Evaluating the Effectiveness of Biodiversity Surrogates for Conservation Planning in the Boreal Region of Canada

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**Abstract (max 350 words)**

**Key Words (max 12 words):** Biodiversity surrogates, effectiveness, conservation planning, boreal region.

# Introduction

Ecological reserves that are designed using modern conservation planning methods should be representative of regional biodiversity (Margules and Pressey 2000). However, comprehensive biodiversity data are generally not available, so conservation practitioners need to use biodiversity surrogates when assessing representation (Caro and O’Doherty 1999, Wiens et al. 2008, Hortal et al. 2009, Urbina-Casanova et al. 2016). This assumes that areas representative of surrogates are also representative of regional biodiversity. Surrogates can be taxonomic (i.e., species) or environmental (Grantham et al. 2010). Environmental surrogates can be discrete classified layers such as physiographic features or land types (e.g., Lombard et al. 2003, Oliver et al. 2004), continuous layers such as climatic variables (e.g., Sarkar et al. 2005, Hanson et al. 2017), or a combination of variables in multivariate space (e.g., Beier and Albuquerque 2015, Albuquerque and Beier 2018). Environmental surrogates have the advantage of being easily mapped over wide areas, and therefore, provide a low-cost alternative for large-scale conservation planning. It is generally assumed that representing a variety of environmental conditions will also represent a range of biodiversity values. However, tests of environmental surrogates have produced varying results (e.g., Oliver et al. 2004, Sarker et al. 2005, Grantham et al. 2010, Mellin et al. 2011, Beier et al. 2015, Engelbrecht et al. 2016), as have tests for biodiversity surrogates in general (e.g., Rodrigues and Brooks 2007). Grantham et al. (2010) suggest that this variability is due to differences in surrogates used, study regions, measures of surrogate effectiveness, and biodiversity features that the surrogates are intended to represent.

Two general types of tests have been used in recent studies to evaluate biodiversity surrogates (Rodrigues and Brooks 2007). Pattern-based tests directly measure the spatial relationship between the surrogate and test features on the landscape (Grantham et al. 2010, Andrefouet et al. 2012). This approach can be used to test, for example, the statistical significance of correlations between surrogates and test features (e.g., Oliver et al. 2004, Su et al. 2004), but does not directly evaluate the effectiveness of surrogates for conservation planning. Selection-based techniques generally involve the selection of conservation areas using the surrogates, then evaluate the representation of the test features in the selected areas (Grantham et al. 2010, Andrefaut et al. 2012). According to Rodrigues and Brooks (2007), this approach focuses on evaluating the extent to which areas selected for surrogates capture the test features.

In addition to biodiversity representation, methods for conservation planning in the boreal forest region of Canada are increasingly accounting for ecosystem dynamics (Leroux et al. 2007, Leroux and Rayfield 2014). For example, the concept of minimum dynamic reserves (MDR) has been suggested for the construction of ecological benchmarks i.e., large, intact reserves designed to maintain large-scale natural disturbances and other ecological processes (Arcese and Sinclair 1997, Wiersma 2005, Schmiegelow et al. 2014). Both aspects of conservation planning are generally lacking in the boreal region. For example, environmental surrogates in the boreal region are under-represented in the current protected areas network (Andrew et al. 2014) and expansions to the network are needed if Canada is to meet targets set by the Convention on Biological Diversity (SCBD 2010). Expansions to the reserve network should be science-based (Coristine et al. 2018), and will require the use of biodiversity surrogates, but little has been done to test the effectiveness of surrogates in this region (but see Warman et al. 2004, Powers et al. 2013). Remotely sensed environmental surrogates are increasingly available for the Canadian boreal (e.g. Powers et al. 2013) and recent advances in the availability of species models in the boreal region (Stralberg et al. 2015) make it possible to test the effectiveness of surrogates to represent a range of species across the entire Canadian boreal region. This presents an opportunity to integrate surrogacy evaluations into existing conservation planning frameworks such as those using the National Ecological Framework for Canada (Ecological Stratification Working Group 1996). The application and evaluation of environmental surrogates could be especially useful in the boreal region where access is limited and species data are scarce (Schmiegelow et al. 2012).

There's a certain amount of confusion in the use of the terms representativeness and representation. According to Kukkala and Moilanen (2013), "representation can be interpreted as the extent of occurrence of a particular species or other biodiversity feature within a specific area", whereas "representativeness can be seen as a broader concept indicating whether a reserve network represents the full variety of biodiversity at all levels of organization." In this study we focus on representativeness by evaluating if networks comprised of ecological benchmarks that are representative of four environmental surrogates are also representative of several test features, specifically boreal caribou, songbird species, and waterfowl guilds. For each test feature (species), we evaluate the hypothesis that there is a positive linear relationship between networks that are representative of the species or group of species and those that are representative of the surrogates. Rather than constructing and selecting networks using subjective area-based targets, we used catchments as building blocks to create benchmark networks based on criteria of size, intactness and hydrological connectivity. We also address representation with a case study of an ecoregion in north-central Canada that identifies benchmark networks that maximize representation (i.e. extent of occurrence) of test species.

# Methods

## Study area

Our study region is the Canadian boreal forest (Brandt 2013), stratified into XX ecoregions using the National Ecological Framework for Canada (Ecological Stratification Working Group 1995; Figure 1). Ecoregions are stratified into areas that are characterized by distinctive regional ecological factors, including climate, physiography, vegetation, soil, water, and fauna. Ecoregions are nested within ecozones, which are large areas delineated on the basis of the interactions of biotic and abiotic factors including human activities. A total of 94 ecoregions occur in the boreal region (Table 1) and, among those, benchmark networks were identified for 72, of which 48 contained networks that were considered representative of their ecoregion based on criteria defined in the following paragraphs. Our focus in this study is on the 48 ecoregions with representative benchmark networks.

**Figure 1 & Table 1**

## Biodiversity surrogates

In this paper, we define surrogates as a set of environmental features that we expect to conserve broader biodiversity when represented in a reserve network. The surrogates serve as indicators of large-scale environmental variation of ecological patterns and processes that are assumed to influence biodiversity at coarse spatial scales. We used four environmental surrogates (Figure 2):

1. Gross primary productivity (GPP) is an indicator of the amount of carbon absorbed by photosynthesis, measured in kg per meter squared per year (C kg/m2/yr). It is calculated as an average of 15 years of data (2000-2014) from the MODIS satellite and has a resolution of 1 km2 (Zhao and Running 2010);
2. Climate moisture index (CMI) is a measure of the water deficit (or surplus) in soil, calculated as the yearly average precipitation minus yearly potential evapotranspiration expressed in units of cm of water per year (Hogg 1997). We used data from Hamann et al. 2013 with resolutions of 1-km2 for western North America and 4-km2 for North America, resampling the latter to 1-km2.
3. Land cover (LCC) is a categorical descriptor of vegetation on the landscape and was measured using the 2010 Land Cover of North America based on 250m MODIS satellite imagery, containing 19 cover types (CEC 2013). Landcover classes associated with anthropogenic disturbance were removed (urban, agriculture).
4. Lake edge density (LED) is an indicator of the density of riparian habitat, measured in km/km2 within 100 km2 circular units (BEACONs 2011). This dataset was created using the 1:1,000,000 lakes and wide rivers coverage from the Atlas of Canada’s National Scale Frameworks Hydrology (v6.0, NRCAN 2009);

**Figure 2**

## Test features

We refer to the biodiversity features that we are trying to represent as test features or test species. We used predictive maps of caribou habitat, songbird densities, and waterfowl densities as test features to evaluate the effectiveness of the four biodiversity surrogates. For caribou, we used a 1-km2 resolution raster map created from a national resource selection function (RSF) model for boreal woodland caribou in Canada. The map was produced by Environment Canada (2011) and quantifies the predicted probability of habitat selection relative to its availability. The national-scale RSF model was developed using animal location data collected by provincial and territorial wildlife departments. Data points from 581 radio-collared caribou distributed among the 27 caribou ranges from 2000 to 2010 were used.

