



RESEARCH ARTICLE OPEN ACCESS

Elevational Range Changes of Tropical Forest Birds on the Small Caribbean Island of Montserrat

Filibert Heim^{1,2} | James R. Daley³ | Calvin Fenton³ | James Boatswain³ | Stephon Hixon³ | Tavis Weekes³ | Lloyd Martin³ | Johannes Kamp¹ | Steffen Oppel^{2,4}

¹Department of Conservation Biology, University of Göttingen, Göttingen, Germany | ²Swiss Ornithological Institute, Sempach, Switzerland | ³Department of Environment, Ministry of Agriculture, Trade, Lands, Housing and the Environment, Brades, Montserrat | ⁴RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, Cambridge, UK

Correspondence: Steffen Oppel (steffen.oppel@vogelwarte.ch)

Received: 11 August 2025 | **Revised:** 17 March 2026 | **Accepted:** 27 March 2026

Keywords: climate change | distribution | dynamic occupancy models | forest | island | range shift

ABSTRACT

Aim: Globally, species are changing their ranges poleward and uphill due to climate warming. This poses a particular risk to biodiversity endemic to islands, where dispersal limitations may hinder latitudinal movement across the sea and elevational range changes can result in a smaller area of potentially suitable habitat. Few studies have examined whether bird species on small tropical islands exhibit changes in elevational ranges. Here we study elevational range changes in a forest bird community that hosts two globally threatened species, of which one is endemic to the small Caribbean Island of Montserrat.

Location: Montserrat, Lesser Antilles, West Indies.

Taxon: Forest birds.

Methods: We analysed point-count data collected between 2011 and 2024 with dynamic occupancy models which explain changes in occupancy over time by colonisation and extinction while accounting for imperfect detection. We assessed the influence of elevation on both colonisation and extinction to gather robust evidence of potential elevational range changes.

Results: We found evidence for range changes in five out of 12 species, with four species changing uphill, including the endemic Montserrat Oriole (*Icterus oberi*), and one species showing a range contraction towards lower elevations. However, model selection uncertainty limited our ability to infer the influence of elevation on occupancy dynamics in five species. We caution that the time span of our study may not have been long enough to detect range changes in all species.

Main Conclusions: Uphill range changes observed in this study may result from synergistic interactions of anthropogenic forest degradation at lower elevations, increasing temperatures due to global warming in the Caribbean, and other consequences of global change such as the impact of hurricanes on high elevation forest structure. Our study suggests that uphill range shifts may reduce the available habitat of a globally threatened bird species endemic to a small tropical island in the Caribbean.

1 | Introduction

Climate change causes significant alterations to the earth's biodiversity and its impact is predicted to increase during the 21st century (Pörtner et al. 2021; Thomas et al. 2004; Urban 2015). Species generally respond to climate change by changing their distribution to keep track with their preferred climate ('range

changes'), or by adapting to the new conditions within the same area ('niche shifts'), with species unable to respond facing extinction (Lenoir and Svenning 2013; Maggini et al. 2011; Parmesan 2006). In the future, a large number of species, especially those with small populations and restricted geographic and climatic ranges, could go extinct due to climate change-mediated range changes towards higher elevations and

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Journal of Biogeography* published by John Wiley & Sons Ltd.

latitudes (Chen et al. 2011; Lenoir and Svenning 2013, 2014; Manes et al. 2021; Parmesan 2006; Parmesan and Yohe 2003; Rubenstein et al. 2023). Species that are endemic to tropical mountains may be threatened first from these range changes (Lenoir and Svenning 2013; Manes et al. 2021), for example due to dispersal limitations and reduced habitat availability at higher elevations (Freeman, Scholer, et al. 2018; Urban 2018).

Range changes are alterations in the distribution of a species over time along at least one of three geographical dimensions—longitude, latitude, or elevation—and result from accompanying changes in the requirements and tolerances of the species (Lenoir and Svenning 2013). Mechanisms underlying range changes include population increases, decreases, colonisation and extinction across a population's core distribution or periphery (Lenoir and Svenning 2013). Different combinations of these changes in occupancy and abundance can lead to various types of range changes, including 'expansion' at one margin of a species' range (the leading edge), 'contraction' at the other margin of a species' range (the trailing edge), or a 'shift' with simultaneous expansion at the leading and contraction at the trailing edge (Breshears et al. 2008; Lenoir and Svenning 2013; Maggini et al. 2011).

Despite a general trend in range changes towards higher elevations and latitudes, changes to lower elevations or latitudes have also been reported (Lenoir et al. 2010; Rubenstein et al. 2023), as well as shifts in variable directions as a consequence of anthropogenic effects (Sanczuk et al. 2024). Many of the global diversity of range changes reflect the spatial heterogeneity of changes in climate and land use variables (Campbell et al. 2021; Lenoir and Svenning 2014) or their diverse impact on any biotic or abiotic factors that influence the range of a species (Neate-Clegg and Tingley 2023). However, which factors affect range changes in specific ecosystems is still poorly understood, especially in tropical regions, where only a few studies have examined range alterations (Colwell and Feeley 2024; Neate-Clegg and Tingley 2023; Rubenstein et al. 2023).

In the tropics, the steeper temperature gradient along elevation rather than latitude compared to temperate regions leads to elevational range changes being a common phenomenon (Colwell et al. 2008; Colwell and Feeley 2024; La Sorte et al. 2014; Urban 2018). Most elevational distribution changes in the tropics have been uphill (Neate-Clegg et al. 2021), partly because the forest ecotones themselves shift uphill due to a warming climate (Pouteau et al. 2018). On tropical islands, the opportunities for species to adjust their geographic ranges are limited by dispersal barriers: a generally shallow latitudinal surface temperature gradient in the tropics (Colwell et al. 2008; Colwell and Feeley 2024; La Sorte et al. 2014) forces species to either find suitable habitat at higher elevations or risk a long journey across the sea to colonise terrestrial habitat at higher latitudes (Colwell et al. 2008; Urban 2018). For many forest species, travelling long distances across open habitat and the sea is difficult or impossible (Rehm and Feeley 2016; Urban 2018). Elevational range changes have been recorded for some Caribbean forest bird species in Puerto Rico between 1998 and 2015 (Campos-Cerqueira et al. 2017). These elevational range changes and dispersal limitations could result in mountaintop extinctions if distributions change to more suitable habitat at higher elevations, which might cover a

smaller surface area and therefore support smaller populations with higher risk of extinction (Freeman, Scholer, et al. 2018; O'Grady et al. 2004; Shoo et al. 2005).

We investigated whether elevational range changes occurred in a tropical forest bird community on an island representing a biodiversity hotspot that is highly vulnerable to climate change (Corlett 2012; Freeman and Class Freeman 2014; Gould et al. 2020; Şekercioğlu et al. 2012). Montserrat, in the Lesser Antilles, is a small volcanic island with a steep elevational gradient and many endemic species (Hemmings et al. 2015; Young et al. 2008). Montserrat's tropical forest hosts the endemic Montserrat Oriole (*Icterus oberi*) and the range-restricted Forest Thrush (*Turdus lherminieri*), which are both globally threatened and reliant on intact forest ecosystems (Bambini et al. 2017; Hilton 2008; Oppel et al. 2015). Because Montserrat's temperature has increased over the last 15 years (Figure S2), an uphill range shift of threatened species could induce population decreases due to a reduction of available habitat at higher elevations (Freeman, Lee-Yaw, et al. 2018; Freeman, Scholer, et al. 2018). We therefore examined patterns of local colonisation and extinction probability along an elevational gradient for 12 forest bird species over the past 14 years using dynamic occupancy models and point-count data. With this study on a small tropical island that has experienced a warming climate, we contribute to an improved understanding of the impacts of environmental change on bird communities in a Caribbean biodiversity hotspot.

2 | Methods

2.1 | Study Area and Bird Species

The small Caribbean island of Montserrat (16°45'N, 62°10'W, size: 104 km², Figure 1) is situated in the northern part of the Lesser Antillean island arc (Nelson 2017; Oppel et al. 2013). It has mainly a tropical rainforest climate, with highly seasonal precipitation and a wet season from June until November (Hemmings et al. 2015). Montserrat's land mass consists of four volcanic massifs, with the Soufrière Hills having been active since a major volcanic eruption in 1995 (Hincks et al. 2005), which resulted in the loss of most tropical forest in the southern half of the island. The Centre Hills (1100 ha in size) now host the majority of the remaining forest (Dalsgaard et al. 2007; Oppel et al. 2013; Young 2008), and are legally protected (Oppel et al. 2015; UNEP-WCMC 2024). This massif is characterised by a remnant volcanic dome forming rugged terrain with steep hills, sharp ridges and deep valleys (Hemmings et al. 2015) and a range of forest types at elevations from 132 to 740 m above sea level (asl), with a decreasing area at higher elevations (Figure S1). The mean temperature on Montserrat has increased by an average of 0.053°C per year (standard error: 0.019, $p = 0.006$) between 2011 and 2025 (Figure S2).

