COMMENTARY

Modeling spatial variation in winter abundance to direct conservation actions for a vulnerable migratory songbird, the Bicknell's Thrush (*Catharus bicknelli*)

Kent P. McFarland,[1]* John D. Lloyd,[1] Sarah J. K. Frey,[2] Patrick L. Johnson,[1] Richard B. Chandler,[3] and Christopher C. Rimmer[1]

[1] Vermont Center for Ecostudies, Norwich, Vermont, USA
[2] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA
[3] Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia, USA
* Corresponding author: kmcfarland@vtecostudies.org

ABSTRACT

The winter range of the Bicknell's Thrush (*Catharus bicknelli*), a globally vulnerable Nearctic–Neotropical migratory songbird, is restricted to the Greater Antilles. Most birds occur on Hispaniola, where the species exhibits sexual habitat segregation, and where the loss of its preferred wet broadleaf habitats has been severe. Conservation of female-dominated habitats has been identified as a top priority for the species' preservation. During 2010, we conducted standardized field surveys for the Bicknell's Thrush in forests of the Dominican Republic's Cordillera Septentrional, an area of high importance for females. We combined occurrence data with environmental variables to create a model of thrush distribution and habitat selection in the region. Elevation (densities peaked at ∼600 m), aspect (northeastern slopes), the amount of forest cover within 1 km, and forest density best described thrush presence and abundance. As an example of how predictive models of abundance can inform conservation, we used the best model that contained only spatially explicit covariates to map predicted winter abundance of the Bicknell's Thrush. With the highest elevations in the study area (∼600 m) and the most intact forest cover, 2 scientific reserves contained the largest areas of high thrush abundance, but many privately held lands contained forest fragments predicted to contain thrushes. Applying criteria from our abundance model to a region-wide assessment of available private properties, we identified a 400-ha abandoned farm situated along the Cordillera Septentrional between existing protected areas that contained environmental conditions suitable for Bicknell's Thrushes. We used this information to identify, purchase, and create the Dominican Republic's first-ever private reserve, the 400-ha Reserva Privada Zorzal. Our model can be used to identify and prioritize additional lands for conservation of the Bicknell's Thrush in the region. Our approach could also be used elsewhere to make informed conservation decisions.

Keywords: Bicknell's Thrush, *Catharus bicknelli*, Dominican Republic, habitat, Nearctic–Neotropical migratory songbird, point count, winter

Modelando la variación espacial en la abundancia invernal de un ave canora migratoria vulnerable, *Catharus bicknelli*, para dirigir las acciones de conservación

RESUMEN

El rango invernal de *Catharus bicknelli*, un ave canora migratoria neártica-neotropical vulnerable a nivel global, está restringido a las Antillas Mayores. La mayoría de las aves están presentes en La Española, donde la especie exhibe segregación sexual de hábitat y donde la pérdida de sus hábitats de hoja ancha húmedos preferidos ha sido severa. La conservación de los hábitats dominados por las hembras ha sido identificada como una alta prioridad. Durante 2010, condujimos muestreos de campo estandarizados para *C. bicknelli* en los bosques de la Cordillera Septentrional de República Dominicana, un área de alta importancia para las hembras. Combinamos datos de ocurrencia con variables ambientales para crear un modelo de distribución y de selección de hábitat de la especie en la región. La elevación (las densidades fueron máximas a ∼600 m), la orientación (laderas noroeste), la cantidad de cobertura boscosa dentro de 1 km y la densidad del bosque describieron mejor la presencia y la abundancia de la especie. A modo de ejemplo de cómo los modelos predictivos de abundancia pueden ayudar a la conservación, usamos el mejor modelo que contuvo solo covariables espacialmente explícitas para mapear la abundancia invernal predicha de *C. bicknelli*. Dos reservas científicas con la mayor elevación en el área de estudio y la mayor cobertura de bosque intacto, albergaron las áreas más grandes con mayor abundancia de *C. bicknelli*, pero muchas tierras privadas albergaron fragmentos de bosque donde se predijo la presencia de la especie. Aplicando los criterios de nuestro modelo de abundancia a una evaluación a escala regional de la disponibilidad de propiedades privadas, identificamos 400 ha de fincas abandonadas situadas a

lo largo de la Cordillera Septentrional entre las áreas protegidas existentes que presentaron condiciones ambientales adecuadas para *C. bicknelli*. Usamos esta información para identificar, comprar y crear la primera reserva privada de la historia de República Dominicana – la Reserva Privada Zorzal de 400 ha. Nuestro modelo puede ser usado para identificar y priorizar tierras adicionales para la conservación en la región. Nuestro enfoque podría usarse en otras partes para tomar decisiones informadas de conservación.

Palabras clave: ave canora migratoria neártica-neotropical, *Catharus bicknelli*, hábitat, invierno, punto de conteo, República Dominicana

INTRODUCTION

Conservation planning and implementation require the identification of high-quality habitats and geographic locations where management actions may improve the viability of target species. The conservation of nonbreeding habitat of many Nearctic–Neotropical migratory songbirds can be especially challenging, yet many studies have shown that winter habitat quality and availability limit populations of migratory songbirds, and that alteration of winter habitat can lead to population declines (e.g., Marra et al. 1993, Sherry and Holmes 1996, Norris et al. 2004).

The Bicknell's Thrush (*Catharus bicknelli*) is considered one of the Nearctic–Neotropical migrants at greatest risk of extinction and thus of highest continental conservation concern (Pashley et al. 2000, Rich et al. 2004, Wells 2007, Townsend et al. 2015). The species is classified as Vulnerable by the International Union for the Conservation of Nature (IUCN) and as Threatened in Canada (Stattersfield and Capper 2000, COSEWIC 2009). Bicknell's Thrush breeding populations are declining in the core and northern parts of the species' range. Breeding Bird Survey data from 16 routes in Canada from 1968 to 2008 showed a significant decline of 9% per year (COSEWIC 2009). Trail-based point count surveys in the White Mountains of New Hampshire, USA, revealed a 7% annual decline from 1993 to 2003 (Lambert et al. 2008). The High Elevation Landbird Program documented annual declines of 17% in New Brunswick, Canada, and 15% in Nova Scotia, Canada, between 2002 and 2009 (Whittam and Campbell 2010).

At both ends of its migratory range, the Bicknell's Thrush has a limited, highly fragmented distribution and faces multiple threats to its habitats that may affect populations (Atwood et al. 1996, Lambert et al. 2005, Townsend et al. 2015). These threats include climate change (Rodenhouse et al. 2008), acid ion deposition (Johnson et al. 1992, Graveland and van der Wal 1996, Hames et al. 2002), mercury contamination (Rimmer et al. 2005, 2010), mountaintop development (Rimmer et al. 2004, Strong et al. 2009, Townsend et al. 2015), forestry operations (Nixon et al. 2001, Chisholm and Leonard 2008, Aubry et al. 2011, McKinnon et al. 2014), interspecific competition (Freeman and Montgomery 2016), and loss and degradation of winter habitats (Rimmer 2005, Town-send et al. 2009b, 2015). Evidence indicates that a complex interplay of ecological and demographic factors on the wintering grounds, exacerbated by forest loss and degradation, may be a primary limiting factor across the annual cycle of the Bicknell's Thrush (Townsend et al. 2009a, 2009b).

