CONSERVATION OF THREE FOREST LANDBIRD SPECIES AT RISK: CHARACTERIZING AND MODELLING HABITAT AT MULTIPLE SCALES TO GUIDE MANAGEMENT PLANNING

by

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for the birds and the trees

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ABSTRACT

To effectively conserve species at risk (SAR), it is important to understand their ecology at multiple scales, including stand-level habitat associations and landscape-level distribution. The Rusty Blackbird (*Euphagus carolinus*), Olive-Sided Flycatcher (*Contopus cooperi*), and Canada Warbler (*Cardellina canadensis*) are listed landbird species at risk (SAR) that breed in wet forest habitat in Canada's Maritimes. To characterize their habitat for stand-scale conservation, I surveyed vegetation cover and structure at 99 known locations in the Southwest Nova Biosphere Reserve. Habitat at sites occupied by each SAR was significantly different from habitat at unoccupied sites. However, occupied habitat near recent forest harvesting (within 1 km) did not differ from that in unharvested areas, suggesting features can be retained in managed forest landscapes. I further categorized habitat using Nova Scotia's Forest Ecosystem Classification (FEC) and found these SAR predominantly occupied the same wet-poor ecosites, potentially allowing for management of all three species as a suite. I also used FEC information to verify spatial data layers commonly used in forest management planning and found their accuracy ranged from poor to fair, depending on layer and buffer size considered.

To support regional-scale protected areas planning, I developed a species distribution model (SDM) for these species. I first evaluated 128 published SDM algorithms, finding that a majority did not accurately report model uncertainty, prediction metric, or both. To aid conservation practitioners in selecting and reporting on SDMs for conservation, I developed a guide based on data type, conservation objective, and experience. I then modeled the population density of the three SAR in four national parks in New Brunswick and Nova Scotia, using Poisson log-linear regression models with a branching hierarchy. When comparing predicted population sizes to regional population estimates, national parks supported habitat for only 3-4% of Canada Warblers and 1-2% of Olive-sided Flycatchers. Thus it is highly unlikely that existing national parks alone are able to maintain viable regional populations. To help prevent extirpation of these species, forestry prescriptions need to be adjusted to conserve habitat, and key locations for management should be identified at a regional scale.

LIST OF ABBREVATIONS USED

AA	Abundance-absence data
BAM	Boreal Avian Modelling Project
CART	Classification and Regression Trees
CASFRI	Common Attribute Schema for Forest Resource Inventories
CAWA	Canada Warbler
DET	Occupancy-detection data
DTW	Depth to water table
ELC	Ecological Land Classification
FEC	Forest Ecosystem Classification
FID	Forest Inventory Database
DTW	Depth to water table
GIS	Geographic Information Systems
HSI	Habitat Suitability Index
ISA	Indicator Species Analysis
IV	Indicator value
MRPP	Multi-response Permutation Procedures
NMDS	Non-metric Multidimensional Scaling
OSFL	Olive-sided Flycatcher
NB	New Brunswick
NS	Nova Scotia
PA	Presence-absence data
PO	Presence-only data
PV	Population viability data
RUBL	Rusty Blackbird
SAR	Species at risk
SB	Species biology data
SDM	Species distribution model
SNBR	Southwest Nova Biosphere Reserve
SPVA	Spatial population viability analysis

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CHAPTER 1 INTRODUCTION

As human-caused disturbance intensifies globally, an increasing number of species are in decline, with many at risk of extinction. Now that at least 80% of the land surface of the Earth experiences direct human impacts (Sanderson et al. 2002), global extinction rates have risen to exceed natural rates of by three to four orders of magnitude (De Vos et al. 2014). As resource exploitation and climate change continue, the prognosis for an increasing number of species is rapidly becoming grim (Vié et al. 2008).

Globally, habitat modifications are directly correlated with numbers of species at risk (SAR), and continued land-use changes are expected to have the greatest future impacts on terrestrial biodiversity (Sala 2000). Though Canada is one of the few places retaining extensive tracts of forest, rates of species endangerment are similar to other countries in the Americas, and are predominantly the result of ongoing habitat loss (Kerr & Deguise 2004). Human modification to natural landscapes, as well as species richness, is greater in the southern regions of Canada (Kerr & Cihlar 2004), including the provinces of New Brunswick and Nova Scotia.