Montserrat hosts 24 land bird species including 10 restricted range species and two that are globally threatened (Oppel et al. 2015): the Forest Thrush suffers from habitat loss and invasive species (Collar 2020; Jean-Pierre et al. 2023; Parashuram et al. 2015), and the endemic Montserrat Oriole has experienced a steep population decline due to forest loss associated with volcanic activity after 1995 (Arendt et al. 1999; Hilton et al. 2003),



FIGURE 1 | The island of Montserrat belongs to the Lesser Antillean Island arc (left) and contains four volcanic hill ranges, namely (from north to south) the Silver Hills, Centre Hills, Soufrière Hills and South- Soufrière Hills (right). Forest bird counts were conducted at 86 sampling locations (red dots), mainly within the Centre Hills Forest Reserve (pale polygon). *Source:* Centre Hills Protected Area Polygon: UNEP-WCMC (2024); Satellite image: Planet Labs PBC (2024).

but later showed increasing population trends from 2011 to 2016 (Bambini et al. 2017). The extremely restricted range and the potential effects of climate change and volcanic activity on available forest habitat render both species prone to environmental extinction risk (BirdLife International 2016).

2.2 | Bird Monitoring

Bird monitoring in the Centre Hills has been conducted using point counts from 2011 to 2024 by the Montserrat Department of Environment. A total of 86 point-count sites were established in the Centre Hills forest covering all forest types and the full elevational range of 608 m (from 132 to 740 m asl; see Figure S2). Adjacent point-count locations were >200 m apart to limit double-counting of birds at adjacent points (see Figure 1).

Surveys took place from late March until mid-May every year (except in 2020 when COVID-19 prevented surveys), thus covering the main breeding season of forest birds on Montserrat (Bambini et al. 2017). Surveys were scheduled to be completed within a period of 5 weeks to meet an assumption of population closure. Observers visited sampling locations three times within those 5 weeks between 5:45 and 13:30 local time and counted all birds

seen or heard for 10 min after a settling time of 3 min. More detailed descriptions of the bird monitoring protocol can be found elsewhere (Bambini et al. 2017; Oppel et al. 2014; Parashuram et al. 2015). For our analyses described here, we reduced the available abundance data to binary detection/non-detection data.

2.3 | Data Analysis

We examined occupancy dynamics for 12 forest bird species that were observed at >45% of survey points in at least one year during the forest bird monitoring. This selection comprised all range-restricted and globally threatened forest bird species of the Centre Hills (Hilton 2008; Oppel et al. 2015). Specifically, we estimated the effects of elevation on colonisation and extinction for Pearly-eyed Thrasher (PETH) *Margarops fuscatus*, Bananaquit (BANA) *Coereba flaveola*, Scaly-naped Pigeon (SNPI) *Patagioenas squamosa*, Forest Thrush (FOTH), Scaly-breasted Thrasher (SBTH) *Allenia fusca*, Antillean Crested Hummingbird (ACHU) *Orthorhyncus cristatus*, Montserrat Oriole (MTOR), Bridled Quail-Dove (BRQD) *Geotrygon mystacea*, Purple-throated Carib (PTCA) *Eulampis jugularis*, Caribbean Elaenia (CAEL) *Elaenia martinica* and Green-throated Carib (GTCA) *Eulampis holosericeus*.

2.3.1 | Inferring Occupancy Dynamics Using Dynamic Occupancy Models

Dynamic occupancy models use repeated sampling data to model both the ecological processes of occupancy, colonisation and extinction, but also the observation process to account for imperfect detection (Fiske and Chandler 2011; Kéry and Royle 2020). Imperfect detection is common in forest bird surveys and can depend on factors such as species, observer, season, daytime, or habitat (Alldredge et al. 2007).

Dynamic occupancy models consist of two hierarchical levels, an ecological state component which describes the true, latent presence-absence dynamics by three Bernoulli distributions, and a detection process component that describes the observation error of the true state. The occurrence state in the first season is governed by a parameter for initial occupancy probability (Ψ), and this state can change over time based on colonisation (γ) and extinction (ϵ) probabilities between consecutive sampling seasons (Fiske and Chandler 2011; Kéry and Royle 2021; MacKenzie et al. 2003). The observation process component of the dynamic occupancy model makes use of the repeated surveys within a season to describe the probability of detecting a presence while accounting for imperfect detection (Kéry and Chandler 2016; Kéry and Royle 2020). The model assumes population closure (no immigration or emigration of a species within the area surrounding each point) during the period of repeated visits (in our case 5 weeks) within a season. Thus, if a species is detected at a sampling point, then all non-detections during other visits within the same season are assumed to result from imperfect detection (Rota et al. 2009). Detection probability can be estimated using site- and occasion-specific covariates (Table S1). Further assumptions include that observations of species are independent between sampling locations, and that there are no false-positive observations (Kéry and Chandler 2016; Kéry and Royle 2020; MacKenzie et al. 2018). The Montserrat forest bird surveys use sampling locations > 200 m apart (Figure 1) and a conservative recording protocol of vocalising birds to ensure that violations of these assumptions are minimised.

To examine whether elevation explained colonisation and extinction probabilities, we fitted dynamic occupancy models using the function 'colext' in the R package 'unmarked' (Fiske and Chandler 2011; Kellner et al. 2023). Because different covariates might potentially determine the detection and initial occupancy probabilities of different bird species, we used a staged approach to first select appropriate detection and initial occupancy models for each species (Section 2.3.3), before addressing our main question of elevational distribution changes (Section 2.3.4) in models exploring different parameterisations for colonisation and extinction (Kéry et al. 2013).

2.3.2 | Covariates to Explain Occupancy Dynamics and Detection

We used survey date (as Julian 'date'), survey time of day ('time'), 'wind' (categorical with four levels), 'rain' (binary 'rain'/'no rain') and general bird 'activity' (calculated as the sum of all bird detections across all species, including species not assessed here)

as observation covariates to explain variation in detection probability. Environmental covariates that remain constant between surveys at the site level included the topography as 'elevation', terrain 'location' (categorical with 'ridge', 'mid-slope', 'valley', 'flat-open'), and forest habitat variables such as diameter at breast-height ('dbh'), tree-height ('treeheight') and canopy cover ('canopy'), which were measured and averaged at each point-count location (Parashuram et al. 2015). The survey year was included as an annually changing site covariate that allowed occupancy and detection to either change linearly over time (hereafter referred to as 'linear_trend') or randomly every year (hereafter referred to as 'random_year'; see Section 2.3.4). All numeric variables were rescaled to a mean of 0 and standard deviation of 1 (Kellner et al. 2023). An overview of covariates with their type, metric and exact definition is provided in Table S1.

2.3.3 | Selecting Species-Specific Formulations for Detection Probability and Initial Occupancy

Prior to addressing our main question of elevational distribution changes, we proceeded in a staged fashion to first select an appropriate detection model, and then an appropriate initial occupancy model for each species (Morin et al. 2020).

To select an adequate detection model for each species, we explored effects of weather (Morelli et al. 2022; O'Connor and Hicks 1980), daytime (Morelli et al. 2022), season (Kéry et al. 2005; Riegert 2022), habitat (Morelli et al. 2022) and observer (Alldredge et al. 2007; Cunningham et al. 1999). We considered 'day' and 'time' because singing intensity changes over the season (Puswal et al. 2021) and with time of day (Gil and Llusia 2020; Keast 1994). The variable 'time' was explored with linear and quadratic effect, because vocalisations can peak at intermediate times of the day. We used the covariates 'wind' and 'rain' as proxies for weather which is known to affect avian singing activity and the ability of observers to detect acoustic cues (Robbins 1981). The variable 'activity' was a general metric to quantify the survey-specific overall bird activity, which can vary tremendously from one day to the next due to behavioural changes and other unmeasured variables (Ke et al. 2022; Sólmos et al. 2018; Zou et al. 2019). Topography described by the covariate 'location' can affect sound propagation (Guibard et al. 2022; Guo et al. 2022), and was therefore also included as a detection covariate. We added these predictors as additive effects on detection probability in the order listed above and fitted a series of dynamic occupancy models that assumed constant initial occupancy, colonisation and extinction to select the most parsimonious combination of detection covariates. The most parsimonious detection model for each species was selected based on the Akaike Information Criterion corrected for small-sample size (AIC_c) (Bolker 2008; Burnham and Anderson 2002), and this combination of detection covariates was then used in the next stage.

