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

One key requirement of protected areas designed using systematic conservation planning methods is to be representative of regional biodiversity (Margules and Pressey 2000). However, comprehensive biodiversity data are generally not available, so conservation practitioners often use biodiversity surrogates to assess representation (Caro and O’Doherty 1999, Wiens et al. 2008, Hortal et al. 2009, Urbina-Casanova et al. 2016). This assumes that areas that are 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 such as physiographic features or land cover types (e.g., Lombard et al. 2003, Oliver et al. 2004), continuous 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, providing 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 the biodiversity features that surrogates are intended to represent.

Two general types of tests have been used in recent studies to evaluate biodiversity surrogates: pattern-based and selection-based (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. In contrast, selection-based techniques first use surrogates to select conservation areas and then evaluate how well those same areas represent test features (Grantham et al. 2010, Andrefaut et al. 2012). According to Rodrigues and Brooks (2007), this approach if preferable for conservation planning since it focuses on evaluating the extent to which areas selected for surrogates also 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. These are 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 of which are generally lacking from conservation planning 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 forest (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 wide range of species across the entire Canadian boreal region. This presents an opportunity to integrate surrogacy evaluations within a conservation planning framework, which could be especially useful in the boreal region where access is limited and species data are scarce (Schmiegelow et al. 2012).

There is some confusion around 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 environmental surrogates are also representative of test features, specifically boreal caribou, songbird assemblages, and waterfowl guilds. Our specific objectives are to:

1. Determine if networks representative of surrogates are also representative of test features;
2. Determine if representative networks are more effective than non-representative networks for test features;
3. Evaluate if the relative importance of environmental surrogates varies by test features; and
4. Assess if the relationship between surrogates and test features are influenced by other factors.

We also address representation with a case study of an ecoregion in north-central Canada that identifies benchmark networks that maximize both representation (i.e. extent of occurrence) and representativeness of test features.

# Methods

## Study area

Our study area covers the Canadian boreal forest (Brandt 2013), stratified into 94 ecoregions based on the National Ecological Framework for Canada (Ecological Stratification Working Group 1995; Figure 1). Ecoregions are contiguous 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. Of the 94 ecoregions, benchmark networks were identified for 72, of which 48 contained networks that were considered representative of their ecoregion based on criteria defined below under “Benchmark networks”. In this study, we focus on the 48 ecoregions with representative benchmark networks (Table 1, Appendix 2). Since some ecoregions had few representative networks, we aggregated ecoregion-level networks to Bird Conservation Regions (BCRs), ecologically distinct regions with similar bird communities, habitats, and resource management issues (Bird Studies Canada and NABCI 2014). We dropped the ecoregions from ecozone 14 (montane cordillera) since it only included a small portion of the ecozone and BCR 10.

**Figure 1 & Table 1**

## Biodiversity surrogates

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 classes (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). We removed landcover classes associated with anthropogenic disturbances (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 evaluated the effectiveness of the four biodiversity surrogates using test features comprised of predictive maps of caribou habitat, songbird densities, and waterfowl densities. 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 (Environment Canada 2011). The map 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 used were recorded from 2000 to 2010 from 581 radio-collared caribou distributed among 27 caribou ranges.

For songbirds and waterfowl, we used 4-km2 resolution raster maps representing the predicted densities of 80 boreal songbird[[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.

For songbird species, we evaluated 12 assemblages representing Conservation (N=4), Habitat (N=4), and Migration groups (N=4). The Conservation groups included all species (AllBirds), forest-associated species (ForestBirds), species whose populations are declining (Declining), and species of low conservation concern (LowConcern). The Habitat groups included conifer-associated species (Conifer), deciduous-associated species (Deciduous), mixedwood-associated species (Mixedwood), and grassland-associated species (Grassland). The Migration groups included neotropical migrants (Neotropical), short-distance migrants (ShortDistance), nomadic species (Nomadic), and year-round resident species (Resident). For waterfowl species, we evaluated 4 assemblages: all waterfowl species (AllWaterfowl), cavity nesters (CavityNesters), ground nesters (GroundNesters), and above water nesters (OverwaterNesters). The composition of songbird and waterfowl species in each group is listed in Appendix 2. For each of the 16 assemblages, we summed the density of the individual species to create a map showing the overall density for that assemblage.

## Benchmark networks

We used ecological benchmark networks as spatial units to evaluate the effectiveness of the four environmental surrogates. For each ecoregion, we generated a set of potential benchmark areas based on three criteria: 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. 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 catchment-level 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 then identified benchmark networks that were representative and non-representative of the four environmental surrogates. We first determined the minimum number of benchmarks required in each ecoregion to identify a representative network using MDR-based representation targets (Appendix 1). To apply MDR-based targets, continuous surrogates were converted to classes. MDR‐based targets are calculated by multiplying the MDR for the ecoregion by the proportion of the surrogate class in the ecoregion. Once the minimum number of benchmarks was determined (ranging from 2 benchmarks per network to 4 benchmarks per network), we compiled a complete set of networks using all possible benchmark combinations, and removed highly overlapping networks to minimize redundancy in the network sample (Appendix S1, Table S1). For the resulting networks, dissimilarity metrics were calculated by comparing the surrogates’ distribution in each network to its distribution in the ecoregion. For the three continuous surrogates, GPP, CMI and LED, we used the Kolmogorov-Smirnov (KS) statistic. For LCC, a categorical surrogate, we used the Bray-Curtis statistic. Both statistics range from 0 to 1 and indicate increasing dissimilarity. Representative networks met at least 90% of all MDR-based representation targets and had dissimilarity metrics ≤ 0.2 for all four surrogates, while non-representative networks had dissimilarity metrics > 0.2 for all four surrogates and failed to meet at least 90% of all MDR-based targets. We used a dissimilarity cutoff of 0.2 to filter out networks that met the MDR-based targets but had skewed distributions due to over-representation of a small number of classes. We have found in analyses across boreal Canada and Alaska that networks with dissimilarity values ≤ 0.2 tend to meet most MDR-based targets and have distributions similar to the ecoregion (reference?). Following the analysis, we grouped the benchmark networks into BCR units based on their ecoregion membership (Table 1).

## Effectiveness of surrogates

To achieve our first objective (are networks representative of surrogates also representative of test features), we calculated the KS statistic for each test feature for each representative and non-representative network using the same approach described previously for surrogates i.e., we compared the distribution of test feature values within a network to its distribution within the ecoregion in which it is embedded. We then calculated, for each test feature, the mean and standard deviation of KS values for all representative and non-representative networks within each BCR unit. As with the surrogates, we used a KS values of 0.2 as a cutoff between representative and non-representative networks for a given test feature.