Efforts to reduce species decline often include habitat conservation or establishment of protected areas in potential breeding habitat (Kerr & Cihlar 2004). Protected areas are important reserves for SAR (Soule & Terborgh 1999), but they may not be sufficient in size or location for conserving biodiversity (Lemieux & Scott 2005). Canada's Species At Risk Act (SARA) was passed without evaluating the potential for existing protected areas to conserve species at risk: as of 2004, there was no relationship between the distribution of federal protected areas and the distribution of federally-listed SAR in Canada (Kerr & Cihlar 2004). The contribution of existing protected areas to available habitat is presently unknown for most taxa (Kerr & Cihlar 2004).

Given increasing threats to habitat, and lack of coverage of the existing network, the expansion of protected areas alone may be insufficient to protect SAR in Canada. However, expanding protected areas is not the only solution: it is urgent that conservation be facilitated in human-dominated landscapes, in cooperative efforts with landowners (Kerr & Deguise 2004; Coristine & Kerr 2011). For many forest-dwelling taxa, the contribution of both protected areas and lands under active forest management is unknown.

For landbirds that use forest habitat, ongoing spatially-extensive changes to this habitat is their greatest threat in the breeding range. Although substantial threats occur during migration and wintering, the relative importance of breeding factors, such as habitat loss, can be more important for some populations (Rushing et al. 2016) Many forest bird species are vulnerable to habitat alteration through logging (e.g. Hutto & Gallo 2006; Lain et al. 2008; Cahall & Hayes 2009; Schlossberg & King 2009). The relationships of birds to their habitat, in both managed and unmanaged lands, needs to be known at local and regional scales in order to develop comprehensive approaches to conservation (Hurme et al. 2005; Cumming et al. 2010b). To protect forest habitat, two commonly used tools are protection (restriction of management activities on the land) and stand-level sustainable forest management (planning that incorporates wildlife values and protects habitat for species at risk). Using these tools for conservation requires at least some prior knowledge of what habitat a given SAR uses, and how that habitat can be identified or located. Thus it is essential to characterize and map the habitat of species in decline to identify candidate areas for protection and effectively manage areas experiencing disturbance.

1.1. THE EFFECTS OF SCALE

When characterizing habitat, it is necessary to choose an appropriate scale for analysis. If the scale of study and the scale of species responses are different, results may be misleading (Savignac et al. 2000; Schaefer & Mayor 2007). Habitat can be modeled or measured at a variety of extents, from microsite to range-wide. Analyses need to consider both the scale at which the organism operates, but also, the scale at which management action will be taken.

Organisms operate at different scales for different elements of their life histories, with each ecological process occurring within an ‘ecological neighbourhood’, where an organism is active or has some influence during a period of time (Addicott et al. 1987). For example, during the breeding season, the ecological neighbourhood could be a nest site, a foraging site, or a territory or home range, depending on the ecological process being studied. However, not all scales are equally valuable for applying conservation action, particularly when trying to design protected areas or guide stand-level forest management planning. Although habitat is often modeled based on existing data, often at relatively coarse scales such as regional or national extents, this may be insufficient to capture species' responses (Burgman et al. 2001; Elith & Leathwick 2009a). Only by studying an organism's habitat at multiple scales can it be determined what scales might be appropriate for conservation action, and if existing management tools can produce meaningful results at these scales.

It is known that patterns of habitat use by bird species differ depending on the spatial scale at which they are measured, and the habitat features that are important at one scale may not be considered important at another. For example, patterns of habitat use by Pileated Woodpeckers (*Dryocopus pileatus* L.) were best explained by different variables at the microhabitat (<0.04-ha radius plots) and macrohabitat scales (>125-ha radius plots; Savignac et al. 2000). Likewise, Girard et al. (2004) studied occurrence of songbirds in plots of 50-, 100-, and 1000-m radii, and found that occurrence in forest of different types (coniferous, deciduous, and mixedwood) in Quebec significantly differed between scales.

