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The Effects of Spruce-Fir Disturbances on Bicknell's Thrush (Catharus bicknelli) Occupancy at Mountain Birdwatch Sampling Sites in Vermont

Jake Campbell

The University of Vermont

Rubenstein School of Environment and Natural Resources

Honors College

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Jake Campbell

Committee

Dr. James Murdoch, Wildlife and Fisheries Biology Program, Rubenstein School of Environment and Natural Resources, University of Vermont (Advisor)

Dr. Jason Hill, Vermont Center for Ecostudies and Rubenstein School of Environment and Natural Resources, University of Vermont

Dr. Beverley Wemple, Department of Geography, College of Arts and Sciences, University of Vermont

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Abstract

Bicknell's Thrush (*Catharus bicknelli*) is one of the most range-restricted forest birds of North America, breeding primarily in the montane spruce-fir forests of the northeastern USA. Population declines over the next decade are expected to be exacerbated by climate change, which is predicted to decrease the amount of spruce-fir forest cover in New England over the next several centuries. The threats faced by Bicknell's Thrush implore scientists to determine what factors drive its distribution throughout montane spruce-fir forest ecosystems. Of particular interest are the impacts of small-scale canopy gaps on Bicknell's Thrush. To examine this relationship, I used lidar-derived forest canopy gap measures and other site characteristics to construct a single-season occupancy model of Bicknell's Thrush based on presence-absence data from 155 Mountain Birdwatch sampling sites in Vermont. I evaluated the relative support of 19 candidate models that included single and additive combinations of elevation, latitude, total canopy gap area, number of canopy gaps, and median canopy gap size. The top-ranking model indicated that latitude, elevation, and median gap size had a positive effect on occupancy while number of gaps had a negative effect on occupancy. These results suggest that Bicknell's Thrush select areas with fewer large gaps over areas with many smaller gaps. This indicates that the additional sunlight received by areas with these canopy gap characteristics could have a positive influence on Bicknell's Thrush foraging success.

Introduction

Bicknell's Thrush (*Catharus bicknelli*) is one of the most range-restricted forest birds of North America, breeding primarily in the montane spruce-fir (*Picea spp. and Abies balsamea)* forests of the northeastern USA, but also in the boreal forests of eastern Canada (Townsend et al. 2020). Surveys for Bicknell's Thrush conducted in the White Mountains of New Hampshire (King et al. 2008; Lambert et al. 2008) documented the decline of Bicknell's Thrush populations between 1993 and 2003. This decline has likely continued throughout the past decade (Vermont Center for Ecostudies [VCE] 2020). These declines are expected to be exacerbated by climate change, which is predicted to decrease the amount of spruce-fir forest in New England by 65% over the next 200 years (Iverson et al. 2017). Bicknell's Thrush is also classified as a species of greatest conservation need and as a special concern species in New York, Vermont, New Hampshire, and Maine (Lambert et al. 2017). Because of the threats faced by the Bicknell's Thrush, it is important to determine what factors drive its distribution throughout the montane spruce-fir forest, as knowledge of these factors can assist in the conservation and management of Bicknell's Thrush habitat.

Previous research indicates that two factors driving the distribution of Bicknell's Thrush are elevation and latitude (Hill and Lloyd 2017). These two factors have a strong positive influence on the distribution of the montane spruce-fir habitat that Bicknell's Thrush depends on for breeding (Reiners and Lang 1979). There are also more local factors driving Bicknell's Thrush distribution. Within montane spruce-fir forests, the highest densities of Bicknell's Thrush are found in disturbed areas (Townsend et al. 2020). This is true not only for natural disturbances, but also for anthropogenic disturbances such as historically logged areas (Aubry et al. 2011) and ski trails (Hill and Campbell 2019), suggesting that other finer scale factors could affect distribution.

Previous studies have used a variety of methods to classify disturbance. Some depend on forest inventory data collected via field assessment (Aubry et al. 2011). These inventories are resource-intensive and often not feasible to conduct at a large spatial scale. Others depend on the National Land Cover Dataset (NLCD), using percent canopy cover to quantify disturbance (Dewitz 2021; Hill and Lloyd 2017). While this allows for analysis to take place on a larger spatial scale, the coarse spatial resolution of the NLCD (30 m) means that small disturbances cannot be reliably identified and included in statistical models. In this study, 0.7 m lidar-derived canopy height models (CHMs) were used to identify disturbed areas, allowing for the identification of small disturbances at a much larger spatial scale than *in situ* forest inventory methods.

The impacts of elevation, latitude, and canopy gaps measures on Bicknell's Thrush distribution were examined using an occupancy model approach (MacKenzie et al. 2002). The objectives of the study were to create an occupancy model for Bicknell's Thrush at Mountain Birdwatch sites in Vermont and to examine the impact that canopy gap characteristics have on Bicknell's Thrush occupancy at these sites. It was hypothesized that when holding latitude and elevation constant, Bicknell's Thrush occupancy would increase with increasing canopy gap quantity and size.

Materials and Methods

Study Area

This study used monitoring data collected by community scientists through the Mountain Birdwatch (MBW) program. Mountain Birdwatch is a long-term community science monitoring program for 10 species of birds, and red squirrel (*Tamiasciurus hudsonicus*) that live in the montane spruce-fir forests of the northeastern United States, including the Bicknell's Thrush (Hill and Lloyd 2017). Mountain Birdwatch sampling routes consist of 3-6 sampling sites located at least 0.25 km apart along hiking trails and logging roads (Hill and Lloyd 2017). At each sampling site, observers conduct four five-minute point counts and record both the birds present and whether each bird was detected at a distance of greater than or ≤50 m. (Hill and Lloyd 2017). Each site is surveyed annually by a lone observer—typically, an experienced birder—on a day with fair weather in June. All the sampling sites along a route are surveyed on the same day in a given year. There are MBW sampling routes in New York (within the Adirondacks and

Catskills), Vermont, New Hampshire, and Maine, but based on the availability and quality of lidar data, only sampling sites within Vermont were considered for this study (VCE 2019). Within Vermont, there are 165 sampling sites representing 29 MBW routes (VCE 2019; Figure 1).

