

Bird community composition along elevation and latitudinal gradients in Alberta's mixedwood forest: analogues for our future climate?

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Preface:

The Alberta Biodiversity Monitoring Institute (ABMI) is an arm's-length, not-for-profit scientific organization. The primary goal of the ABMI is to provide relevant scientific information on the state of Alberta's biodiversity to support natural resource and land-use decision making in the province.

In the course of monitoring terrestrial and wetland ecosystems across the province, the ABMI has assembled a massive biodiversity database, developed reliable measurement protocols, and found innovative ways to summarize complex ecological information.

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Abstract

Elevation and latitude are primary determinant of local climate conditions. As climate change progresses, high elevation and high latitude locations in Alberta are more likely to have suitable climate conditions to allow persistence of forest environments. We conducted a detailed bird and local climate survey across Alberta to determine how birds react to variation in elevation and latitude with the goal of better understanding how bird communities might change with future climate shifts. We found more southerly latitudes and lower elevations currently support more species of birds. The latitudinal – richness response was driven primarily by invasion of lower-latitude species adapted to open grassland, agricultural, and urban environments. In contrast, there was no evidence that changes in richness with elevation were driven by invasion by open habitat species at lower elevations. These data demonstrate the complexities of understanding topographic – climate controls on species distribution and highlight the need for enhanced monitoring of Alberta’s hill systems. As climate change progresses, Alberta’s hills systems will become increasingly important for conserving biodiversity associated with Alberta’s forests.

Introduction

Stralberg et al. (submitted) recently used a series of climate projections, species distribution modelling, and conservation prioritization tools to evaluate a series of realistic scenarios about how birds might change their distribution with climate change across boreal Canada. They demonstrated that as the climate warms much of the boreal plains ecosystem in Alberta will shift to a climate that is far less likely to support trees. This will have negative effects on many bird species that rely on forests. Mapping current bird distributions based on climate they were able to identify climatic refugia (locations where climate will remain within the range of conditions), places that will become more suitable in the future, and places which will no longer be suitable. They found central and northern hill systems will become increasingly important for conserving boreal bird diversity as the climatic shifts in these areas will not be sufficiently extreme to shift from a forest to non-forest state. In some of the more northern hill systems, tree productivity could also increase creating new habitat for some species (Pastor and Post 1988).

The rationale of this approach to understanding climate change on bird communities is that continental and intercontinental patterns of species richness and the distribution of many species are correlated with current climate conditions (Woodward 1987). Typically, the greatest diversity of species occurs in warm, wet areas. Water-energy balance explains almost three-quarters of the variance in bird species richness at a planetary scale (Hawkins et al. 2003) indicating that spatial distributions of extant bird species likely reflect a strong response to climate both directly and through climate's effect on plant biomass or vegetation structure. In Alberta, water-energy balance is strongly correlated with mean annual temperature (hereafter

MAT) which in turn is inversely correlated with latitude along the boreal-parkland-grassland gradient (Figure 1).

MAT will experience a large directional change in the future due to climate warming in Alberta based on climate projection models. Thus, we chose to evaluate how current MAT influences forest bird communities. Our rationale was that the most southerly forests in Alberta might provide analogue examples of what future bird communities might look like in the future. However, climate envelopes will not only shift towards the poles with warming temperatures. MAT is highly correlated with altitude (Daly et al. 1994). Thus, we also evaluated how much bird communities in Alberta might change with elevation at the same latitude. This was done under the premise that bird species and communities may be able to move upslope in response to climate change. Identifying this potential could then be used to locate micro-refugia within hill systems where the probability of forests and forest birds persisting might be higher (Dobrowski 2010).

A limitation of Stralberg's (submitted) models is that little data on bird abundance or climate is known from Alberta's hill systems *per se*. Thus, we collected new field data to determine how bird communities and climate vary along a latitudinal and elevation gradient in Alberta to: 1) establish a baseline for future monitoring; 2) test predictions made by Stralberg et al. (submitted) related to community composition and diversity; and 3) demonstrate how boreal forest systems in northern Alberta might look in the future by comparing forest relics in southern Alberta's hill systems to those further north. Our specific objectives were to determine: 1) if there are elevation specialists in Alberta's mixedwood forests; 2) if there are latitudinal specialists in Alberta's mixedwood forests; 3) if individual species in southern

latitudes have shifted to higher elevations relative to more northern latitudes; 4) if alpha and gamma richness vary with elevation & latitude; and 5) if differences in alpha and beta richness are caused by differential invasion by open habitat species into low elevation and low latitude sites.

Methods

Within four hill systems from the Alberta-Montana to the Alberta-NWT border, we selected an approximately equal number of sample locations within each available 100-m elevation band (ranging from 3 to 4 bands). In this analysis, we used data from 156 locations in the four hill systems across Alberta (Figure 1) We also attempted to achieve equal coverage of four local aspect/landform categories: northeast-facing, southwest-facing, flat, and valley bottom. Preliminary analysis of bird data indicated this variable was rarely important, so it was not included in further analysis. All points were within 5 km of a road and in clusters of four, arranged in a 500-m by 500-m square for optimal deployment of field sampling. Clusters were placed to target the medium-mesic upland forest that was dominated by a white spruce-aspen gradient (i.e., not bogs or pine forests found on poor soils). Each cluster could span a maximum of two elevation categories. Clusters were also placed to avoid cutblocks and other major anthropogenic disturbances. A few individual sample locations that, due to mapping error, fell inside a recent cutblock, open area, or other anthropogenic feature (e.g., well pad, road, cabin), or water body, were moved in the field to the closest mature forest that would still maintain at least 400 m between points.

