Continued Exploration of the Relationship between Downhill Ski Area Edges and Bicknell's Thrush in the Northeastern U.S. Using Mountain Birdwatch Data (2016-2019)

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Summary

Anthropogenic edges have received lots of attention in the wildlife literature, because edges can serve as *ecological traps* for some species by reducing reproductive output or adult survival sufficiently to allow populations to sustain themselves without immigration. Compared to other forest biomes, the influence of edges on bird communities in boreal forests has been less frequently investigated, but natural disturbances (e.g., fir waves) are a common component of these forest biomes. Bicknell's Thrush (Catharus bicknelli) breed exclusively in this forest community in the U.S., and are most common near these natural disturbances. Bicknell's Thrush demographics have been partially investigated with respect to anthropogenic disturbances (downhill ski areas) in Vermont, where researchers found that Bicknell's Thrush nests were clustered at the edges of ski trails. That study was not able to examine patterns of abundance as it relates to downhill ski areas. Therefore, we sought to address this information gap by analyzing patterns of Bicknell's Thrush abundance as they relate to ski area disturbances using *N*-mixture models in a hierarchical Bayesian framework. We analyzed 4 years (2016-2019) of point count data collected on mountains with ski resorts under the Mountain Birdwatch citizen science program at 83 sampling locations in New York, Maine, and Vermont. From 2016 to 2019, Mountain Birdwatch observers conducted 269 5minute point counts at 83 sampling stations along 14 routes. Observers reported 417 Bicknell's Thrush detections. Bicknell's Thrush abundance (corrected for imperfect detection) was greatest immediately adjacent to sites of ski area disturbances, and was smallest at the sampling sites farthest from those disturbances. We estimated Bicknell's Thrush density was, on average, ~15 times higher within 689 m of disturbances compared to areas between 690 and 2784 m from disturbances. However, relatively high animal density does not necessarily indicate high-quality habitat, especially given that previous research was unable to document any fitness benefits for Bicknell's Thrush associated with nesting near anthropogenic disturbances. The possibility exists that anthropogenic edges like downhill ski runs only superficially mimic the fir waves naturally found in Bicknell's Thrush habitat, and that fitness benefits only occur for thrush breeding near natural edges. Although the approach used within this report are statistical defensible and informative, Mountain Birdwatch was not designed to investigate the effects of disturbance on bird abundance. Therefore, a more powerful approach would be to initiate an intentional field study to document the fitness benefits of Bicknell's Thrush (and other boreal forest bird species) as it relates to natural and anthropogenic edges. We outline such a study with the ultimate goal of discovering the actual mechanisms (e.g., food resources or predation risk) that possibly drive these local patterns of abundance.

Introduction

Anthropogenic edges have received lots of attention in the wildlife literature, especially in the context of silvicultural practices (Manolis et al. 2002), utility corridors (Anderson et al. 1977) and energy development (Bayne et al. 2016). Edges and associated *edge effects* can be *ecological traps* for some species by reducing reproductive output or adult survival (Robinson et al. 1995, Manolis et al. 2002) sufficiently to allow populations to sustain themselves without immigration (Pulliam 1988). In contrast to natural edges, anthropogenic edges in forested landscapes tend to be uniform in shape and size, have a more abrupt ecotone, and are often actively maintained through management activities (Ranney et al. 1981, Williams-Linera 1990, Matlack 1993, Rolando 2005). The response of bird species to edges, however, is complex and is often species- or guild-specific and dependent upon the landscape, and edge and forest type (Harper et al. 2005). Numerous studies have documented both positive (e.g., Terraube et al. 2016) and negative (e.g., Laiolo and Rolando 2005, Broadbent et al. 2008, Batáry et al. 2014, Hofmeister et al. 2017) edge effects for forest bird species. Indeed, even interior forest bird species may utilize anthropogenically cleared areas (e.g., clearcuts) during some stage of their lifecycle (Vitz and Rodewald 2006)--perhaps to take advantage of relatively high levels of vegetation and food density in successional forest patches (Pagen et al. 2000, Marshall et al. 2003).

Compared to other forest biomes, the influence of edges on bird communities in boreal forests has been less frequently investigated (Harper et al. 2005). There is reason to speculate that edge effects in boreal forests may be less pronounced, given the short canopy heights and frequent natural disturbances caused by insect outbreaks and windthrow that create natural edges in this biome (Bonan and Shugart 1989, Engelmark 1999, Harper et al. 2005, Kneeshaw et al. 2011). For example, boreal breeding birds associated with young forest stages or mixed habitats are more abundant along forest edges in Alberta, Canada, compared to adjacent interior forest plots (Bayne et al. 2016). In contrast, edge effects in montane boreal forests, associated with ski areas, have been shown to influence plant community diversity from insects to large herbivores (Morrison et al. 1995, Burt and Rice 2009, Kašák et al. 2013). Ski slope edges tend to have lower bird species richness and diversity compared to interior forest patches, and bird species that favor ecotones may prefer non-ski area edges (e.g., forest-glade ecotones) with greater vegetation structural complexity (Rolando 2005).

