated, so the path moves out across the map. The cost of moving along each path is accumulated along that path and summed to calculate the cumulative cost to reach each cell in the map from the nearest source cell (see Adriaensen et al., 2003 and Supplementary Information). The cumulative cost values in the destination cells are used to compare travel costs.

The cost analysis was conducted in two steps for each iteration for each species. Firstly, we calculated the maximum cumulative costs achieved in the current known range expansion between 1999 and 2010. There is a range of costs associated with traveling from different parts of the previous range to different parts of the current range; the maximum cumulative cost expended by the birds to reach the current range represented our belief of the maximum possible cost that each species could accommodate in future range expansions over a similar time frame (ca. 10 years). In this first step the occupied cells in the 1999 survey were treated as the start point and the cumulative costs incurred to travel to the additional cells occupied in the 2010 survey were calculated. Secondly, the predicted cost of future range expansion for

each species was calculated. In this case, cells occupied in the 2010 range were treated as the start points and new cumulative cost maps were generated for the island. The minimum cumulative costs required for the range to expand to the Anse Quito reserve was calculated. We then compared the maximum cost from past range expansions to the minimum required to reach Anse Quito to determine whether we expected colonisation or not (illustrated in Figure 2 using a set of most likely values obtained from experts).

Results

Landscape Preference and Assessment of Anse Quito Reserve

For both species, the preference values assigned to land cover types by the experts resulted in a high predicted preference for mixed forest, low preference for barren and grassland land cover types and medium preference for the intermediate land cover types for both species (Table 1). This is consistent with the landscape types occurring in both species current ranges. The current range of both species consists of more mixed forest than any other land cover type (47% of Fody range and 55% of Warbler; Table 2). As mixed forest, the Anse Quito reserve was scored, on average, by experts as the most highly preferred land cover type for both species (Table 1).

Cost Distance Analysis

Our simulations showed that in 928 of 1,000 simulation runs (92.8%) the Fody was predicted to expand its range to include Anse Quito reserve at the same or less cost than expended during the 10 year expansion made between the 1999 and 2010 surveys (Figure 2 & 3). In contrast, in only 344 of 1,000 runs (34.4%) the Warbler range was predicted to expand to reach Anse Quito reserve. In the majority of simulations, the cumulative cost of reaching Anse Quito was more than that expended in the Warblers previous range expansion between 1999 and 2010 (Figure 2 & 3). Furthermore, in those Fody simulations where colonisation did not occur, the extra cost

they would need to reach the reserve was small (3 to 20% of range of costs; Figure 3), contrasting to the Warbler where there was frequently a substantial cost differential (0.003-54% of range of costs; Figure 3). This result suggests that experts were less convinced that the Warblers will reach Anse Quito within the ten year time horizon than the Fodys.

Discussion

Both the Fody and Warbler have shown remarkable range expansions through their most preferred mixed forest land cover in the period between 1999 and 2010. Unsurprisingly, the predicted cost to reach some un-colonised areas on the island is more than that expended by either species in moving from their historical to current ranges. Most unoccupied area, including the Anse Quito reserve, is in the west of the island. The greater cost to disperse west is because there are more, larger and more inter-connected residential and grassland land cover areas that are unfavourable to both species in that direction, highlighting the fact that dispersal across landscapes strongly depends on the configuration of land cover.

The classification of Anse Quito reserve as mixed forest, the preferred species-specific habitat for both Fody and Warbler, suggests that their current absence in the reserve is not driven solely by the habitat paradigm. Thus we can reject our hypothesis H1. Anse Quito reserve has been the subject of intensive restoration efforts by the Mauritian Wildlife Foundation over the last 20 years. A recognized caveat here is that we are basing our species-specific suitable habitat assessment on a coarse judgment of vegetation structure that may miss important aspects each species requires. The assessment is supported, however, by the fact that the current range of both species consists of more mixed forest than any other land cover type (47% of Fody range and 55% of Warbler; Table 2).