Lidar

Light detection and ranging (lidar) is a remote sensing technology that can be used to measure the three-dimensional structure of a landscape and is well-suited for obtaining accurate estimates of vegetation height and canopy cover (Lefsky et al. 2002). Lidar sensors, typically mounted on level-flying planes, emit a laser pulse and measure the amount of time it takes for that pulse to return to the sensor (Lefsky et al. 2002). When these pulses are sent out at a rapid rate, they will reflect off of features above the ground (such as vegetation) and the ground itself (Lefsky et al. 2002). The time it takes for the pulse to return to the sensor is used to calculate the distance the pulse traveled (Lefsky et al. 2002). This results in the creation of a three-dimensional point cloud containing x-, y-, and z-coordinates for each return (Lefsky et al. 2002). Statewide lidar data for Vermont is available at a spatial resolution of 0.7 m (Vermont Center for Geographic Information [VCGI] 2021), a 43-fold increase in spatial resolution when compared to NLCD data. In these data, each pixel represents a square with side lengths of 0.7 m. The lidar data used in this study were collected between 2014 and 2017 because Vermont does not have statewide lidar data for any single given year (VCGI 2018a).

I used canopy height models downloaded from the Vermont Center for Geographic Information's Vermont lidar finder (2021). Canopy height models represent the height of an object above ground surface and are created by subtracting the elevation of the ground (digital terrain model) from the elevation above sea level of features (such as trees) on the ground (digital surface model). The resulting CHM represents the height of these objects (Figure 2).

I then determined the date of lidar collection for each sampling site by digitizing the collection date maps included with the lidar metadata (VCGI et al. 2018a; Figure 3**)**. I created a 100-m buffer around each MBW sampling site (Environmental Systems Research Institute [ESRI] 2021). For all buffers with a single lidar collection date, I recorded the date as is. For buffers that had multiple lidar collection dates within 30 days of each other, I averaged the collection dates. For buffers that had their lidar data collected on multiple days that were not within 30 days of each other and buffers that did not have complete lidar coverage, I could not determine a collection date.

Elevation and Canopy Cover

I determined percent canopy cover using the Vermont Tree Canopy Dataset, which has a spatial resolution of 0.5 m (University of Vermont Spatial Analysis Lab [UVM SAL] 2019**).** This dataset was created using object-based image analysis technique, which groups pixels with similar spectral and spatial properties into objects (UVM SAL 2019**).** In this dataset, the spatial and spectral properties were derived from lidar and multispectral imagery (UVM SAL 2019**)**. I used this dataset to determine the percent canopy cover within the 100 m buffer around each sampling site. I then used a digital elevation model with a spatial resolution of 0.7 m to determine the elevation at each sampling site (VCGI et al. 2018b).

Gap Delineation

A canopy gap can be defined as, “a ‘hole’ in the forest extending through all levels down to an average height of 2 m above the ground,” (Brokaw 1982). However, this average height is dependent on forest type, with canopy gap height thresholds in previous studies ranging from 1 m (Zielewska-Büttner et al. 2016) to 10 m (Gaulton and Malthus 2008). The minimum canopy gap size is also dependent on forest type, with previous studies setting thresholds between 5 m^2 (Gaulton and Malthus 2008; Vehmas et al. 2011) and 10 m^2 (Zielewska-Büttner et al 2016). In this study, the threshold for canopy gap height was less than or equal to 3 m and the threshold for canopy gap area was greater than or equal to 8 m^2, which are the thresholds used in a recent study identifying forest canopy gaps in the boreal forests of Canada (Goodbody et al. 2020). The boreal forests of Canada are structurally very similar to the montane spruce-fir forests of Vermont.

I completed all gap delineation using ArcGIS Pro 2.9.1 (ESRI 2021). To delineate gaps, I created a raster layer where all CHM pixels with a value less than or equal to 3 m were given a value of one, indicating that they were gap pixels. I then converted the gap raster into an unsimplified polygon (the resulting polygon has a shape identical to that of the gap raster) and deleted all gaps with areas less than 8 m^2. Each set of adjacent pixels was aggregated into a single gap polygon. I then clipped gap polygons to the 100 m buffers surrounding each sampling site and deleted all gap polygons with areas less than 8 m^2. Finally, I determined the sampling site that each gap was associated with.

<u>Data Preparation</u>

I completed all data preparation using R 4.1.2 (R Core Team 2021). I exported geospatial data to a tabular format and joined it with the MBW survey data. I then filtered the data, eliminating surveys that did not take place (indicated by a June day of "NA") or did not take place in Vermont. I also eliminated sampling sites with canopy cover less than 60%, as gap delineation errors were more frequent at sites with less than 60% canopy cover (Zielewska-Büttner et al 2016). Finally, I eliminated sampling sites for which a lidar collection date could not be determined. This resulted in the elimination of a total of ten sampling sites within the study area.

Each sampling site had multiple years of data associated with it, as the MBW dataset includes data from 2010-2021. For each sampling site, I considered only the survey that took place in the year closest to lidar collection date (Figure 4).

For each five-minute point count, I transcribed the counts of Bicknell's Thrush at each sampling site to either values of 0 (no Bicknell's Thrush were detected) or 1 (one or more Bicknell's Thrush were detected). I only considered counts within a distance of 50 m or less (Hill and Lloyd 2017). I then calculated total canopy gap area, number of gaps, and median size of gaps at each sampling site. Total canopy gap area was calculated by summing the area of all canopy gaps while number of gaps was calculated by counting the number of distinct canopy gaps. Finally, I standardized all covariates by subtracting the mean and dividing by the standard deviation. The minimum, maximum, mean, and standard deviation for each variable considered during model fitting is in Table 2.