Understanding the influence of ski area edge effects on bird communities is important in New England and New York, where some of the largest of the ~134 ski resorts (e.g., Killington-Pico, Vermont) contain upwards of 150 km of ski trails (Killington Mountain Ski Resort 2019, SkiCentral 2019, SkiResorts 2019). Despite projected increased winter temperatures and a loss in snow cover, the northeastern U.S. ski industry is not thought to be highly vulnerable to climate change (Scott et al. 2006, Contosta et al. 2019). The forest composition surrounding ski areas, however, is expected to change. Forecasted temperature and precipitation changes in our regional climate are expected to result in substantial conversions (up to 50%) of existing montane spruce-fir forests (*Picea* spp.-*Abies balsamea*) to hardwoods between 2100 and 2300 (Iverson et al. 2008, Rodenhouse et al. 2008, Wang et al. 2016). Given these forecasted changes to our montane areas, it is important to document current patterns of biodiversity and the abundance of rare species like the Bicknell's Thrush (*Catharus bicknelli*).

The Bicknell's Thrush exclusively breeds in the naturally-disturbed montane spruce-fir forests of New York, Vermont, New Hampshire, Maine, and southeast Québec and young forest stands in the highlands of New Brunswick (Wallace 1939, Lambert et al. 2005, Townsend et al. 2015). The Bicknell's Thrush is one of the Nearctic-Neotropical migrants at greatest risk of extinction (Birdlife International 2000, Wells 2007), and is highly vulnerable to climate-driven extirpation (Rodenhouse et al. 2008). Recent demographic research puts the U.S. population estimate around 71,000 individuals, and <120,000 globally. Bicknell's Thrush demographics have been partially investigated with respect to ski areas on Mt. Mansfield and Stratton Mountain, Vermont (Rimmer et al. 2004). In that study, proximity to ski trails had no measurable effect on nest or adult survival, adult behavior or home range size, but Bicknell's Thrush did show some aversion to crossing large ski trails greater than 50 m (Rimmer et al. 2004). Bicknell's Thrush nests were clustered at the edges of ski trails, and ~26% of nests (n = 14, out of 54) were found within 2 m of ski trail edges (Rimmer et al. 2004). However, Rimmer et al. (2004) was not able to investigate Bicknell's Thrush adult density as it pertains to ski trail proximity.

Therefore, we sought to address this information gap by analyzing patterns of Bicknell's Thrush abundance using *N*-mixture models in a hierarchical Bayesian framework. We analyzed 4 years (2016-2019) of point count data collected under the Mountain Birdwatch citizen science program (Vermont Center for Ecostudies 2019). The original scope of this report was to focus on Vermont, but only 9 of 29 (31%) Mountain Birdwatch routes in Vermont occur on mountains with developed downhill ski areas. Therefore, we expanded my analysis to include all Mountain Birdwatch routes in New England and eastern New York on mountains with ski resorts. Given the frequency of nest locations immediately adjacent to ski trails (Rimmer et al. 2004), and the lack of known effects from ski trail proximity on fitness components of Bicknell's Thrush, we hypothesized that Bicknell's Thrush abundance would be positively associated with ski area proximity.

Methods

Mountain Birdwatch Surveys and Covariates

Mountain Birdwatch was designed to monitor breeding populations of 10 species of passerine birds in the mountains of the northeastern United States and southeastern Canada, although the sampling frame and survey methods were designed based on the distribution and ecology of Bicknell's Thrush. In the United States, sampling locations occur in montane spruce–fir forests within New York, Vermont, New Hampshire, and Maine. Initiated in 2000, MBW was substantially restructured and expanded by the Vermont Center for Ecostudies in 2010 to include an updated survey methodology (repeated counts) implemented annually at >700 sampling locations along 129 routes (currently). A Mountain Birdwatch route consists of 3–6 fixed sampling locations, depending upon the patch size of the high-elevation spruce–fir forest, that are spaced at least 0.25 km apart (straight line distance) along a hiking trail. Individual sampling locations range in elevation from 582 to 1502 m and stretched from the Catskill Mountains, NY (41.9° N latitude) to northern Maine (46.0° N latitude).