In the next stage, variation in initial occupancy was accounted for by incorporating site covariates which may explain species-specific habitat preferences (Kéry and Chandler 2016; Kéry and Royle 2016). The covariate 'elevation' accounts for elevational patterns in rainfall and forest type which affect the distribution of forest birds on Montserrat (Hilton 2008; Parashuram

et al. 2015) and other Caribbean Islands (Devenish-Nelson and Nelson 2021). We added the covariates ‘treeheight’ and ‘dbh’ to include the possibility that certain bird species favour higher or older forest. Certain bird species exhibit a preference for dense canopy, as demonstrated by the Forest Thrush on Montserrat (Parashuram et al. 2015). Accordingly, we incorporated canopy cover as a predictor variable in our models. Because tree height decreases with increasing elevation (Hamilton et al. 2008; Homeier et al. 2010; Lieberman et al. 1996), bird species may select different tree heights at different elevations, and we therefore also included an interaction between ‘elevation’ and ‘treeheight’. We added all other covariates as additive effects on initial occupancy in a series of dynamic occupancy models that used the most parsimonious combination of detection covariates and assumed constant colonisation and extinction. As above, we used AIC_c to select the most parsimonious model for each species.

2.3.4 | Estimating the Effect of Elevation on Occupancy Dynamics

After controlling for variation in detection and initial occupancy, we addressed our key ecological question on elevational range changes by fitting 13 plausible candidate models that varied the covariates in the colonisation and extinction models (Table S2). These candidate models reflected the following ecological processes.

We fitted a range ‘shift’ model in which both colonisation and extinction were explained by elevation. This mainly refers to the scenario of an uphill range shift as climate warms and therefore an increasing colonisation at higher elevation (expansion at the leading edge) and increasing extinction at lower elevation (contraction at the trailing edge) (Breshears et al. 2008; Lenoir and Svenning 2013; Maggini et al. 2011).

Furthermore, we built two alternative models (‘expansion’ and ‘contraction’) which predict that only colonisation or extinction, respectively, change with elevation. These represent alternative scenarios in which either the trailing or leading edge remains stationary (Maggini et al. 2011).

Because changes in the occupancy of forest birds could also occur independent of elevation, we fitted alternative models that allowed occupancy to change annually. We allowed occupancy to change gradually over time (‘linear_trend’) or flexibly every year (‘random_year’) to explain both colonisation and extinction by year (Kéry et al. 2013). We used annual variation either as an alternative explanation to elevation, or in addition to elevation in the ‘shift’, ‘expansion’ and ‘contraction’ models to investigate the effect of elevation on colonisation and extinction while accounting for annual variation.

Besides the models representing ecological hypotheses, we also included two reference models that assumed that neither colonisation nor extinction were explained by either elevation or year, but rather that they remained constant. One of these reference models included the most parsimonious combination of detection and initial occupancy covariates (‘constant’), while the second reference model assumed that all four model components were constant (‘intercept-model’).

We selected the most parsimonious of those 13 plausible candidate models using AIC_c as above, and present the relative weight of evidence (ωAIC_c) to acknowledge cases where the most parsimonious model received limited support from the data (Burnham and Anderson 2002). Estimates of effect sizes of elevation on colonisation and extinction were obtained from the most parsimonious model, and the estimated probability of colonisation and extinction was plotted against elevation to demonstrate the effect of elevation (Kellner et al. 2023; Kéry and Chandler 2016; Kéry and Royle 2020).

To assess whether the dynamic occupancy models provided an adequate fit for the data, we used a parametric bootstrapping procedure to simulate 1000 replicate data sets from the model with all covariates for each species and used the χ^2 statistic to evaluate whether there were consistent differences between simulated and actual data. We concluded that models provided an appropriate fit to the data if the p -value was > 0.05 and suggested that simulated and actual data were similarly distributed.

3 | Results

3.1 | Elevational Range Changes

Point-count data for 12 forest bird species on Montserrat were collected in 13 years between 2011 and 2024, yielding 39,120 observations from 3260 surveys.

We found evidence for elevational range changes in five out of the 12 analysed species (Figure 2, Table 1), with the occupancy dynamics of three species (Bridled Quail-Dove, Scaly-breasted Thrasher and Brown Trembler) best explained by the ‘contraction’ model where only extinction depended on elevation, one species (Purple-throated Carib) where colonisation was explained by elevation (‘expansion’ model), and one species (Montserrat Oriole) where both colonisation and extinction were explained by elevation (‘shift’ model). For four species (Bananaquit, Forest Thrush, Pearly-eyed Thrasher and Scaly-naped Pigeon) the most parsimonious model was the ‘constant’ model where both colonisation and extinction were modelled with intercepts only. For another three species (Antillean Crested Hummingbird, Caribbean Eleania and Green-throated Carib) both extinction and colonisation were best explained by an annual trend (‘linear_trend’ model). The χ^2 goodness-of-fit test indicated that observed and simulated data followed a similar distribution ($p > 0.05$ for all species).

3.2 | Model Selection Uncertainty

We found considerable model selection uncertainty in five species including two (Bridled Quail-Dove and Purple-throated Carib) which exhibited elevational range changes. However, for these two species, the uncertainty only included whether elevation affected colonisation, extinction, or both (cumulative ωAIC_c for all elevation models ≥ 0.5 , see Table S3), whereas models without elevation received less support. In two other species (Forest Thrush, Scaly-naped Pigeon), elevation was contained in a competitive, but not the most parsimonious model (see Table S3).

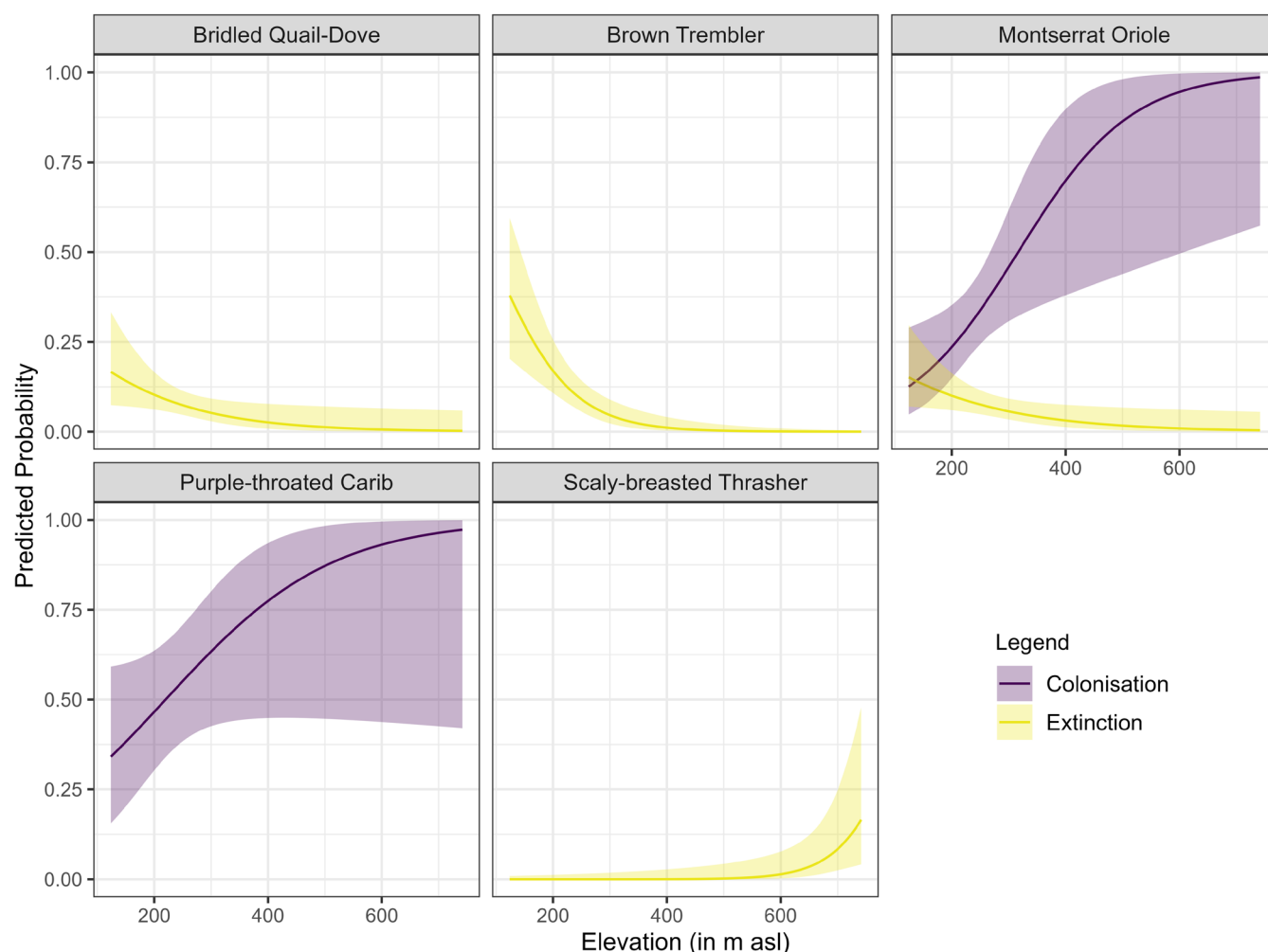


FIGURE 2 | Predicted colonisation and extinction probabilities in relation to elevation of survey points in the Centre Hills forest reserve of Montserrat, Lesser Antilles, for five forest bird species, where elevation was included as a predictor in the most parsimonious dynamic occupancy model based on survey data from 2011 to 2024.