Recent studies in the Dominican Republic have identified wet, broadleaf, montane forest at middle elevations as a potentially crucial habitat for the Bicknell's Thrush (Townsend et al. 2010, 2012). Bicknell's Thrushes exhibit sexual habitat segregation in winter (Townsend et al. 2011, 2012). Female thrushes occur at relatively high densities in moderately disturbed mid-elevation rainforests of the Cordillera Septentrional, compared with densities in the more pristine cloud forests of remote mountain ranges, such as Sierra de Bahoruco and Cordillera Central, where males are encountered 4 times more often than females (Townsend and Rimmer 2006, Townsend et al. 2011). While research is ongoing to elucidate the complex overwintering ecology of Bicknell's Thrushes, the species' primary limiting factor is thought to be winter survivorship of females, including possible seasonal carryover effects (Townsend et al. 2009b).

Despite considerable recent attention focused on Bicknell's Thrush conservation, surprisingly few empirical data exist with which to identify priority conservation areas on the species' Caribbean wintering grounds. At a range-wide scale, presence-only records from the past ~40 yr have been used to quantitatively evaluate winter distribution and habitat selection across the Greater Antilles (McFarland et al. 2013). The Dominican Republic was estimated to contain half of all potential winter habitat, with total winter precipitation, slope aspect, and land cover (particularly moist, broadleaf forests) found to be important predictor variables of thrush occupancy.

To stabilize or increase Bicknell's Thrush populations, immediate action must take place to conserve winter habitat (IBTCG 2010). Our study aimed to (1) estimate the abundance of Bicknell's Thrushes, while accounting for imperfect detection probability, in threatened forests of the Cordillera Septentrional, an area believed to be of high importance for female thrushes, and (2) relate abundance to a suite of habitat, geographic, topographic, and climatic variables. We also endeavored to demonstrate how spatial models of abundance can directly inform conservation

actions for Bicknell's Thrushes in the Dominican Republic through identifying an area that was developed into a private reserve.

METHODS

Study Site

The Cordillera Septentrional runs parallel to the northern coast of the Dominican Republic. Our study area was located in the easternmost region of the mountain range and encompassed 2 scientific reserves, Loma Quita Espuela in the west and Loma Guaconejo in the east, and a 10-km² buffer zone (Appendix Figure 4). The reserves were legally designated as protected areas by the Dominican government in 1990 (Loma Quita Espuela) and 1996 (Loma Guaconejo) because the flora and fauna have exceptionally high rates of endemism and diversity (Sanchez and Hager 1997, SODIN 2002). Both reserves have been designated as Important Bird Areas (IBAs) by BirdLife International on the basis of their national significance for supporting avian biodiversity (Perdomo and Arias 2008). The biodiversity within both reserves has also contributed to Hispaniola receiving the highest ranking of biological importance in a worldwide assessment of bird protection priorities (Stattersfield et al. 1998). Despite the importance of the 2 reserves for supporting regional biodiversity and avian habitat, intensively cultivated land in the buffer zone has caused severe forest fragmentation. The remaining forest habitat is highly threatened. GIS analysis of the study area has indicated that only 4% of land outside protected area boundaries is composed of primary forest (Kerchner et al. 2010).

Bird Surveys

We used a generalized random tessellation stratified (GRTS) sampling design to allow for a spatially balanced probabilistic approach (Stevens and Olsen 2004). For the GRTS sample selection process we divided our study area into 1-km² blocks ($n = 1,100$). We then evaluated each block in the order in which it was selected by the GRTS process and established survey points in the block if it (1) contained enough forested areas to hold at least 4 survey points spaced 200 m apart, and (2) was within 3 km of an access road or within 1 km of a trail. We did not place survey points in blocks that we did not have permission to access. For logistical reasons, we occasionally placed 1–2 points in an adjacent block to create a full route of points. This resulted in 25 blocks containing 1–12 points each.

To assess habitat-specific abundance, we surveyed Bicknell's Thrushes at 99 points (Appendix Figure 4) between January and March, 2010. Two experienced observers visited each point 2 ($n = 3$) or 3 ($n = 96$) times. During each visit, they counted all Bicknell's Thrushes heard or seen during a 20-min survey period that was divided into 8 2.5-min counts, with a 1-min playback of conspecific calls broadcast at min 10 and min 15. Playback recordings included both songs and calls of Bicknell's Thrushes. To avoid the possibility of including transients, surveys were conducted during the middle of the territorial overwintering period (Townsend et al. 2010). We were not able to distinguish the age or sex of individual thrushes from vocalizations or observations. Air temperature, wind speed, cloud cover, and time of day were recorded during each survey. Wind speed and cloud cover were measured on a scale of 0–4, with wind speed following the Beaufort scale and cloud cover ranging from clear (0) to light drizzle (4). Surveys were not conducted during rain showers or when winds exceeded 4 (~29 km hr^{-1}). Because of logistical constraints, we did not maintain regular intervals between consecutive surveys. The number of days between first and second surveys varied from 1 to 62 days ($\bar{x} = 11.37 \pm 17.93$ SD days), while 1 to 49 days elapsed between second and third surveys ($\bar{x} = 23.93 \pm 14.81$ SD days). The total time between first and last surveys ranged from 20 to 63 days ($\bar{x} = 35.0 \pm 11.2$ SD days).

Habitat Data

To determine forest cover in the study area, we used images acquired between 2007 and 2009 from the Landsat Enhanced Thematic Mapper (ETM+) instrument operated by the U.S. Geological Survey and the National Aeronautics Space Administration (NASA). Orthorectification and atmospheric corrections were performed by NASA. Four images were selected to create a composite, cloud-free image of the study region. We used a digital elevation model (DEM) created from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) for terrain data (elevation and aspect). We calculated northness using cos(aspect × π/180) and eastness as sin(aspect × π/180). These aspects likely receive higher annual precipitation from prevailing easterly winds, resulting in the wet forests preferred by Bicknell's Thrushes (McFarland et al. 2013). Because the density of the forest understory is known to be important for the selection of both winter and breeding habitat by Bicknell's Thrushes (Frey et al. 2012, McFarland et al. 2013, Townsend et al. 2015), we measured understory density using ocular estimates of the amount of vegetation covering an imaginary box 1 m wide and 2.5 m tall placed 10 m away from each survey point in each cardinal direction. Average canopy height was estimated to the nearest meter. Two observers conducted all ocular estimates; both were trained in estimation prior to surveys using a gridded frame 1 m wide and 2.5 m tall. Total canopy cover at each survey point was determined using the average densiometer reading from each cardinal direction at the survey center.

Statistical Analysis

All statistical analyses were performed using R statistical software (R Core Team 2012) with package Unmarked 0.11 (Fiske and Chandler 2011). We modeled Bicknell's Thrush population dynamics using the model of Dail and Madsen (2011). This model extends the Royle N-mixture model (Royle 2004) for data collected on open populations (i.e. those experiencing mortality, recruitment, immigration, and emigration).

For each site ($i = 1, \ldots, R$), primary sampling occasion (i.e. the repeated visits to each point; $j = 1, \ldots, J$), and secondary sampling occasion (i.e. the 8 2.5-min counts during each of the 3 repeated visits; $k = 1, \ldots, K$), we recorded the number of individuals detected, denoted as $\{y_{ijk}\}$. Within each of the J primary periods, the population was assumed to have been closed with respect to movement and demographic processes, but closure was not assumed between primary periods.

Abundance in the initial time period (N_{i1}) was treated as an outcome of a Poisson distribution with a mean of λ_i. This can be thought of as the expected abundance of animals following an initial territory establishment process. Subsequent to this initial time period, individuals remained on the plot with probability ω, which is the apparent survival probability, that is, the probability of surviving and not permanently emigrating. New individuals entered the plot at a Poisson rate of γ. The sum of the remaining individuals (S) and recruitment (G) determined future abundance (N_{ij}). These individuals were then detected with probability p. Thus, the model can be described as follows:

$$N_{i1} \sim \text{Poisson}(\lambda_i);$$

$$S_{ij} \sim \text{Binomial}(\omega, N_{ij}-1);$$

$$G_{ij} \sim \text{Poisson}(\gamma);$$

$$N_{ij} = G_{ij} + S_{ij};$$

$$y_{ijk} \sim \text{Binomial}(p, N_{ij}).$$

Each of the 4 parameters (λ_i, γ_i, ω_i, and p_i) can be modeled as a function of covariates. We used a forward manual stepwise approach to select the variables that best explained both detection probability and abundance.