For songbirds and waterfowl, we used a set of raster maps representing the predicted densities of 80 boreal songbirds[[1]](#footnote-1) species and 17 waterfowl species. The maps were developed using boosted regression trees to model the relationship between each species and several biophysical, climate, and ecological variables that were available consistently across the boreal region (Barker et al. 2014, Stralberg et al. 2015). We used map-based predictions rather than the underlying survey data to evaluate test features because, unlike the original data, the maps use bird-habitat relationships to estimate density across the entire region of interest. They are also robust to differences in the variety of field survey methods used across the boreal (Solymos et al. 2013). Moreover, the survey data coverage is not sufficient for the scale of analysis and rarely extends into the large, intact wilderness areas where many of our benchmark networks were identified. Songbird maps were clipped to the species known range boundary (Cornell Lab of Ornithology 2019).

We evaluated two groups of songbird species (AllBirds and ForestBirds), as well as 11 songbird species that were selected in consultation with partner organizations and external experts based on several criteria including threat status, vulnerability to future landscape change, geographic distribution, biology, social/cultural importance, and relevance to forestry (Table 2, Appendix S1). Collectively, these 11 species represent a range of broad habitat types. For AllBirds, we calculated a composite metric by summing all individual songbird densities to create a map showing overall density for 80 species. ForestBirds is also a summed composite metric For waterfowl, we evaluated four metrics, one consisting of all waterfowl species (AllWaterfowl) and three guilds: cavity nesters (CavityNesters), ground nesters (GroundNesters), and above water nesters (OverwaterNesters). The composition of species in each guild is listed in Table 2. For each of the four metrics, we summed individual waterfowl densities to create a map showing the overall density for the species belonging to each guild or, in the case of AllWaterfowl, all 17 waterfowl species.

**Measuring Representation**

<maybe add section here that speaks to how we measure representation??>

## Benchmarks networks

To evaluate the effectiveness of the four environmental features to represent the test features, we used ecological benchmark networks as spatial units. For each ecoregion, we generated a set of potential benchmark areas based on the fundamental properties of size, intactness, and connectivity (Lisgo et al. in prep). Benchmarks were sufficiently large to maintain all flammable vegetation types under the regional fire regime according to Leroux et al.’s (2007) minimum dynamic reserve (MDR) approach (Appendix Sx). Benchmarks were designed to be intact so that ecological processes were operating with minimal human interference. Intactness was measured using GFWC’s (2014) Human Access dataset. To simultaneously address terrestrial and hydrologic connectivity, we used Benchmark Builder software (BEACONs 2017) to assemble catchments along stream networks until the MDR-based area target for the ecoregion was reached. Only catchments with a minimum intactness of 80% were included in the analysis. While Benchmark Builder constructs benchmarks to be hydrologically connected, the ecological framework of Canada does not conform to hydrologic boundaries. As such, we constructed benchmarks for the ecoregion plus its intersecting fundamental drainage areas (FDA; NRCAN 2009). All benchmark construction began with headwater catchments located within the ecoregion, but benchmarks were permitted to grow into surrounding FDAs to preserve hydrologic connectivity.

For each ecoregion, we identified benchmark networks that were representative and non-representative of the four biodiversity surrogates. We first determined the minimum number of benchmarks required in each ecoregion to identify a representative network using MDR-based representation targets and dissimilarity metrics as described in Appendix S1. Once the minimum number of benchmarks was determined, we identified all possible networks of that size, regardless of representation quality, and removed highly overlapping networks to minimize redundancy in the network sample (Appendix S2). We then selected subsets of representative networks and non-representative networks, up to a maximum of 500 networks in each set (Table 1). Representative networks met all MDR-based representation targets and had dissimilarity metrics ≤ 0.2 for all four biodiversity surrogates, while non-representative networks had dissimilarity metrics > 0.2 (see following section). statistics

## Relationship between species and surrogates

For each ecoregion, we developed multiple linear regression models to evaluate the relationship between the representativeness of each test species or species group and the representativeness of the four environmental surrogates within benchmark networks. We quantified representation using KS and BC dissimilarity metrics for the four surrogates (Figure 2) and the KS statistic for test species or species group. For the dissimilarity metrics, the ecoregion served as the reference area. Based on a simple power analysis, we only included ecoregions that had a minimum of 30 networks, with at least 10 representative and 10 non-representative networks (Appendix Sx). The design was not balanced, and we used no more than 10 times as many networks of one network type (i.e., representative vs non-representation, up to a maximum of 500 networks). We developed up to 18 regression models for each ecoregion: AllBirds, ForestBirds, one for each of the 11 songbird species and four waterfowl groups, and caribou. For each model, we related the KS value of the test species (SPP\_KS) to the linear combination of KS and BC values for the predictor variables (CMI\_KS, GPP\_KS, LED\_KS, LCC\_BC):

SPP\_KS = CMI\_KS + GPP\_KS + LED\_KS + LCC\_BC

For each test species, we assessed the fit of the regression models using three statistics: the adjusted R2, the overall F-test, and the Root Mean Square Error (RMSE). The adjusted R2 represents the proportion of total variance that is explained by the model. It is a relative measure of the goodness of fit of the model. The F-test evaluates the null hypothesis that all regression coefficients are equal to zero versus the alternative that at least one is not. A significant F-test indicates that the observed R2 is reliable. The RMSE is the square root of the variance of the residuals. It indicates the absolute fit of the model to the data i.e., how close the observed data points are to the model’s predicted values. In general, a higher R2 value and lower RMSE value indicate better model performance. We evaluated the consistency of the ecoregion-level models within ecozones and across the boreal by calculating their average adjusted R2 values as well as the proportion of models that were considered to be moderate or strong. For the latter, we chose a cut-off of 0.2, although we recognize that other values could be used. We also report the absolute value of the *t*-statistic for each model parameter as an estimate of the contribution of each variable to the model i.e., variable importance (Kuhn and Johnson 2013). All analyses were carried out using R v. 3.7.1 (R Development Core Team 2019). As a final step, we evaluated the influence of five ecoregion-level factors on the strength of the relationship between test species and surrogates: ecozone membership, ecoregion intactness, mean network size as approximated by MDR, mean species density, and species density coefficient of variation (CV) for all species and groups of species except for Caribou. For Caribou, we evaluated mean and CV of habitat quality instead of density.