For our second objective (are representative networks more effective than non-representative networks for test features), we calculated the effect size between representative and non-representative networks to determine if representative networks are more effective than non-representative networks for test features. The effect size (Cohen 1988) was calculated as:

ES = (mean of KSrep) – (mean of KSnonrep) / std dev of KS

where “mean of KSrep“ is the mean KS value for representative networks, “mean of KSnonrep“ is the value of the mean dissimilarity metric for non-representative networks, and “std dev of KS” is the pooled standard deviation of KS values for all networks. Following Cohen (1988), we consider effect sizes of 0.2 as small, 0.5 as medium, and 0.8 as large.

For our third objective (does the relative importance of environmental surrogates vary by test feature), we developed a multiple linear regression model to evaluate the relationship between the representativeness of the test feature and the representativeness of the four environmental surrogates within benchmark networks. For each test feature in each BCR, we developed up to 17 regression models for each BCR unit using all representative networks available:

KStest = KSCMI + KSGPP + KSLED + BCLCC

where KStest is the KS value for a given network, KSCMI, KSGPP and KSLED are the KS value for CMI, GPP and LED, and BCLCC is the Bray-Curtis value for LCC. We used the absolute value of the *t*-statistic for each model parameter as an estimate of variable importance (Kuhn and Johnson 2013). We then tabulated the number of times each surrogate was ranked as the top predictor in each BCR unit.

For our fourth objective (is the relationship between surrogates and test features influenced by other factors), we evaluated the influence of five ecoregion-level factors on the strength of the relationship between test species and surrogates: ecoregion membership, ecoregion intactness, mean benchmark size as approximated by MDR size, mean species density, and species density coefficient of variation (CV) for all test features except for Caribou. For Caribou, we evaluated mean and CV of habitat quality instead of density. For each factor, we compared the regression model described in the previous paragraph to a model which also included the factor. We then calculated the AIC statistic for both models to determine if the factor was influential i.e., there was a reduction in the AIC value between models. We did this for all test features and BCR units. All analyses were carried out using R v. 4.0.3 (R Development Core Team 2020).

## Case study

In the Supporting Information, we provide a case study which illustrates a complementary and alternative approach to evaluating representation, one that is based on maximizing representation using the area-adjusted proportion of the species population or core habitat within the network. Using this approach, representation 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

*Objective 1. Networks representative of surrogates are also representative of test features.*

Benchmark networks that were representative of environmental surrogates were also representative of test features for 47 out of 67 test feature-BCR combinations, based on having an average KS threshold value of ≤0.2 (Table 2). Moreover, the remaining 21 test feature-BCR combinations were within only 0.04 units of the KS threshold. Overall, KS values for representative networks across all test features and BCRs were relatively consistent, averaging 0.19 for all test features, ranging from 0.12 to 0.20 for caribou, 0.16 to 0.24 for songbird assemblages, and 0.14 to 0.19 for waterfowl assemblages. This was more consistent than for non-representative networks, where KS values averaged 0.34 overall, ranging from 0.17 to 0.33 for caribou, 0.25 to 0.48 for songbird assemblages, and 0.21 to 0.34 for waterfowl assemblages.

**Tables 2**

*Objective 2. Representative networks are more effective than non-representative networks.*

Representative networks were more effective than non-representative networks for all test features in all BCRs (Table 2). The effect size, measured using Cohen’s *d* was large (d ≥ 0.8) for 58 test feature-BCR combinations, medium (0.5 ≤ d < 0.8) for 7 test features in 3 BCRs (including 4 in BCR6), and small (0.2 ≤ d < 0.5) for ConiferBirds and Caribou in BCR6. In both cases where the effect size was small, it was mainly due to the relatively low KS value for non-representative networks in those BCRs (KS = 0.26 for ConiferBirds, and KS = 0.17 for Caribou). The effect size was large for all test features in BCR 8 and large for all but 2 test features in BCR4 and BCR8. The effect sizes for caribou were small, medium and large for BCR6, BCR7 and BCR8, respectively.

*Objective 3. The relative importance of environmental surrogates varies by test features*

Overall, Landcover and Gross Primary Productivity were consistently the most important surrogate across all test features and BCR units, being most important in 31 and 24 models, respectively (Table 3). In contrast, Climate Moisture Index was the most important surrogate in only 2 of the models and Lake Edge Density in 10 of the models. Among songbird groups, Landcover and Gross Primary Productivity were the most important surrogates in 24 and 17 of the models, respectively. Conversely, Lake Edge Density and Climate Moisture Index were most important in only 5 and 2 models, respectively. ResidentBirds were the only group where only one surrogate, Landcover, was most important across BCRs. Among waterfowl groups, Gross Primary Productivity, Landcover, and Lake Edge Density were almost equal in importance across BCRs while Climate Moisture Index was never selected as the most important variable. Landcover was the most important surrogate for the caribou models in two BCRs and Gross Primary Productivity in the third.

**Tables 3**

*Objective 4.* *The relationship between surrogates and test features are rarely influenced by other factors.*

We found few patterns when we evaluated the influence of five factors on the strength of the relationship between test features and environmental surrogates (Table 4). Across the 67 test feature-BCR models, only 18 were influenced by one of the factors. Ecoregion membership did not influence any of the models. Benchmark size (MDR) and Density coefficient of variation were included in 3 models each, while Ecoregion Intactness and Density were included in 6 models each. Among groups of songbirds, DeciduousBirds was the only group that was affected by 3 of the factors: Benchmark size, Density and Density coefficient of variation. Five of the songbird groups were influenced by two of the factors. The five factors had no influence on the Caribou models and only a minor influence on the waterfowl groups. Among the latter, Benchmark size and Density were found to have a significant effect on the GroundNesters group. None of the five factors had an influence on any of the other waterfowl groups.

**Tables 4**

# Discussion

Our main objective was to evaluate the effectiveness of four environmental surrogates that were recently used to represent biodiversity in systematic conservation planning in the boreal forest of Canada (Bauduin et al. 2020 – add to introduction and remove from here). Our results show that, for the majority of test features and Bird Conservation Regions (BCRs) that we evaluated, benchmark networks that were representative of environmental surrogates were also representative of test features. Moreover, in all cases, representative networks were more effective than non-representative networks, and in most cases the effect size was medium or large. In other words, across all test features and BCRs, no networks that were representative for surrogates performed poorly for test features. Overall, the consistency of results across BCRs and test features is encouraging and provides some evidence for using the four environmental surrogates for conservation planning in the boreal region. This consistency may also help explain why, with few exceptions, the relationship between surrogates and test features were rarely influenced by other ecoregion-level factors (does this need to be explained in more detail?). Although the focus of our study was to evaluate the four environmental surrogates together rather then individually, we also ranked surrogates in terms of their importance for different test features. Among the four surrogates, Land Cover Class and Gross Primary Productivity were most often selected as the top surrogate across all test features. Conversely, CMI was almost never selected as the top surrogate while Lake Edge Density was relatively more important among waterfowl assemblages than other test features. The contrasting importance of Lake Edge Density between songbirds and waterfowl provides an important reminder of the need to use multiple surrogates in conservation planning exercises.