A citizen scientist adopts a Mountain Birdwatch route, and then conducts point counts at the sampling stations on that route during a single morning in June each year. Each observer conducts four 5-minute back-to-back point counts at each of the sampling stations along their adopted route; all 5-minute counts are independent of one another. Observers record the initial detection distance (0-50 m or >50 m) for each individual bird detected, and they keep track of bird movements to avoid double-counting individuals within a 5-minute point count. For this report and statistical analysis, we combined Bicknell's Thrush counts across both distance bins. In our experience, detections of Bicknell's Thrush beyond 100 m are rare; therefore, detections of Bicknell's Thrush in the Mountain Birdwatch dataset likely represent individuals using the area immediately adjacent to sampling stations. Nearly all of the Mountain Birdwatch surveys were conducted by citizen scientists who self-identified as experienced birders and who received in-person or online training; a small number of surveys were conducted annually by professional biologists who fill in for citizen-scientists who were unable to complete their assigned route.

Mountain Birdwatch Route Selection

Using aerial photography in Google Earth (Google, Mountain View, CA), we identified Mountain Birdwatch routes that occurred on mountains with downhill ski areas. For these analyses, we included all sampling stations from those identified routes and all associated Mountain Birdwatch Bicknell's Thrush count data from 2016-2019. We chose this timeframe for multiple reasons. First, we included multiple years of Mountain Birdwatch point count data to increase the sample size and statistical power to detect relationships between Bicknell's Thrush abundance and the suite of covariates. Second, most of the aerial imagery in Google Earth was captured during this time period, and we used that imagery in connection with my assessment of land cover changes (described below). Third, Mountain Birdwatch participation and route coverage were relatively low in 2016 and 2017, before rebounding to 88-95% route coverage in 2018 and 2019, respectively. Fourth, previous analyses with Bicknell's Thrush Mountain Birdwatch data found substantial inter-annual variation in counts (Hill and Lloyd 2017); just using one year of count data would increase the chances of identifying spurious relationships between Bicknell's Thrush abundance and the covariates.

National Land Cover Data (NLCD)

We used ArcGIS PRO (ESRI, Redlands, CA) to quantify National Land Cover Data (NLCD) from 2011 (Homer et al. 2015) and 2016 (the most recent National Land Cover dataset; Yang and et al. 2018) around Mountain Birdwatch sampling stations located on mountains with developed downhill ski areas. The NLCD are summarized every five years, released at a 30x30 m scale, and are directly comparable between releases (Yang and et al. 2018). Ecological processes that affect organismal abundance occur at multiple spatial scales (Wiens 1989), so we initially quantified land cover at two (arbitrary, but reasonable) spatial scales: 0.2 and 0.5 km. However, there was little change in land cover and no change in evergreen forest coverage at the 0.2 km spatial scale surrounding sampling stations from 2011 to 2016 (Jake Campbell unpublished data). Based on these findings, and those of similar investigations (e.g., Rolando 2005), we selected an intermediate spatial scale of 0.5 km for my analyses.

Using raster analysis tools in ArcGIS PRO, we quantified the proportion of the area within 0.5 km of Mountain Birdwatch sampling stations that existed as evergreen forest, mixed evergreen-deciduous forest, and all four categorizations of human development (pooled) in both 2011 and 2016. The NLCD defines evergreen forest as, "areas dominated by trees generally greater than 5 m tall, and greater than 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage." In our experience, however, the NLCD evergreen category also categorizes Bicknell's Thrush habitat in the northeastern U.S. with tree canopies <5 m (Hill and Lloyd 2017). We categorized the proportion of the landscape that was mixed forest around sampling stations for descriptive purposes (i.e., that measurement was not intended to be used in our statistical models).

Proximity of Sampling Stations to Anthropogenic Disturbance

Originally, we had planned to include the distance to ski area disturbance as a covariate in our model selection. Types of ski area disturbances include downhill ski trails and other ski area infrastructure, such as chairlift terminals. We modified this approach after examining the aerial imagery around Mountain Birdwatch routes on mountains with ski slopes. On those mountains, there is usually a mix of infrastructure and anthropogenically cleared areas that are obviously related to the ski area, and then other similar and adjacent infrastructure that may not be directly involved in ski operations. In these cases, the effects (if any) of the non-ski area and ski area infrastructure are likely confounded and would be exceedingly difficult to separate in this analysis (Figure 1).