For the detection probability component of the model, we considered time of day, date, observer, playback, temperature, an index of wind speed, and an index of cloud cover as covariates. Date was represented as the day of the year starting on January 1. We began by running a global model that included all detection covariates, with abundance held constant. We used the P-values from the global model to determine the order in which potential covariates were added during the stepwise selection process (e.g., the first model included only the covariate with the smallest P-value, the second model included the covariates with the 2 smallest P-values, and so on). In subsequent abundance models, as per Burnham and Anderson (2002), we retained any detection variables present in models within 2 Akaike's information criterion points (ΔAIC) of the top model. We kept apparent survival constant in all models. Recruitment was also modeled as constant and was estimated to allow for immigration and to account for serial correlation.

Once we had determined the best set of covariates for describing detection probability, we moved on to identify the best set of covariates for characterizing abundance. Holding detection to be a function of the best set of covariates, we used the same stepwise procedure as described for selecting detection covariates to identify the best model of abundance. We considered the following covariates: (1) a quadratic effect of elevation (hereafter, Elev^2), (2) the percentage of native forest cover within 1 km of the survey point (For1km), (3) aspect (Northness and Eastness), (4) canopy height (Ht), (5) canopy cover (Cov), and (6) understory vegetation density (Den). Variables 1–3 were derived from remote sensing data, and variables 4–6 were determined from on-the-ground vegetation surveys. We selected these variables based on previous field experience and range-wide modeling results (McFarland et al. 2013).

RESULTS

We visited 3 of the 99 survey points twice and 96 of the points 3 times, yielding a total of 2,352 secondary sampling occasions. We detected Bicknell's Thrushes at 30 of the 99 survey points. Eighty percent of detections during surveys were of single individuals, and we never detected more than 2 thrushes at a single point. Thrushes were detected during just 5% of the secondary sampling occasions.

Only 39 detections (36%) occurred before the first playback period, illustrating the importance of using broadcast vocalizations for detection of this cryptic species. Playback and air temperature at the start of a survey were present in all supported models for detection probability (Table 1) and were the most significant variables (Table 2). Detection probability was predicted to nearly double after broadcasting vocalizations (Figure 1A). At the coolest temperatures ($\sim 16^\circ$C), detection probability was predicted to be ~ 0.4, dropping linearly to < 0.2 when temperatures reached 27°C (Figure 1B). Additionally, observer and wind speed were important in some plausible models, with predicted effects on detection probability of ~ 0.1 between the 2 observers and for the
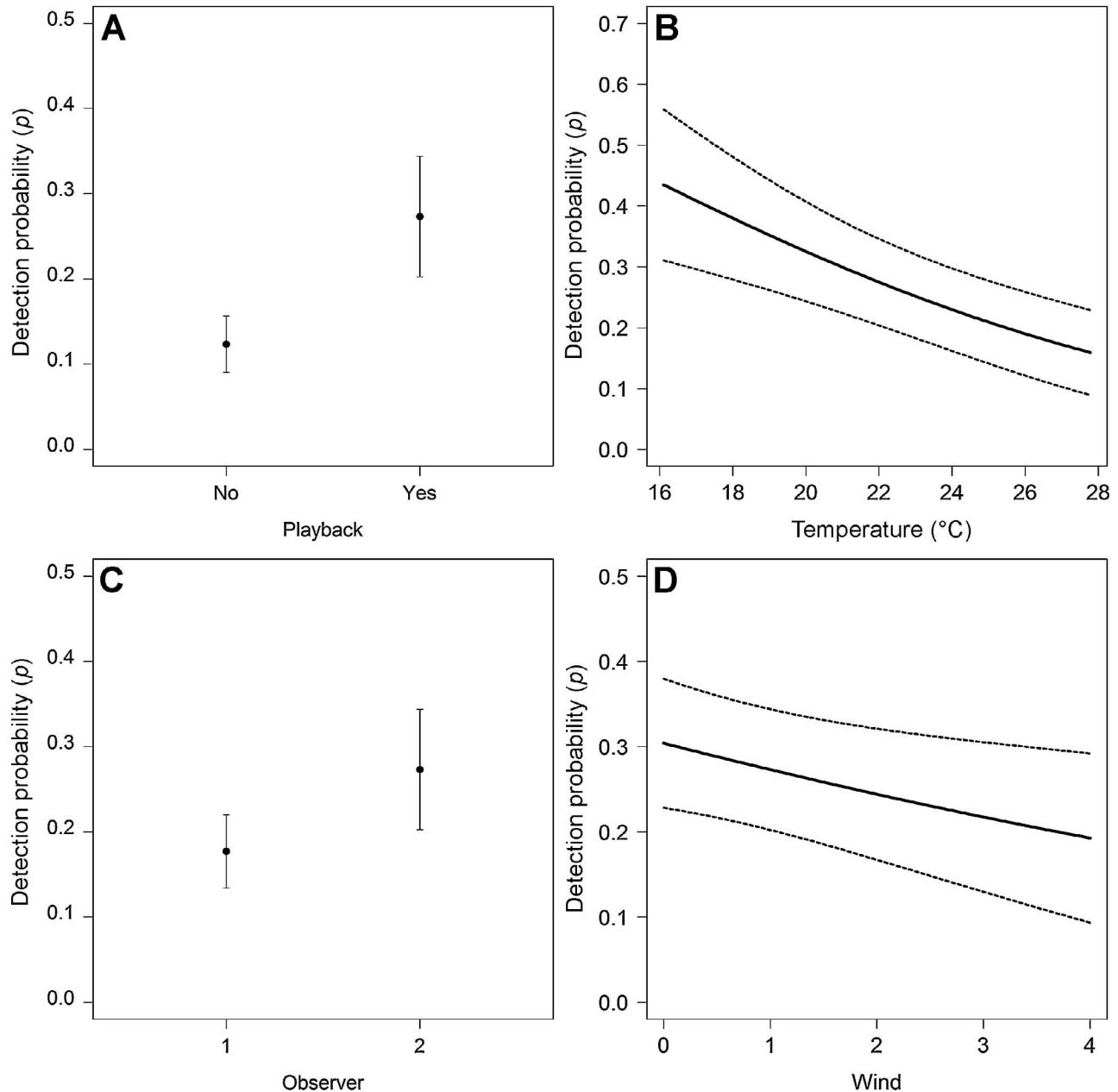
FIGURE 1. Detection of Bicknell's Thrush in relation to (**A**) playback use, (**B**) air temperature (°C), (**C**) observer, and (**D**) wind speed in the eastern Cordillera Septentrional, Dominican Republic, January–March, 2010. Error bands and bars are ± 1 SE.

lowest to highest wind speeds during surveys (Figures 1C and 1D).