Anse Quitar reserve is small and a long distance from the current ranges of both Fody and Warbler. Thus, the current absence of both species is better explained by the metapopulation paradigm. Our cost analysis for Warblers indicated natural colonization was less likely, supporting our hypothesis H2 that the reserve, although suitable, may not be easily accessible. Fody and Warbler already occupy most of the available mixed forest habitat on Rodrigues; 75% within the current range of the Fody and 77% within the current range of the Warbler (Table 2), meaning Anse Quitar provides rare unoccupied and suitable habitat for both species. There may, therefore, be a greater need for reintroduction to establish a population of Warbler at Anse Quitar reserve. In contrast, Fodys are thought likely to naturally colonise Anse Quitar and a recent possible sighting of a Fody at the reserve (Alfred Begue, personal communication) is encouraging.

The predicted travel costs to colonise Anse Quitar reserve are based on the judgement of experts in the absence of detailed dispersal data. It is not unusual for management decisions for threatened species to rely on judgments of experts (Yamada et al., 2003; Murray et al., 2009; Runge et al., 2011; Martin et al., 2012). Acknowledging this and then utilizing best-practice protocols to obtain these judgments allows for decisions based on the highest possible quality information and it provides an alternative to investing in further field research on dispersal capacity (Yamada et al., 2003; Murray et al., 2009; Gregory et al., 2012; Converse et al., 2013).

The conclusions obtained from experts effectively constitute hypotheses about the dispersal capacity and colonization potential of Anse Quitar by each species. Our study was done within the context of limited resources available to directly study dispersal behaviour of each species and the need to support decisions about reintroduction. Decision makers can place some confidence in the expert belief that Fody will reach Anse Quitar within 10 years. This was not the case for Warblers, where only about one third of our simulations showed they would reach

Anse Quitor reserve unassisted. An interesting future application could be to carefully monitor ongoing range expansion and compare to the predictions made by experts. A choice of whether to invest in detailed monitoring, particularly to resolve uncertainty in the probability of Warbler to reach Anse Quitor, could be formalized through a value of information analysis (Runge et al., 2011, Canessa et al., 2015). Value of information analysis may help justify the cost of learning about Warbler dispersal in terms of selecting between reintroduction and self-colonisation to achieve the manager's restoration objectives. Without further learning then our use of expert judgement makes the management decisions more transparent and accountable (Beier et al., 2009; Burgman et al., 2011; Gregory et al., 2012).

Our study and the support it provides to decision makers is necessarily based on numerous assumptions. Perhaps the most important one is using expert judgment of land cover preference as a surrogate for resistance to dispersal. However, without investing in learning the resistance values of different land cover types we believe it the best available solution. Our justification is two-fold; firstly the experts discussed and agreed with this assumption for the purposes of this decision. By definition, this group of people have most knowledge about these species and the island within which they are found. Secondly, work on dispersal in other threatened forest dwelling island passerines shows that preference and preferred dispersal routes are tightly aligned (Richard & Armstrong 2010; Richardson 2015). Furthermore, detection probability and the methods of previous surveys may not accurately represent historic range and recent range expansion. It is certain that there has been a remarkable recovery but uncertainty in just how much. Again, this is the available information for experts and decision makers. Finally, we are making a dichotomy between natural colonization, or not, within ten years. Although in many cases the Warbler was not predicted to naturally colonise within this time frame they may still do so. The decision maker in this case is fully aware of this ten-year cut-off.

Determining how a species can move through heterogeneous landscapes is a challenge for decision makers involved in reintroduction planning (Armstrong & Seddon, 2008; Richard & Armstrong, 2010; Osbourne & Seddon, 2012; IUCN, 2013). The information we have generated here will assist decision makers in weighing up whether or not intervening through reintroduction for either species is desirable. The relative ease of natural colonization of Anse Quitor reserve by either species is likely to be only one of many factors that decision makers will consider when choosing whether to implement reintroduction. It is likely to depend on the wider objectives of Anse Quitor restoration. For example, if either Fody or Warblers provide important ecosystem services that would benefit the continued restoration of the Anse Quitor reserve and the risks to both species source populations are low, then reintroduction to speed colonization may be favoured (similar to justifications made by Morrison et al., 2011). Conversely, if natural colonization is deemed likely within a reasonable time frame, both species are unlikely to face extinction, and the benefits to the reserve are minimal, then waiting for natural colonization may be chosen. The preferred decision depends on the agreed objectives for management and trade-offs between those objectives (Converse et al., 2013). Our study is not designed to make the decision to reintroduce or not, rather it is to provide an important piece of information to include within that decision process.