Figure 1. An example from Mt. Mansfield, Vermont, with multiple types of forest disturbances within close proximity to Mountain Birdwatch sampling stations 3 and 4 on route 155. Multiple ski runs are visible in the upper half of the imagery, and a chairlift terminal and ski patrol hut in the middle of the imagery. The auto road on Mt. Mansfield (gray line crossing between the two sampling stations) overlaps ski runs for much of its length, making it difficult to separate any potential effects of the ski runs and infrastructure and auto road on the abundance of Bicknell's Thrush.

The decision to use the distance to any anthropogenic disturbance (hereafter simply *disturbance*), compared to ski area-only disturbance, had a minimal effect on the final results (JMH unpublished data); those two covariates were highly correlated (*r* = 0.93 (95%)

CI: 0.89, 0.95), P<0.001), and the two distances were identical for 63% of the sampling stations used in the analysis (mean difference = 232 m). Within Google Earth, we calculated the Euclidean distance (m) from each sampling station to the edge of the nearest disturbance larger than a hiking trail (e.g., downhill ski trail or road). For sampling stations located in the middle of downhill ski runs, we recorded the distance to disturbance as 0 m.

Candidate Models and Model Selection

There is no agreement upon best model section method for hierarchical N-mixture models (Kéry and Royle 2015). Therefore, we fit *N*-mixture models in a frequentist framework using the *pcount* function in R version 3.6.1 (R Core Team 2019) package "unmarked" version 0.13-0 (Fiske and Chandler 2011). Multi-year models can be accommodated by stacking the multiple years of data in a vertical format (Hill and Lloyd 2017). In the *pcount* function, we set K (the upper index of integration) to 50 so that it did not affect parameter estimates. We developed a base model from a much larger and longer analysis of Mountain Birdwatch Bicknell's Thrush data (Hill and Lloyd 2017). For each 5-minute point count, we considered the survey start time (decimal hours) and day of the month of June (e.g., 1 June = 1 and 30 June = 30) as potential detection covariates. In the base model, the detection function (ρ) was informed by an overall intercept and two potential detection covariates, and the abundance component (λ) was described by an overall intercept, elevation of the sampling station, and the distance to disturbance and its quadratic term. We did not consider more complex model structures (as in Hill and Lloyd 2017), because *N*-mixture models require large amounts of data and preliminary analyses suffered from poor model fit and model convergence issues with more complex structures (JMH unpublished data).

We selected models using Akaike's information criterion for small sample sizes (AICc; Burnham and Anderson 2002), and used the same systematic procedure outlined in Hill and Lloyd (2017). From the base model, we first identified the parsimonious ρ structure by removing the detection covariates one at a time. Then we singly removed the abundance covariate for the quadratic term for distance to disturbance; we did not consider models without any distance to disturbance covariates as that was the primary focus of our analysis. We included an abundance covariate for elevation in all models, because previous analyses have shown that elevation has the strongest effect on Bicknell's Thrush abundance (Hill and Lloyd 2017). Elevation and distance to disturbance were not significantly correlated (r = 0.10, P = 0.31). All covariates were grand-mean centered and scaled by their standard deviation to improve the performance of the final model.

Fitting the Final Model in a Bayesian Framework

Using the approach of Hill and Lloyd (2017), we used JAGS version 4.3.0 (Plummer 2003) and R to fit the parsimonious N-mixture model identified using the pcount function, in a multi-season hierarchical Bayesian framework. Hierarchical models with random effects are not currently supported within the unmarked package (Fiske and Chandler 2011), so we added a random site effect for abundance to account for overdispersion and an unequal number of sampling events between sampling stations (Kéry and Schaub 2011). We also considered random observer effects to account for differences in observer ability, but those model structures were too complex for our relatively small dataset (i.e., those models failed goodness-of-fit and convergence tests). We used uninformed priors for all parameters: a uniform distribution (min = 0, max = 5) for the standard deviation of the random site effect, and a more diffuse draw from a uniform distribution (min = -10, max = 10) for all other parameters. We based my conclusions on 3000 iterations (1000 iterations saved from three Markov chain Monte Carlo chains) saved from a model run with 400,000 iterations, thinned at a rate of 1:200 after we discarded the first 200,000 iterations as burnin. We examined plots of residuals, traceplots of the posteriors, and insured that all parameter Gelman-Rubin statistics (\hat{r}) were <1.01 (Gelman and Rubin 1992). We also developed a posterior predictive check, simulated data under our estimated model parameters, and calculated \hat{c} : values near 1.0 indicate adequate model fit (Kéry and Royle 2015).