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 (Beier et al. 2015, Engelbrecht et al. 2016). 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.

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 or species density in our analysis. Other surrogacy tests 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 benchmark networks that have the same distribution of habitat quality or species density as in its surrounding 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 features (ConiferBirds, DeciduousBirds, MixedwoodBirds, GrasslandBrids) 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 features. 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 moderately between BCRs, we did not identify any consistent factors responsible for this variation. We evaluated the influence of five factors on the strength of the relationship between test features 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). Finally, we aggregated benchmark networks to BCR units but recognize that the analyses could equally have been conducted at the ecoregion level, albeit with low sample sizes for several ecoregions.

The use of biodiversity surrogates is an important part of systematic conservation planning, including 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 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>:

* Appendix 1. Construction and filtering of benchmark networks.
* Appendix 2. Number of networks by ecoregion.
* Appendix 3. Common and scientific names of for test species along with their assemblage membership(s).
* Case study demonstrating the difference between evaluating representativeness and representation in one ecoregion.

# Literature Cited

Andrew, M.E., M.A. Wulder, and J.A. Cardille. 2014. Protected areas in boreal Canada: a baseline and considerations for the continued development of a representative and effective reserve network. Environmental Reviews 22:135-160.

Arcese, P., and A.R.E. Sinclair. 1997. The role of protected areas as ecological baselines. Journal of Wildlife Management 61:587-602.

Albuquerque, F., and P. Beier. 2018. Improving the use of environmental diversity as a surrogate for

species representation. Ecology and Evolution 8:852-858.

Andrefouet, S., M.A. Hamel, and M. Dalleau. 2012. Distinction between effective pattern-based

and selection-based biodiversity surrogates is essential: caveats for managers. Marine Ecology Progress Series 452:287-295.

Araújo, M. B., C. J. Humphries, P. J. Densham, R. Lampinen, W. J. M. Hagemeijer, A. J. Mitchell-Jones, and J. P. Gasc. 2001. Would environmental diversity be a good surrogate for species diversity? Ecography 24:103–110.

Barker, N. K. S., S. G. Cumming, and M. Darveau. 2014. Models to predict the distribution and abundance of breeding ducks in Canada. Avian Conservation and Ecology 9(2): 7.

http://dx.doi.org/10.5751/ACE-00699-090207

Bauduin S, Cumming SG, St-Laurent M-H, McIntire EJB (2020) Integrating functional connectivity in designing networks of protected areas under climate change: A caribou case-study. PLoS ONE 15(9): e0238821. https://doi.org/10.1371/journal.pone.0238821

BEACONs. 2011. Lake-edge density version 2.0 dataset. Canadian BEACONs Project, University of Alberta, Edmonton, AB.

BEACONs. 2017. Manual Benchmark Builder Version 3.3.15. BEACONs Project, University of Alberta, Edmonton. AB.

Beier, P., and F. Albuquerque 2015. Environmental diversity as a surrogate for species representation. Conservation Biology 29: 1401-1410.

Beier, P., P. Sutcliffe, J. Hjort, D.P. Faith, R.L. Pressey, and F. Alburqurque. 2015. A review of selection-based tests of abiotic surrogates for species representation. Conservation Biology 29(3):668-679.

Bird Studies Canada and NABCI.  2014.  Bird Conservation Regions.  Published by Bird Studies Canada on behalf of the North American Bird Conservation Initiative.   [https://www.birdscanada.org/bird-science/nabci-bird-conservation-regions](https://www.birdscanada.org/bird-science/nabci-bird-conservation-regions/) Accessed:  February 28, 2021.

Brandt J. P., M.D. Flannigan, D.G. Maynard, and I. D. Thompson. 2013. An introduction to Canada’s boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environmental Reviews 226:207–226.

Carmel, Y., and L. Stroller-Cavari. 2006. Comparing environmental and biological surrogates for biodiversity at a local scale. Israel Journal of Ecology and Evolution 52:11–27.

Caro, T.M. and G. O’Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology 13(4):805-814.

Carvalho, S. B., J. C. Brito, E. J. Crespo, and H. P. Possingham. 2011. Incorporating evolutionary processes into conservation planning using species distribution data: a case study with the western Mediterranean herpetofauna. Diversity and Distributions 17:408–421.

CEC. 2013. 2010 Land Cover of North America at 250 meters, Edition 1.0. Commission for Environmental Cooperation, Montréal, QC.

Coristine, L.E., A.L. Jacob, R. Schuster, S.P. Otto, N.E. Baron, N.J. Bennett, S.J. Bittick, C. Dey, B. Favaro, A. Ford, L. Nowlan, D. Orihel, W.J. Palen, J.L. Polfus, D.S. Shiffman, O. Venter, and S. Woodley. 2018. Informing Canada’s commitment to biodiversity conservation: A science-based framework to help guide protected areas designation through Target 1 and beyond. FACETS 3 :531-562.

Cornell Lab of Ornithology. 2019. All About Birds. Cornell Lab of Ornithology, Ithaca, New York. https://www.allaboutbirds.org Accessed: August 8, 2019.

Ecological Stratification Working Group. 1995. A National Ecological Framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa/Hull. Report and national map at 1:7500 000 scale.

Engelbrecht, I., M. Robertson, M. Stolz, and J.W. Joubert. 2016. Biological Conservation 197:171-179.

Environment Canada. 2011. Scientific Assessment to Inform the Identification of Critical Habitat for Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada: 2011 update. Ottawa, Ontario, Canada. 102 pp. plus appendices.

Ferrier, S., and G. Watson. 1997. An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity. Environment Australia, Canberra, Australia.

GFWC. 2014. Human Access of Canada's Landscapes. Global Forest Watch Canada. https://databasin.org/datasets/0c54d369b225471ea7e9f7999ce94cc0

Grantham, H. S., R.L. Pressey, J. Wells, J., and A. J. Beattie. 2010. Effectiveness of biodiversity surrogates for conservation planning: different measures of effectiveness generate a kaleidoscope of variation. PLoS ONE 5(7):e11430.

Hamann A, Wang TL, Spittlehouse DL, Murdock TQ. 2013. A comprehensive, high‐resolution database of historical and projected climate surfaces for Western North America. Bulletin of the American Meteorological Society, 94, 1307–1309.

Hanson, J.O., J.R. Rhodes, C. Riginos, and R.A. Fuller. 2017. Environmental and geographic variables are

effective surrogates for genetic variation in conservation planning. PNAS 114(48):12755-12760.