Automated recording units (ARUs) were deployed at each site during the first visit. ARUs recorded sounds of various birds, mammals, and amphibians every hour for 10 minutes for a period of 2 – 7 days depending on logistical constraints. We then listened to four 3-minute periods at each ARU. All recordings were processed at the same time of day, specifically 5 AM. Data are reported as the maximum number of individuals of each species that were recorded across the four listening events.

To evaluate our hypotheses related to individual species, we used Poisson regression to determine how latitude and residual elevation, time of year, and dominant tree species influenced the relative abundance of birds. We assumed that the detection radius of the ARU was the same in all environments and that any variation in detectability was random with respect to latitude and residual elevation. Akaike's Information Criteria (AIC) was used to rank the fit of various models. In all models we included time of year and dominant tree species. We then evaluated whether the fit of this base model could be improved by including residual elevation and latitude as linear functions, residual elevation and latitude as quadratic functions, and residual elevation and latitude as a multiplicative term (interaction). This was done individually for each species. The quadratic terms allowed us to test if there was evidence of birds that were mid-latitude or mid-elevation specialists. The multiplicative model allowed us to test if there was consistency in how birds react to residual elevation when controlling for latitude. If the best-fitting model had a $\Delta AIC > 2$ we reported the response of the bird based on that model. When more than one model had similar fit we summarized the result based on the principle of parsimony whereby the model with the fewest parameters was selected. For example, a linear response to residual elevation and/or latitude was deemed a more

parsimonious explanation than a quadratic or multiplicative effect. We also evaluated the 90% confidence intervals for the best selected model to determine if the estimated coefficients included zero or not when making our determination of the best model fit.

When the multiplicative model was supported we then evaluated whether our hypothesis that individual bird species in more southern latitudes may have shifted to higher elevations by looking at the predicted values from the model. We also evaluated the predicted values when the quadratic model was selected to determine if it supported a mid-latitude or mid-elevation specialization.

Ordinary least squares regression was used to assess how species richness, total bird abundance, and the composition of the community were influenced by residual elevation and latitude. The same modelling framework was used as for individual species. The response variable for community composition was the proportion of species detected that were capable of living in open habitats. We classified a species as capable of living in open habitat if models from the Alberta Biodiversity Monitoring Institute found they were abundant in agricultural, grassland, or urban areas. Species associated with wetlands were not included in this definition. When modelling proportion of community adapted to living in open habitats, we also included species richness in the base model. When modelling total bird abundance we included species richness in the base model.

Results

We detected a total of 94 bird species at 156 locations. This is approximately 1/3 of Alberta's bird species. However, 56 were rare and found at less than 10% of survey points. We

chose not to analyze these species for latitude or residual elevation responses as the sample size precluded robust confidence in our parameter estimates for these species. They were included in all estimates of alpha and gamma richness.

Of the 38 species that were sufficiently abundant to model their response, we found the Chipping Sparrow and Dark-eyed Junco did not respond to residual elevation or latitude. The Red-eyed Vireo and Western Tanager were more common at lower elevations but showed no response to latitude while the Savannah Sparrow was more common at higher elevations.

For 17 species, inclusion of latitude as a linear function provided a better model fit. Black-capped Chickadee, Brown-headed Cowbird, Brown Creeper, Clay-colored Sparrow, Common Yellowthroat, Dusky Flycatcher, House Wren, Least Flycatcher, Mourning Dove, Tree Swallow, Veery, Warbling Vireo, and White-crowned Sparrow were more likely to be found in southern latitudes. Hermit Thrush, Rose-breasted Grosbeak, Ovenbird, and Tennessee Warbler were more likely to be found in northern latitudes. For 8 species, a quadratic model provided the best model fit. The Blue-headed Vireo, Golden-Crowned Kinglet, Gray Jay, Red-breasted Nuthatch, Ruffed Grouse, White-throated Sparrow, Winter Wren, and Yellow-rumped Warbler were more abundant at mid-latitudes.

An additional 8 species showed evidence of an interactive effect of residual elevation and latitude. This suggests the response to residual elevation was not consistent along latitudinal gradients. Species with this response included the American Redstart, American Robin, Black-throated Green Warbler, Magnolia Warbler, Ruby-crowned Kinglet, Swainson's Thrush, Yellow-bellied Sapsucker, and Yellow Warbler. The main reason for this interactive effect was many species were rare at some latitudes and common at others making an

evaluation of how they responded to residual elevation at all latitudes difficult. When we removed the interaction term, we found the American Robin, Yellow-bellied Sapsucker, and Yellow Warbler were more common in southern latitudes. The Black-throated Green Warbler, Magnolia Warbler, and Swainson's Thrush were more common at northern latitudes. The American Redstart and Ruby-Crowned Kinglet showed no strong evidence of latitudinal effects with this model structure.