Results and Discussion

We identified 14 Mountain Birdwatch routes in Maine (*n* = 1), New York (*n* = 4), and Vermont (*n* = 9) that were located on mountains with downhill ski areas. Those 14 routes consisted of 83 sampling stations, and there were 15 sampling stations from three routes (Sugarloaf in Maine, and Mansfield and Killington in Vermont) that were located within ski runs (i.e., distance to disturbance = 0 m). On average, the 83 sampling stations were located 790 m from anthropogenic disturbances (min = 0, max = 2784, median = 486 m; Figure 2), and located at a mean elevation of 1089 m (min = 784, max = 1330, median = 1082 m). From a model selection perspective, it would likely be more desirable to have a uniform distribution of distances to sampling stations; such a covariate distribution would likely reduce the possibility of large sample sizes (at small disturbance distances) driving the model selection. Put more simply, with few sampling stations at far distances from disturbances, we have few opportunities to generate large counts of Bicknell's Thrush far from disturbances.



Figure 2. Histogram of the distance to anthropogenic disturbance for 83 Mountain Birdwatch sampling stations located in Vermont, New York, and Maine.

National Land Cover Data change

In 2016, the mean proportion of disturbance around sampling stations was 2.50% (min = 0.00, max = 39.49, median = 0.00%), and there was no change in the proportion of disturbance surrounding sampling stations (at the 0.5 km scale) between 2011 and 2016. An examination of Google Earth aerial imagery from ~2012 to ~2018 revealed no obvious additional anthropogenic disturbances in the 0.5-km area surrounding sampling stations. A new large-scale disturbance (e.g., the creation of a new ski run) during this period would have been a convenient natural experiment, and allowed for the examination of pre- and post-disturbance bird counts. Such a natural experiment could shed insight into how quickly Bicknell's Thrush (and other forest bird species) respond to disturbance. Given that Bicknell's Thrush occupies naturally disturbed habitat on the breeding grounds, we would speculate that adult thrush would rapidly (<1 year) respond to a new disturbance.

The typical Mountain Birdwatch sampling station in 2016 was surrounded by 66.32% of evergreen forest (min = 0.00, max = 1.00, median = 71.64%), and an additional 17.92% of mixed evergreen-deciduous forest (min = 0.00, max = 95.07, median = 8.39%). Between 2011 and 2016, the area of evergreen forest surrounding sampling stations (within 0.5 km) declined by an average of 2.54% (largest gain of evergreen forest = 1.46%, largest loss of evergreen forest = 4.5%, median = 0.00%). Losses in mixed evergreen-coniferous forests between 2011 and 2016 were less common; only one sampling station gained mixed forest (0.36%) and 11 sampling stations lost between 0.11% and 10.31% of 2011 mixed forest (mean = 0.42%, median = 0.00%). We were skeptical of these forest loss estimates for high elevation forests, and we subsequently quantified grassland cover change from 2011 to 2016 as well. Changes from forest to grassland cover could indicate additional ski trail development, but ski trails are generally classified as *open development* (NLCD code 21; JMH personal observation) in the national land cover products.

Over those years (2011-2016), grassland cover increased by an average of 2.55% around samplings stations, and the vast majority of those changes (96.08%) came from the area surrounding the sampling stations on the three Mt. Mansfield, Vermont routes. These changes were not visually apparent when we examined imagery from Google Earth and the National Agriculture Imagery Program (NAIP) from ~2009 through 2018. A side-by-side comparison of NLCD products from 2011 and 2016 on Mt. Mansfield, however, revealed the cause of these apparent changes. The 2016 NLCD apparently misclassified large portions of the east face of the Mansfield ridgeline as grassland (Figure 3); 2018 Google Earth imagery clearly shows these new grassland area as intact forest, and personal experience confirms that this area is still forested (JMH personal observation). Perhaps a late snow cover on the east slope of the Mansfield ridgeline is responsible for the misclassification of forest cover.



Figure 3. National land cover (mis-)classification of the Mt. Mansfield ridgeline (extending north to south in the center of both panels) in 2011 (panel A) and 2016 (panel B). Dark green represents evergreen forest, red colors indicate development (e.g. the ski areas from Stowe Mountain Resort and the auto road), and yellow indicates grassland (nontilled herbaceous cover). The 2016 NLCD falsely indicates that large portions of the eastern slope of the Mansfield ridgeline have been converted to grasslands.

Changes between forest types surrounding sampling stations were also difficult to detect by only examining aerial photography in Google Earth. We could not visually detect a difference in forest cover in any of the cases when a 2011 evergreen forest cell (30x30 m) switched to a different forest classification in 2016. Along with the misclassification of grassland habitat, these results suggest that there was very little change in forest cover suitable for Bicknell's Thrush around the Mountain Birdwatch sampling stations.