Modeling Approach

I developed a single-season occupancy model that predicts occupancy probability while accounting for imperfect detection (MacKenzie et al. 2002). Occupancy models assume either that occupancy and detection probabilities remain constant across all sites or are a function of covariates (MacKenzie et al. 2002). Covariates for occupancy probability should be time constant and site specific while covariates for detection can be time varying and site specific (MacKenzie et al. 2002).

The covariates of interest for detection (p) were June day (all surveys occurred in June) and time (minutes after midnight). Since the four independent point counts at each sampling site take place over a twenty minute time period (Hill and Lloyd 2017), the start time of the first five-minute point count was used as the detection covariate for each of the four point counts at a single survey point. The covariates of interest for occupancy (ψ) were latitude (decimal), elevation (m) and its quadratic term, total gap area (m^2), median gap size (m^2), and number of gaps. Percent canopy cover was excluded from analysis due to its high correlation with canopy gap area (r = -0.727). See Table 1 for the predicted effect of each covariate.

Model Fitting

All occupancy analysis was conducted using the *unmarked* package for R (Fiske and Chandler 2011). I fit the models using a sequential-by-sub-model strategy. The relative support of each model was determined using Akaike's Information Criterion adjusted for a small sample size (AICc) and models with ΔAICc ≤5 were considered to have strong empirical support (Morin et al. 2020). I first identified all detection substructures that had strong support. The occupancy substructure for all these models was a global model, which considered the additive combination of all occupancy covariates. I then identified all occupancy substructures with strong support. The detection substructure for all these models was the global detection model (Day + Time). Finally, I created a model that combined all strongly supported substructures for both detection and occupancy (Morin et al. 2020). Occupancy substructures considered all single variable and additive bivariate combinations of elevation, latitude, number of gaps, total gap area, and median gap size. Since elevation and latitude are known to be strong predictors of Bicknell's Thrush distribution, the additive effects of elevation, latitude, and each canopy gap measure were also considered (Hill and Lloyd 2017).

During all stages of the model fitting process, each model was checked for uninformative parameters. An uninformative parameter is a variable that does not have a relationship with the response and does not improve the log-likelihood of a model but is ranked close to models with informative parameters based on AICc (Leroux 2019). A model with one more parameter than a higher-ranked model that was within ΔAICc 2 of that higher ranked model was considered to potentially contain an uninformative parameter (Leroux 2019). If the log-likelihood of the model potentially containing an uninformative parameter was within ±1 log-likelihood of the higher ranked and less parameterized model and the parameter estimate for the potentially uninformative parameter had a 95% confidence interval that crossed zero, that parameter was considered uninformative and the model containing it was removed from consideration (Leroux 2019).

Results

Observers detected Bicknell's Thrush at 35 of 155 sites (naïve occupancy = 22.6%). Model selection results for detection probability indicated three models with strong empirical support, which were the single variable models for June day and time and their additive effect (Table 3). As a result, the detection substructure for the final model considered the additive effect of June day and time. Both June day and time had a negative effect on detection probability.

Model selection results for occupancy probability indicated three models with strong empirical support (Table 4). In all three of these models, elevation and latitude were covariates. In addition to latitude and elevation, both number of gaps and median gap size were present in at least one of these models. All variables considered by these three models with strong empirical support were combined into a single substructure, which considered the additive effects latitude, elevation, number of gaps, and median gap size on occupancy probability. No other models were within Δ5 AICc of the three models with strong empirical support (Morin et al. 2020).

The final model considered the additive effect of June day and time on detection and the additive effect of elevation, latitude, number of gaps, and median gap size on occupancy. Predictions from this final model indicate that elevation and latitude have a strong positive effect on occupancy probability. Median gap size and number of gaps have weaker effects on occupancy probability, with median gap size increasing occupancy probability and number of gaps decreasing occupancy probability (Table 5, Figure 5). The fit of the model was assessed using the goodness-of-fit test for single season occupancy models (MacKenzie and Bailey 2004) ($\chi2 = 26.235$, $p = 0.015$) .

Discussion

Bicknell's Thrush occupancy probability was strongly and positively associated with elevation and latitude, positively associated with median gap size, and negatively associated with number of gaps. This indicates that Bicknell's Thrush distribution is driven not only by landscape-scale geographic factors, such as elevation and latitude, but also by small-scale canopy gap characteristics. Detection probability was negatively associated with June day and time.

Most Bicknell's Thrush vocalization is confined to 15-20 minute periods at dawn and dusk (Townsend et al. 2020). According to MBW protocol, surveys should start no earlier than dawn, which is consistent with the negative relationship between detection probability and time. In terms of June day, Bicknell's Thrush vocalizations peak in mid-June and decline sharply by late June (Townsend et al. 2020). While parameter estimates indicate a continuous decline with increasing June day, the negative relationship could be driven by the sharp decline in late June, which could account for the larger standard error associated with the June day parameter estimate.

Elevation and latitude were strongly and positively correlated with occupancy probability, which is consistent with observations that Bicknell's Thrush are restricted to chronically disturbed montane spruce-fir forests (Townsend et al. 2020). In Vermont, the two montane natural communities dominated by spruce-fir forest are subalpine krummholz and montane spruce-fir forest (Thompson et al. 2019). Subalpine krummholz is typically found at elevations above 1,067 m while montane spruce-fir forest is typically found at elevations between 762 m and 1,067 m (Thompson et al. 2019). As a result, increasing elevation increases the amount of potential Bicknell's Thrush habitat. At lower latitudes, the lower elevation cutoff for montane spruce-fir forest is increased, resulting in smaller amounts of this natural community present in southern areas when compared to northern areas with similar physical characteristics (Thompson et al. 2019).