When considering the distribution of species, variables measured at local or fine scales are often better predictors. For example, relative abundances of breeding forest birds in New England forests were better predicted by local-scale variables (forest stand structure) than stand-scale variables (cover type or size class of trees; DeGraaf et al. 1998). Similarly, Betts et al. (2006c) found that site occupancy of a suite of songbird species depended more on fine-scale variables than coarse-scale variables for most species, but that landscape configuration also played an important role. When considering the needs of a species, microhabitat features should not be ignored. Diversity of breeding forest bird species is reliant on the vertical structures of forests, or forest strata (MacArthur & MacArthur 1961). As such, field study of fine-scale habitat features should be included to better understand bird-habitat relationships prior to engaging in predictive modeling for conservation.

It should be cautioned that although many studies compare the effects of scale, some neglect to quantify the operating scales, and terms are not equivalent between studies. For example, there seems to be little agreement on the size implied by 'landscape scale', which has been used to refer to areas as small as 3 ha (Richmond et al. 2012), to 500 ha (Taylor & Krawchuk 2005), and even as large as 8000 ha (Bloom et al. 2013). In this thesis, I use the local or stand scale to describe the ecological neighbourhood immediately around the bird sighting (0.8 ha, 50 m radius circle), and assign landscape scale based on the largest territory size (MacKay et al. 2014) for these SAR (20 ha, 250 m radius circle).

1.2. STUDY SPECIES AND CONTEXT

The Rusty Blackbird (*Euphagus carolinus* Müller) Olive-Sided Flycatcher (*Contopus cooperi* Swainson), and Canada Warbler (*Cardellina [Wilsonia] canadensis* L.) are listed forest landbird species at risk in Canada, with the Rusty Blackbird designated as Special Concern and the other two species as Threatened (Government of Canada 2011). Most of the breeding range for these three migrants falls within Canada, housing over 70% of Rusty Blackbird and Canada Warbler populations, and over 50% of the Olive-sided Flycatcher population (Blancher 2003). The Maritimes represent the easternmost extent of the range of these species. Estimates from long-term monitoring show that population declines for these species have been devastating in the last half-century.

The Rusty Blackbird has experienced >88% global population reduction since 1960, but this decline has likely been continuing for a century or more (Greenberg & Droege 1999; Niven et al. 2004). Since 1968, the Olive-sided Flycatcher global population has declined by approximately 79%, and the Canada Warbler population has declined by approximately 85%. For all three species, annual rate of decline in Atlantic Canada in recent years has exceeded mean range-wide decline by two-to-four times (Environment Canada 2014a; Sauer et al. 2014). Evidence of breeding range contraction has been observed for the Rusty Blackbird in Maine (Powell 2008), New Hampshire (Deming 2009), and the southern boreal forest (Greenberg et al. 2011). Extirpation risk may be high in Nova Scotia, particularly as it is home to a unique subspecies of Rusty Blackbird (*E. c. nigrans*).

In the eastern portion of their range, all three species rely on forested habitat in or adjacent to wet areas (Altman & Sallabanks 2010; Reitsma et al. 2010; Avery 2013a), in natural and managed stands (Powell 2008; Robertson & Hutto 2013; Hunt et al. 2015). All three species are insectivorous on the breeding grounds, though their modes of acquiring food differ. Rusty Blackbirds forage by wading into shallow water, or feed in deeper water from a platform of floating vegetation or debris (Bergtold 1927; Greenberg et al. 2011; Avery 2013a). Olive-sided Flycatchers sally from perches on tall trees to capture flying insects, and Canada Warblers forage aerially or occasionally on the ground in dense, shrubby habitats (Reitsma et al. 2010).

These three species have been receiving increased conservation interest in recent years, with international research and conservation consortiums forming around them (e.g. International Rusty Blackbird Working Group; Canada Warbler International Conservation Initiative) and national and provincial governments and non-government organizations addressing them in management planning. A number of organizations and researchers have identified an urgent need to collect data regarding the availability and quality of habitat (e.g. Hobson et al. 2010), particularly in areas with vulnerable populations.