Mountain Birdwatch sampling efforts

From 2016 to 2019, Mountain Birdwatch observers conducted 269 5-minute point counts at 83 sampling stations along 14 routes. Observers reported 417 Bicknell's Thrush detections from a total of 46 sampling stations (naive occupancy rate for sampling stations = 0.55) on 11 routes (naive occupancy rate for routes = 0.79). These occupancy results are naïve, because they do not take into account false zero counts (i.e., when an observer fails to detect any Bicknell's Thrush at a location despite thrushes being present) like the *N*-mixture models.

Model selection results and interpretation

In our model selection procedure, we identified the point count start time and the June day of the survey as informative detection covariates (Table 1). Counts occurred between 4:00 am and 8:47 am in my sample, and an observer was 1.95 times more likely to detect a Bicknell's Thrush at 4:00 am compared to that same Bicknell's Thrush at 8:47 am (Figure 4). Similarly, an observer was 3.22 times more likely to detect a Bicknell's Thrush on June 1 compared to a Thrush on June 30. These results are similar to those reported by Hill and Lloyd (2017). These results should not be interpreted to mean that surveys for Bicknell's Thrush should only occur in the pre-dawn darkness of early June (which would be logistically infeasible for large areas). Indeed, these results support the use of surveys throughout the mornings and month of June, and then statistically accounting for differences in detection probability associated with time and date.

Detection probabilities <1.0 are typical in wildlife surveys, where detection rates may vary based on vocal behavior, phenology of the breeding season, and numerous other factors (Wilson and Bart 1985, Diefenbach et al. 2007, Anderson et al. 2015). Across all years and surveys, mean detection probability averaged 0.29 (SD = 0.03, 95% credible interval = 0.22 to 0.36) and was very consistent--ranging between 0.27 and 0.33. These results support the use of citizen scientists to monitor for Bicknell's Thrush (*sensu* Fore et al. 2008), and they resemble the mean detection probability reported for Bicknell's Thrush from a much larger dataset (95% CI: 0.25 to 0.37; Hill and Lloyd 2007). Large variations in mean detection probability from year to year would suggest potential problems with the survey methodology or discrepancies in observer abilities (Meentemeyer et al. 2015).

Table 1. Model selection results using the pcount function in the R package "unmarked" to estimate Bicknell's Thrush abundance (N) and detection probability (p) from Mountain Birdwatch point count data (2016–2019). Models were ranked by their change in Akaike's information criterion for small sample sizes (Δ AICc) and corresponding model weight (w_i).

Model	ΔAICc	Wi	к	Log likelihood
ρ(count time + June day), λ(elevation + disturbance + disturbance²)	0.00	0.61	7	-723.21
ρ(count time + June day), λ(elevation + disturbance)	1.56	0.28	6	-725.04
ρ(count time), λ(elevation + disturbance + disturbance²)	3.61	0.10	6	-726.07
ρ (June day), λ(elevation + disturbance + disturbance ²)	10.47	<0.01	6	-729.50

Models, with K parameters, were sorted by their reduction in Akaike's information criterion for small sample sizes (\Delta AICc) compared to the model with the lowest AICc score. All models contained separate intercepts (not shown for clarity) for abundance and detection. The term disturbance² represents the quadratic term for distance to disturbance.



Figure 4. Bicknell's Thrush mean detection probability from Mountain Birdwatch surveys (2016-2019) declined steadily throughout the morning (left panel) and month of June (right panel). Detection probability is the probability of detecting a thrush that is present and available for detection. Point counts began up to 45-minutes before dawn, which can be as early as 4:00 am at high elevations in Maine. Thick lines (both panels) represent the mean relationship between survey start time (left panel) and day of June (right panel). Thin lines (both panels) represent individual estimates of detection probability for those covariates that were generated from the model posterior. A traditional figure with 95% credible intervals would like very similar to the below figure, but we find this format to be more informative.

Along with elevation, the distance to disturbance covariate (and its quadratic term), were included in the parsimonious model (Table 2). The parameter estimate (Table 2) for elevation was positive--a predictable result given the well-demonstrated positive relationship between Bicknell's Thrush abundance and elevation (Hill and Lloyd 2017). Bicknell's Thrush abundance, with respect to elevation, varies with latitude; Bicknell's Thrush populations reach their greatest density in northern New Hampshire and Maine at ~1000 m and elsewhere at ~1400 m (Hill and Lloyd 2017). The dataset used in this analysis was too small to consider interaction terms, but one might consider an interaction between elevations, where Bicknell's Thrush are already most abundant, might have a proportionally smaller effect on Bicknell's Thrush local abundance than a similar disturbance at lower elevations with lower Bicknell's Thrush density. The naïve occupancy results and the parameter estimates (Table 2) for elevation and distance to disturbance 4).