The affinity of Bicknell's Thrush for chronically disturbed areas is well documented, but no direct study has been made of the impact of small-scale canopy gap characteristics (Townsend et al. 2020). The increase in occupancy probability associated with median gap size and the decrease in occupancy probability associated with number of canopy gaps indicates that Bicknell's Thrush occupancy is highest in areas that have smaller numbers of larger disturbances. This is true within the range of median gap size (10.78 m^2 -31m^2) and number of gaps (18-187) that was present across sampling sites. Previous research found that sites occupied by Bicknell's Thrush had a greater abundance of snags, stumps, and large dead fallen trees (Connolly 2000). Both hurricane patches and fir waves are larger disturbances that result in snags, stumps, and large dead fallen trees (Reiners and Lang 1979). Since these disturbance mechanisms are more localized, as compared to smaller but more numerous gaps caused by trees breaking or bending under the weight of rime ice or snow, the more localized disturbance mechanisms result in a higher overall stem density after regeneration (Reiners and Lang 1979). Bicknell's Thrush prefer areas with high stem density, as they tend to build their nests in very dense balsam fir (*Abies balsamea*) thickets (Connolly 2000). This could indicate that Bicknell's Thrush prefers the canopy structure generated by large localized disturbances over the canopy structure generated by smaller more dispersed disturbances. See figure 6 for examples of these two canopy structures.

A reason for this preference could be that the gaps generated by these large localized disturbances provide better foraging opportunities. Bicknell's Thrush is an insectivore, generally feeding on or close to the ground during the breeding season (Wallace 1939). Beetles and ants make up the majority of its food (Wallace 1939). The center of canopy gaps receives 9-23% of full sunlight while the edges of canopy gaps receive 3-11% of full sunlight (Denslow et al. 1990). In these otherwise dark and dense understories, canopy gaps provide a source of sunlight (Thompson et al. 2019). This increased sunlight could increase the number of insects (Braun-Reichert et al. 2021), but further research, which could include counts and inventories of insects in areas with a variety of forest gap characteristics, is needed to explore this idea in more detail. Further research could also incorporate the inclusion of a canopy gap shape measure, such as area to perimeter ratio or gap shape complexity index (Koukoulas and Blackburn 2004) into an occupancy model.

One limitation of this study was the inability to account for forest canopy gaps that extended over the boundary of the 100 m buffer around each sampling site. The 100 m size of buffer was chosen to avoid buffer overlap, which would have resulted in single canopy gaps being considered for multiple sampling stations. Since each gap was clipped to the buffer, the gap area outside of the 100 m buffer was discarded. An individual gap that is relatively small within the study area could be connected to a gap ten times the size of the study area. This means that the true size of the gap would not be captured. Another limitation is that all adjacent pixels were considered part of the same gap. This means that in some cases, two gaps that are connected by a small number of gap pixels would be considered one gap but would effectively function as two separate gaps. Both of these limitations result in the canopy gap data being abstracted from the actual physical conditions. This abstraction could account for the relatively large range of 95% confidence intervals for the parameter estimates of gap statistics.

The findings that the median gap size and number of gaps influence Bicknell's Thrush occupancy has the potential to inform management. Elevation and latitude, the primary factors influencing Bicknell's Thrush occupancy probability, cannot be changed through management practices, as these are fixed landscape-level characteristics. However, small-scale canopy gap characteristics can be altered. To improve the quality of habitat where Bicknell's Thrush is present in low densities due to either low latitude or low elevation, active silvicultural management could be explored as a potential management tool. Cutting trees in a way that simulates the natural processes that create the canopy structure favored by Bicknell's Thrush (relatively few large canopy gaps) has the potential to aid in the species' recovery.