We found no support for our hypothesis that any individual species in southern latitudes has shifted to higher elevations relative to the more northern latitudes. In Appendix 1, the raw mean abundance for the four major latitudinal areas in four residual elevation categories for these 38 species are shown.

Alpha richness showed a very strong linear response to latitude and residual elevation (Figure 2). There was no evidence of a mid-latitude or mid-elevation response. The interaction between residual elevation and alpha richness improved model fit and suggested that alpha richness declined with elevation more rapidly in the most southerly sites. However, a decline in alpha richness with elevation occurred at all latitudes (Figure 4). Based on standardized beta coefficients, latitude ($\beta = -0.387$, $P < 0.001$) had a slightly greater effect on alpha richness than residual elevation ($\beta = -0.315$, $P < 0.001$).

The proportion of the community comprised of open habitat species was strongly influenced by latitude but was not related to residual elevation (Figure 3). There was no evidence of an interaction between residual elevation and latitude for the proportion of open habitat species (Figure 4). There was also no evidence of a quadratic relationship. Based on

standardized beta coefficients, latitude ($\beta = -0.895$, $P < 0.001$) had a much greater effect on alpha richness than residual elevation ($\beta = -0.036$, $P = 0.503$).

Removing the open habitat species from the estimate of alpha richness resulted in no significant interaction between residual elevation and latitude ($\beta = 1.966$, $P = 0.111$). Instead we found residual elevation ($\beta = -0.435$, $P < 0.001$) had a much greater effect on alpha richness of forest species than latitude when modelled as a linear term ($\beta = 0.194$, $P = 0.042$). The best fitting model for alpha richness of forest species indicated more species were found in mid-latitudes as the quadratic model had better model fit (Figure 5).

The patterns we saw in alpha richness were similar when we estimated gamma richness (cumulative number of species observed) for each latitudinal cluster with species accumulation curves (Figure 6). Species accumulation with increasing number of survey sites was more rapid for the southerly latitudes, intermediate at mid-latitudes, and shallowest at high latitudes.

Total bird abundance was strongly correlated with alpha richness ($r^2 = 0.94$). However, based on AIC there was some evidence of better model fit relative to the base model when latitude was included ($\beta = -0.053$, $P = 0.04$).

Discussion

Latitude was generally a better predictor of species specific bird abundance than relative elevation. Very few species showed evidence of being specialized to a particular elevation. Far more species showed distinct latitudinal gradients. Only 18% of species showed no numerical response to latitude, 42% were relatively more abundant in more southern latitudes, 21% in mid-latitudes, and 18% in northern latitudes. The Cypress Hills (the southern

relict forest) had the highest mean alpha species richness as well as the highest gamma richness. We suggest four possible explanations for the increased number of species we observed in the most southerly sites and the greater number of species that seem to be more abundant in southern latitude forests.

The species diversity - energy hypothesis suggests the amount of available energy sets limits to the richness of the system (Evans et al. 2005). Increased solar energy at low latitudes (when water is abundant) may increase net primary productivity, allowing more individuals to be supported per unit area in such forests. When we controlled for species richness, we found weak evidence that the total number of birds detected differed as a function of residual elevation or latitude suggesting that our southern sites may have been slightly more productive than the more northerly sites.

Alternatively, colder temperatures at higher latitudes may restrict the number of species that can occur due to physiological tolerance limitations (Currie 1991). However, the fact that the majority of bird species detected were migratory species, not affected by low winter temperatures, limits the applicability of this hypothesis here. More likely is that the diversity of plants comprising food and nesting resources experience is affected by physiological limitations (Ferber et al. 2014)

Thus a third explanation is that forests in more southerly forests are more diverse in their internal vegetation structure and composition than the more northern forests thereby supporting a greater diversity of species (Glenn-Lewin 1977). While we did control for leading tree species, we did not include shrub attributes or other factors such as vertical or horizontal structure that do influence species richness. Future analyses will test this hypothesis to

determine how native understory plant structure varies as a function of residual elevation and latitude. However, we suspect this will not explain the pattern in alpha richness of birds. Relatively few of the bird species that are strongly associated with complex shrub and canopy structure (i.e. American Redstart, Canada Warbler, Magnolia Warbler) were detected more often in southern forests, suggesting that complexity of understory forest vegetation is not strongly varying with latitude or residual elevation (Hobson and Bayne 2000).