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Table 1. Mean values of expert opinion (mean most likely, mean lowest and mean highest) of preference scores (scale 0-1) for each land cover type on Rodrigues island for Rodrigues Fody and Rodrigues Warbler. Opinions were elicited from eleven experts on a three-point scale including the lowest, highest and most likely values such that the expert was 100% confident the true value would fall within their range. *The Anse Quitor reserve is mixed forest and we have greyed that habitat column to highlight the opinion for the destination sites' suitability.

Species	Built up	Agricultural	Casuarina Forest	Acacia Forest	Eucalyptus Forest	Grassland	Barren	Residential agricultural	Residential	*Mixed Forest
Fody	0.52 (0.33-0.75)	0.38 (0.16-0.55)	0.02 (0.01-0.07)	0.1 (0.03-0.18)	0.44 (0.25-0.61)	0.08 (0.04-0.11)	0.01 (0.01-0.02)	0.5 (0.28-0.4)	0.4 (0.3-0.5)	0.82 (0.6-1.0)
Warbler	0.27 (0.11-0.47)	0.32 (0.15-0.55)	0.05 (0.01-0.08)	0.04 (0.01-0.09)	0.49 (0.42-0.7)	0.03 (0.01-0.07)	0 (0-0)	0.47 (0.33-0.66)	0.33 (0.24-0.63)	0.85 (0.65-0.98)

Table 2. Proportion of the current ranges of Fody and Warbler under each landscape type and as a proportion of the total area of that landscape available on Rodrigues. Mixed forest, the most preferred habitat in the experts' opinion is in bold.

Landscape Type	Fody		Warbler	
	% of range	% of total on Rodrigues	% of range	% of total on Rodrigues
Mixed Forest	47	75	55	77
Residential Agriculture	21	48	15	29
Agriculture	15	46	15	40
Grassland	7	12	8	12
Residential	4	54	3	43
Eucalyptus Forest	3	42	2	21
Acacia Forest	1	11	1	10
Built-up	1	20	1	13
Barren	1	30	1	24
Casuarina Forest	0	0	0	0

Figure 1. Land cover types of Rodrigues Island. Anse Quito reserve is shown in black.