Given the increased rate of population declines in the eastern part of the range, conservation in the Maritimes may be important for retaining the existing range of these species. On the breeding grounds, habitat destruction through wetland loss and forestry activities has been hypothesized as a cause of population declines (Greenberg & Droege 1999; Riordan et al. 2006; Greenberg et al. 2011). In New Brunswick and Nova Scotia, all three species are known to occupy wet forest landscapes in both protected areas, as well as areas of recent forest harvesting and management. In Nova Scotia, provincial protected areas are designated based on remoteness, rarity, species richness, restoration potential, and connectivity potential (Province of Nova Scotia 2013), and in New Brunswick, they are designated based on ecologically sensitive features vulnerable to human activity and representative or rare ecosystems (Government of New Brunswick 2012). Neither province establishes protected areas specifically for conserving species at risk. Outside of protected areas, landscapes in these provinces feature high levels of habitat heterogeneity as well as extensive active forest harvesting operations, and have been substantially altered by anthropogenic development in recent years (Loo & Ives 2003; Mosseler et al. 2003). However, they have received relatively little study in Atlantic Canada (but see undergraduate theses by Fargher 2011; Harper 2011). Until now, there has been a lack of specific and quantifiable information regarding fine-scale habitat associations of these species in Nova Scotia, nor have there been targeted regional predictive habitat models (although see Bale et al. in prep).

1.3. RESEARCH OBJECTIVES AND THESIS STRUCTURE

The main goals of my thesis were to characterize fine-scale habitat for these SAR in Nova Scotia in order to suggest habitat-maintaining forest management practices (Chapters 2 and 3), choose a regional-scale modelling method informed by conservation objectives (Chapter 4), and develop predictive models for protected areas to help guide management planning (Chapter 5).

Chapter 2 begins at the scale of individual forest stands occupied by these three SAR. I measure and characterize vegetation cover and habitat structure in Nova Scotia, contrast vegetation characteristics between sites occupied and unoccupied by a given species, and compare occupied sites in areas of recent harvesting to those in areas not recently harvested. I use multivariate methods of analysis and testing of means for non-parametric data (including indicator species analysis, non-metric multi-dimensional scaling, and classification and regression trees) to identify vegetation characteristics associated with particular site treatments for each species. Based on variables that emerge as significant for each species and site condition, I recommend forest management strategies to maintain habitat features during forest harvesting operations.

Chapter 3 answers the question: what tools are appropriate for stand-scale forest management planning when trying to conserve these three SAR? I characterize habitats occupied by these three SAR using Nova Scotia’s Forest Ecosystem Classification (FEC) System, and test frequency distributions to see if particular bird species are associated with particular forest groups, vegetation types, soil types, and ecosites more than expected by chance. I use FEC data to verify digital spatial layers commonly used in management planning, and compare classified and reference categories using error matrices and Kappa statistics. Based on inaccuracies in digital data for wet forest habitats, I suggest FEC as a stand-level management tool that could be integrated into existing forest management methods.

At regional-to-national scales, modern SAR management often involves the construction of species distribution models (SDM) to predict species' habitat, occurrence, occupancy, or abundance across the landscape. In Chapter 4, I classify 128 published SDM algorithms by conservation objective(s) and prediction metric, and find that the majority of models do not report an appropriate level of uncertainty with their prediction, which could have impacts for applied conservation and management. Taking lessons learned from these models, I develop a novel framework that guides the user through SDM selection based on their conservation objective, while taking into account data type and appropriateness of model algorithm for their desired prediction metric. I close with recommendations for best practices to aid users in developing robust SDMs to help guide species conservation.