The last explanation, and the one we feel might have the strongest effect, is that the most southerly forested sites are relatively close to open grassland areas that have been devoid of trees for many centuries. The trees of the Cypress Hills are typically found on north-facing slopes in steep terrain where streams and higher soil moisture occur. On the plateau of the hills, south facing slopes, and the valley bottoms, native grassland is more likely to predominate (Newsome and Dix 1968). As such, higher species richness may reflect a greater number of major ecosite classes being present within the sampling radius of the ARU so that in the Cypress Hills we may be counting birds that are outside of the forest patches themselves. Alternatively, open habitat species may be more likely to “invade” forests in southern latitudes because the overall landscape is more suitable for them. That the proportion of species adapted to open habitat was so strongly correlated with latitude and that forest bird richness was not linearly related to latitude provides support for this hypothesis. Careful examination of all of the species more common at southern latitudes indicates they are often found in shrubby areas near the edge of forests and open. That being said, there were three species that were more common in southern forests that have a strong association with mature trees suggesting there are forest specialists who are more common in southern latitudes. The Warbling Vireo is often

described as preferring deciduous forest although they also use some mixed coniferous and deciduous habitats. The Brown Creeper is described as using mature evergreen or mixed evergreen-deciduous forests. The Veery is typically found in deciduous woodlands with a well-developed understory (All About Birds 2015).

Overall, these results suggest that as climate changes in Alberta that more northern hill systems may become more diverse than they currently are. This assumes that Cypress Hills is a good analogue of the future for northern hill systems. At face value this might suggest to some that climate change will generally be positive for birds that use aspen-mixedwood forests. However, the higher diversity of birds in the Cypress Hills is driven primarily by increases in open habitat species most commonly found in agricultural, grassland, and urban environments. These species presumably have a greater climate tolerance and are not species of concern currently nor are likely to be in the future. Numerous species that are reasonably common in the northern portion of Alberta like the Black-throated Green Warbler, Blue-headed Vireo, and Hermit Thrush were not found in the Cypress Hills. Whether this reflects the fact that these species never colonized this area or whether they were present but are now locally extinct is unknown.

Common northern birds like the Ovenbird, Rose-breasted Grosbeak, Ruby-crowned Kinglet, Swainson's Thrush, and White-throated Sparrow should be carefully monitored in the Cypress Hills. These species currently exist in the Cypress Hills in sufficient numbers to detect population trends. However, they occur at much lower numbers than further north and thus may provide an early warning system of extinction risk related to climate change. Much of the Cypress Hills exists within protected areas and is subjected to fewer impacts from industrial

activities like forestry and energy development than forests further north. Having a directed ARU monitoring program in the Cypress Hills would provide a good opportunity to separate the effects of climate change from land-use on birds in an area where the shift from a forested to grassland ecosystem has a fairly high degree of certainty.

At a species level there was very little evidence of strong responses to residual elevation. Alpha richness however, was strongly related to elevation. The same three hypotheses used to explain bird response to latitude could be used to explain patterns related to residual elevation. Residual elevation did not explain any of the variation in total bird abundance suggesting that productivity *per se* is not the key driver. Admittedly, we have not yet tested for changes in vegetation structure with elevation so we can't exclude the possibility that forest complexity is higher at lower elevations. Previous studies have shown this to be true in mountain systems (Glenn-Lewin 1977).

The hypothesis that proximity to non-treed ecosites might drive patterns of decreased richness at higher elevations can't be excluded but seems a weaker explanation for the richness – elevation pattern we observed. In the most southerly Cypress Hills site, the valleys and plateaus are often relatively flat and more likely to be grassland than forest. Thus, we might actually have expected higher species richness to occur at higher elevations if invasion or increased detection of open habitat species was the cause of this pattern. Furthermore, the plateaus of the northern hills we studied were generally forested so we expected to see an interaction between latitude and residual elevation for richness and proportion of the community adapted to open habitats. This did not occur.

The relationship between richness, residual elevation, and latitude did show evidence of an interactive effect. The greatest difference in alpha richness as a function of latitude occurred at low elevations with a relatively small difference in alpha richness observed between latitudes at the highest elevations. At this point the primary driver of the elevation – richness pattern we observed remains unclear. Regardless, the existence of this gradient does provide an explicit test for monitoring the effects of climate change. Detailed monitoring at low versus high elevation sites in the boreal plains should be undertaken to determine if elevation shifts in bird communities will help compensate for the habitat change that is expected at lower elevations as climate change progresses.

The existence of elevation – richness gradients along the relatively narrow altitudinal range studied here demonstrates the importance of studying climate – topography controls on forest ecosystems and how this influences birds. If we hope to conserve the biodiversity of Alberta's forests, more effort is needed to understand, protect, and monitor what is occurring in Alberta's hill systems as these areas may become the only boreal forests available to future generations of Albertan's to enjoy. The past focus of most monitoring of boreal birds has taken place in the flat plains of the boreal mainly driven by concerns about industrial development in these areas. That hill systems are more difficult to develop from an industrial perspective gives them a degree of *de facto* protection that is invaluable in trying to separate the relative importance of land-use and climate change for boreal biodiversity. However, to achieve this directed monitoring of these areas is required.