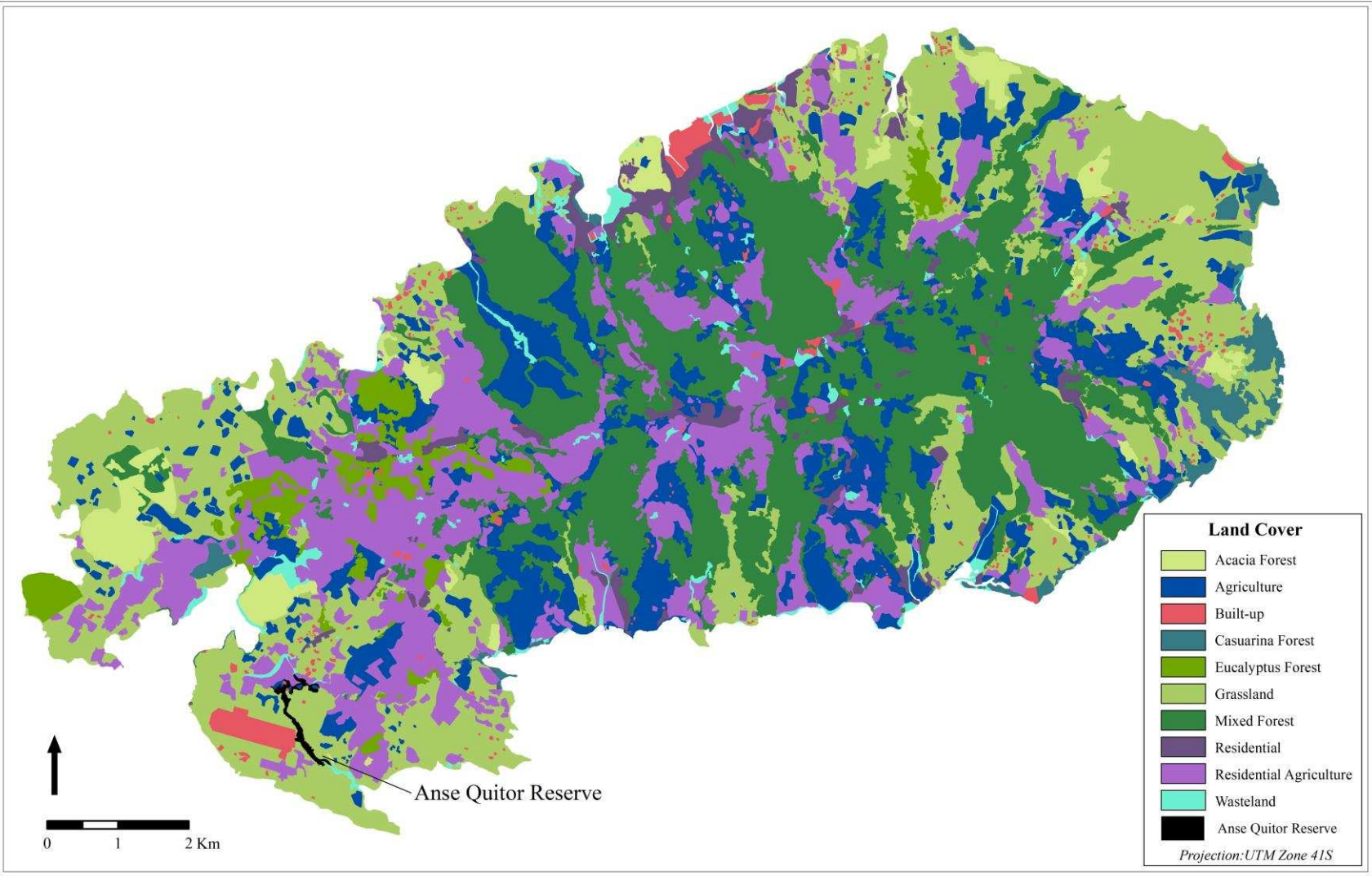


Figure 2. Example of the predicted approximate 10 year future range expansion of the Rodrigues Fody (A) and Rodrigues Warbler (B), based on the cumulative cost expended during expansions across different land cover types between the 1999 and 2010 surveys using the mean of the experts' most likely values. Each map shows historic range (estimated at 1999), current range expansion (estimated at 2010) and future predicted range expansion over a similar time period. Striped zones represent regions of Rodrigues unlikely to be colonised within a similar timeframe and cumulative cost as was previously achieved in the 1999-2010 expansions. The Anse Quitor reserve is shown in black.