In Chapter 5, I develop regional-scale SDMs for the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in national parks in New Brunswick and Nova Scotia. I choose a hierarchical set of covariates expected to influence habitat selection by drawing upon habitat associations derived in Chapters 2 and 3. Using an extensive avian point count dataset from the Boreal Avian Modelling (BAM) Project, I predict population density of these bird species in Maritime National Parks using Poisson log-linear regression models with a branching hierarchy, in conjunction with Dr. Peter Solymos (University of Alberta). I use these predictions to estimate population sizes within National Parks, and compare them to regional population estimates to determine if national parks protect enough habitat to help buffer population declines in the region. This work was submitted as a report to Parks Canada on behalf of BAM. Trish Fontaine (University of Alberta) and Dr. Erin Bayne (University of Alberta) assisted with data acquisition and report preparation.

Finally, I conclude the thesis with discussion of the management implications of my findings, and specific recommendations for preventing extirpation of these three species from Nova Scotia and New Brunswick. I explore the limitations of my methods, and recommend future research that should be undertaken to engage in the most effective conservation for these landbird SAR.

CHAPTER 2 HABITAT ASSOCATIONS IN NOVA SCOTIA

2.1. INTRODUCTION

On public and private forest lands, sustainable forest management dictates that operators must balance objectives of timber harvest with wildlife and ecosystem values. Conservation or protection of SAR is often mandated, either through government legislation or wood supply certification schemes (Becker et al. 2011). To effectively manage for SAR, biological information about the species should be measured locally to maximize its reliability, relevance, and applicability (Hurme et al. 2005; Sallabanks et al. 2006; Cumming et al. 2010b). This is particularly important for species in decline, as conservation efforts may rely heavily on estimates of the extent of known habitat (Schlossberg & King 2009).

The Rusty Blackbird, Olive-Sided Flycatcher, and Canada Warbler are listed forest landbird species at risk in Canada that have experienced significant population declines (Government of Nova Scotia 2007; Government of Canada 2011; Environment Canada 2014a). The Committee on the Status of Endangered Wildlife in Canada has assessed the Rusty Blackbird as special concern (COSEWIC 2006), and the Olive-sided Flycatcher and Canada Warbler as threatened (COSEWIC 2007, 2008). In the Southwest Nova Biosphere Reserve (SNBR) all three species are known to occupy wet forest landscapes in both protected areas as well as areas of active forest harvesting and management. Many of these landscapes feature high levels of habitat heterogeneity as well as extensive forest harvesting operations, and have been substantially altered by anthropogenic development (Loo & Ives 2003; Mosseler et al. 2003).

In Nova Scotia, protected areas cover roughly 12% of the landmass, and the national parks components of these areas are insufficient to maintain regional populations of these three species (Westwood et al. 2015; Chapter 5). In order for populations of these species to recover, they will need to persist in landscapes undergoing various levels of forest management. However, in much of Nova Scotia, natural forest dynamics are driven by the creation of small gaps resulting from low fire frequency and/or relatively small and sporadic insect outbreaks (Neily et al. 2008). As such, songbird communities in these types of forests may be sensitive to the changes in landscape structure that result from forest harvesting practices, the scale of which differs considerably from local natural disturbance regimes (Taylor & Krawchuk 2005). By directly linking tools for measuring species at risk habitat to forest inventory measures, it is possible to facilitate conservation and monitoring efforts within existing forestry protocols (Psyllakis & Gillingham 2009). Occurrence of a species in a given habitat is linked to forest vegetation structures. Understanding these specific features is important to help predict and mitigate the impacts of timber harvest (Marzluff et al. 2000; Sallabanks et al. 2006).

Very little information about the response of these SAR to forest harvesting and management practices is available (but see Powell et al. 2010a; Robertson & Hutto 2013; Hunt et al. 2015), and none has been collected in eastern Canada. Although not explicitly tested, forest management on the breeding grounds is hypothesized to significantly contribute to population declines for these species (COSEWIC 2007, 2008; Environment Canada 2014b). In Pennsylvania, Becker et al. (2011) found strong declines in Canada Warbler abundance over 14 years, corresponding with a reduction in area of mature deciduous and mixed forest, and an increase of clear cut and early seral stage vegetation. From 1998-2000, Harrison et al. (2005) reported local extinction of Canada Warblers from an experimental forest undergoing harvesting; however, it is unclear if these trends are due to harvesting or region-wide declines in abundance. Despite recent efforts to evaluate these species at broader spatial scales (e.g. Haché et al. 2014; Westwood et al. 2015), specific habitat requirements are unknown for most of their Canadian range. Nova Scotia, the easternmost extent of the range, may support a unique subspecies of Rusty Blackbird (*E. c. nigrans*), making it particularly important to determine regionally-specific habitat information (Godfrey 1986; although genetic evidence for this sub-population has not been documented, Hobson et al. 2010 supported a separate flyway for populations breeding east of the Appalachians).