Hogg, E. H. 1997. Temporal scaling of moisture and the forest – grassland boundary in western Canada. Agriculture and Forest Meteorology 84:115‐122.

Hortal, J., M.B. Araujo, and J. M. Lobo. 2009. Testing the effectiveness of discrete and continuous environmental diversity as a surrogate for species diversity. Ecological Indicators 9(1):138-149.

Januchowski-Hartley, S. R., V. Hermoso, R. L. Pressey, S. Linke, J. Kool, R. G. Pearson, B. J. Pusey, and J. VanDerWal. 2011. Coarse-filter surrogates do not represent freshwater fish diversity at a regional scale in Queensland, Australia. Biological Conservation 144:2499–2511.

Kukkala, A. S., and A. Moilanen. 2013. Core concepts of spatial prioritisation in systematic conservation planning. Biological Reviews 88:443-464. http://dx.doi.org/10.1111/brv.12008

Kuhn, M., and K. Johnson. 2013. Applied Predictive Modeling. Springer

Leroux, S.J., and B. Rayfield. 2014. Methods and tools for addressing natural disturbance dynamics in conservation planning for wilderness areas. Diversity and Distributions 20:258–271.

Leroux, S. J., F.K. Schmiegelow, R.B. Lessard, and S. G. Cumming. 2007. Minimum dynamic reserves: a framework for determining reserve size in ecosystems structured by large disturbances. Biological Conservation 138(3):464-473.

Lindenmayer, D. B., P. S. Barton, P. W. Lane, M. J. Westgate, L. McBurney, D. Blair, P. Gibbons, and G. E. Likens. 2014. An empirical assessment and comparison of species-based and habitat-based surrogates: a case study of forest vertebrates and large old trees. Plos One 9.

Lisgo, K., F. Schmiegelow, S. Leroux, S. Cumming, M. Krawchuk, and P. Vernier. In prep. Benchmarks across the Boreal: Designing large protected areas in one of the World’s remaining wilderness regions.

Lombard, A.T., R.M. Cowling, R.L., Pressey, and A.G. Rebelo. 2003. Effectiveness of land classes as surrogates for species in conservation planning for the Cape Floristic Region. Biological Conservation 112:45-62.

McArthur, M. A., B. P. Brooke, R. Przeslawski, D. A. Ryan, V. L. Lucieer, S. Nichol, A. W. McCallum, C. Mellin, I. D. Cresswell, and L. C. Radke. 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuarine Coastal and Shelf Science 88:21–32.

Margules, C.R., and R.L. Pressey. 2000. Systematic conservation planning. Nature 405(6783):243-253.

Mellin, C., S. Delean, J. Caley, G. Edgar, M. Meekan, R. Pitcher, R. Przeslawski, R., A. Williams, and C. Bradshaw. 2011. Effectiveness of biological surrogates for predicting patterns of marine biodiversity: A global meta-analysis. PLoS ONE 6(6):e20141.

NRCan. 2009. Atlas of Canada 1,000,000 National Frameworks Data, Hydrology Version 6.0: A practical guide to the datasets. Natural Resources Canada, Ottawa, ON. <ftp://ftp.geogratis.gc.ca/pub/nrcan_rncan/archive/vector/framework_cadre/drainage_areas/1M_HYDRO_GUIDE_EN_2009.pdf>

Oliver, I., A. Holmes, J.M. Dangerfield, M. Gillings, A.J. Pik, D.R. Britton, M. Holley, M.E. Montgomery, M. Raison, V. Logan, R.L. Pressey, and A.J. Beatie. 2004. Land systems as surrogates for biodiversity in conservation planning. Ecological Applications 14(2):485-503.

Otto, S.A. (2019, Jan.,7). How to normalize the RMSE [Blog post]. Retrieved from https://www.marinedatascience.co/blog/2019/01/07/normalizing-the-rmse/

Powers, R.P., N.C. Coops, J.L. Morgan, W.A. Wulder, T.A. Nelson, C.R. Drever, and S.G. Cumming. 2012. A remote sensing approach to biodiversity assessment and regionalization of the Canadian boreal forest. Progress in Physical Geography 37(1):36-62.

R Development Core Team. 2019. R: a language and environment for statistical computing. R Foundation

for Statistical Computing, Vienna, Austria.

Radeloff, V. C., M. Dubinin, N. C. Coops, A. Allen, T. M. Brooks, M. Clayton, G. Costa, C. H. Graham, D. Helmers, A. R. Ives, D. Kolesov, A. M. Pidgeon, G. Rapacciuolo, E. Razenkova, N. Suttidate, B. E. Young, L. Zhu, and M. Hobi. 2019. The Dynamic Habitat Indices (DHIs) from MODIS and global biodiversity. Remote Sensing of Environment 222: 204-214

Rodrigues, A. S. L., and T. M. Brooks. 2007. Shortcuts for Biodiversity Conservation Planning: The Effectiveness of Surrogates. Annual Review of Ecology, Evolution, and Systematics 38(1):713-737.

Sarkar, S., J. Justus, T. Fuller, C. Kelley, J. Garson, and M. Mayfield. 2005. Effectiveness of Environmental Surrogates for the Selection of Conservation Area Networks. Conservation Biology 19(3):815-825.

Schindler, S., H. von Wehrden, K. Poirazidis, T. Wrbka, and V. Kati. 2013. Multiscale performance of landscape metrics as indicators of species richness of plants, insects and vertebrates. Ecological Indicators 31:41–48.

Schmiegelow, F. et al. 2012. Predictive tools for the monitoring and assessment of boreal birds in Canada, 2009-2012. Annual Report to Environment Canada by the Boreal Avian Modelling Project.

Schmiegelow, F.K.A., S.G. Cumming, K.A. Lisgo, K.A., S.J. Leroux, and M.A. Krawchuk. 2014. Catalyzing Large Landscape Conservation in Canada’s Boreal Systems: The BEACONs Project Experience, in: Lewitt, J.N. (Ed.), Conservation Catalysts: The Academy as Nature’s Agent. Lincoln Institute of Land Policy, Cambridge Massachusetts, pp. 97–122.

Secretariat of the convention on biological diversity. 2010. COP-10 decision X/2. https://www.cbd.int/decision/cop/?id=12268

Stralberg, D., S.M. Matsuoka, A. Hamann, E.M. Bayne, P. Solymos, F.K.A. Schmiegelow, X. Wang, S.G. Cumming and S.J. Song. 2014. Projecting boreal bird responses to climate change: the signal exceeds the noise. Ecological Applications, 25, 52‐69.

Stralberg, D., S.M. Matsuoka, A. Hamann, E.M. Bayne, P. Sólymos, F.K.A. Schmiegelow, X. Wang, S.G. Cumming, and S.J. Song. 2015. Projecting boreal bird responses to climate change: the signal exceeds the noise. Ecological Applications 25(10):52-69.