Initial abundance varied among points as demonstrated by the inclusion of multiple covariates in all supported models (Table 3). The importance of 5 covariates was clear (Table 4). A quadratic effect of elevation ($Elev^2$) was present in all models (Table 3), with abundance predicted to peak at 552 m (Figure 2A). As expected for a forest-interior songbird, an effect of the amount of forest cover

within 1 km^2 of a survey point was strongly supported, with abundance predicted to rise cubically to >2 thrushes per survey point with >80% forest cover (Figure 2B). Thrushes were predicted to potentially be present at low densities even when forest cover was <20%. Mountain slopes with more easterly and northerly aspects were predicted to have higher thrush abundance (Figures 2C and 2D); these aspects generally correspond to higher precipitation (eastern and northern slopes intercept moist
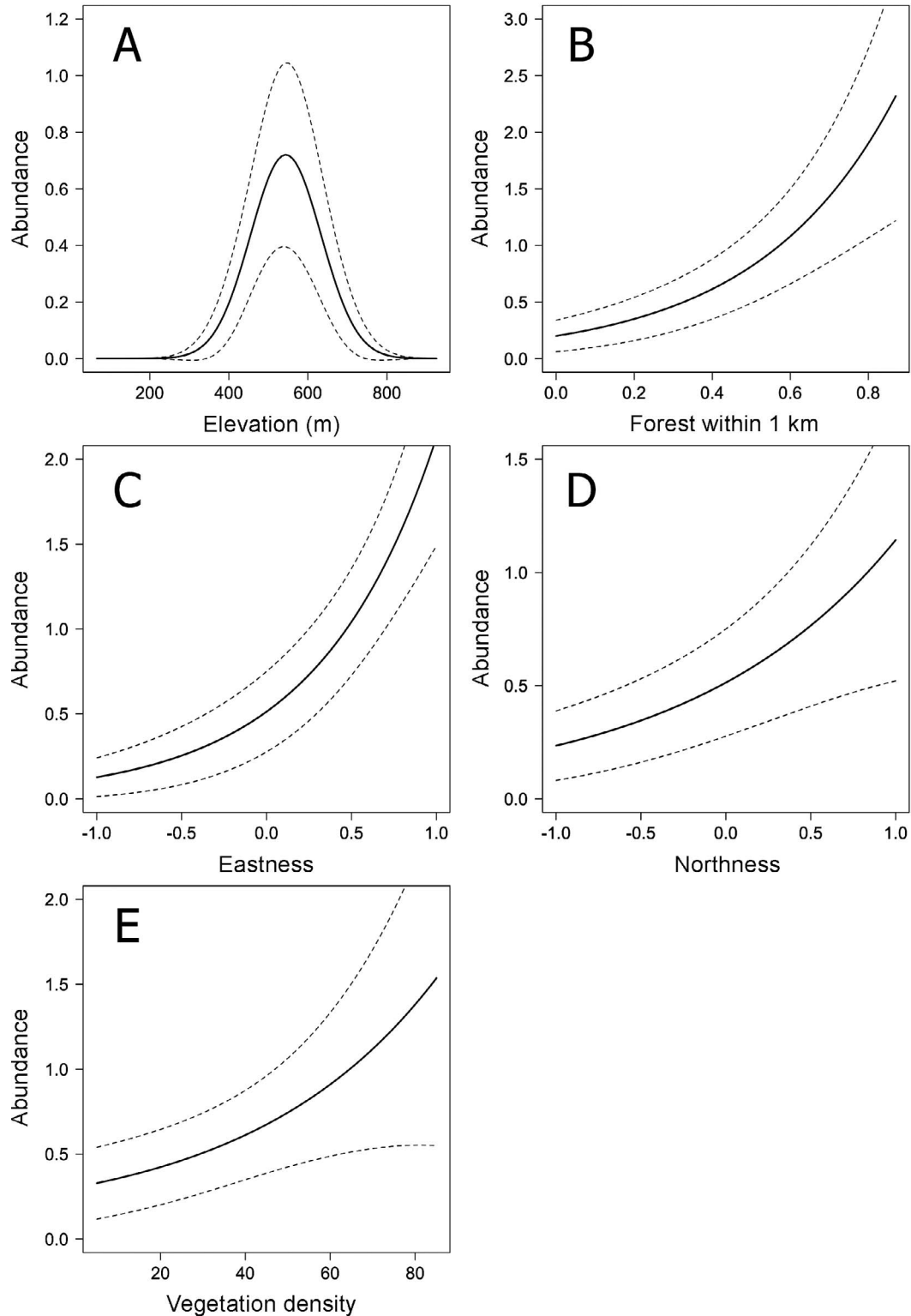
FIGURE 2. Estimates of expected abundance of Bicknell's Thrush in the eastern Cordillera Septentrional, Dominican Republic, January–March, 2010, in relation to (**A**) elevation (m), (**B**) the percentage of native forest cover within 1 km of survey points, (**C**) slope aspect eastness, (**D**) slope aspect northness, and (**E**) understory vegetation density based on the top-ranked model (Table 3). Error bands are ± 1 SE.
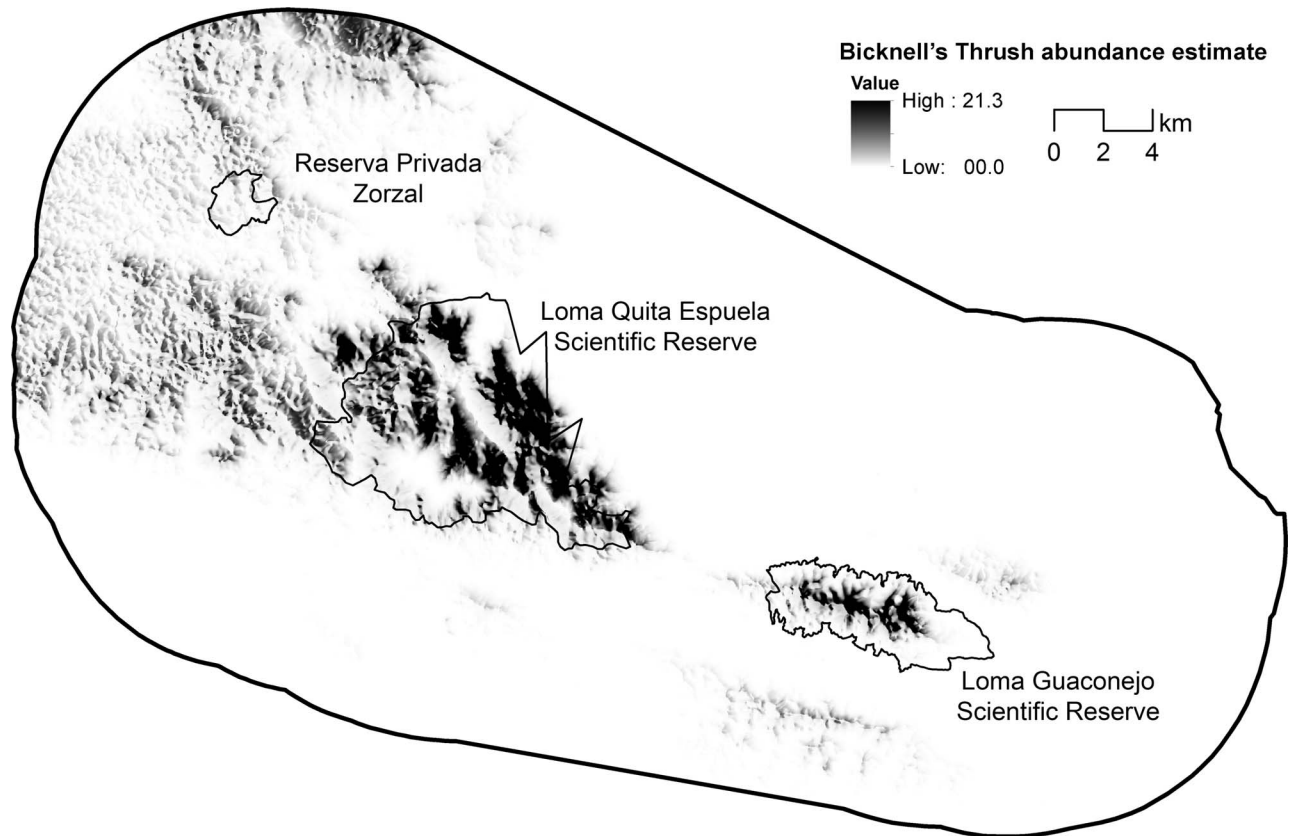
FIGURE 3. Expected abundance of Bicknell's Thrush in the eastern Cordillera Septentrional, Dominican Republic, if a count were conducted at the centroid of each 30 m^2 raster cell, predicted using the model λ(Elev^2 + E + For1km + N) p(Playback + Temp + Obs + Wind + Time) γ(constant) ω(constant). See Tables 1 and 3 for parameter definitions and model details.

easterly trade winds, leaving west- and south-facing slopes in a substantial rain shadow), and possibly greater wind damage from tropical storms. Vegetation density, a local-scale habitat covariate, was also a good predictor of thrush abundance (Figure 2E), and indicated that Bicknell's Thrush abundance would be greater in naturally disturbed mature forest and advanced secondary forest.