2.1.1. Habitat structure and patchiness

Vegetation structure generally refers to the horizontal and vertical distribution of canopy elements, and influences species distribution and abundance through the creation of microclimates and microhabitats (Goetz et al. 2010). Forest vegetation structure has long been thought to play an important role in determining bird species diversity, explaining more variation than vegetation composition alone (MacArthur & MacArthur 1961). Forest vegetation structure is commonly used when describing songbird communities, particularly as a predictor of species richness and diversity (Heikkinen et al. 2004; Sallabanks et al. 2006; Goetz et al. 2007; Psyllakis & Gillingham 2009).

For a particular species of concern, it is necessary to derive species-specific structural features associated with habitat use (e.g. Goetz et al. 2010). In Maine and New Hampshire, Canada Warbler abundance was better explained by vegetation size-class and structure than cover type, with the highest abundances predicted in early seral stage forests (DeGraaf et al. 1998). Structural attributes of territories have been characterized for Canada Warbler in New Hampshire (Reitsma et al. 2013) and Alberta (Hunt et al. 2015). Canada Warblers also show evidence of clustered distributions (Len Reitsma, unpubl. data), suggesting suitable habitats may have to extend beyond the size of a single territory (0.4 ha to 0.75, COSEWIC 2008). However, as they have much larger territory sizes, the ecological neighbourhoods (Addicott et al. 1987) that Olive-sided Flycatcher and Rusty-Blackbird occupy more likely consist of non-contiguous patches in a heterogeneous landscape.

The variation of structure within forest stands has been thought in some cases to be more important than variability between cover types in determining habitat suitability and use (DeGraaf et al. 1998; Hurme et al. 2005). For many songbird species, especially those with large territories, resources will be distributed unevenly across the territory. Some patches will be useful for foraging and nesting, and others will not. If vegetation is patchy and heterogeneous across the territory, structural variation is high, whereas homogenous vegetation results in low structural variation (Bleho 2009).

Understanding the scale at which vegetation characteristics are most strongly associated with bird life processes is important for management (Richmond et al. 2012). Patchiness (or variability in forest stands) has been considered at the landscape scale, particularly in the context of large natural disturbances (e.g. Schmiegelow et al. 1997; Niemela 1999; Lain et al. 2008), but rarely within territories. For interior forest swamp species in Rhode Island, total habitat availability was thought to be more important than patch size, with species focusing their use on very small patches (<1 ha) within a heterogeneous landscape (Golet et al. 2001). At fine scales, within-habitat characteristics become important, such as horizontal heterogeneity or vegetation height and composition (Böhning-Gaese 1997). Small-scale patchiness may be particularly important in southwestern Nova Scotia, where the natural disturbance regime is dominated by small gap creation, and the topography is variable, leading to a diversity of microsites (Neily et al. 2003). Whereas vegetation structure is a well-documented predictor for the occurrence of many species, variation of vegetation structure across a territory has been less studied.

I aimed not only to characterize the vegetation cover and structure in sites occupied by the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in the Southwest Nova Biosphere Reserve (SNBR), but also to capture the variation across individual sites to better understand the role of habitat patchiness for these species. The SNBR consists of the five southernmost counties of southwestern Nova Scotia, and includes large protected areas and areas under timber management. My objectives were to (1) characterize habitat occupied by these three species in the SNBR, both in terms of vegetation composition and habitat structure and its variability, by comparing occupied habitat to unoccupied habitat; (2) compare characteristics of occupied habitat in a landscape matrix of forest harvesting to that in non-harvest matrices, and (3) determine whether general management recommendations can be formulated to conserve common habitat needs of these three species.