4 | Discussion

We found elevational range changes in five out of 12 forest bird species on Montserrat, with four of these species changing their range uphill as expected under climate warming. These elevational range changes either occurred through a shift (Montserrat Oriole), by uphill expansion (Purple-throated Carib), or contraction at lower elevations (Bridled Quail-Dove and Brown Trembler), and different mechanisms may explain those dynamics for the different species. Despite the relatively short period of 14 years, some elevational range changes were evident that may ultimately result in changes in population size because less habitat is available for each species at higher elevations (Figure S1).

4.1 | Substantial Variation in Range Changes on Montserrat

The substantial variation in species elevational range changes that we found on Montserrat is consistent with previous studies (Campos-Cerqueira et al. 2017; Freeman, Lee-Yaw, et al. 2018;

Lenoir et al. 2010; Rubenstein et al. 2023). For some species, we found no evidence of elevation affecting occupancy dynamics, and any changes in occupancy were better explained by temporal variation than elevation. Some of the species for which we did not detect elevational range shifts include the most common species (Bananaquit, Pearly-eyed Thrasher, Forest Thrush, Scaly-naped Pigeon), for which the estimated occupancy was close to one (Figure S3). Changes in the distribution of those widespread species may not be detectable with occupancy but may require data on abundance (Joseph et al. 2006; Steen et al. 2023; Steenweg et al. 2019). Likewise, the rarest and decreasing species of the Centre Hills (Green-throated Carib and Caribbean Elaenia) had low and decreasing occupancy throughout the study area (Figure S3), possibly reducing the power to detect any changes in the elevational distribution. Thus, for some species our data and models may not have been powerful enough to detect elevational changes (Banner et al. 2019; Fuller et al. 2022; Southwell et al. 2019). However, for the species where we did find evidence for elevation to affect occupancy dynamics, potentially competing models simply reflected uncertainty in the exact process how occupancy changed with elevation, but not the fact that elevation was an important predictor

TABLE 1 | Parameter estimates (mean and 95% confidence intervals) for elevation on initial occupancy Ψ , colonisation γ and extinction ϵ probability for 12 forest bird species at 86 sampling locations (leading to 3260 detection/non-detection observations per species) in the Centre Hills forest reserve on the island of Montserrat, Lesser Antilles, between 2011 and 2024 estimated with dynamic occupancy models accounting for detection probability (p).

Species	Dynamic occupancy model formulation					Effect (mean and 95% confidence intervals) of elevation on		Detection probability (95% confidence intervals)	
	Ψ	γ	ϵ	p		Ψ	γ	ϵ	p
ACHU	elevation+treeheight	linear_trend	linear_trend	day+time+rain+wind+activity+location		24.55 (151.16, 200.26)			0.6 (0.57, 0.63)
									0.35
BANA	constant	constant	constant	day+time+rain+wind+activity					0.97 (0.96, 0.98)
BRQD	treeheight+canopy	constant	elevation	day+time+rain+wind+activity				-1.07 (-1.89, -0.26)	0.48 (0.45, 0.51)
									0.46
CAEL	treeheight+canopy	linear_trend	linear_trend	day+ time ² +rain+wind+activity					0.21 (0.16, 0.26)
FOTH	constant	constant	constant	day+time+rain+wind+activity+location					0.88 (0.86, 0.9)
GTCA	constant	linear_trend	linear_trend	day+time+rain+wind+activity					0.13 (0.1, 0.17)
MTOR	elevation:treeheight+canopy	elevation	elevation	day+time+rain+wind+activity+location		-1.23 (-2.31, -0.15)	1.48 (0.5, 2.46)	-0.91 (-1.59, -0.23)	0.54 (0.51, 0.57)
									0.62
PETH	constant	constant	constant	day+time ² +rain+wind+activity					1 (1, 1)
PTCA	treeheight	elevation	constant	day+time+rain+wind+activity+location			1.01 (0.08, 1.93)		0.54 (0.5, 0.57)
									0.3
SBTH	elevation:treeheight	constant	elevation	day+time+rain+wind+activity+location		5.33 (-16.24, 26.9)		2.75 (0.9, 4.59)	0.92 (0.9, 0.93)
									0.65
SNPI	constant	constant	constant	day+time+rain+wind+activity+location					0.87 (0.85, 0.89)
TREM	treeheight+canopy	constant	elevation	day+time+rain+wind+activity+location				-2.12 (-2.99, -1.25)	0.39 (0.36, 0.42)
									0.76

Note: The detection probabilities were estimated at mean observation covariate values, dry weather and mid-slope locations. Note that parameter estimates of elevation are only shown if elevation was retained in the most parsimonious model. The support for the most parsimonious model is shown as weight of evidence (ω_{AIC_c}). All effect sizes are reported on the logit-scale. See Table S1 for definition of predictor variables and Table S3 for a complete list of all other candidate models for each species. *Species:* ACHU = Antillean Crested Hummingbird; BANA = Bananaquit; BRQD = Bridled Quail-Dove; CAEL = Caribbean Elaenia; FOTH = Forest Thrush; GTCA = Green-throated Carib; MTOR = Montserrat Oriole; PETH = Pearly-eyed Thrasher; PTCA = Purple-throated Carib; SBTH = Scaly-breasted Thrasher; SNPI = Scaly-naped Pigeon; TREM = Brown Trembler.

of colonisation or extinction. We are therefore confident that we can infer elevational changes for these five species.

4.2 | Possible Explanations for Observed Range Changes

Our main hypothesis suggests that climate change caused uphill range changes as shown for species globally (Lenoir and Svenning 2013; Rubenstein et al. 2023), tropical birds (Campos-Cerqueira et al. 2017; Neate-Clegg et al. 2018, 2021) and amphibians (Campos-Cerqueira and Aide 2017; Gould et al. 2020) in the Caribbean. For example, changes on Puerto Rico were linked to rising temperatures in birds and amphibians: eight of 21 studied birds changed their range uphill (Campos-Cerqueira et al. 2017) while six out of 12 frog species were extirpated at lower elevations (Campos-Cerqueira and Aide 2017; Gould et al. 2020). Thus, we assume that a generally increasing temperature trend in the Caribbean (Almazroui et al. 2021; Campbell et al. 2021; Jones et al. 2016) and on Montserrat (Figure S2) forced species either directly (based on physiological responses) or indirectly (via biotic or abiotic interactions) to change towards higher elevations to remain in their species' climatological or ecological niche (Cahill et al. 2013; Freeman and Class Freeman 2014; Lenoir and Svenning 2013; Neate-Clegg and Tingley 2023). For two species the uphill 'range contraction' was caused by increasing extinction at lower elevations. At these elevations the forest margins of our study area are exposed to anthropogenic land-use change despite the formal preservation as forest reserve (Oppel et al. 2015). That may affect species such as the Bridled Quail-Dove and Brown Trembler sensitive to anthropogenic disturbance and land-use change (Boal and Madden 2022; Rivera-Milán et al. 2021). The uphill contraction of those two species' ranges may have therefore been caused by direct disturbance and forest loss rather than any mechanisms of a warming climate.

Besides direct anthropogenic disturbance, climate change may also induce weather phenomena that lead to natural forest disturbances, which may explain the observed uphill range changes of Montserrat Oriole and Purple-throated Carib. Increasingly powerful hurricanes exacerbated by climate change (Emanuel 2005; Walsh et al. 2019) can induce forest disturbance by defoliation and tree loss (Askins and Ewert 2021; Hilton 2008; Tanner et al. 1991), especially in the most exposed parts at higher elevations. These natural disturbances can create openings in the forest that can support large numbers of early successional species such as *Heliconia* plants (Hogan et al. 2022; Meléndez-Ackerman et al. 2003; Oppel et al. 2020). *Heliconia caribaea* and *H. bihai* (Hamilton et al. 2008) are essential for nectar feeding of Purple-throated Caribs (Dalsgaard et al. 2010; Martín-Rodríguez et al. 2011), and provide nesting and feeding habitat for Montserrat Orioles (Allcorn et al. 2012; Oppel et al. 2013, 2020; Young 2008). Thus, powerful hurricanes Maria and Irma in 2017 could have caused increased abundance of *Heliconia* at higher elevations where trees are more susceptible to the destructive force of the wind (Tanner et al. 1991). Such an increased *Heliconia* abundance could have led to uphill range changes of Montserrat Orioles and Purple-throated Caribs. However, we acknowledge that we neither have supporting data on the abundance and distribution changes of *Heliconia*

on Montserrat nor any other forest habitat characteristics that might have changed during the study period which limits our ability to infer the exact mechanism leading to the observed elevational range changes.