Predicted apparent recruitment over the winter season was low, whereas predicted apparent survivorship was ~98% (90% CI: 96–99%; Table 5). Estimates of total abundance for the survey points ranged from 50 (90% CI: 27–105) Bicknell's Thrushes during survey period 1, to 46 thrushes (90% CI: 28–81) during survey 2, down to 42 (90% CI: 25–72) during the final survey.

We used the best model that contained only spatially explicit covariates—λ(Elev^2 + Eastness + For1km + Northness) p(Playback + Temp + Obs + Wind) γ(constant) ω(constant)—to map predicted winter abundance of the Bicknell's Thrush (Figure 3). With the highest elevations in the study area (~600 m) and the most intact forest cover, the 2 scientific reserves were predicted to contain the largest areas of high thrush abundance.

DISCUSSION

Understanding patterns of distribution and habitat use is fundamental to informing conservation actions, especially those aimed at rare and vulnerable species. Identifying high-quality habitat is crucial for effectively conserving species that are experiencing population declines as a result of habitat loss, such as the Bicknell's Thrush. This wet-forest specialist is exceedingly cryptic on its restricted Greater Antillean wintering grounds, which has constrained efforts to elucidate its habitat-specific abundance and evaluate its conservation needs. Yet, without comprehensive knowledge of the species' nonbreeding demographics and habitat use, conservation resources may be inappropriately applied and population declines may be exacerbated.

As an example of how predictive models of abundance can inform conservation, we used the spatially explicit nature of our models to identify locations in the study area predicted to support Bicknell's Thrushes. Applying criteria from our abundance model to a region-wide assessment of available private properties, we identified a 400-ha

TABLE 1. Model selection results for Bicknell's Thrush detection probability (p). All models included expected initial abundance (λ) ~ global, rate of immigration (γ) ~ constant, and apparent survival probability (ω) ~ constant. Data were collected at 99 survey points in the eastern Cordillera Septentrional, Dominican Republic, January–March, 2010. K is the number of model parameters, $-2\ln L$ is the maximized log-likelihood, ΔAIC is the difference from the top model in Akaike's information criterion, and w_i is the Akaike model weight.

Model [a]	K	$-2\ln L$	ΔAIC	w_i
Playback + Temp + Obs	15	395.30	0.00 [b]	0.32
Playback + Temp + Obs + Wind + Time	17	393.81	1.03	0.19
Playback + Temp + Obs + Wind	16	394.82	1.06	0.19
Playback + Temp	14	397.17	1.74	0.19
Playback	13	398.78	2.96	0.07
Playback + Temp + Obs + Wind + Time + Date	17	394.80	3.02	0.07
Global [c]	19	393.48	4.37	0.03
Null	12	411.70	26.81	0.01

[a] Playback = a dummy variable indicating whether or not a recorded vocalization was broadcast during the survey; Temp = the air temperature at the time of the survey; Obs = a dummy variable indicating the identity of the observer conducting the survey; Wind = wind speed during the survey estimated using the Beaufort scale; Time = the time of day at the beginning of the survey; and Date = the date on which the survey was conducted.
[b] Minimum AIC = 820.59.
[c] The global model included Playback + Temp + Obs + Wind + Time + Date + Cloud. Cloud = estimated cloud cover at the time of the survey on a scale of 0–4 (0 = clear, 1 = partly cloudy, 2 = mostly cloudy, 3 = completely cloudy, 4 = light drizzle).

TABLE 2. Parameter estimates and P-values from the global detection (p) model for Bicknell's Thrush (Table 1).

Parameter [a]	Estimate	SE	P-value
β_0	−2.605	0.274	<0.001
Playback	0.978	0.190	<0.001
Temp	−0.306	0.147	0.04
Obs	0.648	0.353	0.07
Wind	−0.183	0.167	0.27
Time	0.135	0.118	0.25
Date	0.112	0.147	0.45
Cloud	−0.068	0.149	0.65

[a] β_0 = intercept; Playback = a dummy variable indicating whether or not a recorded vocalization was broadcast during the survey; Temp = the air temperature at the time of the survey; Obs = a dummy variable indicating the identity of the observer conducting the survey; Wind = wind speed during the survey estimated using the Beaufort scale; Time = the time of day at the beginning of the survey; Date = the date on which the survey was conducted; and Cloud = estimated cloud cover at the time of the survey on a scale of 0–4 (0 = clear, 1 = partly cloudy, 2 = mostly cloudy, 3 = completely cloudy, 4 = light drizzle).

abandoned farm that contained environmental conditions suitable for Bicknell's Thrushes and that was situated along the Cordillera Septentrional between the 2 existing protected areas to the southeast (Loma Quita Espuela and Loma Guaconejo scientific reserves) and La Salcedoa Scientific Reserve to the northwest, just beyond our study area. Conservation of this area thus offered the possibility of increasing landscape connectivity and protecting potential habitat for the Bicknell's Thrush. Based in part on this assessment, the area was purchased as part of a larger land deal and has now been established as the Dominican Republic's first-ever private conservation reserve, Reserva Privada Zorzal (Figure 3). Named after the local moniker for Bicknell's Thrush, most (~70%) of the reserve has been set aside for passive and active reforestation designed to create habitat for Bicknell's Thrushes, with the remaining area used for active cultivation of agricultural crops, including shade-grown cacao. Field surveys in 2016 detected Bicknell's Thrushes at

48 of 107 survey points in forest fragments and regenerating stands of secondary forest on this property (H. Almonte personal communication), where our model predicted that Bicknell's Thrushes would occur at low to moderate abundance. Although other enabling factors were critical, notably a legal framework for creating a private nature reserve and the possibility of generating income from part of the property, the potential value of the area for conservation of the Bicknell's Thrush was crucial for making the case for establishing the reserve. We believe that this provides a compelling example of how distributional models, when properly applied, can directly inform conservation action.

We suggest that using our model to identify and prioritize additional lands for conservation of the Bicknell's Thrush in the region is an important next step. The Cordillera Septentrional provides critical wintering habitat for females (Townsend et al. 2011), which are believed to experience disproportionate winter habitat limitations (Townsend et al. 2009a), and is experiencing ongoing deforestation (Kerchner et al. 2010), making the region a top priority for range-wide conservation efforts. Reforestation of degraded lands, by both passive (e.g., natural regeneration) and active means (e.g., planting native trees, controlling invasive species), will be a key component of an overall strategy to conserve winter habitat for this species. Our model provides an initial framework to identify parcels of suitable habitat, the first critical step in ensuring their protection.