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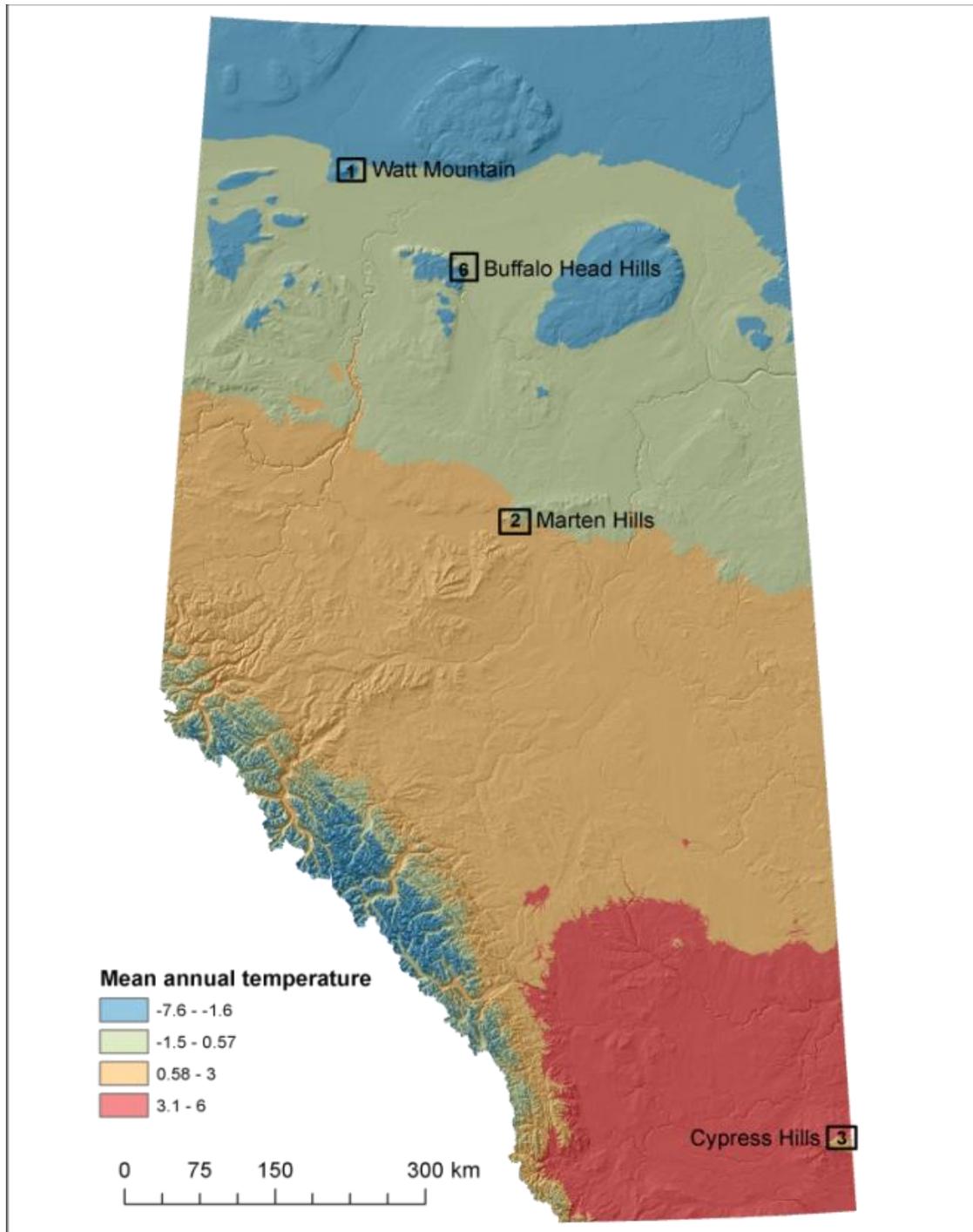


Figure 1 – Mean annual temperature across Alberta and the locations of the four latitudinal clusters where birds and climate were sampled by CCEMC funding in 2014.