Abundance changes offer another possible explanation for the observed range changes in both the Montserrat Oriole and Purple-throated Carib. As populations of both species have grown during the study period (Bambini et al. 2017; Figure S3), the area needed to support this increasing population would also need to increase unless density in the occupied habitat changes. On Montserrat, shrubs and dry forest habitat at lower elevations are not suitable for Montserrat Orioles and Purple-throated Caribs due to the absence of *Heliconia* plants, and the populations might therefore rather expand towards wet forests at higher elevations (Hamilton et al. 2008; Hilton 2008).

One species, the Scaly-breasted Thrasher, showed a counter-intuitive downhill range change caused by increasing extinction at higher elevations. This species also exhibited a preference for higher trees (Table 1; Brown and Collier 2003; Madden and Zanten 2020), and the same process that may have facilitated the expansion of other species to higher elevations (tree loss and defoliation following hurricanes) may have led to a contraction of the Scaly-breasted Thrasher's range to lower elevations. However, we acknowledge that the mechanisms underlying our observed range changes are poorly understood and would require further research.

5 | Conclusion

In conclusion, we provide evidence for elevational range changes (uphill and downhill) in five forest bird species on the small Caribbean island of Montserrat over a period of 14 years. Given accelerating climate change and its impacts on biodiversity during the 21st century, we would expect to observe continued range shifts in the future. Consequently, the four uphill shifting species, including the endemic Montserrat Oriole, could face a decreasing surface area of available suitable habitat at higher elevations in the Centre Hills (see Figure S1), which could result in smaller population sizes increasingly prone to extinction due to stochastic events. Thus, we suggest continuing monitoring of the Centre Hills forest bird community to enable future assessments of population dynamics under climate change.

Author Contributions

F.H. and S.O. conceived the ideas, designed the methodology and analysed the data. J.R.D., C.F., J.B., S.H., T.W., L.M., S.O. and F.H. collected the data and administered the project. F.H. and S.O. led the writing of the manuscript. J.K. reviewed and improved the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank G. Hilton, R. Allcorn, S. Jones, A. Tribe, L. Bambini, D. Gibbons, G. Tyler, D. Pain, K. Smith, S. Sanders, M. O'Brien, J. Millett (all RSPB), J. Greenaway, J. Martin, D. Duberry, A. Homer and L. Aymer (Montserrat forest rangers), Coral Cay Conservation, P. Murrain, M. Brierley and

J. Wright for assistance with fieldwork and data entry. The Montserrat National Trust provided invaluable logistical support. Parts of this work were funded by the UK Foreign and Commonwealth Office, the American Bird Conservancy and the EU BEST initiative. R. Chandler and M. Kéry provided stimulating thoughts on data analysis. The research presented here was conducted by members of the Department of Environment of the Government of Montserrat, and no specific permits were required to count birds.

Funding

This work was supported by the United Kingdom Foreign and Commonwealth Office, the American Bird Conservancy and the European Union BEST initiative.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code to replicate the analysis are available at <https://doi.org/10.5281/zenodo.19366281>.

References

- Allcorn, R. I., G. M. Hilton, C. Fenton, et al. 2012. "Demography and Breeding Ecology of the Critically Endangered Montserrat Oriole." *Condor* 114, no. 1: 227–235. <https://doi.org/10.1525/cond.2011.110033>.
- Allredge, M. W., T. R. Simons, and K. H. Pollock. 2007. "Factors Affecting Aural Detection of Songbirds." *Ecological Applications* 17, no. 3: 948–955. <https://doi.org/10.1890/06-0685>.
- Almazroui, M., M. N. Islam, F. Saeed, et al. 2021. "Projected Changes in Temperature and Precipitation Over the United States, Central America, and the Caribbean in CMIP6 GCMs." *Earth Systems and Environment* 5, no. 1: 1–24. <https://doi.org/10.1007/s41748-021-00199-5>.
- Arendt, W. J., D. W. Gibbons, and G. Gray. 1999. "Status of the Volcanically Threatened Montserrat Oriole *Icterus oberi* and Other Forest Birds in Montserrat, West Indies." *Bird Conservation International* 9, no. 4: 351–372. <https://doi.org/10.1017/S09592709000352X>.
- Askins, R. A., and D. N. Ewert. 2021. "Resistance and Resilience of Virgin Islands Bird Populations Following Severe Hurricanes." *Wilson Journal of Ornithology* 132, no. 4: 898–910. <https://doi.org/10.1676/20-00044>.
- Bambini, L., J. R. Daley, C. Fenton, et al. 2017. "Current Population Status of Four Endemic Caribbean Forest Birds in Montserrat." *Journal of Caribbean Ornithology* 30, no. 1: 2–9.
- Banner, K. M., K. M. Irvine, T. J. Rodhouse, D. Donner, and A. R. Litt. 2019. "Statistical Power of Dynamic Occupancy Models to Identify Temporal Change: Informing the North American Bat Monitoring Program." *Ecological Indicators* 105: 166–176. <https://doi.org/10.1016/j.ecolind.2019.05.047>.
- BirdLife International. 2016. "IUCN Red List of Threatened Species: *Icterus oberi*." IUCN Red List of Threatened Species. <https://www.iucnredlist.org/species/22724147/119465859>.
- Boal, C. W., and H. M. Madden. 2022. "Bridled Quail-Dove (*Geotrygon mystacea*)." In *Birds of the World*, edited by S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.brqdv1.02>.
- Bolker, B. M. 2008. *Ecological Models and Data in R*. Princeton University Press. <https://doi.org/10.2307/j.ctvcm4g37>.
- Breshears, D. D., T. E. Huxman, H. D. Adams, C. B. Zou, and J. E. Davison. 2008. "Vegetation Synchronously Leans Upslope as Climate Warms." *Proceedings of the National Academy of Sciences* 105, no. 33: 11591–11592. <https://doi.org/10.1073/pnas.0806579105>.
- Brown, A. C., and N. Collier. 2003. "Recent Colonization of St. Martin by the Scaly-Breasted Thrasher (*Margarops fuscus*)." *Journal of Caribbean Ornithology* 16: 24–25.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd ed. Springer.
- Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, et al. 2013. "How Does Climate Change Cause Extinction?" *Proceedings of the Royal Society B: Biological Sciences* 280, no. 1750: 20121890. <https://doi.org/10.1098/rspb.2012.1890>.
- Campbell, J. D., M. A. Taylor, A. Bezanilla-Morlot, et al. 2021. "Generating Projections for the Caribbean at 1.5, 2.0 and 2.5°C From a High-Resolution Ensemble." *Atmosphere* 12, no. 3: 328. <https://doi.org/10.3390/atmos12030328>.
- Campos-Cerqueira, M., and T. M. Aide. 2017. "Lowland Extirpation of Anuran Populations on a Tropical Mountain." *PeerJ* 5: e4059. <https://doi.org/10.7717/peerj.4059>.
- Campos-Cerqueira, M., W. J. Arendt, J. M. Wunderle Jr., and T. M. Aide. 2017. "Have Bird Distributions Shifted Along an Elevational Gradient on a Tropical Mountain?" *Ecology and Evolution* 7, no. 23: 9914–9924. <https://doi.org/10.1002/ece3.3520>.
- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. "Rapid Range Shifts of Species Associated With High Levels of Climate Warming." *Science* 333, no. 6045: 1024–1026. <https://doi.org/10.1126/science.1206432>.
- Collar, N. 2020. "Forest Thrush (*Turdus lherminieri*)." In *Birds of the World*, edited by S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.forthr1.01>.
- Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. "Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics." *Science* 322, no. 5899: 258–261. <https://doi.org/10.1126/science.1162547>.
- Colwell, R. K., and K. J. Feeley. 2024. "Still Little Evidence of Poleward Range Shifts in the Tropics, but Lowland Biotic Attrition May Be Underway." *Biotropica* 57, no. 1: e13358. <https://doi.org/10.1111/btp.13358>.
- Corlett, R. T. 2012. "Climate Change in the Tropics: The End of the World as We Know It?" *Biological Conservation, Advancing Environmental Conservation: Essays in Honor of Navjot Sodhi* 151, no. 1: 22–25. <https://doi.org/10.1016/j.biocon.2011.11.027>.
- Cunningham, R. b., D. B. Lindenmayer, H. A. Nix, and B. D. Lindenmayer. 1999. "Quantifying Observer Heterogeneity in Bird Counts." *Australian Journal of Ecology* 24, no. 3: 270–277. <https://doi.org/10.1046/j.1442-9993.1999.00971.x>.
- Dalsgaard, B., G. M. Hilton, G. A. L. Gray, et al. 2007. "Impacts of a Volcanic Eruption on the Forest Bird Community of Montserrat, Lesser Antilles: Volcanic Impacts on Forest Birds." *Ibis* 149, no. 2: 298–312. <https://doi.org/10.1111/j.1474-919X.2006.00631.x>.
- Dalsgaard, B., A. Timmermann, A. M. M. González, J. M. Olesen, J. Ollerton, and L. H. Andersen. 2010. "Heliconia-Hummingbird Interactions in the Lesser Antilles: A Geographic Mosaic?" *Caribbean Journal of Science* 46, no. 2–3: 328–331. <https://doi.org/10.18475/cjos.v46i2.a22>.
- Devenish-Nelson, E. S., and H. P. Nelson. 2021. "Abundance and Density Estimates of Landbirds on Grenada." *Journal of Caribbean Ornithology* 34: 88–98. <https://doi.org/10.55431/jco.2021.34.88-98>.
- Emanuel, K. 2005. "Increasing Destructiveness of Tropical Cyclones Over the Past 30 Years." *Nature* 436, no. 7051: 686–688. <https://doi.org/10.1038/nature03906>.