In the Supplementary Information, we provide a case study and example code for running the evaluation of representativeness. We also include an additional analysis of representation which allows for a comparison of the two approaches. For this latter analysis, we evaluated representation using the area-adjusted proportion of the species population or core habitat within the network. This is measured as the ratio of the proportion of population (or core habitat) within a network to the proportion of the ecoregion that is in the network. A ratio near 1 indicates that the network contains a representative proportion of the population, based on its relative area to the ecoregion. Values below 1 would indicate a lower potential proportion of the population. This approach is in contrast to the representativeness analysis which evaluates the ability of surrogates to capture the full distribution of test features for each of the test species.

# Results

A sufficient number of representative and non-representative networks were identified to develop multiple regression models for 48 of XX boreal ecoregions (add figure highlighting the 48 ecoregions, or add to an existing figure). A total of 662 multiple regression models were developed (test species x ecoregion), of which 634 were significant based on an F-test (Bonferroni corrected p-value ≤ 0.0001). In general, there was a moderate to strong positive linear relationship (adjusted R2 > 0.2) between the representativeness of test species and the representativeness of the four surrogates for 79% of models, with the strongest relationships in the Boreal Shield and Taiga Plains ecozones <insert Figure X (see below) > (Table 3; supp info). ~~CMI and LCC were the most important surrogates across all test species in 204 regression models each and for songbird species for 154 and 141 of 470 models, respectively (Table 4; supp info). In contrast, LED was the most important variable for waterfowl (64 of 192 models) and least important for songbirds (11% of models).~~

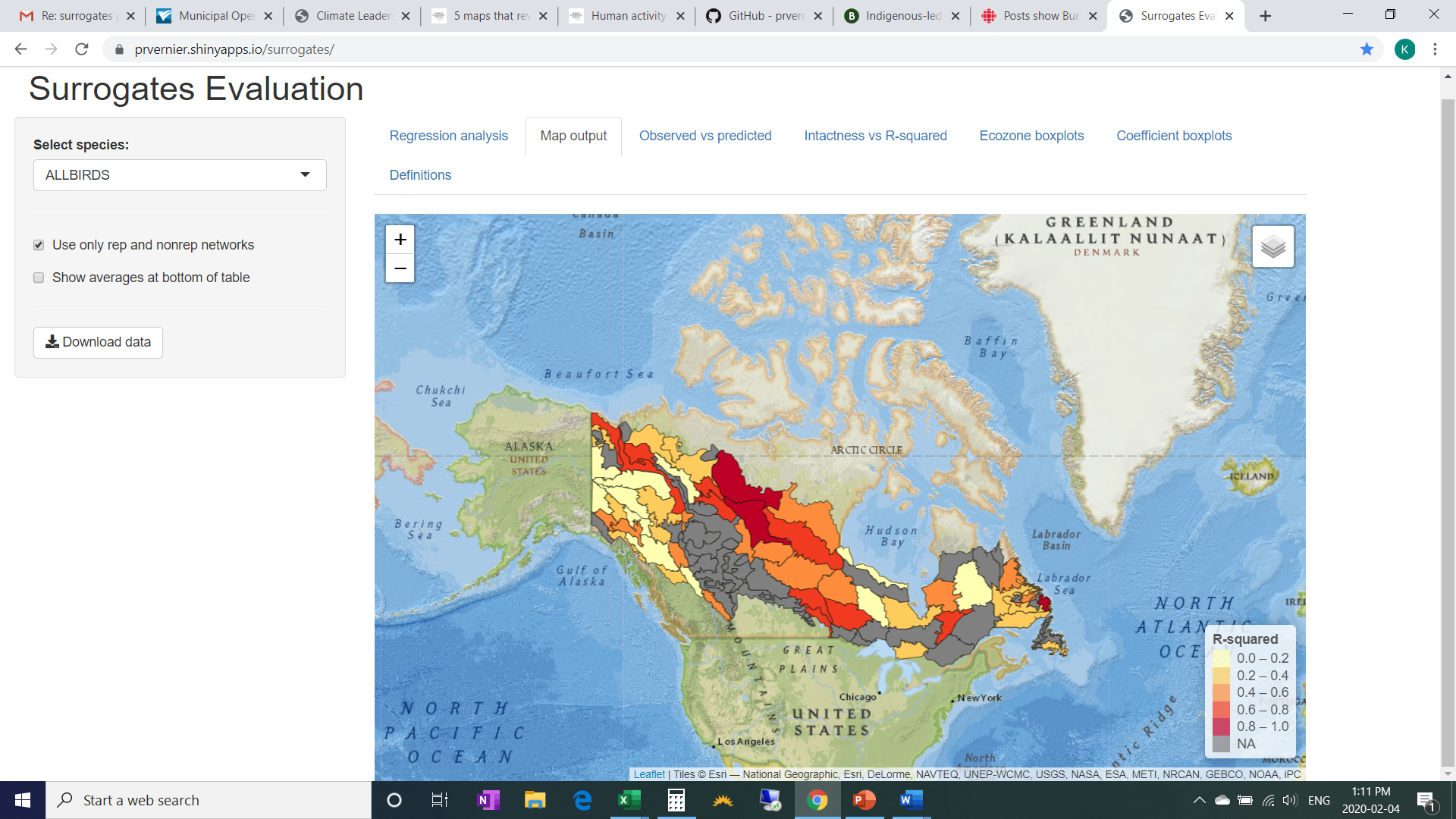


Figure X. Add ecozones, change R-squared to mean adjusted R-squared.

**Tables 3 & 4**

**Individual Songbirds**

The number of individual species per ecoregion varied across the boreal, ranging from X to Y (median = Z; Table 2). On average, the strength of the relationship between individual species and surrogates across all ecoregions was moderate to strong?, ranging from a mean adjusted R2 of 0.38 for Olive-sided Flycatcher to 0.66 for Blackburnian Warbler (Table 3; supp info). In particular, the relationship was strongest for the four warbler species: BTGN, CAWA, etc.. Across all species, the relationship was moderate to strong in 79% of the ecoregions. The strength of the relationship was moderate to strong for over 60% of the ecoregions for all test species, ranging from 64% for the Olive-sided Flycatcher to 100% for Black-throated Green Warbler and Canada Warbler. Twelve of the 18 test species had moderate to strong relationships in at least 75% of the ecoregions in which they occurred. In general, the relationship between surrogates and individual species was relatively strong, with only one species, Olive-sided Flycatcher, having an average adjusted R2 value less than 0.44. Several other species (Boreal Chickadee, Brown Creeper, Swainson’s Thrush, Pine Grosbeak, and White-winged Crossbill) also had relatively moderate to strong relationships in at least 75% of the ecoregions in which they occurred. The average strength of their relationship with surrogates was also relatively high, ranging between 0.45 for White-winged Crossbill to 0.54 for Swainson’s Thrush. Olive-sided Flycatcher had the lowest overall mean model strength (adjusted R2 = 0.38) and the lowest proportion of ecoregions with moderate to strong relationships (64%). It had weak relationships (adjusted R2 < 0.2) in the 14 of 39 ecoregions, with most of these located in the western boreal ecoregions, specifically those located in Taiga Cordillera, Boreal Cordillera, and Montane Cordillera ecozones. At the ecozone level, the Taiga Plains and Boreal Shield A ecozones had the highest average model strength across individual species, with mean adjusted R2 values of 0.58 and 0.57, respectively. At the ecoregion-level, however, for all songbird species, there was large variability in model strength across ecoregions. Among surrogates, CMI and GPP were consistently the most important surrogate across all songbird species, being most important in 127 and 107 models, respectively (Table 4; supp info). In contrast, LED was the most important surrogate in only 10% of the models (36 out of 344 test species x ecoregion models).