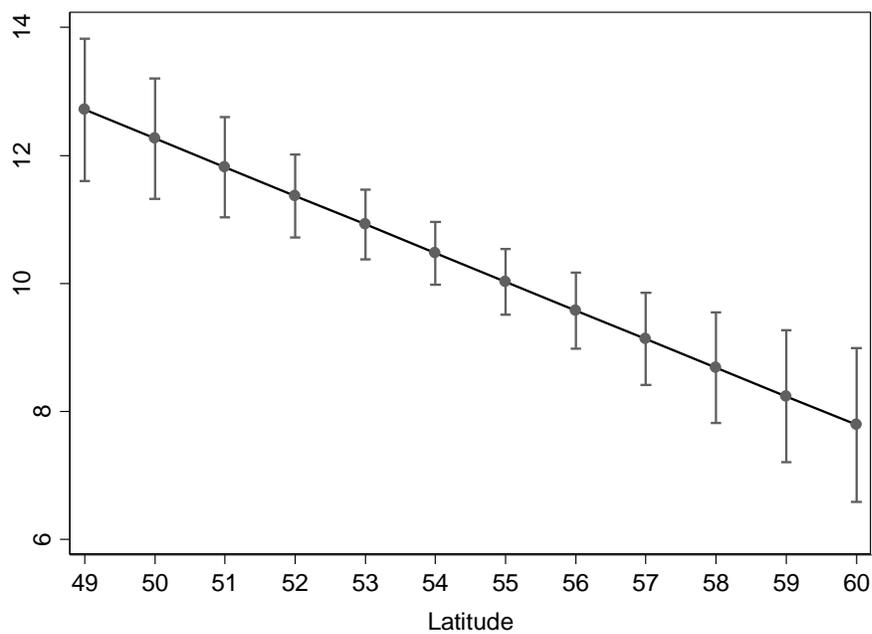
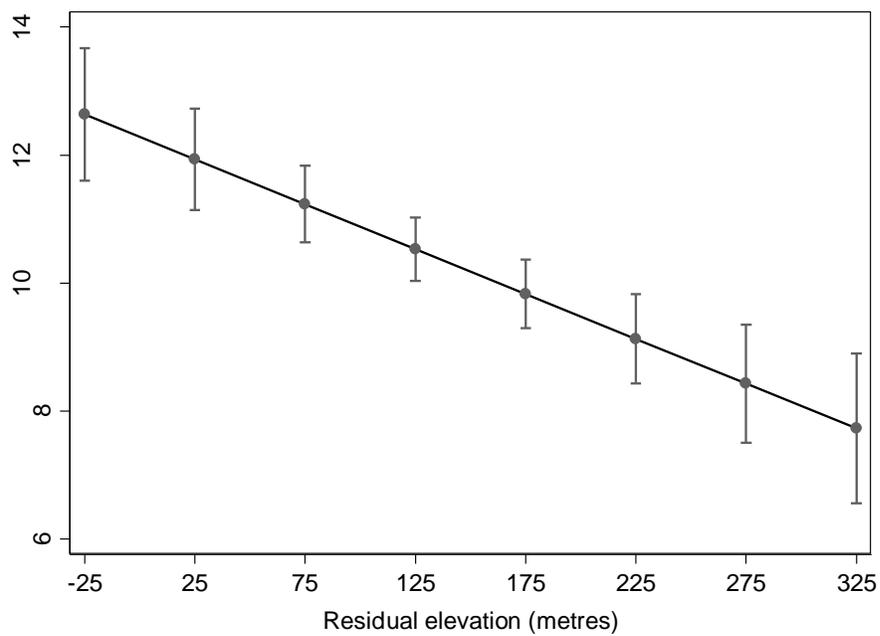


Figure 2 - Number of bird species (alpha richness) detected per station as a function of residual elevation (metres) (TOP) and latitude (BOTTOM). Error bars are 95% confidence intervals.