- Fiske, I., and R. Chandler. 2011. "Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance." *Journal of Statistical Software* 43: 1–23. <https://doi.org/10.18637/jss.v043.i10>.
- Freeman, B. G., and A. M. Class Freeman. 2014. "Rapid Upslope Shifts in New Guinean Birds Illustrate Strong Distributional Responses of Tropical Montane Species to Global Warming." *Proceedings of the National Academy of Sciences* 111, no. 12: 4490–4494. <https://doi.org/10.1073/pnas.1318190111>.
- Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. "Expanding, Shifting and Shrinking: The Impact of Global Warming on Species' Elevational Distributions." *Global Ecology and Biogeography* 27, no. 11: 1268–1276. <https://doi.org/10.1111/geb.12774>.
- Freeman, B. G., M. N. Scholer, V. Ruiz-Gutierrez, and J. W. Fitzpatrick. 2018. "Climate Change Causes Upslope Shifts and Mountaintop Extirpations in a Tropical Bird Community." *Proceedings of the National Academy of Sciences* 115, no. 47: 11982–11987. <https://doi.org/10.1073/pnas.1804224115>.
- Fuller, A. K., B. C. Augustine, D. J. Morin, et al. 2022. "The Occupancy-Abundance Relationship and Sampling Designs Using Occupancy to Monitor Populations of Asian Bears." *Global Ecology and Conservation* 35: e02075. <https://doi.org/10.1016/j.gecco.2022.e02075>.
- Gil, D., and D. Llusia. 2020. "The Bird Dawn Chorus Revisited." In *Coding Strategies in Vertebrate Acoustic Communication*, edited by T. Aubin and N. Mathevon, 45–90. Springer International Publishing. https://doi.org/10.1007/978-3-030-39200-0_3.
- Gould, W. A., J. Castro-Prieto, and N. L. Álvarez-Berrios. 2020. "Climate Change and Biodiversity Conservation in the Caribbean Islands." In *Encyclopedia of the World's Biomes*, 114–125. Elsevier. <https://doi.org/10.1016/B978-0-12-409548-9.12091-3>.
- Guibard, A., F. Sèbe, D. Dagna, and S. Ollivier. 2022. "Influence of Meteorological Conditions and Topography on the Active Space of Mountain Birds Assessed by a Wave-Based Sound Propagation Model." *Journal of the Acoustical Society of America* 151, no. 6: 3703–3718. <https://doi.org/10.1121/10.0011545>.
- Guo, S., W. Wu, Y. Liu, X. Kang, and C. Li. 2022. "Effects of Valley Topography on Acoustic Communication in Birds: Why Do Birds Avoid Deep Valleys in Daqinggou Nature Reserve?" *Animals* 12, no. 21: 21. <https://doi.org/10.3390/ani12212896>.
- Hamilton, M. A., C. Clubbe, S. K. Robbins, and S. Bárrios. 2008. "Plants and Habitats of the Centre Hills and Montserrat." In *A Biodiversity Assessment of the Centre Hills, Montserrat*, vol. 1, 40–55. Durrell Wildlife Conservation Trust. <https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=20b23c1cc41e17b50e9b4be9a283c1ca40f4869e>.
- Hemmings, B., F. Whitaker, J. Gottsmann, and A. Hughes. 2015. "Hydrogeology of Montserrat Review and New Insights." *Journal of Hydrology: Regional Studies* 3: 1–30. <https://doi.org/10.1016/j.ejrh.2014.08.008>.
- Hersbach, H., B. Bell, P. Berrisford, et al. 2023. "ERA5 Hourly Data on Single Levels from 1940 to Present." *Copernicus Climate Change Service (C3S) Climate Data Store (CDS)*. <https://doi.org/10.24381/cds.adbb2d47>.
- Hilton, G. M. 2008. "Birds of the Centre Hills." In *A Biodiversity Assessment of the Centre Hills, Montserrat*, vol. 1, 40–55. Durrell Wildlife Conservation Trust. <https://citeseerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=20b23c1cc41e17b50e9b4be9a283c1ca40f4869e>.
- Hilton, G. M., P. W. Atkinson, G. A. L. Gray, W. J. Arendt, and D. W. Gibbons. 2003. "Rapid Decline of the Volcanically Threatened Montserrat Oriole." *Biological Conservation* 111, no. 1: 79–89. [https://doi.org/10.1016/S0006-3207\(02\)00252-5](https://doi.org/10.1016/S0006-3207(02)00252-5).
- Hincks, T., S. Sparks, P. Dunkley, and P. Cole. 2005. "Montserrat." In *Volcanic Hazard Atlas of the Lesser Antilles*, 147–169. Seismic Research Center. <https://uwisismic.com/wp-content/uploads/2021/10/Montserrat.pdf>.
- Hogan, J. A., J. M. Sharpe, A. Van Beusekom, et al. 2022. "Solar Radiation and Soil Moisture Drive Tropical Forest Understory Responses to Experimental and Natural Hurricanes." *Ecosphere* 13, no. 7: e4150. <https://doi.org/10.1002/ecs2.4150>.
- Homeier, J., S.-W. Breckle, S. Günter, R. T. Rollenbeck, and C. Leuschner. 2010. "Tree Diversity, Forest Structure and Productivity Along Altitudinal and Topographical Gradients in a Species-Rich Ecuadorian Montane Rain Forest: Ecuadorian Montane Forest Diversity and Structure." *Biotropica* 42, no. 2: 140–148. <https://doi.org/10.1111/j.1744-7429.2009.00547.x>.
- Jean-Pierre, A., G. Loranger-Merciris, L. J. Saint-Louis, et al. 2023. "Factors Affecting Spatial Occupancy and Local Abundance of the Forest Thrush, *Turdus lherminieri*, in Guadeloupe Forests." *European Journal of Wildlife Research* 69: 76. <https://doi.org/10.1007/s10344-023-01698-8>.
- Jones, P. D., C. Harpham, I. Harris, et al. 2016. "Long-Term Trends in Precipitation and Temperature Across the Caribbean." *International Journal of Climatology* 36, no. 9: 9. <https://doi.org/10.1002/joc.4557>.
- Joseph, L. N., S. A. Field, C. Wilcox, and H. P. Possingham. 2006. "Presence–Absence Versus Abundance Data for Monitoring Threatened Species." *Conservation Biology* 20, no. 6: 1679–1687. <https://doi.org/10.1111/j.1523-1739.2006.00529.x>.
- Ke, A., R. Sollmann, L. O. Frishkoff, and D. S. Karp. 2022. "A Hierarchical N-Mixture Model to Estimate Behavioral Variation and a Case Study of Neotropical Birds." *Ecological Applications* 32, no. 6: e2632. <https://doi.org/10.1002/eap.2632>.
- Keast, A. 1994. "Temporal Vocalisation Patterns in Members of a Eucalypt Forest Bird Community: The Effects of Weather on Song Production." *Emu – Austral Ornithology* 94, no. 3: 172–180. <https://doi.org/10.1071/MU9940172>.
- Kellner, K. F., A. D. Smith, J. A. Royle, M. Kéry, J. L. Belant, and R. B. Chandler. 2023. "The Unmarked R Package: Twelve Years of Advances in Occurrence and Abundance Modelling in Ecology." *Methods in Ecology and Evolution* 14: 2041–210X.14123. <https://doi.org/10.1111/2041-210X.14123>.
- Kéry, M., and R. Chandler. 2016. "Dynamic Occupancy Models in Unmarked." <https://doi.org/10.1002/9781118203313.ch12>.
- Kéry, M., G. Guillera-Aroita, and J. J. Lahoz-Monfort. 2013. "Analysing and Mapping Species Range Dynamics Using Occupancy Models." *Journal of Biogeography* 40, no. 8: 1463–1474. <https://doi.org/10.1111/jbi.12087>.
- Kéry, M., and J. Royle. 2020. *Applied Hierarchical Modeling in Ecology Analysis of Distribution, Abundance and Species Richness in R and BUGS: Volume 2—Dynamic and Advanced Models*. Vol. 2. 1st ed. Elsevier.
- Kéry, M., and J. A. Royle. 2016. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS: Volume 1 - Prelude and Static Models*. Vol. 1. Elsevier/AP.
- Kéry, M., and J. A. Royle. 2021. "Modeling Species Distribution and Range Dynamics, and Population Dynamics Using Dynamic Occupancy Models." In *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS*, 207–297. Elsevier. <https://doi.org/10.1016/B978-0-12-809585-0.00004-1>.
- Kéry, M., J. A. Royle, and H. Schmid. 2005. "Modeling Avian Abundance From Replicated Counts Using Binomial Mixture Models." *Ecological Applications* 15, no. 4: 1450–1461. <https://doi.org/10.1890/04-1120>.
- La Sorte, F. A., S. H. M. Butchart, W. Jetz, and K. Böhning-Gaese. 2014. "Range-Wide Latitudinal and Elevational Temperature Gradients for the World's Terrestrial Birds: Implications Under Global Climate Change." *PLoS One* 9, no. 5: e98361. <https://doi.org/10.1371/journal.pone.0098361>.