I think a figure would also be helpful here … colour ecoregions by % number of species with R2 >0.X.

**Songbird groups**

The patterns for the two songbird groups, AllBirds and ForestBirds, were quite similar due to the number of common species in both groups. Surrogate models were developed for both groups in all 48 ecoregions with representative and non-representative networks. The relationship between representativeness of AllBirds and ForestBirds and representativeness of surrogates was significant, positive and linear in all cases except for ecoregion 183 for ForestBirds where there was no relationship. The relationship between surrogates and AllBirds and ForestBirds was weaker than for individual species on average, but still moderate to strong in 75% and 81% of the 48 ecoregions, respectively (Table 3; supp info). Similarly, the average strength of the relationship was slightly higher for ForestBirds (adjusted R2=0.44) in comparison to AllBirds (adjusted R2=0.41), varying from 0.0 in ecoregion 183 to 0.90 in ecoregion 69 for ForestBirds and from 0.02 in ecoregion 168 to 0.89 in ecoregion 69 for AllBirds. Most ecozones had fairly consistent results for both groups of birds with the exception of those in the Boreal Cordillera where only 4 of 9 ecoregions had moderate to strong models. Model uncertainty, as measured by RMSE, was relatively low and consistent across the boreal ecoregions, ranging between 0.04 to 0.15 for AllBirds and 0.04 to 0.14 for ForestBirds. Overall, the most important surrogate for the AllBirds models was LCC (16 ecoregions) followed by CMI and GPP (13 and 12 ecoregions, respectively) (Table 4; supp info). Similarly, the most important surrogate for ForestBirds was GPP (18 ecoregions) followed by CMI and LCC (14 and 12 ecoregions, respectively). For both AllBirds and ForestBirds, LED was the most important surrogate for only 7 and 4 ecoregions, respectively.

**Waterfowl guilds**

The relationship between representativeness of waterfowl groups and representativeness of surrogates was significant, linear and positive with 3 exceptions where there was no relationship: ecoregions 59 and 183 for OverwaterNesters and ecoregion 183 for AllWaterfowl. The mean strength of the models was similar among the four guilds, ranging from 0.37 for GroundNesters and 0.43 for CavityNesters (Table 3; supp info). However, for all guilds, there was a very large variation across ecoregions. The majority of the models (135 out of 192) had a moderate to strong relationship. Among waterfowl groups, CavityNesters and AllWaterfowl had moderate to strong relationships in 73% and 75% of the ecoregions, respectively. For the other two guilds, OverwaterNesters and GroundNesters, the numbers were slightly lower, with 69% and 65% of ecoregions having moderate to strong relationships. Average model adjusted R2 varied between 0.43 for CavityNesters to 0.37 for GroundNesters. Four ecozones, the Taiga Plains, the Boreal Shield A, the Taiga Cordillera and the Boreal Cordillera, had similar means and ranges of adjusted R2 values (0.39 to 0.44). The Boreal Plains ecozone, with only one ecoregion had the highest average adjusted R2 value (0.61) among the four groups. Model uncertainty, as measured by RMSE, was also relatively low and very consistent among the four waterfowl groups with the average lowest values ranging between 0.02 and 0.03 and average highest values ranging between 0.14 and 0.16. In contrast to the other taxa, LED was the most important surrogate in 38% of all waterfowl models (Table 3; supp info). This was followed by GPP and LCC which were most important in 30% and 23% of all models. CMI was the most important surrogate in only 15 of the 164 waterfowl models (9%).

**Caribou**

Caribou-surrogate models were developed for 30 ecoregions that were located within predicted boreal caribou habitat and which had representative and non-representative networks. With the exception of ecoregion 70, the relationship between representativeness of caribou habitat and surrogates was significant, positive and linear (Table 3; supp info). The mean strength of the models was 0.42, varying from 0.02 in ecoregion 74 to 0.97 in ecoregion 94. The majority of the models (23 out of 30) had a moderate to strong relationship, with five of them explaining >75% of the variation in surrogate KS values. The Taiga Plains and Boreal Shield A ecozones had the highest consistency in model strength with 6 of 7 and 9 of 10 ecoregions having models with adjusted R2 > 0.2, respectively. Model strength in the Boreal Plains was also very high (adjusted R2 = 0.79), but this ecozone was only represented by one of 6 ecoregions for which representative and non-representative networks could be developed. Model uncertainty, as measured by RMSE, was relatively lower and more consistent within the ecoregions of the Taiga Plains and Boreal Shield A ecozones. Overall, the most important surrogate for the caribou models was GPP (13 ecoregions) followed by CMI and LCC (7 ecoregions each) (Table 4; supp info). In contrast, LED was the most important surrogate for only 3 ecoregions.

**Influence of covariates**

We evaluated the influence of five factors on the strength of the relationship between test species and surrogates and found few patterns. Species density had a moderate but negative influence on the strength of the Blackburnian Warbler and Canada Warbler models. Ecoregion intactness had a moderate negative and positive influence on the strength of the Caribou and Blackburnian Warbler models, respectively. Ecozone membership also had a moderate influence on two species, Black-throated Green Warbler and Cape May Warbler. Density CV and network size, as approximated by MDR, had no influence on any of the relationships. For songbird and waterfowl groups, there were no evident patterns between model strengths and any of the four ecoregion-level factors.

**Shiny app**

In this study we develop 662 multiple linear regression models between test species and environmental surrogates. Due to the large amount of resultant model output, we developed a Shiny app to enable readers and conservation planners in the boreal region to explore the results of the analysis and identify species and ecoregion combinations that are adequately or inadequately represented by benchmark networks selected using surrogates of large-scale environmental variation. The Supporting Information provides instructions on how to run the app from a local machine and also provides summary tables with all input data used in the analyses and the app.

# Discussion

The use of biodiversity surrogates is an important part of systematic conservation planning and, specifically, the identification and selection of conservation areas (Margules and Pressey 2000, Rodrigues and Brooks 2007, Caro 2010, Grantham et al 2010). This is especially true in large remote landscapes with limited field-based information on the distribution and abundance of species, such as the boreal region of Canada. In this study, we evaluated the effectiveness of four environmental surrogates that were recently used to identify ecological benchmark areas for 48 ecoregions occurring in the boreal region (Lisgo et al. *in prep*). Our main focus was on determining if networks designed to be representative of the four surrogates would also be representative of other elements of the regions' biodiversity, specifically boreal caribou, songbirds, and waterfowl.