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Figures and Tables

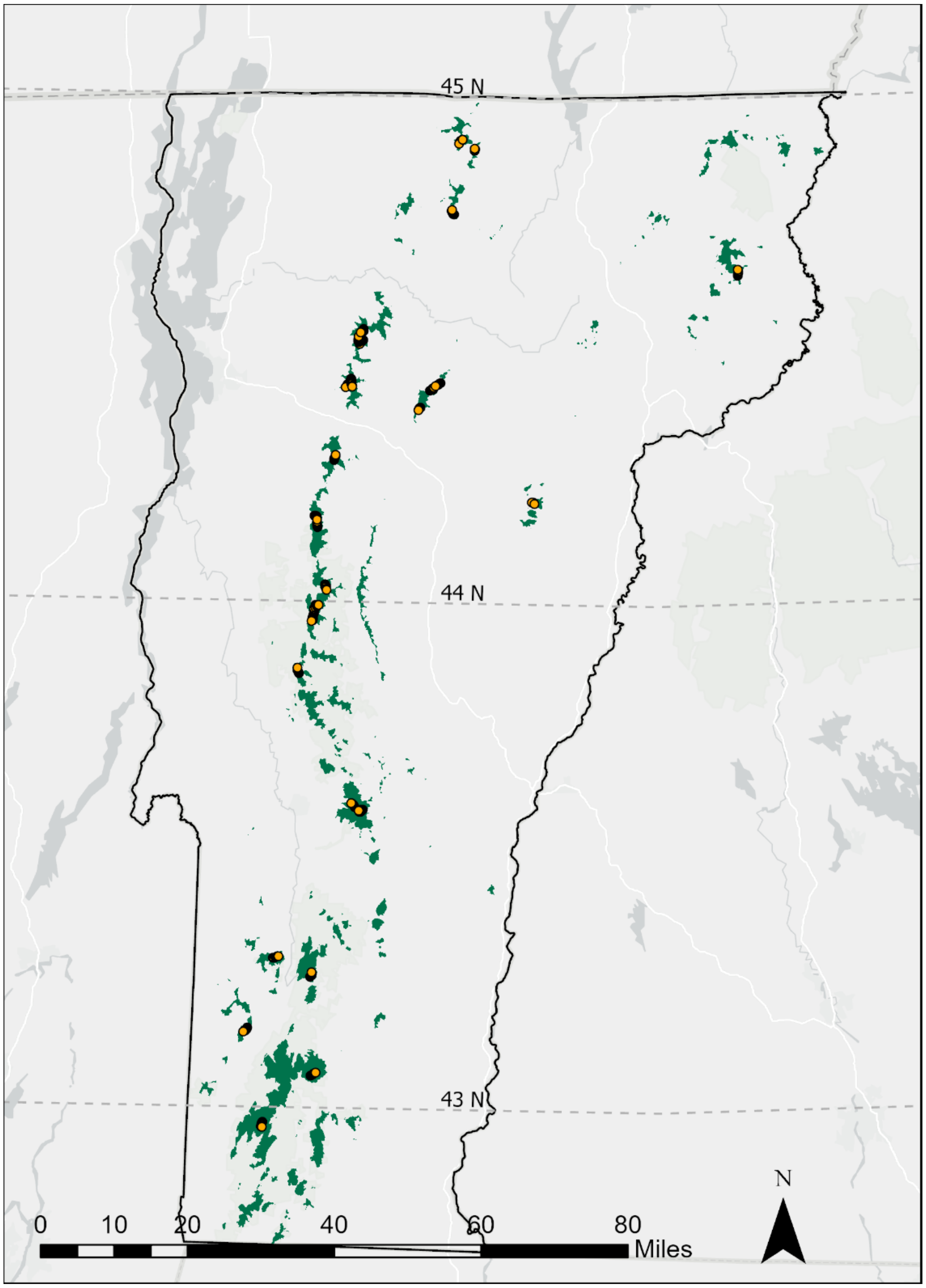

Figure 1: The 165 Mountain Birdwatch sampling stations annually monitored in Vermont by community scientists. These sites are surveyed once per year each June for the presence of 10 bird species, including Bicknell’s Thrush. Areas shaded in green have an elevation greater than 762 meters (the lower elevation threshold for spruce-fir forests). Map data sources: ESRI 2021, VCGI 2021, VCGI 2018b, VCE 2019.

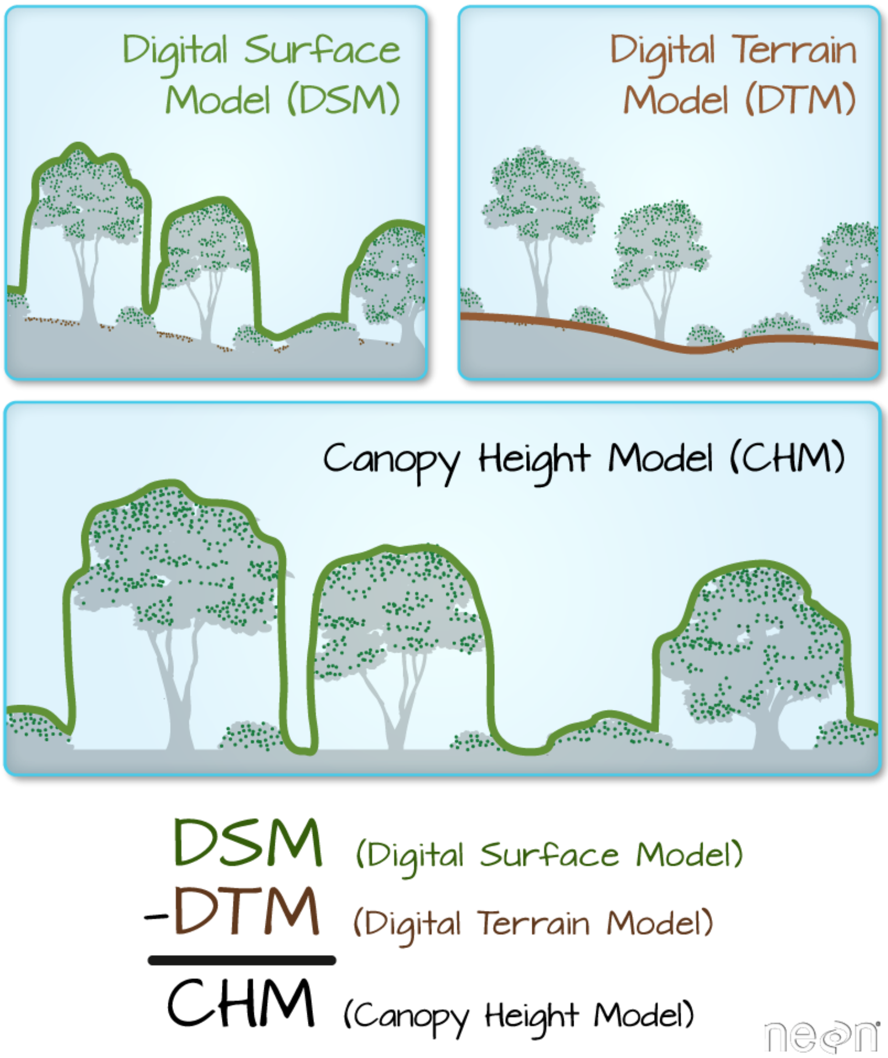

Figure 2: A graphic representation of the process used to create a canopy height model from a digital surface model and a digital terrain model. Source: Wasser et al. 2021.