More broadly, our findings reinforce the importance of mid-elevation and wet broadleaf forests for conservation of the Bicknell's Thrush. The reliance of Bicknell's Thrushes

TABLE 3. Model selection results for Bicknell's Thrush initial abundance (λ). All models included detection probability (p) ~ Playback + Temp + Obs + Wind + Time, rate of immigration (γ) ~ constant, and apparent survival probability (ω) ~ constant. Data were collected at 99 survey points in the eastern Cordillera Septentrional, Dominican Republic, January–March, 2010. K is the number of model parameters, $-2\ln L$ is the maximized log-likelihood, ΔAIC is the difference from the top model in Akaike's information criterion, and w_i is the Akaike model weight.

Model [a]	K	$-2\ln L$	ΔAIC	w_i
Elev^2 + E + For1km + N + Den	15	393.93	0.00 [b]	0.51
Elev^2 + E + For1km + N + Den + Ht	16	393.83	1.80	0.21
Elev^2 + E + For1km + N + Den	14	396.02	2.19	0.17
Elev^2 + For1km + N + E + Den + Ht + Cov	17	393.81	3.76	0.08
Elev^2 + E + For1km	13	398.94	6.02	0.03
Elev^2 + E	12	402.10	10.25	0.00
Elev^2	11	405.10	14.27	0.00
Constant abundance	9	420.88	41.89	0.00

[a] Elev^2 = quadratic effect of elevation (elevation + elevation^2) at the survey location; E = eastness, calculated as sin(aspect $\times$ π/180) and measuring the degree to which the survey location faced east into prevailing winds; For1km = percent native forest cover within a 1-km-radius circle around the survey location; N = northness, calculated as cos(aspect $\times$ π/180) and measuring the degree to which the survey location faced north into prevailing winds; Den = density of understory plant cover; Ht = canopy height; and Cov = canopy cover.
[b] Minimum AIC = 817.86.

TABLE 4. Parameter estimates and P-values from the global initial abundance (λ) model for Bicknell's Thrush (Table 3).

Parameter [a]	Estimate	SE	P-value
β_0	−0.691	0.489	0.16
Elev	2.105	0.916	0.02
Elev^2	−3.077	1.026	0.002
For1km	0.651	0.248	0.009
E	1.456	0.504	0.004
N	0.799	0.387	0.04
Den	0.470	0.225	0.04
Ht	0.080	0.211	0.71
Cov	0.050	0.210	0.81

[a] β_0 = intercept; Elev = Elevation; Elev^2 = quadratic effect of elevation (elevation + elevation^2) at the survey location; For1km = percent native forest cover within a 1-km-radius circle around the survey location; E = eastness, calculated as sin(aspect $\times$ π/180) and measuring the degree to which the survey location faced east into prevailing winds; N = northness, calculated as cos(aspect $\times$ π/180) and measuring the degree to which the survey location faced north into prevailing winds; Den = density of understory plant cover; Ht = canopy height; and Cov = canopy cover.

on a narrow range of biophysical conditions leaves the species highly vulnerable to ongoing deforestation (wet montane forest remains the most endangered habitat on Hispaniola; Perdomo and Arias 2008) and to climate change, which is predicted to yield a substantial drying trend throughout the Caribbean region (Neelin et al. 2006). Long-term conservation of the Bicknell's Thrush, as well as the many endemic and other resident fauna with which they co-occur during winter, will hinge on concerted habitat protection and restoration. Given the limited public resources available for management of protected areas, expanding conservation efforts by enlisting willing private landowners, as with the case study that we have described here, should be considered.

ACKNOWLEDGMENTS

Ethics statement: Permission to conduct research in the Dominican Republic was granted by the Secretaria de Estado de Medio Ambiente y Recursos Naturales (permit #0000023). Locally, surveys within the 2 scientific reserves were approved by reserve managers. Outside the reserves, private property owners, if identifiable, were informed of and approved bird surveys. The entire study was observational. Bird counts were conducted both visually and aurally by trained field biologists and were of short duration, minimizing any potential disturbance to the count area. Playback of conspecific

TABLE 5. Parameter estimates and 90% confidence limits (CL) from the most general dynamic abundance model considered for Bicknell's Thrush surveyed at 99 point count locations in the eastern Cordillera Septentrional, Dominican Republic, January–March, 2010.

Parameter	Estimate	SE	Lower 90% CL	Upper 90% CL
Initial abundance (individuals per plot)	0.496	0.484	0.192	1.281
Apparent recruitment	0.004	0.002	0.001	0.010
Apparent survival	0.982	0.007	0.964	0.991

vocalizations was held to short durations and followed the *Guidelines to the Use of Wild Birds in Research*.

Author contributions: K.P.M. and C.C.R. conceived the idea for this project. K.P.M., C.C.R., P.L.J., and R.B.C. created the experimental design. P.L.J. conducted the fieldwork. S.J.K.F., J.D.L., R.B.C., and K.P.M. analyzed the data. K.P.M., R.B.C., and S.J.K.F. wrote the initial draft of the manuscript, and K.P.M., S.J.K.F., C.C.R., and J.D.L. collaboratively wrote and edited subsequent drafts of the manuscript.

Data deposits: Data has been deposited with the Knowledge Network for Biocomplexity (KNB) and can be accessed at https://knb.ecoinformatics.org/#view/doi:10.5063/F11834NT
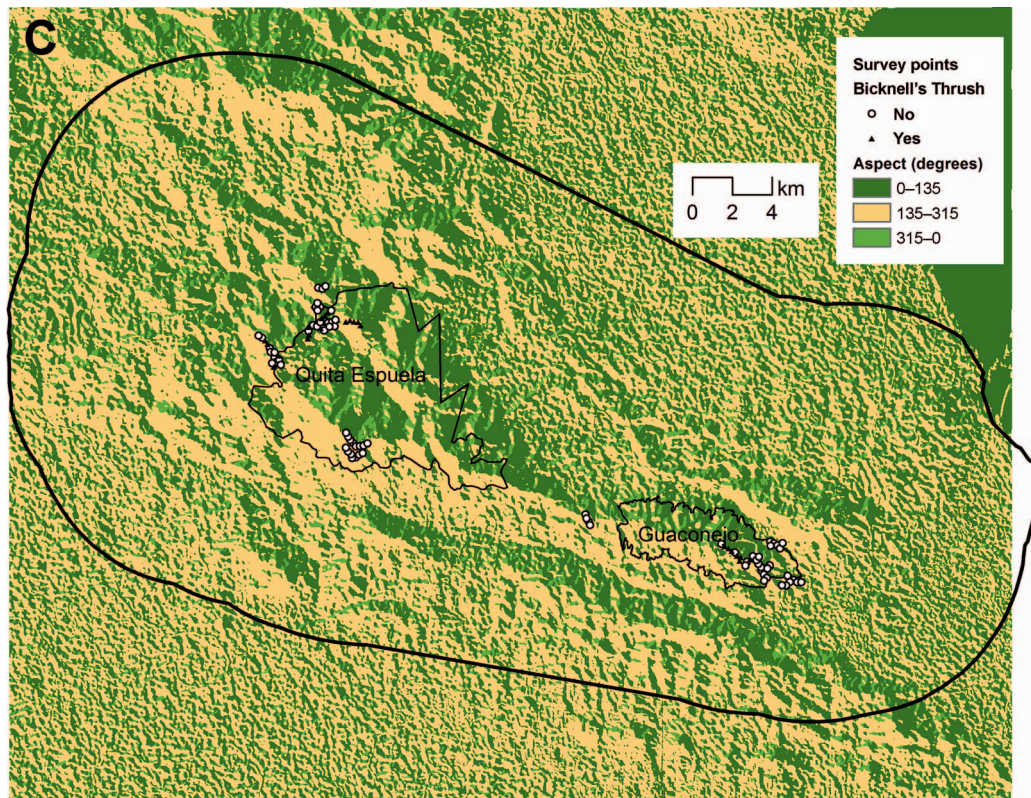
LITERATURE CITED

Atwood, J. L., C. C. Rimmer, K. P. McFarland, S. H. Tsai, and L. R. Nagy (1996). Distribution of Bicknell's Thrush in New England and New York. The Wilson Bulletin 108:650–661.