In general, the relationship between representativeness of test species and representativeness of surrogates was moderate to strong for the majority of the study ecoregions. Moreover, the average strength of the relationships was often stronger for individual songbird species than for groups of songbirds or waterfowl. In particular, results were positive and consistent across ecoregions for the four warbler species that were included in the analysis (Blackburnian Warbler, Black-Throated Warbler, Canada Warbler, and Cape May Warbler). Among other species, the consistency of the relationships varied by species and ecoregions. Results for caribou were restricted to the 30 ecoregions for which habitat was mapped; the effectiveness of surrogates were strongest and most consistent in the Taiga Plains and Boreal Shield ecozones. When the results are viewed across ecoregions, several ecoregions had moderate to strong relationships with all test species while a few ecoregions had moderate to strong relationships with all test species. However, in most ecoregions, there were some weak relationships for at least one of the test species. Conversely, there were only three ecoregions where surrogates were not found to be effective for a majority of test species. The three ecoregions were all located in the western boreal region in the cordillera ecozones. This could be a consequence of lower densities for a number of boreal species that are at the periphery of their distributions in the cordillera. Overall, the consistency of results across ecoregions and test species is encouraging and provides some evidence for the effectiveness of the four surrogates in the boreal region.

In this study, the main focus was on evaluating the four environmental surrogates together rather individually. However, the regression approach we used also permitted us to rank the surrogates in terms of their importance for different species and taxa. Among the four surrogates, Climate Moisture Index and Gross Primary Productivity were the most important for individual and groups of songbird species. Conversely, Lake Edge Density stood out as being the least important surrogate. In contrast, for the waterfowl guilds, Lake Edge Density and Gross Primary Productivity were the most important surrogates. The contrasting importance of Lake Edge Density between songbirds and waterfowl provides an important reminder of the importance of using multiple surrogates in conservation planning. For Caribou, the most and least important surrogate were Gross Primary Productivity and Lake Edge Density, respectively.

The variation in the effectiveness of surrogates between ecoregions and test species suggest that there might be some factors that may explain why test species vary in their responses between ecoregions and within ecozones. We evaluated five possible factors including ecozone membership, ecoregion intactness, network size, species density, and the coefficient of variation of species density. None of the factors had an important influence on the strength of models for songbird and waterfowl groups while, among the individual species, three of the five factors had a minor influence on the four warbler species and Caribou models. The strength of the Black-throated and Cape May Warblers varied with ecozone membership, with the boreal shield ecozone having the strongest models for both species, coinciding largely with the core of their breeding range. In the case of species density, the influence was negative on both Blackburnian and Canada Warbler. Similarly, habitat quality had a small but negative influence on the Caribou model. For intactness, the influence was positive for Blackburnian Warbler and negative for Caribou. However, in both cases, this was likely caused by a statistical artifact due to the influence of one outlier ecoregion in the boreal shield ecozone.

There are relatively few evaluations of studies using environmental surrogates and, among those, differences in methods, scale, region and indicators make comparisons and generalizations difficult. In general, among studies that have evaluated environmental surrogates by themselves or in conjunction with surrogate species, the results have varied. Several recent studies have evaluated environmental surrogates using attributes such as physiographic features or land types (e.g. Lombard et al. 2003, Oliver et al. 2004), climatic variables (e.g. Sarkar et al. 2005, Hanson et al. 2017), and more recently, a combination of variables defined in multivariate space (e.g. Beier and Albuquerque 2015, Albuquerque and Beier 2018). Some studies have suggested that environmental surrogates can be effective on their own or in conjunction with surrogate species to enhance reserve selection and conservation planning (Carmel and Stroller-Cavari 2006, Carvalho et al. 2011, Lindenmayer et al. 2014, Di Minin and Moilanen 2014). In contrast, other studies indicate that environmental surrogates are not effective indicators of species diversity (Araujo et al. 2001, Rodrigues and Brooks 2007, Januchowski-Hartley et al. 2011). However, differences in the set of surrogates used in each study makes comparisons of the importance of specific surrogates difficult. Consequently, there are no generally agreed upon set of environmental surrogates that best represent other elements of biodiversity. This is exacerbated by the growing number of large-scale environmental surrogates that are being developed as remote sensing data becomes increasingly accessible to researchers e.g., Dynamic Habitat Indices (Radeloff et al. 2019). In general, the overall effectiveness of using surrogates such as productivity, land cover, or other physical conditions for conservation planning may depend in large part on scale, geographic region and the species that are targeted for conservation (Ferrier and Watson 1997, Grantham et al. 2010, McArthur et al. 2010, Carvalho et al. 2011, Lindenmayer et al. 2014). Our study contributes to this growing literature and supports the idea that environmental surrogates are effective for conservation planning in the boreal region of Canada.

Similarly, there are no generally agreed upon methods for evaluating surrogates (Rodrigues and Brooks 2007, Caro 2010). Because of the largely intact nature of our study region, our focus was on assessing representativeness as opposed to maximizing representation of selected species (*sensu* Kukkala and Moilanen 2013). Essentially, we wanted to evaluate whether our surrogates were effective at identifying conservation areas that also represented the range of habitat conditions and species densities that occur in the boreal region. To achieve this, we used a reserve selection approach to evaluate if networks comprised of ecological benchmarks that are representative of four environmental surrogates are also representative of boreal caribou, songbirds, and waterfowl. Our choice of using the Kolmogorov–Smirnov (KS) statistic as a measure of representativeness was based on using a simple approach that uses the full range of habitat quality of species density for our analysis. Other surrogacy tests seem to focus on species richness or meeting abundance targets with the assumption that high environmental diversity will lead to high biodiversity by creating lots of habitat types. In our study, we are prioritizing benchmarks that have the same distribution of habitat quality of species density as the ecoregion. The focus is thus on maintaining representativeness of relatively intact landscapes rather than maximizing representation for selected species. In our view, both approaches are valid, with the former approach beneficial in large relatively intact landscapes and the latter approach being complementary but more suited to targeting reserves for species at risk.

We demonstrated both approaches using a case study for one ecoregion in the central boreal region (Supp Info). Based on those results, it seems that adequate representation and representativeness can be achieved for the case study test species (Boreal Chickadee, Cape May Warbler, Rusty Blackbird, and Caribou) but that the same networks don’t necessarily maximize both measures at the same time i.e., networks that maximize representation are not necessarily the same ones that maximize representativeness, and vice versa. So, if the objective was to maximize representation of high quality habitat for a species of concern, a supplementary representation analysis would be advised, with additional networks selected. Although it is encouraging that surrogates are effective using both approaches, this is based on one ecoregion and four test species. A larger scale analysis would be required to determine if this was the case for other species and ecoregions in the boreal region. Although simple to apply for one species, an approach which attempts to maximize representation based on species’ habitat would become increasingly complex with the consideration of additional species of concern. In general, the two approaches are complementary. The representativeness analysis that we applied in this study is a coarse filter approach that is more efficient and effective for representing numerous elements of biodiversity concurrently (*sensu* coarse filter) whereas the representation analysis is more of a fine filter approach that can be used to address gaps in protection.