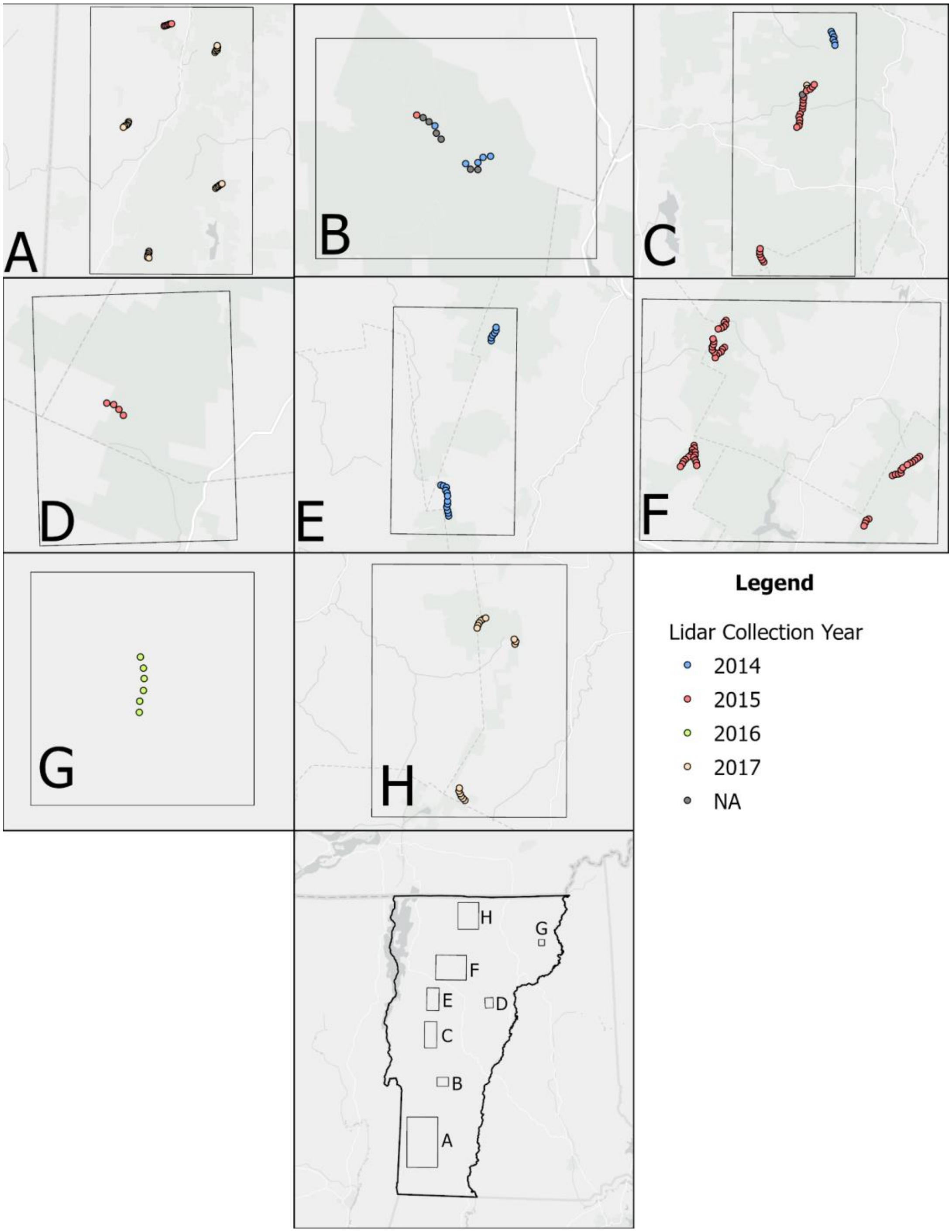

Figure 3: Lidar collection dates for lidar in the 100 meter buffer around each Mountain Birdwatch sampling site. A value of NA means either that a buffer had multiple lidar collection dates more than 30 days apart or that the lidar collection date for that buffer could not be determined. Map data sources: ESRI 2021, VCGI 2021, VCE 2019.

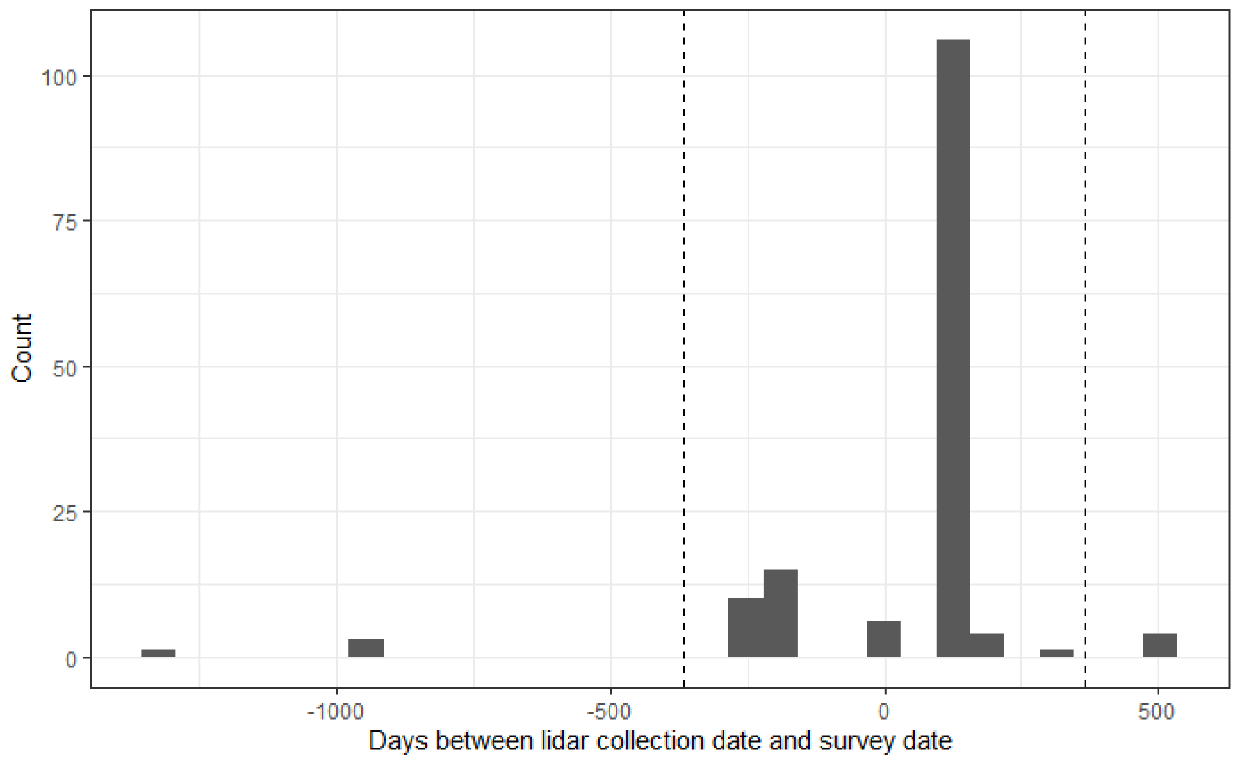

Figure 4: Distribution of days of difference between lidar collection date and Mountain Birdwatch survey date. The area within the dashed vertical lines represents a range of ±365 days.