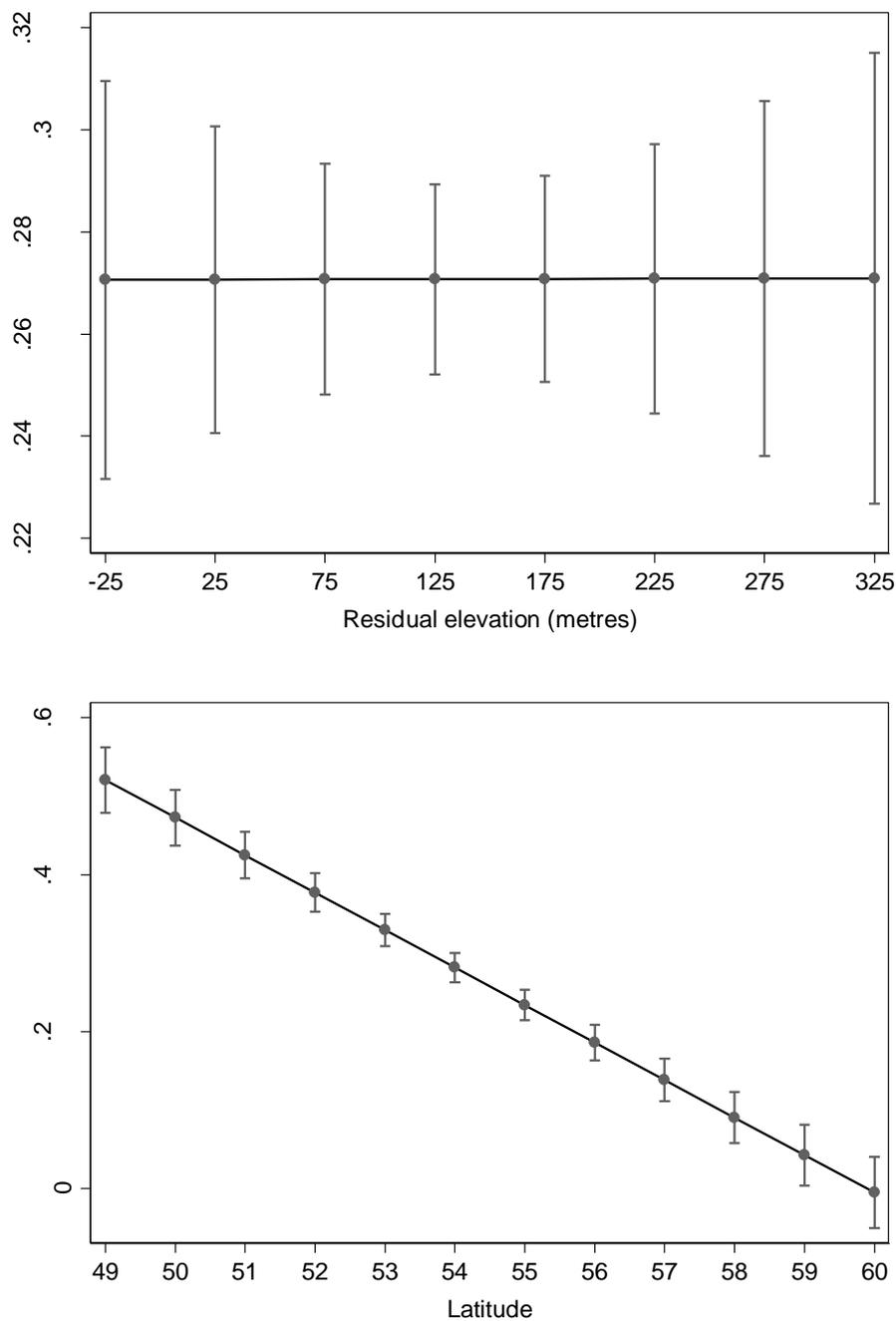


Figure 3 - Proportion of bird community that are capable in living in grassland, agricultural, or urban areas (aka open habitats) as a function of residual elevation (metres) (TOP) and latitude (BOTTOM). Error bars are 95% confidence intervals.

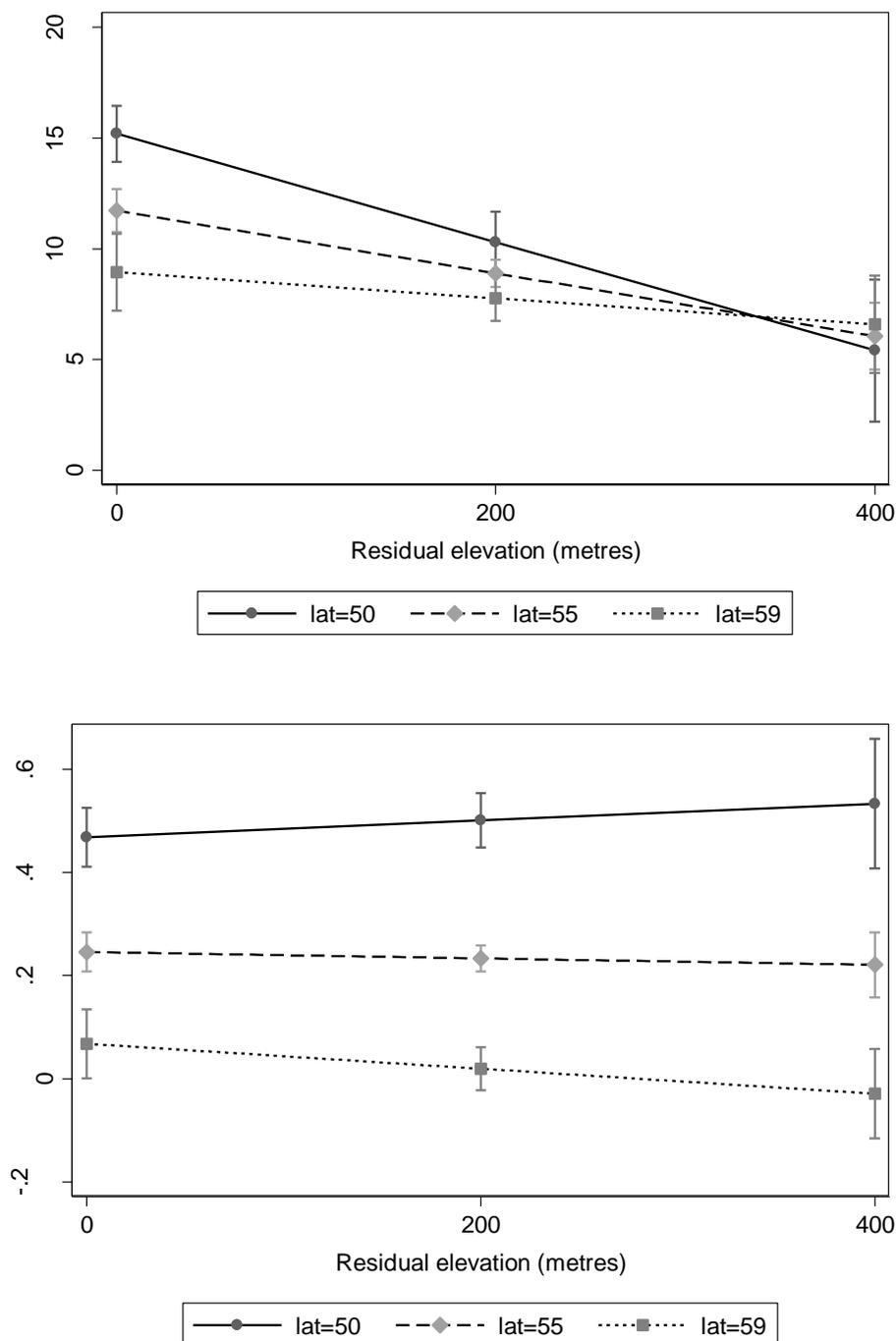


Figure 4 - (TOP) Number of species (alpha richness) and (BOTTOM) proportion of bird community adapted to open habitats as a function of residual elevation (metres) and latitude when modelled as a multiplicative effect. Error bars are 95% confidence intervals.