Aubry, Y., A. Desrochers, and G. Seutin (2011). Response of Bicknell's Thrush (*Catharus bicknelli*) to boreal silviculture and forest stand edges: A radio-tracking study. Canadian Journal of Zoology 89:474–482.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer-Verlag, New York, NY, USA.

Chisholm, S. E., and M. L. Leonard (2008). Effect of forest management on a rare habitat specialist, the Bicknell's Thrush (*Catharus bicknelli*). Canadian Journal of Zoology 86: 217–223.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2009). Unsolicited update: COSEWIC status report on the Bicknell's Thrush *Catharus bicknelli* in Canada. Submitted to the Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON, Canada.

Dail, D., and L. Madsen (2011). Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67:577–587.

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.

Freeman, B. G., and G. Montgomery (2016). Interspecific aggression by the Swainson's Thrush (*Catharus ustulatus*) may limit the distribution of the threatened Bicknell's Thrush (*Catharus bicknelli*) in the Adirondack Mountains. The Condor: Ornithological Applications 118:169–178.

Frey, S. J. K., A. M. Strong, and K. P. McFarland (2012). The relative contribution of local habitat and landscape context to metapopulation processes: A dynamic occupancy modeling approach. Ecography 35:581–589.

Graveland, J., and R. van der Wal (1996). Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. Oecologia 105:351–360.

Hames, R. S., K. V. Rosenberg, J. D. Lowe, S. E. Barker, and A. A. Dhondt (2002). Adverse effects of acid rain on the distribution of the Wood Thrush *Hylocichla mustelina* in North America. Proceedings of the National Academy of Sciences USA 99:11235–11240.

IBTCG (International Bicknell's Thrush Conservation Group) (2010). A Conservation Action Plan for Bicknell's Thrush (*Catharus bicknelli*) (J. A. Hart, C. C. Rimmer, R. Dettmers, R. M. Whittam, E. A. McKinnon, and K. P. McFarland, Editors). International Bicknell's Thrush Conservation Group. www. bicknellsthrush.org

Johnson, A. H., S. B. McLaughlin, M. B. Adams, E. R. Cook, D. H. DeHayes, C. Eagar, I. J. Fernandez, D. W. Johnson, R. J. Kohut, V. A. Mohnen, N. S. Nicholas, et al. (1992). Synthesis and conclusions from epidemiological and mechanistic studies of red spruce decline. In Ecology and Decline of Red Spruce in the Eastern United States (C. Eager and M. B. Adams, Editors). Springer-Verlag, New York, NY, USA. pp. 385–411.

Kerchner, C., M. Honzák, R. Kemkes, A. Richardson, J. Townsend, and C. C. Rimmer (2010). Designing spatially explicit incentive programs for habitat conservation: A case study of the Bicknell's Thrush wintering grounds. Ecological Economics 69:2108–2115.

Lambert, J. D., D. I. King, J. P. Buonaccorsi, and L. S. Prout (2008). Decline of a New Hampshire Bicknell's Thrush population, 1993–2003. Northeastern Naturalist 15:607–618.

Lambert, J. D., K. P. McFarland, C. C. Rimmer, S. D. Faccio, and J. L. Atwood (2005). A practical model of Bicknell's Thrush distribution in the northeastern United States. The Wilson Bulletin 117:1–11.

Marra, P. P., T. W. Sherry, and R. T. Holmes (1993). Territorial exclusion by a long-distance migrant warbler in Jamaica: A removal experiment with American Redstarts (*Setophaga ruticilla*). The Auk 110:565–572.

McFarland K. P., C. C. Rimmer, J. E. Goetz, Y. Aubry, J. M. Wunderle, Jr., A. Sutton, J. M. Townsend, A. Llanes Sosa, and A. Kirkconnell (2013). A winter distribution model for Bicknell's Thrush (*Catharus bicknelli*), a conservation tool for a threatened migratory songbird. PLOS One 8:e53986.

McKinnon, E. A., H. Askanas, and A. W. Diamond (2014). Nest-patch characteristics of Bicknell's Thrush in regenerating clearcuts, and implications for precommercial thinning. Northeastern Naturalist 21:259–270.

Neelin, J. D., M. Münnich, H. Su, J. E. Meyerson, and C. E. Holloway (2006). Tropical drying trends in global warming models and observations. Proceedings of the National Academy of Sciences USA 103:6110–6115.

Nixon, E. A., S. B. Holmes, and A. W. Diamond (2001). Bicknell's Thrushes (*Catharus bicknelli*) in New Brunswick clear cuts: Their habitat associations and co-occurrence with Swainson's Thrushes (*Catharus ustulatus*). The Wilson Bulletin 113:33–40.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society of London, Series B 271:59–64.

Pashley, D. N., C. J. Beardmore, J. A. Fitzgerald, R. P. Ford, W. C. Hunter, M. S. Morrison, and K. Rosenberg (2000). Partners in Flight: Conservation of the Land Birds of the United States. American Bird Conservancy, The Plains, VA, USA.

Perdomo, L., and Y. Arias (2008). Dominican Republic. In Important Bird Areas in the Caribbean: Key Sites for Conservation (D. C. Wege and V. Anadón-Irizarry, Editors). Birdlife International, Cambridge, UK. pp. 157–174.

R Core Team (2012). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Iñigo-Elias, J. A. Kennedy, et al. (2004). Partners in Flight North American Landbird Conservation Plan. Cornell Lab of Ornithology. Ithaca, NY, USA.

Rimmer, C. C. (2005). Bird conservation in Haiti: It's now or never to save Haiti's birds. Journal of Caribbean Ornithology 18:86–87.

Rimmer, C. C., K. P. McFarland, D. C. Evers, E. K. Miller, Y. Aubry, D. Busby, and R. J. Taylor (2005). Mercury concentrations in Bicknell's Thrush and other insectivorous passerines in montane forests of northeastern North America. Ecotoxicology 14:223–240.

Rimmer, C. C., K. P. McFarland, J. D. Lambert, and R. B. Renfrew (2004). Evaluating the Use of Vermont Ski Areas by Bicknell's Thrush: Applications for Whiteface Mountain, New York. Report by the Vermont Institute of Natural Science, Woodstock, VT, USA, submitted to Olympic Regional Development Authority, Lake Placid, NY, USA.

Rimmer, C. C., E. K. Miller, K. P. McFarland, R. J. Taylor, and S. D. Faccio (2010). Mercury bioaccumulation and trophic transfer in the terrestrial food web of a montane forest. Ecotoxicology 19:697–709.

Rodenhouse, N. L., S. N. Matthews, K. P. McFarland, J. D. Lambert, L. R. Iverson, A. Prasad, T. S. Sillett, and R. T. Holmes (2008). Potential effects of climate change on birds of the Northeast. Mitigation and Adaptation Strategies for Global Change 13:517–540.

Royle, J. A. (2004). *N*-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Sanchez, R. O., and J. Hager (1997). Loma Quita Espuela and its renewable natural resources, its current status, and a proposal for integrated management. In The Dominican Republic: A Country between Rain Forest and Desert (E. Bolay, Editor). Margraf Verlag, Weikersheim, Germany. pp. 260–269.