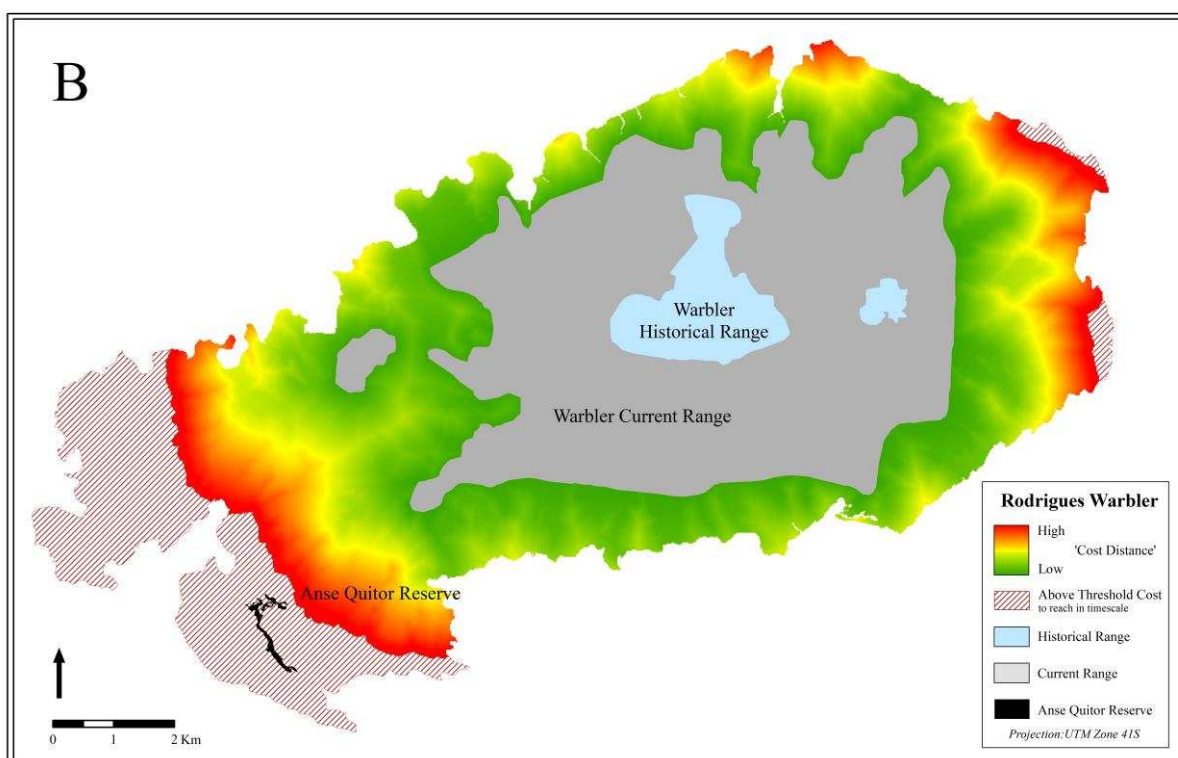
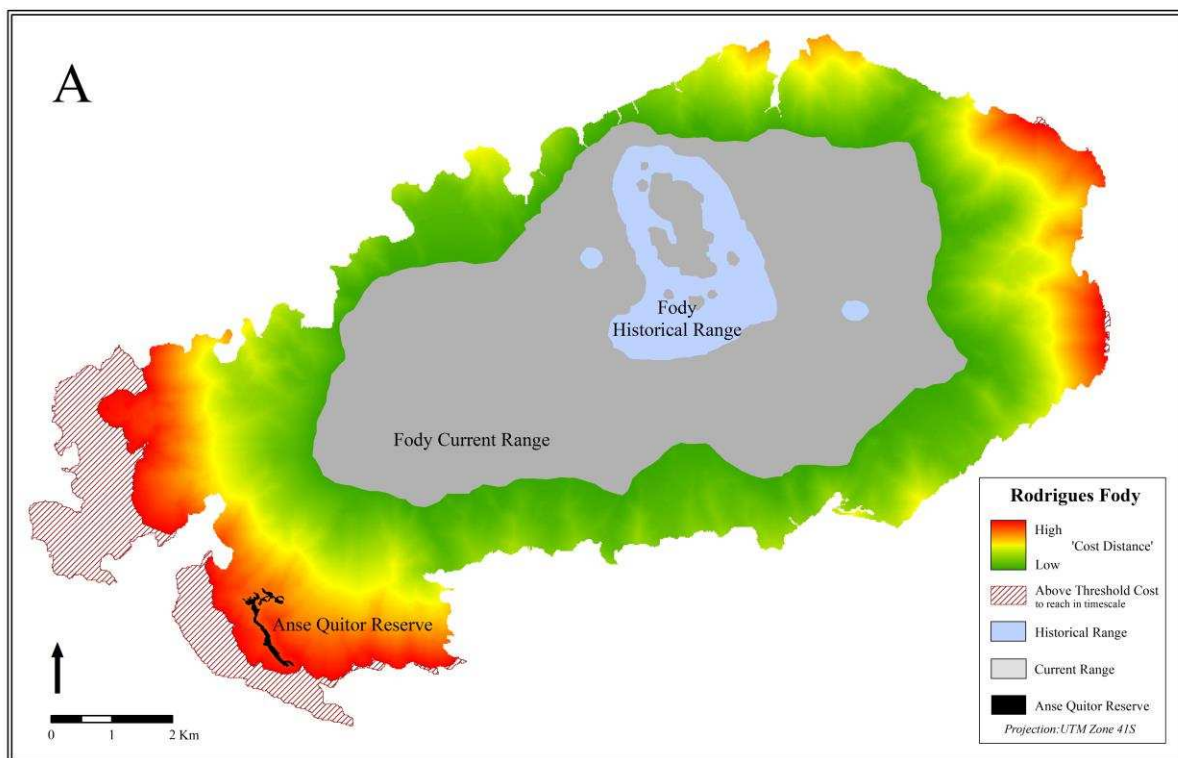