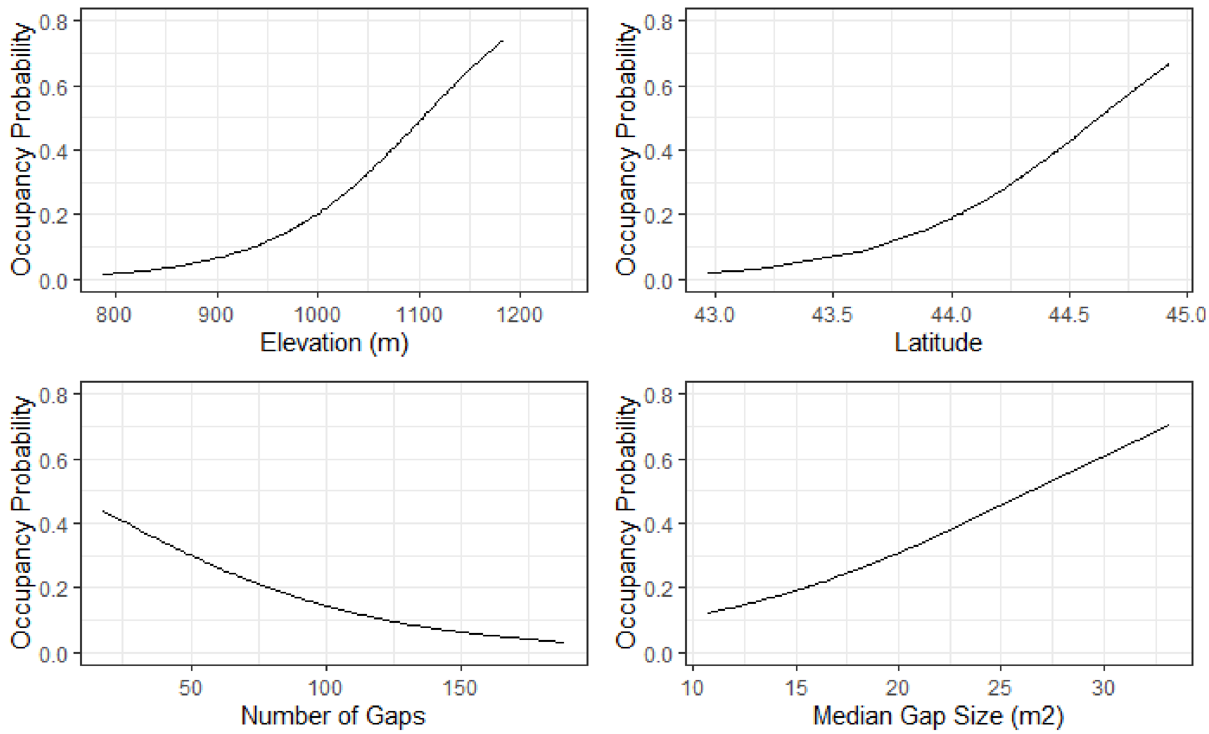

Figure 5: Predicted average occupancy probability of Bicknell's Thrush based on the detection covariates present in the final model. Occupancy was predicted using the logit-link function for the covariate of interest and the average value for all other covariates.