Su, J.C., D.M. Debinski, M.E. Jakubauskas, and K. Kindscher. 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. Conservation Biology 18(1):167-173.

Urbina-Casanova, R., F. Leubert, P. Pliscoff, and R. A. Scherson. 2016. Assessing floristic representativeness in the protected areas national system of Chile: are vegetation types a good surrogate for plant species? Environmental Conservation 43:1-9.

Walz, U. 2011. Landscape structure, landscape metrics and biodiversity. Living Reviews in Landscape Research 5:3–35.

Warman, L.D., M. Forsyth, A.R.E. Sinclair, K. Freemark, H.D. Moore, T.W. Barrett, R.L. Pressey, and D. White. 2004. Species distributions, surrogacy, and important conservation regions in Canada. Ecology Letters 7:374-379.

Wiersma, Y.F. 2005. Environmental benchmarks vs. ecological benchmarks for assessment and monitoring in Canada: Is there a difference? Environmental Monitoring and Assessment 100:1-9.

Wiens, J. A., G. D. Hayward, R. S. Holthausen, and M. J. Wisdom. 2008. Using surrogate species and groups for conservation planning and management. Bioscience 58:241–252.

Zhao, M., and S. W. Running. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329:940-943.

# Tables

**Table 1.** Number of representative and non-representative benchmark networks in each Bird Conservation Region (BCR) used in the evaluation of surrogates. Criteria used to differentiate representative and non-representative networks are described in the methods section.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| BCR # | BCR name | No. of ecoregions  (birds / caribou) | Bird networks  (rep / non-rep) | Caribou networks  (rep / non-rep) |
| 4 | Northern Interior Forest | 14 / 5 | 3703 / 2897 | 0 / 0 |
| 6 | Boreal Taiga Plains | 8 / 8 | 2816 / 2457 | 1514 / 1303 |
| 7 | Taiga Shield and Hudson Plains | 12 / 11 | 5067 / 3803 | 5067 / 3803 |
| 8 | Boreal Softwood Shield | 11 / 11 | 3924 / 2199 | 3898 / 1699 |
| 10 | Northern Rockies | 3 / 2 | 421 / 0 | 615 / 0 |

\* Northern Rockies was dropped because there were no non-representative networks and it only represents a very small proportion of the BCR unit.