- Lenoir, J., J.-C. Gégout, A. Guisan, et al. 2010. "Going Against the Flow: Potential Mechanisms for Unexpected Downslope Range Shifts in a Warming Climate." *Ecography* 33, no. 2: 295–303. <https://doi.org/10.1111/j.1600-0587.2010.06279.x>.
- Lenoir, J., and J.-C. Svenning. 2013. "Latitudinal and Elevational Range Shifts Under Contemporary Climate Change." In *Encyclopedia of Biodiversity*, 599–611. Elsevier. <https://doi.org/10.1016/B978-0-12-384719-5.00375-0>.
- Lenoir, J., and J.-C. Svenning. 2014. "Climate-Related Range Shifts—A Global Multidimensional Synthesis and New Research Directions." *Ecography* 38, no. 1: 15–28. <https://doi.org/10.1111/ecog.00967>.
- Lieberman, D., M. Lieberman, R. Peralta, and G. S. Hartshorn. 1996. "Tropical Forest Structure and Composition on a Large-Scale Altitudinal Gradient in Costa Rica." *Journal of Ecology* 84, no. 2: 137. <https://doi.org/10.2307/2261350>.
- MacKenzie, D. I., J. Nichols, J. Royle, K. Pollock, L. Bailey, and J. Hines. 2018. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. 2nd ed. Academic Press.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. "Estimating Site Occupancy, Colonization and Local Extinction When a Species Is Detected Imperfectly." *Ecology* 84, no. 8: 2200–2207. <https://doi.org/10.1890/02-3090>.
- Madden, H., and A. Zanten. 2020. "Monitoring of Terrestrial Avifauna in Six Habitats on St. Eustatius, Caribbean Netherlands, 2009–2017." *Caribbean Journal of Science* 50, no. 1: 23–36. <https://doi.org/10.18475/cjos.v50i1.a4>.
- Maggini, R., A. Lehmann, M. Kéry, et al. 2011. "Are Swiss Birds Tracking Climate Change?" *Ecological Modelling* 222, no. 1: 21–32. <https://doi.org/10.1016/j.ecolmodel.2010.09.010>.
- Manes, S., M. J. Costello, H. Beckett, et al. 2021. "Endemism Increases Species' Climate Change Risk in Areas of Global Biodiversity Importance." *Biological Conservation* 257: 109070. <https://doi.org/10.1016/j.biocon.2021.109070>.
- Martén-Rodríguez, S., W. John Kress, E. J. Temeles, and E. Meléndez-Ackerman. 2011. "Plant–Pollinator Interactions and Floral Convergence in Two Species of Heliconia From the Caribbean Islands." *Oecologia* 167, no. 4: 1075–1083. <https://doi.org/10.1007/s00442-011-2043-8>.
- Meléndez-Ackerman, E., C. Calisto-Pérez, M. Morales-Vargas, and J. Fumero-Cabán. 2003. "Post-Hurricane Recovery of a Herbaceous Understorey Plant in a Tropical Rain Forest in Puerto Rico." *Journal of Tropical Ecology* 19, no. 6: 677–684. <https://doi.org/10.1017/S0266467403006072>.
- Morelli, F., V. Brlik, Y. Benedetti, et al. 2022. "Detection Rate of Bird Species and What It Depends on: Tips for Field Surveys." *Frontiers in Ecology and Evolution* 9: 671492. <https://doi.org/10.3389/fevo.2021.671492>.
- Morin, D. J., C. B. Yackulic, J. E. Diffendorfer, et al. 2020. "Is Your Ad Hoc Model Selection Strategy Affecting Your Multimodel Inference?" *Ecosphere* 11, no. 1: e02997. <https://doi.org/10.1002/ecs2.2997>.
- Neate-Clegg, M. H. C., S. E. I. Jones, O. Burdekin, M. Jocque, and Ç. H. Şekerciöğlu. 2018. "Elevational Changes in the Avian Community of a Mesoamerican Cloud Forest Park." *Biotropica* 50, no. 5: 805–815. <https://doi.org/10.1111/btp.12596>.
- Neate-Clegg, M. H. C., S. E. I. Jones, J. A. Tobias, W. D. Newmark, and Ç. H. Şekerciöğlu. 2021. "Ecological Correlates of Elevational Range Shifts in Tropical Birds." *Frontiers in Ecology and Evolution* 9: 621749. <https://doi.org/10.3389/fevo.2021.621749>.
- Neate-Clegg, M. H. C., and M. W. Tingley. 2023. "Building a Mechanistic Understanding of Climate-Driven Elevational Shifts in Birds." *PLOS Climate* 2, no. 3: e0000174. <https://doi.org/10.1371/journal.pclm.0000174>.
- Nelson, E. 2017. *Montserrat*, edited by C. D. Allen, 117–134. Springer International Publishing. https://doi.org/10.1007/978-3-319-55787-8_9.
- O'Connor, R. J., and R. K. Hicks. 1980. "The Influence of Weather Conditions on the Detection of Birds During Common Birds Census Fieldwork." *Bird Study* 27, no. 3: 137–151. <https://doi.org/10.1080/00063658009476672>.
- O'Grady, J. J., D. H. Reed, B. W. Brook, and R. Frankham. 2004. "What Are the Best Correlates of Predicted Extinction Risk?" *Biological Conservation* 118, no. 4: 513–520. <https://doi.org/10.1016/j.biocon.2003.10.002>.
- Oppel, S., A. Cassini, J. Daley, and C. Fenton. 2020. "Montserrat Oriole (*Icterus oberi*)." In *Birds of the World*, edited by S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.monori1.01>.
- Oppel, S., A. Cassini, C. Fenton, J. Daley, and G. Gray. 2014. "Population Status and Trend of the Critically Endangered Montserrat Oriole." *Bird Conservation International* 24, no. 2: 252–261. <https://doi.org/10.1017/S0959270913000373>.
- Oppel, S., G. Gray, D. James, et al. 2015. "Important Bird Areas—Montserrat." *British Birds* 108, no. 2: 80–96.
- Oppel, S., G. M. Hilton, R. Allcorn, C. Fenton, A. J. Matthews, and D. W. Gibbons. 2013. "The Effects of Rainfall on Different Components of Seasonal Fecundity in a Tropical Forest Passerine." *Ibis* 155, no. 3: 464–475. <https://doi.org/10.1111/ibi.12052>.
- Parashuram, D., S. Oppel, C. Fenton, et al. 2015. "The Forest Thrush *Turdus therminieri* Prefers Mature Mesic Forest With Dense Canopy." *Bird Conservation International* 25, no. 4: 503–513. <https://doi.org/10.1017/S0959270914000495>.
- Parnesan, C. 2006. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology, Evolution, and Systematics* 37, no. 1: 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>.
- Parnesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts Across Natural Systems." *Nature* 421, no. 6918: 37–42. <https://doi.org/10.1038/nature01286>.
- Planet Labs PBC. 2024. "CC BY-NC-SA 2.0 [Data set]. Planet QGIS Plugin." <https://www.protectedplanet.net/555622117>.
- Pörtner, H.-O., R. J. Scholes, J. Agard, et al. 2021. *Scientific Outcome of the IPBES-IPCC Co-Sponsored Workshop on Biodiversity and Climate Change (Version 5)*. Zenodo. <https://doi.org/10.5281/ZENODO.4659158>.
- Pouteau, R., T. W. Giambelluca, C. Ah-Peng, and J.-Y. Meyer. 2018. "Will Climate Change Shift the Lower Ecotone of Tropical Montane Cloud Forests Upwards on Islands?" *Journal of Biogeography* 45, no. 6: 1326–1333. <https://doi.org/10.1111/jbi.13228>.
- Puswal, S. M., M. Jinjun, and F. Liu. 2021. "Effects of Temperature and Season on Birds' Dawn Singing Behavior in a Forest of Eastern China." *Journal of Ornithology* 162, no. 2: 447–459. <https://doi.org/10.1007/s10336-020-01848-8>.
- Rehm, E., and K. J. Feeley. 2016. "Many Species Risk Mountain Top Extinction Long Before They Reach the Top." *Frontiers of Biogeography* 8: e277788. <https://doi.org/10.21425/F5FBG27788>.
- Riegert, J. 2022. "Detectability of Birds Under Different Sampling Efforts and During the Breeding Season: A Case Study From Central Europe." *Journal of Vertebrate Biology* 71, no. 20207: 22027.1–12. <https://doi.org/10.52525/jvb.22027>.
- Rivera-Milán, F. F., H. Madden, and K. Verdel. 2021. "Bridled Quail-Dove *Geotrygon mystacea* Population Assessment After Hurricanes Irma and Maria, St. Eustatius, Caribbean Netherlands." *Bird Conservation International* 31, no. 4: 656–667. <https://doi.org/10.1017/S0959270920000647>.
- Robbins, C. S. 1981. "Bird Activity Levels Related to Weather." *Studies in Avian Biology* 6: 301–310.
- Rota, C. T., R. J. Fletcher Jr., R. M. Dorazio, and M. G. Betts. 2009. "Occupancy Estimation and the Closure Assumption." *Journal of*

Applied Ecology 46, no. 6: 1173–1181. <https://doi.org/10.1111/j.1365-2664.2009.01734.x>.