Our approach has some limitations, some of which could be addressed in future research. First, we evaluated the effectiveness of surrogates using current predicted species distributions rather than the underlying field survey data. This was done because of the gaps in the distribution of sampling sites across the boreal region. However, future research should consider using actual bird survey data to evaluate effectiveness of benchmark networks, at least for those regions of the boreal where there is sufficient point data. In addition, it would be of interest to use predicted future distributions of habitats and species densities to evaluate effectiveness of benchmark networks under a range of alternative climate change scenarios. Second, our study, like most that evaluate surrogates, is not directly comparable with other studies because of differences in surrogates used, study regions, measures of surrogate effectiveness, and biodiversity features that the surrogates are intended to represent (Grantham et al. 2010). This has hampered the development of general guidelines and best practices for identifying, selecting, and evaluating biodiversity indicators, including environmental surrogates. Third, although the effectiveness of surrogates varied between ecoregions and within ecozones, it is not clear what factors are responsible for this variation. We evaluated the influence of five factors on the strength of the relationship between test species and surrogates and found few significant patterns. In the future, it would be beneficial to explore additional factors at the network- and ecoregion-levels including topography, landscape composition and structure, land use, and natural and anthropogenic disturbance history (Walz 2011, Schindler et al. 2012).

In this study, we evaluated the effectiveness of four environmental surrogates that were recently used to identify representative ecological benchmarks in the boreal region. Benchmarks were first built based on best practices for ensuring intactness, size and hydrologic connectivity (Lisgo et al. *in prep*). Networks of benchmarks were then ranked in terms of ecological representation using the four surrogates. From the large pool of benchmark networks assembled, representative and non-representative networks were selected and used in the evaluation. Our results suggest that, in general, networks of ecological benchmarks that are selected for high levels of surrogate representation, are also effective at representing caribou, songbirds, and waterfowl in the boreal region. The approach thus lends itself well to the design of an effective conservation network that is representative of a regions' biodiversity. Moreover, the use of map-based surrogates that are representative of other elements of biodiversity greatly facilitates large-scale conservation planning in a cost-effective way across remote areas with many information gaps such as the boreal region of Canada.

# Acknowledgements

# Supporting Information

Additional material is available at <https://github.com/prvernier/surrogates>:

* Appendices S1 and S2 - Construction and filtering of benchmark networks.
* Table S1. Common and scientific names of test species.
* Table S2. Summary of multiple linear regression models relating surrogates KS values to species KS values for all ecoregions with representative and non-representative networks in the boreal region of Canada.
* Case study demonstrating the difference between evaluating representativeness and representation in one ecoregion.
* Shiny app for exploring the results in more detail.

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# Tables

**Table 1.** Number of representative and non-representative benchmark networks in each ecoregion used in the evaluation of surrogates within the ecozones of the boreal region of Canada. Criteria used to differentiate representative and non-representative networks are described in the methods section. Networks were also filtered to reduce spatial overlap. The number of ecoregions used in the analysis varied by species based on the extent of their ranges.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Ecozone | Ecoregion | Area (km2) | MDR (km2) | Intactness | Rep networks | Non-rep networks |
| Taiga Plains | 51 | 60,678 | 23,713 | 0.957 | 49 | 192 |
|  | 52 | 108,362 | 2,534 | 0.959 | 357 | 141 |
|  | 53 | 30,405 | 10,592 | 0.875 | 76 | 500 |
|  | 55 | 42,575 | 1,075 | 0.917 | 21 | 145 |
|  | 59 | 27,249 | 1,015 | 0.995 | 500 | 152 |
|  | 60 | 44,429 | 7,191 | 0.976 | 470 | 93 |
|  | 62 | 13,607 | 1,909 | 0.890 | 41 | 80 |
| Taiga Shield | 68 | 136,899 | 841 | 0.998 | 233 | 208 |
|  | 69 | 119,383 | 8,281 | 0.987 | 500 | 500 |
|  | 70 | 180,498 | 2,396 | 1.000 | 500 | 129 |
|  | 71 | 197,117 | 4,225 | 0.996 | 500 | 167 |
|  | 72 | 124,365 | 8,551 | 0.900 | 500 | 210 |
|  | 74 | 187,073 | 1,089 | 0.948 | 500 | 173 |
|  | 77 | 71,274 | 1,299 | 0.988 | 500 | 398 |
|  | 78 | 86,308 | 1,369 | 0.853 | 500 | 365 |
|  | 80 | 56,605 | 272 | 0.981 | 69 | 419 |
| Boreal Shield A | 87 | 78,046 | 7,838 | 0.968 | 121 | 36 |
|  | 88 | 195,469 | 5,041 | 0.950 | 500 | 29 |
|  | 89 | 142,030 | 5,929 | 0.935 | 500 | 28 |
|  | 90 | 146,924 | 3,516 | 0.861 | 500 | 101 |
|  | 94 | 81,673 | 736 | 0.545 | 251 | 500 |
|  | 95 | 110,849 | 2,809 | 0.962 | 500 | 109 |
|  | 100 | 91,993 | 3,040 | 0.745 | 500 | 500 |
|  | 103 | 98,512 | 1,003 | 0.978 | 500 | 78 |
|  | 104 | 19,583 | 3,240 | 0.974 | 26 | 13 |
|  | 105 | 21,350 | 506 | 0.941 | 500 | 305 |
| Boreal Shield B | 108 | 16,027 | 111 | 0.916 | 26 | 500 |
| Boreal Plains | 136 | 51,068 | 10,745 | 0.914 | 31 | 49 |
| Taiga Cordillera | 165 | 26,826 | 5,976 | 0.993 | 151 | 223 |
|  | 166 | 14,651 | 4,236 | 0.976 | 21 | 160 |
|  | 168 | 39,452 | 3,388 | 0.990 | 500 | 18 |
|  | 170 | 87,067 | 529 | 0.996 | 500 | 433 |
|  | 171 | 72,426 | 2,348 | 0.986 | 130 | 320 |
| Boreal Cordillera | 172 | 38,746 | 3,057 | 0.919 | 500 | 26 |
|  | 175 | 26,986 | 1,985 | 0.939 | 500 | 81 |
|  | 176 | 57,428 | 2,401 | 0.944 | 100 | 153 |
|  | 177 | 35,868 | 3,100 | 0.924 | 37 | 61 |
|  | 178 | 35,526 | 614 | 0.969 | 166 | 352 |
|  | 179 | 24,845 | 1,723 | 0.976 | 500 | 127 |
|  | 180 | 105,582 | 569 | 0.968 | 500 | 420 |
|  | 181 | 34,466 | 4,225 | 0.931 | 67 | 500 |
|  | 183 | 37,830 | 1,495 | 0.958 | 31 | 23 |
| Montane Cordillera | 199 | 35,022 | 145 | 0.777 | 12 | 500 |
|  | 200 | 37,064 | 399 | 0.698 | 100 | 10 |
|  | 207 | 39,210 | 279 | 0.863 | 309 | 105 |
| Hudson Plains | 215 | 64,034 | 111 | 0.990 | 265 | 500 |
|  | 216 | 131,100 | 1,432 | 0.992 | 500 | 500 |
|  | 217 | 176,809 | 2,001 | 0.967 | 500 | 234 |