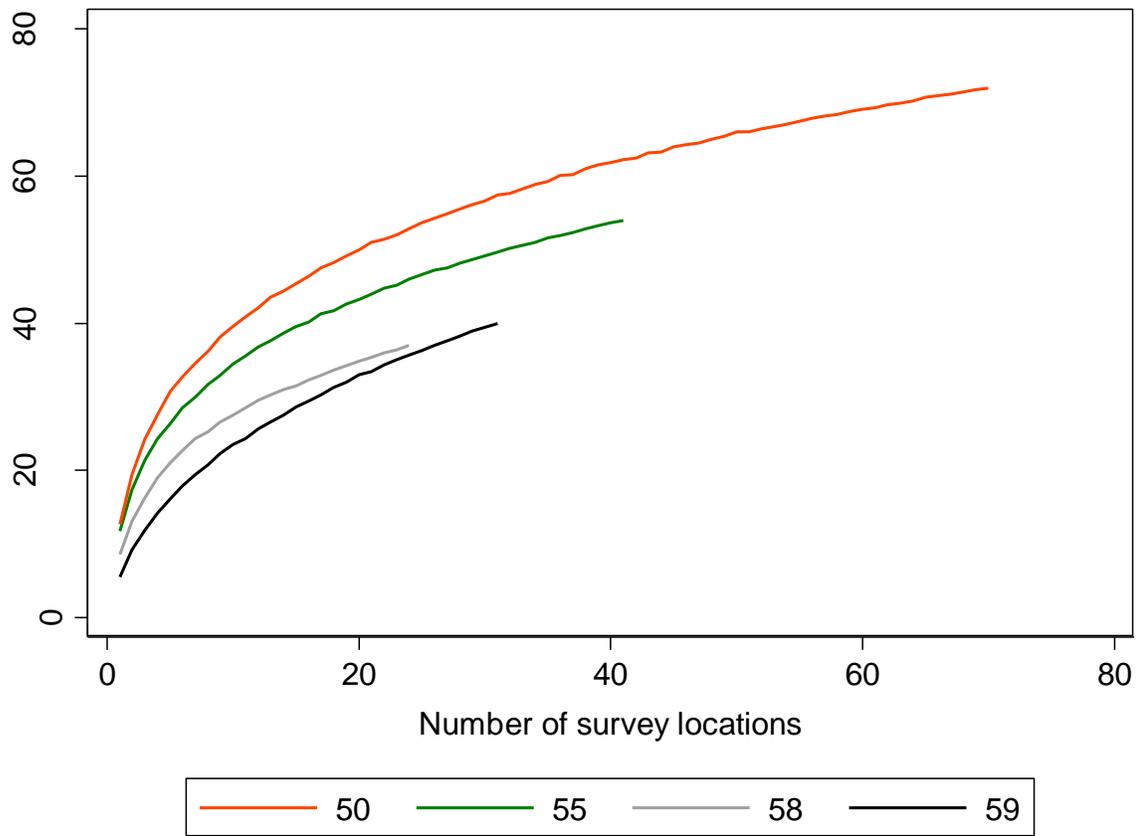


Figure 5 – Cumulative number of species observed (gamma richness) as a function of number of survey locations in each latitudinal cluster. The legend shows the average latitude for each cluster (50° - Cypress Hills, 55° - Marten Hills, 58° - Buffalohead Hills, 59° - Watt Mountain).

savs	0.05	0.31	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
swth	1.05	0.25	0.41	1.70	2.14	1.70	1.57	1.00	0.50	1.20	0.67	2.00	1.67	1.88	1.88
tewa	0.09	0.00	0.23	1.70	1.86	0.40	0.29	0.22	0.50	0.40	0.83	0.50	0.83	1.63	1.38
tres	0.68	0.69	0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
veer	0.77	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
wavi	1.00	0.56	0.50	0.40	0.86	0.20	0.14	0.00	0.00	0.40	0.17	0.00	0.17	0.50	0.63
wcsp	1.09	1.19	1.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
weta	0.05	0.06	0.09	0.50	0.43	0.00	0.07	0.00	0.00	0.10	0.00	0.50	0.17	0.13	0.13
wiwr	0.05	0.00	0.05	0.70	1.00	1.30	1.36	0.33	0.00	0.40	0.83	0.50	0.17	0.50	0.00
wtsp	0.05	0.06	0.00	1.70	2.57	1.00	0.21	0.00	0.00	0.80	0.17	0.00	0.17	0.38	0.25
ybsa	0.86	0.44	0.09	0.10	0.29	0.30	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
yrwa	0.36	0.69	0.55	1.80	1.57	1.90	1.79	0.78	0.17	0.80	0.67	0.50	1.00	1.13	1.00
ywar	0.41	0.56	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

- Codes can be linked to species common and scientific names can be found at www.wec.ufl.edu/birds/SurveyDocs/species_list.pdf