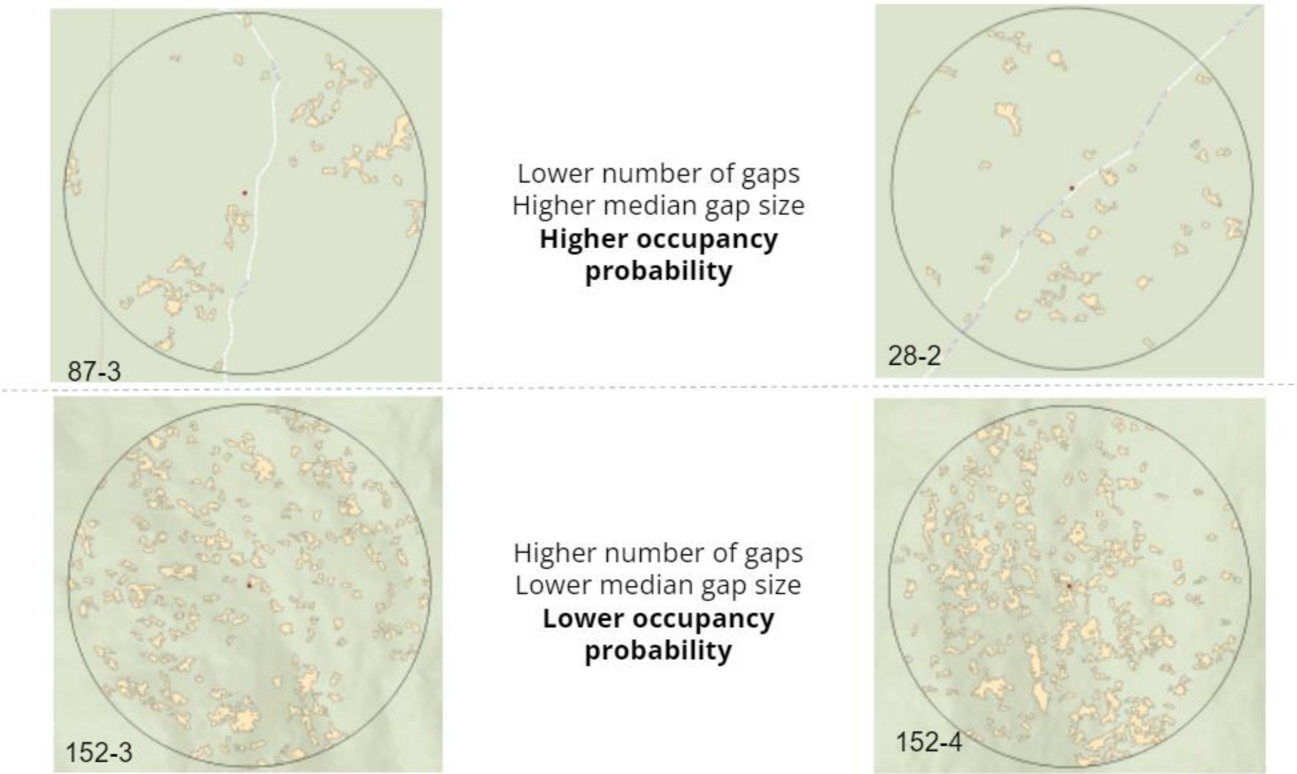

Figure 6: Examples of Mountain Birdwatch sampling sites that have lower number of gaps with a higher median gap size and a higher number of gaps with a lower median gap size. The yellow polygons represent canopy gaps. Sampling sites with a lower number of gaps and a higher median gap size are associated with increased Bicknell's Thrush occupancy.

Table 1: Covariates considered when modeling Bicknell's Thrush occupancy and detection probability.

Covariate	Covariate Measure	Parameter	Predicted effect	Source
Survey start time	Minutes after midnight	Detection	Negative	Hill and Lloyd, 2017
Survey June day	Day of June	Detection	Negative	Hill and Lloyd, 2017
Elevation	Meters above sea level	Occupancy	Nonlinear (see below)	Hill and Lloyd 2017
$Elevation^2$	$Meters^2$ above sea level	Occupancy	Greatest at intermediate values	Hill and Lloyd 2017
Latitude	Degrees north	Occupancy	Positive	Hill and Lloyd 2017 (within range present in VT)
Total canopy gap area (Lidar-derived)	$Meters^2$	Occupancy	Positive	Townsend et al., 2020
Number of canopy gaps (Lidar-derived)	Count	Occupancy	Positive	Townsend et al., 2020
Median canopy gap size (Lidar-derived)	Meters squared	Occupancy	Unknown	N/A

Table 2: Summary statistics for all variables considered during model fitting of Bicknell's Thrush occupancy data in Vermont.

Variable	Minimum	Maximum	Mean	Standard Deviation
JuneDay	3	30	16.9	7.0
Time	240	495	345.5	58
Latitude	42.97	44.92	44.10	0.5
Elevation	788.8	1243.7	1010.1	86.5
ElevationSquared	622214	1546803	1027758	175332
TotalGapArea	357.6	19545.4	3805.1	3797
MedianGapSize	10.78	33.20	16.64	3.1
NGaps	18	188	70.91	30.9

Table 3: Model selection results for detection probability of Bicknell's Thrush in Vermont. The global model includes the additive effects of elevation, latitude, percent canopy cover, number of gaps, and median gap size. The dot represents an intercept-only model.

Model	K	AICc	ΔAICc	AICc Weight	Cumulative Weight	Log-likelihood
ψ(global),p(Day+Time)	9	327.05	0.00	0.74	0.74	-153.91
ψ(global),p(Day)	8	330.09	3.03	0.16	0.91	-156.55
ψ(global),p(Time)	8	331.50	4.45	0.08	0.99	-157.26
Ψ(global),p(.)	7	335.22	8.17	0.01	1.00	-160.23

Table 4: Model selection results of occupancy data of Bicknell's Thrush in Vermont. Models with uninformative parameters have AICc weights and cumulative weights of NA and were not considered. The *p* substructure for all models was *p*(Day + Time).

Ψ Substructure	K	AICc	Delta AICc	AICc Weight	Cumulative Weight	Log-likelihood
Elevation + Latitude + NGaps	7	329.07	0.00	0.46	0.46	-157.16
Latitude + Elevation	6	329.79	0.72	0.32	0.78	-158.61
Elevation + Latitude + MedianGapSize	7	330.61	1.54	0.21	1.00	-157.92
Elevation + Latitude + GapArea	7	331.10	2.03	NA	NA	-158.17
Latitude	5	342.00	12.92	0.00	1.00	-165.80
Elevation + MedianGapSize	6	342.19	13.12	0.00	1.00	-164.81
Latitude + MedianGapSize	6	343.18	14.10	NA	NA	-165.30
Latitude + GapArea	6	343/29	14.22	NA	NA	-165.36
Latitude + NGaps	6	343.42	14.35	NA	NA	-165.43
Elevation + GapArea	6	346.03	16.96	0.00	1.00	-166.73
Elevation	5	346.10	17.02	0.00	1.00	-167.85
Elevation + ElevationSquared	6	346.86	17.78	0.00	1.00	-167.14
Elevation + NGaps	6	347.81	18.74	NA	NA	-167.62
GapArea	5	349.44	20.37	0.00	1.00	-169.52
MedianGapSize	5	349.91	20.84	0.00	1.00	-169.75
GapArea + MedianGapSize	6	350.00	20.93	0.00	1.00	-168.72

NGaps + GapArea	6	351.54	22.46	0.00	1.00	-169.49
NGaps + MedianGapSize	6	352.07	23.00	NA	NA	-169.75
NGaps	5	353.81	24.74	0.00	1.00	-171.70

Table 5: Parameter estimates (betas) with standard errors for the final model of Bicknell’s Thrush occupancy in Vermont.

Covariate	Sub-model	β	SE	Upper 95% confidence interval	Lower 95% confidence interval	p(>|z|)
Intercept	Ψ	-1.238	0.327	-0.911	-1.565	<0.001
Number of gaps	Ψ	-0.581	0.334	-0.247	-0.915	0.081
Median gap size	Ψ	0.399	0.280	0.679	0.119	0.153
Elevation	Ψ	1.144	0.459	1.603	0.685	0.013
Latitude	Ψ	1.288	0.401	1.689	0.887	0.001
Intercept	p	-0.507	0.335	-0.172	-0.842	0.130
Time	*p*	-0.408	0.186	-0.222	-0.594	0.028
June Day	*p*	-0.580	0.265	-0.315	-0.845	0.028