**Table 2**. Average and standard deviation of KS values (dissimilarity metric) in representative and non-representative benchmark networks for each test feature in each Bird Conservation Region. Cohen’s d is also reported as a measure of the effect size between representative and non-representative networks.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Group** | **Test\_feature** | **BCR** | **N rep** | **KS rep**  **mean (sd)** | **N non-rep** | **KS non-rep**  **Mean (sd)** | **Cohen’s d (CI)** |
| Caribou | Caribou | BCR6 | 1545 | 0.14 (0.06) | 1352 | 0.17 (0.10) | 0.37 (0.30, 0.44) |
|  |  | BCR7 | 4163 | 0.20 (0.13) | 3084 | 0.28 (0.14) | 0.62 (0.58, 0.67) |
|  |  | BCR8 | 3898 | 0.12 (0.06) | 1699 | 0.33 (0.17) | 2.03 (2.23, 2.23) |
| Conservation | AllBirds | BCR4 | 3703 | 0.17 (0.09) | 2897 | 0.25 (0.11) | 0.79 (0.74, 0.84) |
|  |  | BCR6 | 1545 | 0.19 (0.07) | 1352 | 0.30 (0.13) | 1.09 (1.01, 1.17) |
|  |  | BCR7 | 5067 | 0.20 (0.09) | 3803 | 0.40 (0.18) | 1.48 (1.62, 1.62) |
|  |  | BCR8 | 3924 | 0.18 (0.08) | 2199 | 0.37 (0.16) | 1.67 (1.47, 1.93) |
|  | ForestBirds | BCR4 | 3703 | 0.17 (0.09) | 2897 | 0.30 (0.15) | 1.12 (1.07, 1.17) |
|  |  | BCR6 | 1545 | 0.19 (0.07) | 1352 | 0.28 (0.14) | 0.88 (0.80, 0.96) |
|  |  | BCR7 | 5067 | 0.22 (0.09) | 3803 | 0.42 (0.18) | 1.49 (1.64, 1.64) |
|  |  | BCR8 | 3924 | 0.19 (0.08) | 2199 | 0.38 (0.16) | 1.71 (1.88, 1.88) |
|  | DecliningBirds | BCR4 | 3703 | 0.17 (0.10) | 2897 | 0.33 (0.14) | 1.35 (1.19, 1.56) |
|  |  | BCR6 | 1545 | 0.21 (0.10) | 1352 | 0.32 (0.13) | 0.98 (0.90, 1.06) |
|  |  | BCR7 | 5067 | 0.21 (0.10) | 3803 | 0.35 (0.18) | 1.06 (0.93, 1.22) |
|  |  | BCR8 | 3924 | 0.21 (0.08) | 2199 | 0.46 (0.16) | 2.22 (2.44, 2.44) |
|  | LowConcernBirds | BCR4 | 3703 | 0.16 (0.08) | 2897 | 0.31 (0.14) | 1.32 (1.16, 1.52) |
|  |  | BCR6 | 1545 | 0.20 (0.07) | 1352 | 0.37 (0.14) | 1.54 (1.46, 1.63) |
|  |  | BCR7 | 5067 | 0.22 (0.09) | 3803 | 0.45 (0.17) | 1.73 (1.91, 1.91) |
|  |  | BCR8 | 3924 | 0.19 (0.08) | 2199 | 0.40 (0.17) | 1.85 (2.04, 2.04) |
| Habitat | ConiferBirds | BCR4 | 3703 | 0.17 (0.09) | 2897 | 0.27 (0.13) | 0.88 (0.83, 0.94) |
|  |  | BCR6 | 1545 | 0.24 (0.10) | 1352 | 0.26 (0.14) | 0.20 (0.13, 0.28) |
|  |  | BCR7 | 5067 | 0.22 (0.11) | 3803 | 0.36 (0.16) | 1.06 (0.93, 1.22) |
|  |  | BCR8 | 3924 | 0.20 (0.07) | 2199 | 0.42 (0.17) | 1.90 (2.09, 2.09) |
|  | DeciduousBirds | BCR4 | 3703 | 0.16 (0.09) | 2897 | 0.40 (0.15) | 2.00 (2.21, 2.21) |
|  |  | BCR6 | 1545 | 0.19 (0.07) | 1352 | 0.39 (0.13) | 1.87 (1.78, 1.96) |
|  |  | BCR7 | 5067 | 0.22 (0.09) | 3803 | 0.38 (0.16) | 1.32 (1.45, 1.45) |
|  |  | BCR8 | 3924 | 0.22 (0.09) | 2199 | 0.38 (0.16) | 1.30 (1.25, 1.36) |
|  | MixedwoodBirds | BCR4 | 3703 | 0.18 (0.10) | 2897 | 0.35 (0.16) | 1.27 (1.12, 1.47) |
|  |  | BCR6 | 1545 | 0.23 (0.10) | 1352 | 0.37 (0.14) | 1.17 (1.09, 1.25) |
|  |  | BCR7 | 5067 | 0.24 (0.09) | 3803 | 0.48 (0.17) | 1.79 (1.97, 1.97) |
|  |  | BCR8 | 3924 | 0.21 (0.08) | 2199 | 0.43 (0.16) | 1.94 (2.13, 2.13) |
|  | GrasslandBirds | BCR4 | 3703 | 0.16 (0.09) | 2897 | 0.38 (0.15) | 1.84 (2.02, 2.02) |
|  |  | BCR6 | 1545 | 0.17 (0.07) | 1352 | 0.35 (0.15) | 1.57 (1.49, 1.66) |
|  |  | BCR7 | 5067 | 0.22 (0.09) | 3803 | 0.42 (0.15) | 1.64 (1.81, 1.81) |
|  |  | BCR8 | 3924 | 0.20 (0.08) | 2199 | 0.40 (0.14) | 1.89 (2.08, 2.08) |
| Migration | NeoMigrantBirds | BCR4 | 3703 | 0.17 (0.10) | 2897 | 0.31 (0.13) | 1.15 (1.10, 1.21) |
|  |  | BCR6 | 1545 | 0.19 (0.07) | 1352 | 0.31 (0.14) | 1.15 (1.08, 1.23) |
|  |  | BCR7 | 5067 | 0.20 (0.09) | 3803 | 0.40 (0.17) | 1.53 (1.69, 1.69) |
|  |  | BCR8 | 3924 | 0.21 (0.08) | 2199 | 0.37 (0.15) | 1.50 (1.32, 1.74) |
|  | ShortMigrantBirds | BCR4 | 3703 | 0.16 (0.09) | 2897 | 0.25 (0.12) | 0.86 (0.81, 0.91) |
|  |  | BCR6 | 1545 | 0.18 (0.08) | 1352 | 0.24 (0.15) | 0.52 (0.45, 0.60) |
|  |  | BCR7 | 5067 | 0.24 (0.09) | 3803 | 0.43 (0.17) | 1.43 (1.57, 1.57) |
|  |  | BCR8 | 3924 | 0.19 (0.08) | 2199 | 0.44 (0.19) | 1.91 (2.10, 2.10) |
|  | NomadicBirds | BCR4 | 3703 | 0.18 (0.09) | 2897 | 0.26 (0.13) | 0.71 (0.66, 0.76) |
|  |  | BCR6 | 1545 | 0.21 (0.07) | 1352 | 0.27 (0.14) | 0.57 (0.50, 0.64) |
|  |  | BCR7 | 5067 | 0.23 (0.10) | 3803 | 0.39 (0.16) | 1.23 (1.08, 1.42) |
|  |  | BCR8 | 3924 | 0.21 (0.08) | 2199 | 0.38 (0.14) | 1.62 (1.42, 1.87) |
|  | ResidentBirds | BCR4 | 3703 | 0.17 (0.08) | 2897 | 0.37 (0.16) | 1.62 (1.78, 1.78) |
|  |  | BCR6 | 1545 | 0.23 (0.09) | 1352 | 0.38 (0.18) | 1.11 (1.03, 1.19) |
|  |  | BCR7 | 5067 | 0.22 (0.09) | 3803 | 0.46 (0.18) | 1.72 (1.89, 1.89) |
|  |  | BCR8 | 3924 | 0.20 (0.09) | 2199 | 0.44 (0.17) | 1.89 (2.08, 2.08) |
| Waterfowl | AllWaterfowl | BCR4 | 3703 | 0.17 (0.10) | 2897 | 0.32 (0.13) | 1.36 (1.20, 1.57) |
|  |  | BCR6 | 1545 | 0.19 (0.10) | 1352 | 0.32 (0.15) | 1.04 (0.96, 1.12) |
|  |  | BCR7 | 5067 | 0.18 (0.10) | 3803 | 0.30 (0.13) | 1.05 (1.01, 1.10) |
|  |  | BCR8 | 3924 | 0.14 (0.07) | 2199 | 0.28 (0.14) | 1.32 (1.26, 1.37) |
|  | CavityNesters | BCR4 | 3703 | 0.19 (0.10) | 2897 | 0.33 (0.13) | 1.30 (1.14, 1.50) |
|  |  | BCR6 | 1545 | 0.16 (0.06) | 1352 | 0.21 (0.10) | 0.54 (0.46, 0.61) |
|  |  | BCR7 | 5067 | 0.17 (0.08) | 3803 | 0.32 (0.14) | 1.41 (1.55, 1.55) |
|  |  | BCR8 | 3924 | 0.14 (0.07) | 2199 | 0.28 (0.14) | 1.40 (1.23, 1.61) |
|  | GroundNesters | BCR4 | 3703 | 0.19 (0.10) | 2897 | 0.30 (0.14) | 0.84 (0.78, 0.89) |
|  |  | BCR6 | 1545 | 0.18 (0.09) | 1352 | 0.33 (0.15) | 1.18 (1.10, 1.26) |
|  |  | BCR7 | 5067 | 0.19 (0.10) | 3803 | 0.33 (0.16) | 1.03 (0.98, 1.07) |
|  |  | BCR8 | 3924 | 0.17 (0.07) | 2199 | 0.27 (0.14) | 0.92 (0.86, 0.97) |
|  | OverwaterNesters | BCR4 | 3703 | 0.17 (0.10) | 2897 | 0.32 (0.14) | 1.35 (1.19, 1.56) |
|  |  | BCR6 | 1545 | 0.19 (0.10) | 1352 | 0.34 (0.16) | 1.15 (1.07, 1.23) |
|  |  | BCR7 | 5067 | 0.19 (0.09) | 3803 | 0.27 (0.14) | 0.65 (0.60, 0.69) |
|  |  | BCR8 | 3924 | 0.15 (0.07) | 2199 | 0.34 (0.16) | 1.76 (1.93, 1.93) |