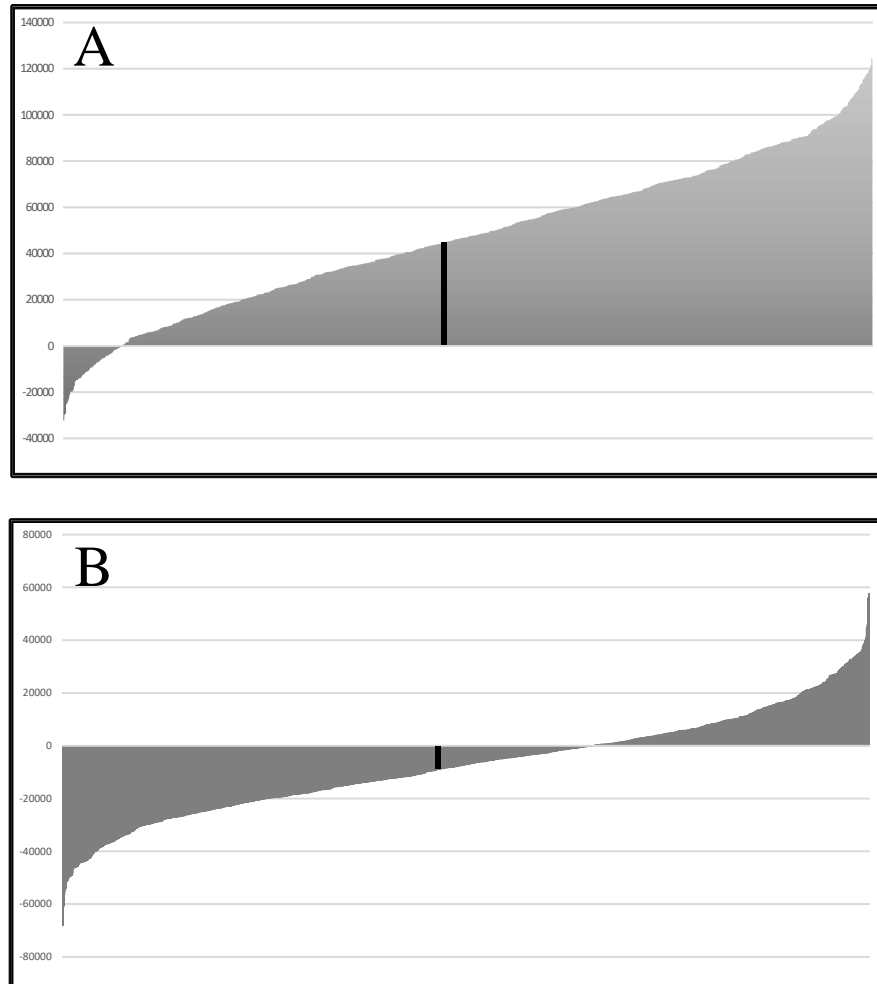