Sherry, T. W., and R. T. Holmes (1996). Winter habitat quality, population limitation, and conservation of Neotropical–Nearctic migrant birds. Ecology 77:36–48.

SODIN (Sociedad para el Desarrollo Integral del Nordeste) (2002). Proyecto Piloto: Ordenamiento Territorial de la Zona de Amortiquamiento de la Reserva Cientifica Loma Guaconejo. Final Report. SODIN, Nagua, Dominican Republic.

Stattersfield, A. J., and D. R. Capper (Editors) (2000). Threatened Birds of the World. Lynx Editions, Barcelona, Spain, and BirdLife International, Cambridge, UK.

Stattersfield, A. J., M. J. Crosby, A. J. Long, and D. C. Wege (1998). Endemic Bird Areas of the World: Priorities for Biodiversity Conservation. BirdLife Conservation Series 7, BirdLife International, Cambridge, UK.

Stevens, D. L., Jr., and A. R. Olsen (2004). Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.

Strong, A. M., C. C. Rimmer, K. P. McFarland, and K. Hagan (2009). Effects of mountain resorts on wildlife. In Mountain Resorts: Ecology and the Law (J. E. Milne, J. LeMense, and R. A. Virginia, Editors). Ashgate Publishing, Surrey, UK, and Burlington, VT, USA. pp. 99–126.

Townsend, J. M., and C. C. Rimmer (2006). Known natal and wintering sites of a Bicknell's Thrush. Journal of Field Ornithology 77:452–454.

Townsend, J. M., K. P. McFarland, C. C. Rimmer, W. G. Ellison, and J. E. Goetz (2015). Bicknell's Thrush (*Catharus bicknelli*), version 2.0. In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.592

Townsend, J. M., C. C. Rimmer, J. Brocca, K. P. McFarland, and A. K. Townsend (2009a). Predation of a wintering migratory songbird by introduced rats: Can nocturnal roosting behavior serve as predator avoidance? The Condor 111:565–569.

Townsend, J. M., C. C. Rimmer, and K. P. McFarland (2009b). Investigating the limiting factors of a rare, vulnerable species: Bicknell's Thrush. In Tundra to Tropics: Connecting Birds, Habitats and People. Proceedings of the Fourth International Partners in Flight Conference (T. D. Rich, C. Arizmendi, D. W. Demarest, and C. Thompson, Editors). Partners in Flight. pp. 91–95.

Townsend, J. M., C. C. Rimmer, and K. P. McFarland (2010). Winter territoriality and spatial behavior of Bicknell's Thrush (*Catharus bicknelli*) at two ecologically distinct sites in the Dominican Republic. The Auk 127:514–522.

Townsend, J. M., C. C. Rimmer, K. P. McFarland, and J. E. Goetz (2012). Site-specific variation in food resources, sex ratios, and body condition of an overwintering migrant songbird. The Auk 129:683–690.

Townsend, J. M., C. C. Rimmer, A. K. Townsend, and K. P. McFarland (2011). Sex and age ratios of Bicknell's Thrush wintering in Hispaniola. The Wilson Journal of Ornithology 123:367–372.

Wells, J. V. (2007). Birder's Conservation Handbook: 100 North American Birds at Risk. Princeton University Press, Princeton, NJ, USA.

Whittam, R., and G. Campbell (2010). High Elevation Landbird Program: 2009 Report. Bird Studies Canada, Sackville, NB, Canada.
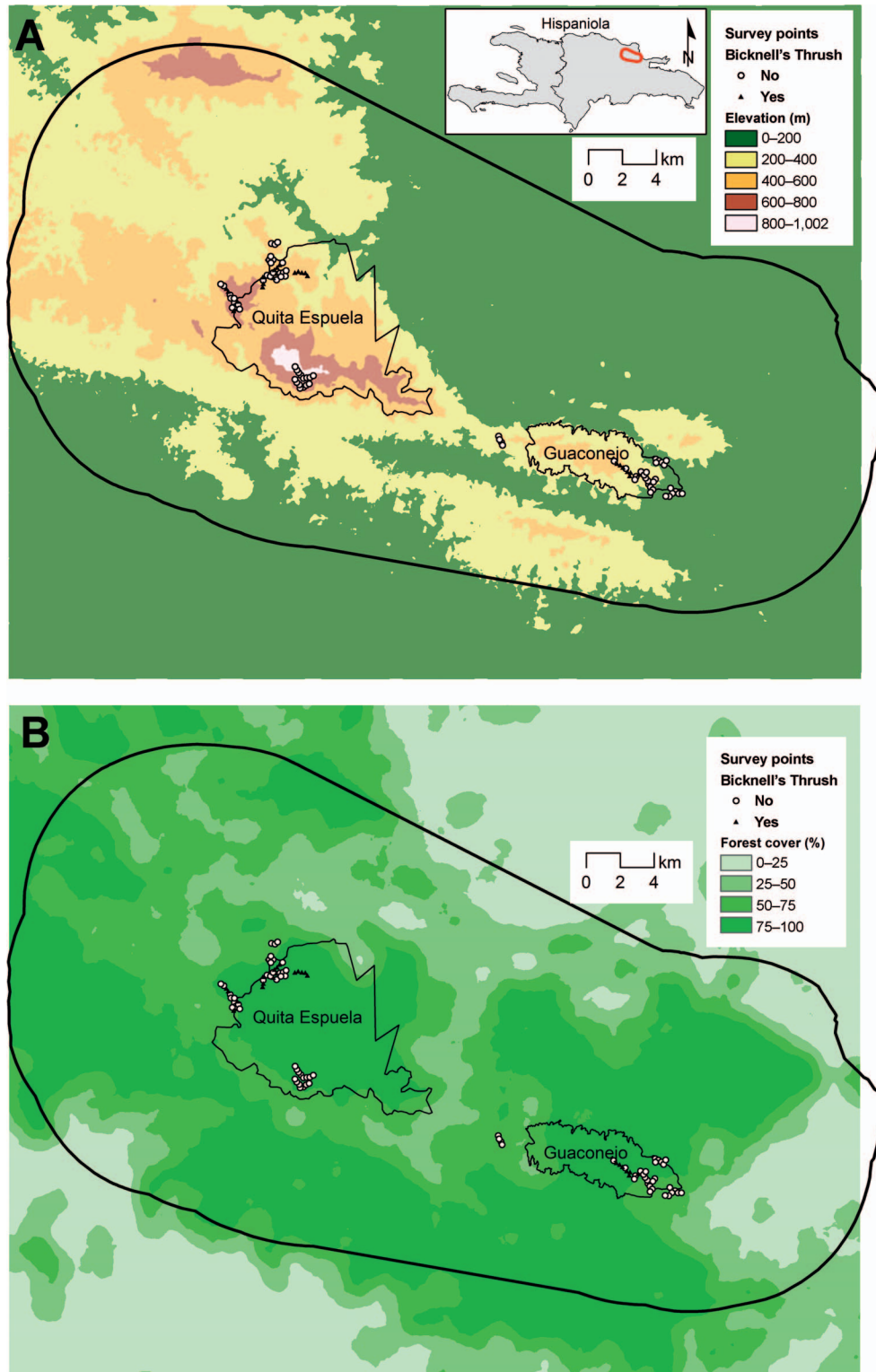
APPENDIX FIGURE 4. Map of the study area showing the locations of the 99 points surveyed for Bicknell's Thrush in the eastern Cordillera Septentrional, Dominican Republic, in winter (January–March) of 2010, with (**A**) elevation, (**B**) percent native forest cover within 1 km of the centroid of each 30 m^2 raster cell, and (**C**) slope aspect. The inset map displays the study area location on the island of Hispaniola.

APPENDIX FIGURE 4. Continued.