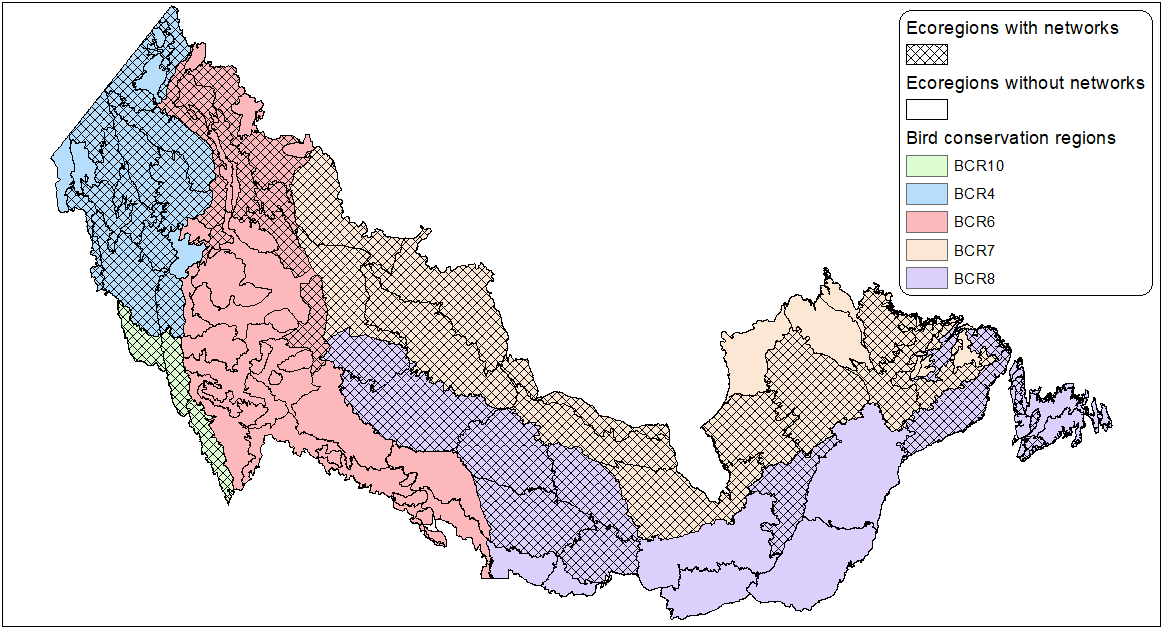
**Table 3.** The number of times CMI, GPP, LED, and LCC was selected as the most important variable, based on the absolute value of the t-statistic in each test feature / BCR model, for songbirds and waterfowl test features. The relative importance of CMI, GPP, LED, and LCC based on the standardized absolute value of the t-statistic in each test feature / BCR model, for songbirds and waterfowl test features.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Group** | **Test feature** | **BCRs** | **CMI** | | **GPP** | | **LED** | | **LCC** | |
|  |  |  | **Top** | **Wgt** | **Top** | **Wgt** | **Top** | **Wgt** | **Top** | **Wgt** |
| Caribou | Caribou | 3 | 0 | 0.17 | 1 | 0.23 | 0 | 0.18 | 2 | 0.42 |
| Conservation | AllBirds | 4 | 0 | 0.16 | 0 | 0.26 | 1 | 0.25 | 3 | 0.33 |
|  | ForestBirds | 4 | 0 | 0.20 | 0 | 0.15 | 2 | 0.29 | 2 | 0.37 |
|  | Declining | 4 | 0 | 0.12 | 2 | 0.40 | 0 | 0.14 | 2 | 0.34 |
|  | LowConcern | 4 | 0 | 0.15 | 2 | 0.33 | 0 | 0.24 | 2 | 0.27 |
|  | Sub-total | 16 | 0 | 0.16 | 4 | 0.29 | 3 | 0.23 | 9 | 0.33 |
| Habitat | Conifer | 4 | 0 | 0.11 | 2 | 0.28 | 0 | 0.15 | 2 | 0.46 |
|  | Deciduous | 4 | 0 | 0.16 | 2 | 0.38 | 0 | 0.13 | 2 | 0.33 |
|  | Mixedwood | 4 | 0 | 0.11 | 2 | 0.40 | 0 | 0.14 | 2 | 0.34 |
|  | Grassland | 4 | 1 | 0.20 | 2 | 0.29 | 0 | 0.26 | 1 | 0.26 |
|  | Sub-total | 16 | 1 | 0.15 | 8 | 0.34 | 0 | 0.17 | 7 | 0.35 |
| Migration | Neotropical | 4 | 1 | 0.23 | 2 | 0.25 | 0 | 0.10 | 1 | 0.42 |
|  | ShortDistance | 4 | 0 | 0.12 | 1 | 0.25 | 1 | 0.21 | 2 | 0.42 |
|  | Nomadic | 4 | 0 | 0.15 | 2 | 0.35 | 1 | 0.22 | 1 | 0.27 |
|  | Resident | 4 | 0 | 0.10 | 0 | 0.16 | 0 | 0.19 | 4 | 0.55 |
|  | Sub-total | 16 | 1 | 0.15 | 5 | 0.25 | 2 | 0.18 | 8 | 0.41 |
| Waterfowl | AllWaterfowl | 4 | 0 | 0.14 | 1 | 0.23 | 2 | 0.34 | 1 | 0.28 |
|  | CavityNesters | 4 | 0 | 0.10 | 0 | 0.23 | 2 | 0.27 | 2 | 0.40 |
|  | GroundNesters | 4 | 0 | 0.11 | 2 | 0.33 | 1 | 0.28 | 1 | 0.29 |
|  | OverwaterNesters | 4 | 0 | 0.14 | 3 | 0.36 | 0 | 0.23 | 1 | 0.27 |
|  | Sub-total | 16 | 0 | 0.12 | 6 | 0.29 | 5 | 0.28 | 5 | 0.31 |
| **All features** | **Total** | **67** | **2** | **0.15** | **24** | **0.28** | **10** | **0.21** | **31** | **0.36** |