Table 2. Parameter estimates (β) on the log (N) and logit (p) scale from the final N-mixture model used to predict Bicknell's Thrush population response to disturbance, with standard deviation (SD) and 95% credible intervals (LCI, UCI).

Parameter	β	SD	LCI	UCI
<i>p</i> . intercept	-0.93	0.19	-1.33	-0.59
<i>p</i> : count time	-0.18	0.11	-0.41	0.03
<i>p</i> : June day	-0.41	0.11	-0.63	-0.20
<i>N</i> : intercept	-0.71	0.34	-1.45	-0.08
<i>N</i> : elevation	0.61	0.20	0.03	0.98
<i>N</i> : distance to disturbance	-0.75	0.30	-1.37	-0.19
σ: distance to disturbance^2	<-0.01	0.25	-0.51	0.47
σ: SD of random site effect	1.35	0.24	0.94	1.89



Figure 4. Six Mountain Birdwatch sampling stations (1-6) from the Sugarloaf route (#69) in Maine; all sampling stations are located within the ski runs of the Sugarloaf Ski Area in Carrabassett Valley, ME. Sampling station 69-1 is located near the top of Sugarloaf Mountain. During surveys, an observer detected Bicknell's Thrush at sampling stations 69-1 (1239 m) and 69-2 (1172 m), but not the lower elevation sites (3-6; ≤1081 m) on the route between 2016 and 2019. These results suggest the possibility of an elevation*disturbance interactive effect, because Bicknell's Thrush were not detected at lower elevation sites (surrounded by evergreen forest) adjacent to disturbances.

The model selection procedure supported a quadratic term for distance to disturbance (Table 1), but the final parameter estimate (Table 2) widely eclipses zero-suggesting a weak effect. However, Bicknell's Thrush abundance was still greatest immediately adjacent to sites of disturbance (Table 2 and Figure 5), and was smallest at the sampling sites farthest from disturbances. These abundance results are supportive of prior research into the effects of ski area disturbances on Bicknell's Thrush. Rimmer et al. (2004) examined characteristics of Bicknell's Thrush populations at two ski areas on mountains in Vermont–Mt. Mansfield, and Stratton Mountain. In that study, Bicknell's Thrush nest density was greatest near edges: 31 of 54 nests (57%) were within 10 m of ski trail edges and 45% of those nests were within 2 m from the edge (Rimmer et al. 2004). Furthermore, distance to ski trails and distance to hiking trails were uninformative predictors of nest survival in their models. Instead, red squirrel (Sciurus vulgaris) annual occurrence drove nest survival patterns, and red squirrels were not attracted to ski trail edges (Rimmer et al. 2004). Rimmer et al. (2004) did not conduct surveys for adult birds, but they did observer behavior of adults at nests and monitor adult movements via radio tracking. There was no evidence that ski slope edge proximity influenced adult thrush behavior at nests, and radio-tagged thrushes regularly crossed ski runs <30 m in width but rarely gaps >50 m (Rimmer et al. 2004).



Distance to disturbance (m)

Figure 5. The relationship between Bicknell's Thrush abundance and distance to disturbance, as estimated from the final N-mixture model and Mountain Birdwatch surveys (2016-2019). The red lines are associated with the left Y-axis drawn in red: the dark thick red line is the mean relationship between abundance and distance to disturbance, and the thin red lines are 500 individual estimates randomly pulled from the model posterior. The blue line is associated with the right Y-axis, and it represents the cumulative percent of Bicknell's Thrush abundance with respect to distance to disturbance. For example, ~50% of the Bicknell's Thrush in the analysis occurred at distances of 689 m or less from disturbances. Put more simply, there were as many Bicknell's Thrush in areas within 689 m of disturbances, as there were in areas that were between 690 and 2784 m.

The raw count data support Figure 5 as well. Beyond ~1100 m, observers reported a maximum of 1 Bicknell's Thrush during 5-minute point counts. In contrast, observers routinely detected 2-3 thrushes are distances less than that, and occasionally 4-5 birds during 5-minute point count periods. These results are logical, given the concentration of Bicknell's Thrush nests at ski slope edges (Rimmer et al. 2004) and the uncommon mating system of this species, where multiple males (2-4) may provision nestlings in a single nest (Goetz et al. 2003).