Figure 3. Differences between maximum costs expended in previous range expansion and predicted costs to reach AQ reserve in 1000 simulations for Fody (A) and Warbler (B). Those above zero difference in cost are predicted to make it to AQ reserve. The mean of the most likely expert values results are highlighted (A Fody: 45,166 and B Warbler -7,851). *Note different scales.



Supplementary Information

Surveys

In brief, territory mapping was carried out during the breeding season. Territory mapping involved attracting birds by sound while walking along parallel transects in core bird areas. Surveys used a “phishing” technique (the surveyor makes a “phishing” sound that attracts both species to the surveyor) (Impey et al., 2002), or song playback, either as a full replacement to “phishing” (Showler et al., 2002, Steward, 2010), or in addition to it (Norfolk, 2010). Population estimates were calculated by assuming there were two birds to each territory.

Landscape Map

A landscape map (6m resolution) with 20 land cover types created from aerial imagery taken between 2006 and 2008 was used (kindly provided by The Mauritius Ministry of Agro Industry and Food Security, The Forestry Service Ministry of Agro-Industry and Fisheries and the Mauritius Sugarcane Industry Research Institute). We modified this existing map by reducing these 20 human-centric land cover types to 10, based on the key land cover types identified to be of importance to the Fody and Warbler in the population surveys (Impey et al., 2002; Norfolk, 2010; Showler et al., 2002; Steward, 2010). In addition, the broad forest classes of the original map were expanded to better capture forest types that were more important to each species (Figure 1; see Supportive Information Table 1 for original and modified forest types). To distinguish and separate forest cover types and reclassify them, all 208 forest polygons were visited by one of us (Olivia Davies).

The landscape map was verified in two ways. Land cover types were checked against Google Earth 2012 satellite imagery to identify any large discrepancies between land cover type polygons on the vector map and more recent satellite imagery. Additionally, the map was ground-truthed by creating 50 area and land cover type-weighted random location points, which were visited to within

4m-100m, depending on access, to visually check or identify the land cover type, but with very little change required.

Table 1. Description of the original land cover types used in the habitat map and the ten land cover types used in the analysis.

Original land cover type	Description	Study land cover type	
Forest	Natural or exotic trees with a closed canopy.	Mixed Forest	Coastal Casuarina Forest
		Eucalyptus Forest	Acacia Forest
Grassland	Coastal vegetation of short grasses and occasional wide-spaced trees.	Grassland	
Shrub	Natural or exotic vegetation of open woody bush or bare rock.	Barren	
Marsh	Aquatic or regularly flooded vegetation.		
Beach	Beaches		
Sea	Inland saltwater body		
River	River estuaries.		
Wasteland	Natural or man-made soil or concrete without vegetation.		
Agricultural	Small-sized fields of rain fed crops.	Agricultural	
Terrace	Used or abandoned agricultural fields on a steep slope.		
Residential Agricultural	Wide spaced (>30m) housing with agricultural land attached.	Residential Agricultural	
Residential	Closer spaced (<30m) housing with no agricultural land.	Residential	
Farmstead	Farm out-buildings and isolated farm housing.	Built-up	
Buildings	Official buildings and shops.		
Hotel	Hotel		
Cemetery	Cemetery		
Sports	Sports fields		
Drain	Large storm drains.		
Airport	Airport		

Cost Distance Analysis

The cost distance tool of ESRI ArcGIS 10.3 was utilised to calculate accumulated cost distance. The method is detailed in Adriaensen et al 2003, and described as follows in the ESRI user documentation;

When moving from a cell to one of its four directly horizontally or vertically connected neighbours, the cost to move to the neighbouring is 1 times the cost of cell 1, plus the cost of cell 2, divided by 2: $a1 = (\text{cost1} + \text{cost2}) / 2$. Where cost1 = the cost of cell 1, cost2 = the cost of cell 2, a1 = the total cost of the link from cell 1 to cell 2.

If the movement is diagonal (a longer distance from the centre of the cell to the centre of a diagonally connected neighbouring cell than from the centre of the cell to the centre of a horizontally or vertically connected neighbouring cell), the cost to travel over the link is 1.414214 (or the square root of 2) times the cost of cell 1 plus the cost of cell 2, divided by 2:

$a1 = 1.414214 (\text{cost1} + \text{cost2}) / 2$. Where cost1 = the cost of cell 1, cost2 = the cost of cell 2, a1 = the total cost of the link from cell 1 to cell 2.