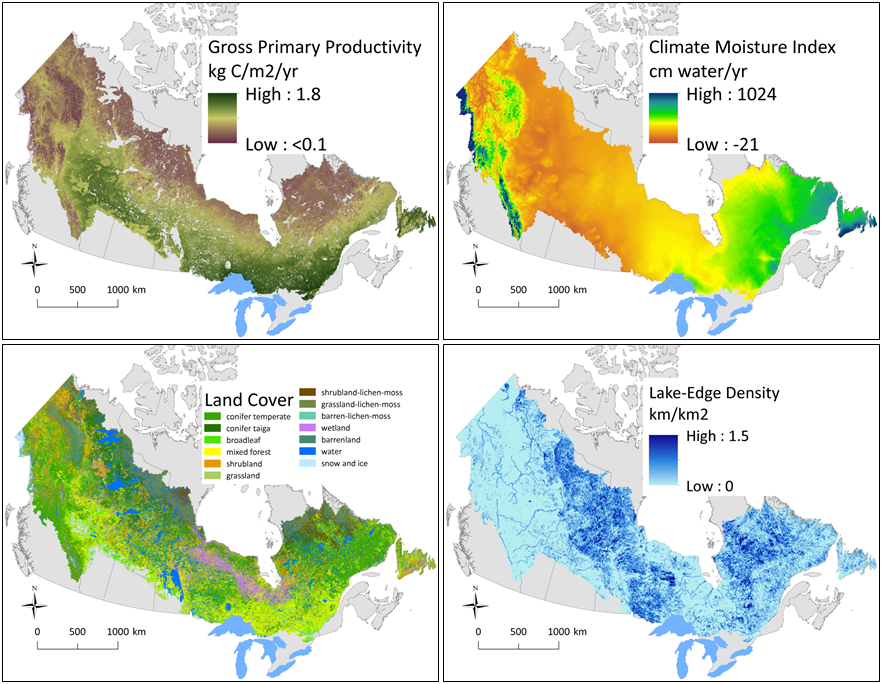
**Table 4.** The number of times each of the five co-factors were found to be influential based on the difference in AIC values between models that include a factor and those that don’t. Ecoregion= ecoregion membership; MDR = MDR (benchmark) size; Intactness = ecoregion intactness; Density = species density or, in the case of Caribou, of RSF values; Density CV = coefficient of variation of density values or, in the case of Caribou, of RSF values.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Group** | **Test feature** | **BCRs** | **Ecoregion** | **MDR** | **Intactness** | **Density** | **Density CV** |
| Caribou | Caribou | 3 | 0 | 0 | 0 | 0 | 0 |
| Conservation | AllBirds | 4 | 0 | 0 | 1 | 1 | 0 |
|  | ForestBirds | 4 | 0 | 0 | 0 | 0 | 1 |
|  | Declining | 4 | 0 | 0 | 0 | 0 | 0 |
|  | LowConcern | 4 | 0 | 0 | 2 | 0 | 0 |
|  | Sub-total | 16 | 0 | 0 | 3 | 1 | 1 |
| Habitat | Conifer | 4 | 0 | 0 | 0 | 0 | 0 |
|  | Deciduous | 4 | 0 | 1 | 0 | 1 | 1 |
|  | Mixedwood | 4 | 0 | 0 | 1 | 0 | 0 |
|  | Grassland | 4 | 0 | 0 | 1 | 1 | 0 |
|  | Sub-total | 16 | 0 | 1 | 2 | 2 | 1 |
| Migration | Neotropical | 4 | 0 | 0 | 0 | 1 | 0 |
|  | ShortDistance | 4 | 0 | 0 | 0 | 0 | 0 |
|  | Nomadic | 4 | 0 | 1 | 1 | 0 | 0 |
|  | Resident | 4 | 0 | 0 | 0 | 1 | 1 |
|  | Sub-total | 16 | 0 | 1 | 1 | 2 | 1 |
| Waterfowl | AllWaterfowl | 4 | 0 | 0 | 0 | 0 | 0 |
|  | CavityNesters | 4 | 0 | 0 | 0 | 0 | 0 |
|  | GroundNesters | 4 | 0 | 1 | 0 | 1 | 0 |
|  | OverwaterNesters | 4 | 0 | 0 | 0 | 0 | 0 |
|  | Sub-total | 16 | 0 | 1 | 0 | 1 | 0 |
| **All features** | **Total** | **67** | **0** | **3** | **6** | **6** | **3** |

# Figures

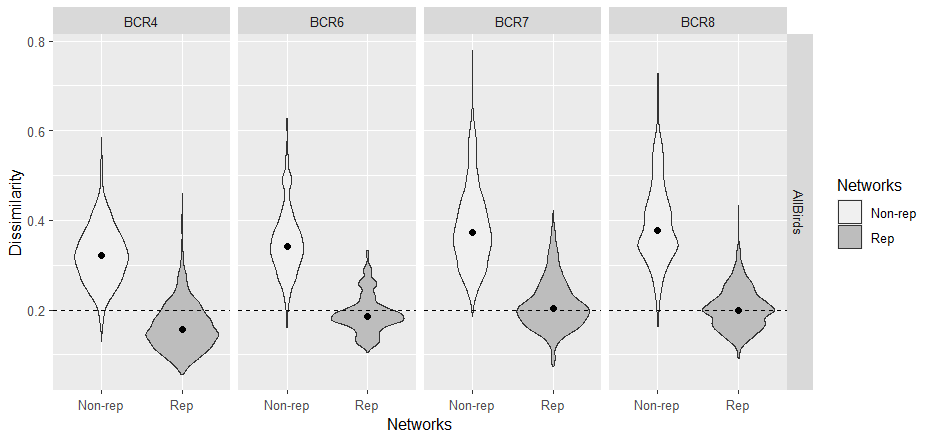


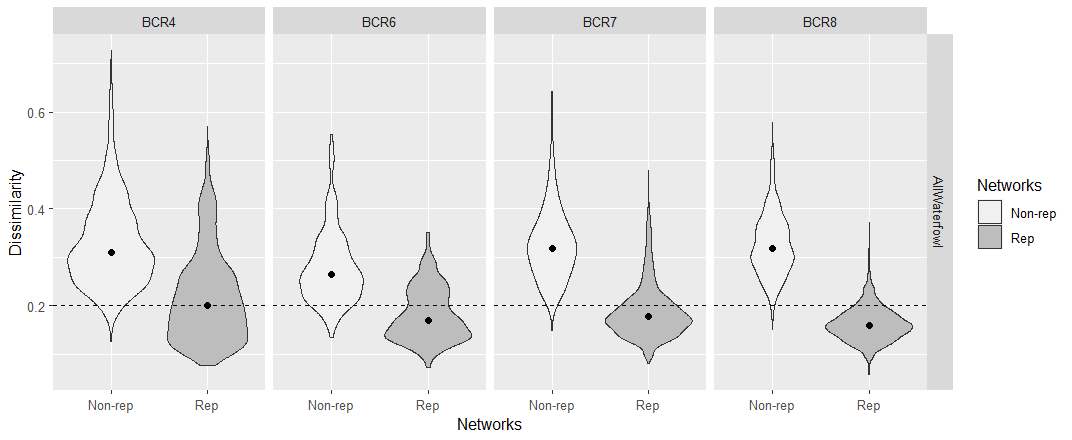
**Figure 1.** The boreal region of Canada was stratified into five Bird Conservation Regions (BCRs; Bird Studies Canada and NABCI 2014), each containing some ecoregions with representative benchmark networks (cross-hatched polygons) and some without.



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

**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.





**Figure 3.** Violin plots showing the difference in KS value distributions between representative and non-representative networks for AllBirds (top) and AllWaterfowl (bottom) assemblages. The dashed horizontal line indicates the 0.2 threshold separating representative from non-representative networks.

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