Are ski slopes beneficial to Bicknell's Thrush?

Multiple forms of evidence suggest that Bicknell's Thrush adult and nesting densities are greatest adjacent to disturbances—anthropogenic and natural (Rimmer et al. 2004, Townsend et al. 2015, this study). However, fitness benefits (i.e., increased survival or reproductive output) have so far not been demonstrated for Bicknell's Thrush breeding near disturbances (Rimmer et al. 2004); these benefits have thus far been thoroughly investigated only with respect to ski slope edges. Indeed, relatively high animal density does not necessarily indicate high-quality habitat (Van Horne 1983, Mosser et al. 2009, Beerens et al. 2015). The possibility exists that anthropogenic edges (e.g., ski runs) only superficially mimic the fir wave edges naturally found in Bicknell's Thrush habitat, and that fitness benefits only occur for thrush breeding near natural edges.

There is evidence to suggest that the location or size of the disturbance may be important for how disturbances are perceived by Bicknell's Thrush. First, observers consistently did not detect Bicknell's Thrush at some lower elevation Mountain Birdwatch sampling sites (in appropriate Bicknell's Thrush habitat), despite those sites being adjacent to ski slope edges. Second, Bicknell's Thrush frequently cross small forest gaps (e.g., ski slopes) <30 m wide, but rarely navigate forest gaps >50 m (Rimmer et al. 2004); so at some (unknown) size, a disturbance edge is likely perceived as a barrier (and not an attractant) by Bicknell's Thrush.

The density of some avian species may peak near disturbances initially, only because displaced individuals with strong site fidelity are crowded into the remaining habitat (Hagan et al. 1996). Over time, this inflated density near disturbance declines as site-faithful birds senesce, and younger birds fail to take up residency near the site of disturbance. That scenario is unlikely for the Bicknell's Thrush in this study for two reasons. Our analysis used data from a four-year period, and examination of NLCD and Google Earth imagery indicated no notable disturbances near sampling stations during the study or the immediate years before.

It is likely, however, that some Bicknell's Thrush are displaced by the initial creation of ski runs in spruce-fir habitat, and those activities also fragment the remaining forest habitat. Bicknell's Thrush occupancy patterns are affected by processes at both the local and landscape scale, but local forest patch size is positively related to occupancy probability in this species (Frey et al. 2011). A large ski resort (e.g., Killington Mountain Ski Resort, Vermont) may contain over 100 km of ski runs (Killington Mountain Ski Resort 2019); assuming 40-m wide runs, that would result in 400 ha of cleared forest—a large enough area to contain the home ranges of 74-125 female Bicknell's Thrush (Collins 2007). Are these displaced individuals simply absorbed into the immediate landscape, or do they resettle elsewhere? If new breeding adults are attracted to the new ski area disturbance, are their enough recruited individuals to replace the former residents who resettled elsewhere (i.e., does the net population of Bicknell's Thrush on the mountain change)? These questions would best be answered by conducting surveys before and after new ski slope development activity, but the perimeter-to-area ratio of forest patches may be a more informative predictor of Bicknell's Thrush occupancy and local abundance than forest patch size alone (*sensu* Hill and Diefenbach 2014).

These unanswered questions acknowledge an important limitation of the analysis in this report. Mountain Birdwatch was not designed to specifically investigate patterns of Bicknell's Thrush abundance as it relates to anthropogenic disturbances. Although the analysis and approach undertaken in this report are statistically defensible, these results are entirely correlational. A more powerful approach would be to initiate an intentional field study to address the questions raised in the preceding paragraph, and to simultaneously document how the other boreal forest bird community members respond to disturbance. We would recommend a study design based on repeated sampling at stations along elevational gradients spanning ski trails across New England and New York. We would also recommend standardizing ski run width (if possible) and quantifying recreational activities (e.g., hiking, dog walking, and mountain biking) near sampling stations, as these activities can negatively affect local bird populations (Steven et al. 2011, but see Deluca and King 2014). Such an investigative effort would be best paired with identical sampling from mountains without ski resorts, setting up transects perpendicular to fir waves, as positive fitness benefits may only be present at naturallydisturbed sites. Ultimately, the goal of such research should be to discover the actual mechanisms driving these local patterns of abundance. Therefore, it would also be insightful to simultaneously quantifying food resources (or a proxy such as light levels or soil temperature), offspring condition (e.g., size at fledging) or survival, and predation risk along these natural and anthropogenic edges.

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Author Contributions

J. Campbell quantified land cover changes surrounding Mountain Birdwatch sampling locations, and J. Hill conducted all statistical modeling and wrote the manuscript.

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