Table 2. Common and scientific names for test features (species) used in the evaluation of surrogates. See Appendix 1 for codes, common names, and scientific names for all species included in the composite indicators.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Group | Code | Common name | Latin name | No. of Ecoregions “where models created” | Average R2 |
| Ungulates | Caribou | Boreal caribou | *Rangifer tarandus* |  |  |
| Songbirds | BLBW | Blackburnian Warbler | *Setophaga fusca* |  |  |
|  | BOCH | Boreal Chickadee | *Poecile hudsonicus* |  |  |
|  | BRCR | Brown Creeper | *Certhia americana* |  |  |
|  | BTNW | Black-throated Green Warbler | *Setophaga virens* |  |  |
|  | CAWA | Canada Warbler | *Cardellina canadensis* |  |  |
|  | CMWA | Cape May Warbler | *Setophaga tigrina* |  |  |
|  | OSFL | Olive-sided Flycatcher | *Contopus cooperi* |  |  |
|  | PIGR | Pine Grosbeak | *Pinicola enucleator* |  |  |
|  | RUBL | Red-winged Blackbird | *Agelaius phoeniceus* |  |  |
|  | SWTH | Swainson's Thrush | *Catharus ustulatus* |  |  |
|  | WWCR | White-winged Crossbill | *Loxia leucoptera* |  |  |
|  | ForestBirds | All forest birds | 53 species |  |  |
|  | AllBirds | All birds | 80 species |  |  |
| Waterfowl | CavityNesters | Cavity nesting waterfowl | 6 species |  |  |
|  | GroundNesters | Ground nesting waterfowl | 11 species |  |  |
|  | OverwaterNesters | Overwater nesting waterfowl | 6 species |  |  |
|  | AllWaterfowl | All waterfowl | 23 species |  |  |

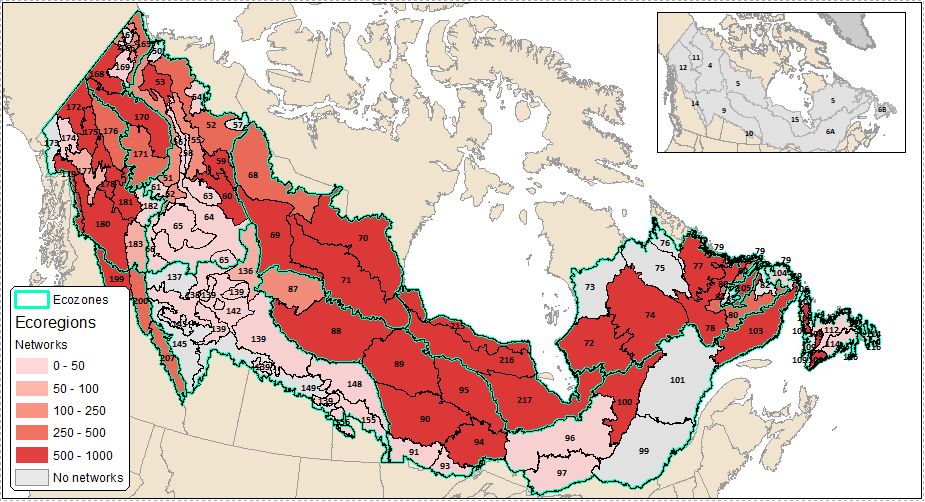
**Table 3.** Summary of ecoregion-level regression models relating species KS to surrogates for All Birds, Forest Birds, Caribou, and 11 individual bird species. N is the #of ecoregions where a model was created? () indicates the number of ecoregions with R2>0.X. Ecoregions and Nets indicates the number of ecoregions and networks, respectively, that were used in each ecozone/test species’ model. For each of the four surrogates, we provide the coefficients and *t*-statistic as an estimate of the contribution of each variable to the model; bold coefficients indicate the most important surrogate for a particular species/ecozone model.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Species | N | CMI | GPP | LED | LCC | Mean? R2 | RMSE |
| CARIBOU | 30 () | 0.01 (-0.53-0.72) | 0.32 (-0.82-1.60) | 0.05 (-1.16-0.89) | 0.08 (-1.43-1.18) | 0.42 (-0.11-0.96) | 0.07 (0.01-0.12) |
| blbw | 6 | 0.45 (0.20-0.95) | 0.53 (-0.01-1.04) | -0.03 (-0.37-0.10) | -0.08 (-1.63-0.61) | 0.66 (0.19-0.92) | 0.06 (0.04-0.09) |
| boch | 48 | 0.19 (-0.68-1.00) | 0.25 (-0.85-1.78) | 0.09 (-0.88-2.31) | 0.23 (-0.67-1.03) | 0.47 (0.03-0.89) | 0.09 (0.03-0.14) |
| brcr | 20 | 0.21 (-0.27-0.84) | 0.34 (-0.69-1.58) | 0.09 (-0.34-0.87) | 0.20 (-0.40-1.35) | 0.45 (0.02-0.78) | 0.08 (0.06-0.12) |
| btnw | 16 (16) | 0.28 (-0.37-0.92) | 0.57 (-0.15-1.43) | -0.06 (-0.94-0.99) | 0.08 (-1.03-1.09) | 0.58 (0.23-0.95) | 0.07 (0.04-0.11) |
| cawa | 10 (10) | 0.27 (0.11-0.43) | 0.49 (-0.26-1.03) | 0.10 (-0.42-0.56) | 0.04 (-1.24-0.94) | 0.57 (0.24-0.98) | 0.07 (0.02-0.12) |
| cmwa | 15 | 0.22 (-0.20-0.93) | 0.36 (-0.47-1.31) | 0.12 (-0.26-0.66) | 0.22 (-0.27-1.36) | 0.52 (0.02-0.91) | 0.08 (0.05-0.13) |
| osfl | 39 | 0.22 (-0.53-1.11) | 0.20 (-2.57-1.30) | 0.09 (-0.88-1.59) | 0.05 (-1.29-0.78) | 0.38 (0.01-0.95) | 0.08 (0.03-0.15) |
| pigr | 48 | 0.27 (-0.39-1.19) | 0.28 (-0.38-1.43) | -0.02 (-1.29-1.10) | 0.09 (-1.52-1.63) | 0.48 (0.04-0.97) | 0.07 (0.02-0.14) |
| rubl | 48 | 0.17 (-0.74-1.01) | 0.27 (-1.14-1.50) | 0.05 (-0.66-0.83) | 0.17 (-0.68-2.22) | 0.45 (0.01-0.95) | 0.08 (0.03-0.14) |
| swth | 46 | 0.29 (-1.08-1.26) | 0.18 (-0.70-1.42) | 0.02 (-0.83-1.72) | 0.39 (-0.52-1.45) | 0.54 (0.06-0.97) | 0.08 (0.02-0.14) |
| wwcr | 48 | 0.20 (-1.05-1.24) | 0.29 (-0.93-2.11) | 0.03 (-0.82-1.79) | 0.12 (-2.65-1.25) | 0.44 (0.02-0.91) | 0.08 (0.04-0.14) |
| ForestBirds | 48 | 0.10 (-1.02-0.65) | 0.33 (-0.89-2.04) | 0.05 (-1.72-2.67) | 0.19 (-1.26-1.36) | 0.44 (-0.00-0.90) | 0.09 (0.04-0.14) |
| AllBirds | 48 | 0.12 (-0.79-1.09) | 0.23 (-1.26-1.51) | 0.06 (-2.58-2.44) | 0.21 (-1.46-1.76) | 0.41 (0.02-0.89) | 0.08 (0.04-0.14) |
| CavityNesters | 48 | 0.08 (-0.47-0.67) | -0.05 (-1.26-0.59) | 0.29 (-1.21-1.33) | 0.30 (-0.58-1.72) | 0.43 (0.02-0.88) | 0.07 (0.03-0.15) |
| GroundNesters | 48 | 0.10 (-0.61-0.69) | 0.21 (-0.78-1.67) | 0.16 (-0.70-1.84) | 0.10 (-0.84-1.80) | 0.37 (0.01-0.96) | 0.09 (0.03-0.15) |
| OverwaterNesters | 48 | 0.16 (-0.41-0.96) | 0.13 (-1.40-1.02) | 0.17 (-0.88-1.40) | 0.06 (-0.90-1.73) | 0.39 (0.00-0.97) | 0.08 (0.02-0.14) |
| AllWaterfowl | 48 | 0.09 (-0.51-0.77) | 0.10 (-0.95-1.56) | 0.29 (-0.46-1.64) | 0.11 (-0.94-1.30) | 0.39 (0.01-0.96) | 0.08 (0.02-0.16) |