Rubenstein, M. A., S. R. Weiskopf, R. Bertrand, et al. 2023. “Climate Change and the Global Redistribution of Biodiversity: Substantial Variation in Empirical Support for Expected Range Shifts.” *Environmental Evidence* 12, no. 1: 7. <https://doi.org/10.1186/s13750-023-00296-0>.

Sanczuk, P., K. Verheyen, J. Lenoir, et al. 2024. “Unexpected Westward Range Shifts in European Forest Plants Link to Nitrogen Deposition.” *Science* 386, no. 6718: 193–198. <https://doi.org/10.1126/science.ado0878>.

Şekercioğlu, Ç. H., R. B. Primack, and J. Wormworth. 2012. “The Effects of Climate Change on Tropical Birds.” *Biological Conservation* 148, no. 1: 1–18. <https://doi.org/10.1016/j.biocon.2011.10.019>.

Shoo, L. P., S. E. Williams, and J.-M. Hero. 2005. “Climate Warming and the Rainforest Birds of the Australian Wet Tropics: Using Abundance Data as a Sensitive Predictor of Change in Total Population Size.” *Biological Conservation* 125, no. 3: 335–343. <https://doi.org/10.1016/j.biocon.2005.04.003>.

Sólymos, P., S. M. Matsuoka, S. G. Cumming, et al. 2018. “Evaluating Time-Removal Models for Estimating Availability of Boreal Birds During Point Count Surveys: Sample Size Requirements and Model Complexity.” *Condor: Ornithological Applications* 120, no. 4: 765–786. <https://doi.org/10.1650/CONDOR-18-32.1>.

Southwell, D. M., L. D. Einoder, J. J. Lahoz-Monfort, A. Fisher, G. R. Gillespie, and B. A. Wintle. 2019. “Spatially Explicit Power Analysis for Detecting Occupancy Trends for Multiple Species.” *Ecological Applications* 29, no. 6: e01950. <https://doi.org/10.1002/eap.1950>.

Steen, V. A., A. Duarte, and J. T. Peterson. 2023. “An Evaluation of Multistate Occupancy Models for Estimating Relative Abundance and Population Trends.” *Ecological Modelling* 478: 110303. <https://doi.org/10.1016/j.ecolmodel.2023.110303>.

Steenweg, R., M. Hebblewhite, J. Whittington, and K. McKelvey. 2019. “Species-Specific Differences in Detection and Occupancy Probabilities Help Drive Ability to Detect Trends in Occupancy.” *Ecosphere* 10, no. 4: e02639. <https://doi.org/10.1002/ecs2.2639>.

Tanner, E. V. J., V. Kapos, and J. R. Healey. 1991. “Hurricane Effects on Forest Ecosystems in the Caribbean.” *Biotropica* 23, no. 4: 513–521. <https://doi.org/10.2307/2388274>.

Thomas, C. D., A. Cameron, R. E. Green, et al. 2004. “Extinction Risk From Climate Change.” *Nature* 427, no. 6970: 145–148. <https://doi.org/10.1038/nature02121>.

UNEP-WCMC. 2024. “Protected Area Profile for Centre Hills From the World Database on Protected Areas (Version AW3D30v3.1.3.2) [Data set]. Protected Planet.” <https://www.protectedplanet.net/555622117>.

Urban, M. C. 2015. “Accelerating Extinction Risk From Climate Change.” *Science* 348, no. 6234: 571–573. <https://doi.org/10.1126/science.aaa4984>.

Urban, M. C. 2018. “Escalator to Extinction.” *Proceedings of the National Academy of Sciences* 115, no. 47: 11871–11873. <https://doi.org/10.1073/pnas.1817416115>.

Walsh, K. J. E., S. J. Camargo, T. R. Knutson, et al. 2019. “Tropical Cyclones and Climate Change.” *Tropical Cyclone Research and Review* 8, no. 4: 240–250. <https://doi.org/10.1016/j.tcr.2020.01.004>.

Young, R. P., ed. 2008. *A Biodiversity Assessment of the Centre Hills, Montserrat*. Vol. 1. Durrell Wildlife Conservation Trust. <https://cites.eerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=20b23c1cc41e17b50e9b4be9a283c1ca40f4869e>.

Young, R. P., G. M. Hilton, and L. Martin. 2008. “Biodiversity of the Centre Hills: Importance, Key Features, Conservation Priorities and Recommended Actions.” In *A Biodiversity Assessment of the Centre Hills, Montserrat*, vol. 1, 9–29. Durrell Wildlife Conservation Trust. <https://cites.eerx.ist.psu.edu/document?repid=rep1&type=pdf&doi=20b23c1cc41e17b50e9b4be9a283c1ca40f4869e>.

Zou, F., Q. Zhang, M. Zhang, et al. 2019. “Temporal Patterns of Three Sympatric Pheasant Species in the Nanling Mountains: N-Mixture Modeling Applied to Detect Abundance.” *Avian Research* 10, no. 1: 42. <https://doi.org/10.1186/s40657-019-0181-6>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Distribution of grid cells representing the frequency of surface area derived from a digital elevation model of the Centre Hills forest reserve on Montserrat, Lesser Antilles (red bars) and the elevational distribution of survey points for long-term bird monitoring (blue bars). Source digital elevation model: OpenTopography, 2016; Centre Hills Protected Area Polygon: UNEP-WCMC 2024. **Figure S2:** Long-term (1940 to 2026) (a) and short-term changes over the study period (2011 to 2024), (b) in the monthly mean air temperature on Montserrat. The data indicate monthly averaged air temperatures obtained from ERA5 (Hersbach et al., 2023) which provides long-term climate data through reanalysis and downscaling from global weather observations. Trends are depicted in blue (95% confidence intervals in grey) and are calculated for (a) using a loess function with a smoothing parameter of 0.5 and for (b) using a linear trend regression resulting in a slope of 0.053 (standard error: 0.019, $p=0.006$). **Figure S3:** Estimated annual probability of occupancy between 2011 and 2024 for 12 forest bird species at 86 sampling locations in the Centre Hills forest reserve on Montserrat, Lesser Antilles, derived from dynamic occupancy models. No surveys were conducted in 2020. Occupancy probability was calculated from estimated posterior distributions using the empirical Bayes method and averaged across all point count locations for each survey year, thus yielding the average proportion of sites occupied. **Table S1:** Definitions of environmental variables used as covariates to explain occupancy dynamics and detection probability of 12 species of forest birds in dynamic occupancy models based on bird survey data from 2011 to 2024. Type indicates whether variables varied by observation (obsCov), by location (siteCov), or by survey year (yearlySiteCov). All numeric variables were rescaled to a mean of 0 and standard deviation of 1. **Table S2:** Symbolic representation of the model components for the 13 candidate models that were explored to test biological hypotheses of range shifts of forest birds on Montserrat. Note that only the colonisation and extinction components of the models are specified, while the detection and initial occupancy components varied by species and covariates for those components were selected during preliminary stages for each species and then held constant for each species when fitting these candidate models. Note that the ‘intercept-model’ is not shown in this table, as it is identical to the ‘constant’ model in colonisation and extinction probabilities, but also uses only an intercept for the detection and initial occupancy components. **Table S3:** Model selection table of dynamic occupancy models investigating the effect of elevation on occupancy in 12 forest bird species at 86 sampling locations in a forest reserve on Montserrat, Lesser Antilles, between 2011 and 2024. Fitted models for all modelling are aggregated for each species but note that model fitting proceeded sequentially. After correcting for detection and initial occupancy as nuisance parameters, the models for colonisation and extinction were fitted to address the main research question on range shifts. Models for each species are ordered by the second-order Akaike Information Criterion corrected for small sample sizes (AIC_c) and the most parsimonious model is displayed in bold. ΔAIC_c is the difference between the AIC_c of a model and the most parsimonious model for that species, nPars is the number of parameters and ωAIC_c is the relative weight of evidence for a model. See Table S1 for description of covariates.