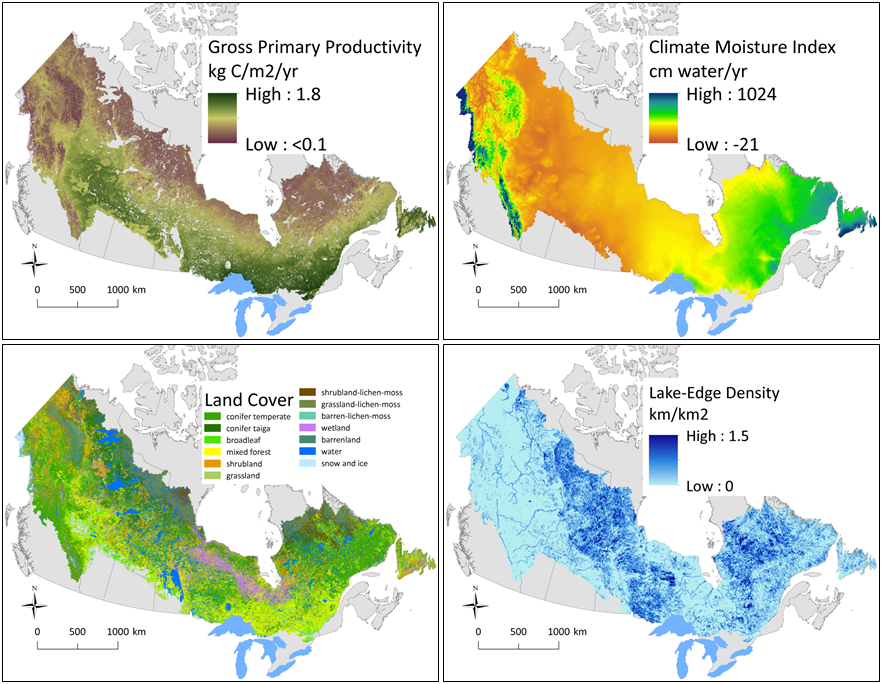
**Table 4.** The number of times CMI, GPP, LED, and LCC was selected as the most important variable, based on the absolute value of the t-statistic in each test feature / ecozone model, for songbirds and waterfowl test features. See Appendix 1 for results for each test feature/ecozone model.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Group** | **Test feature** | **Ecoregions** | **CMI** | **GPP** | **LED** | **LCC** |
| Ungulates | Caribou | 30 | 7 | 13 | 3 | 7 |
| Songbirds | Blackburnian Warbler | 6 | 2 | 2 | 1 | 1 |
|  | Boreal Chickadee | 48 | 20 | 16 | 2 | 10 |
|  | Brown Creeper | 20 | 8 | 6 | 1 | 5 |
|  | Black-throated Green Warbler | 16 | 7 | 5 | 1 | 3 |
|  | Canada Warbler | 10 | 2 | 4 | 2 | 2 |
|  | Cape May Warbler | 15 | 4 | 7 | 3 | 1 |
|  | Olive-sided Flycatcher | 39 | 14 | 16 | 5 | 4 |
|  | Pine Grosbeak | 48 | 19 | 15 | 2 | 12 |
|  | Rusty Blackbird | 48 | 12 | 19 | 8 | 9 |
|  | Swainson’s Thrush | 46 | 21 | 9 | 2 | 14 |
|  | White-winged Crossbill | 48 | 18 | 8 | 9 | 13 |
|  | Sub-total (songbird species) |  | 127 | 107 | 36 | 74 |
|  | ForestBirds group | 48 | 14 | 18 | 4 | 12 |
|  | AllBirds group | 48 | 13 | 16 | 7 | 12 |
|  | Sub-total (songbird groups) |  | 27 | 34 | 11 | 24 |
| Waterfowl | CavityNesters guild | 48 | 6 | 7 | 19 | 16 |
|  | GroundNesters guild | 48 | 10 | 17 | 14 | 7 |
|  | OverwaterNesters guild | 48 | 16 | 14 | 14 | 4 |
|  | AllWaterfowl guild | 48 | 11 | 12 | 15 | 10 |
|  | Sub-total (waterfowl) |  | 43 | 50 | 62 | 37 |
| All species | Total |  | 204 | 204 | 112 | 142 |

# Figures



**Figure 1.** The boreal region of Canada was stratified into XX ecoregions (black outlines) using the National Ecological Framework for Canada (Marshall et al. 1999). The number of networks meeting size and intactness criteria by ecoregion are indicated by the value in the centre of the polygon as well as the shading of the polygon i.e., increasing shades of grey indicates higher number of networks. Inset map displays forested ecozones of the boreal region: Taiga Plains (4), Taiga Shield (5), Boreal Shield A (6A), Boreal Shield B (6B), Boreal Plains (9), Taiga Cordillera (11), Boreal Cordillera (12), Montane Cordillera (14), Hudson Plains (15).



|  |  |
| --- | --- |
|  |  |

**Figure 2.** Top four maps show the distribution of the four environmental surrogates in the boreal region. From top left to bottom right: Gross Primary Productivity (GPP), Climate Moisture Index (CMI), North America Land Cover 2005 (LCC), and Lake-edge Density (LED). The bottom two maps show the predicted density of Canada Warbler and habitat suitability of boreal caribou.

1. Data and report for songbirds: <https://zenodo.org/search?page=1&size=20&q=Stralberg> [↑](#footnote-ref-1)