2.2. METHODS

2.2.1. Study area and focal species

The SNBR, a UNESCO-designated biosphere reserve, covers 1 546 374 ha and includes the five southernmost counties of Nova Scotia (65°24’7”W, 44°13’58N; UNESCO 2007;

Figure 2.1). Its forests are located in the south mountain, rossignol, lahave drumlins, and western barrens ecodistricts of the western ecoregion (Nova Scotia Department of Natural Resources 2003). The area supports a predominantly coniferous forest with associations of pine, spruce, and hemlock (Neily et al. 2008). Areas of moist to wet soils disturbed by hurricanes serve as the substrate for forests dominated by red maple (*Acer rubrum*) and black spruce (*Picea mariana*). On less wet sites, associations of eastern hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), and white pine (*Pinus strobus*) occur. The SNBR includes several major towns and many small communities, as well as large land holdings devoted to forest harvesting. It also includes extensive protected areas, the largest being Kejimkujik National Park and the Tobeatic Wilderness Area.

The Rusty Blackbird breeds in swamps, wooded bogs, and along the borders of lakes and streams (Greenberg & Droege 1999; Powell et al. 2010b), placing nests predominantly in conifers 1-3 m high (Matsuoka et al. 2010b; Powell et al. 2010a) in both natural and managed stands (Powell 2008). Olive-sided Flycatchers predominantly occupy sites near patches of early seral vegetation (Altman & Sallabanks 2010). In Nova Scotia, they occur in treed wetlands, along natural and anthropogenic forest edges, and in open and semi-open forests that are dominated by conifers (Fargher 2011). Nests are located along the mid-to-upper branches in coniferous trees slightly shorter than the surrounding canopy (Dixon 1920). The Canada Warbler requires a well-developed shrub layer (Reitsma et al. 2010), and can also be locally abundant in regenerating forests (i.e., 6–30 years post-disturbance) following anthropogenic or natural disturbances (Lambert & Faccio 2005). Though found in a variety of forest types, in its eastern range, the Canada Warbler is most common in wet mixed forest (Reitsma et al. 2010).

2.2.2. Site selection and bird surveys

As information on the target species at risk was limited in the SNBR, it was necessary to increase the inventory of detection sites. To maximize the likelihood of locating birds when surveying new locations, I constructed preliminary habitat suitability index (HSI) models to guide ground surveys to areas of potentially suitable habitat (Tirpak et al. 2008). Suitability indices, derived from literature review and expert opinion, were assigned to

Geographic Information Systems (GIS) layers describing key environmental covariates, with analyses conducted using ArcGIS 10.2.2 (Esri Inc. 2014). Polygons were calculated with HSI values ranging between 0.0 (habitat not suitable) and 1.0 (habitat of maximum suitability; detailed methods available in Westwood 2012). Final models were divided into areas of high, medium, and low suitability and the three species' HSIs were averaged as a composite.

Detection surveys (point counts and playbacks) surveys were conducted from April-July 2012 and 2013 in randomly selected polygons of high suitability at a minimum of 10 ha in the composite HSI, stratified by ecodistrict and management type (non-harvest for matrix versus areas in a harvest matrix). In each polygon, I established three survey plots at least 250 m apart and ≥100 m from a road or other discontinuity. I also surveyed locations with previous detections made by other observers, and made opportunistic playback surveys (not accompanied by point counts) at locations when potentially suitable habitat was encountered *en route* to designated survey polygons (e.g. roadside, border of non-target wetland).

Surveys were conducted between sunrise and 1130h in fair weather conditions (no rain and wind <30 km/h). Each survey consisted of a 5-min unlimited-radius point count followed by a 30-s playback for each species, interspersed by 2-min listening periods (if the target species was detected, its listening period was extended to 5 min). Distance and direction was noted to adjust UTM coordinates to reflect actual bird location. In total, 337 surveys were completed, with Rusty Blackbird detected at 25 locations (19 novel detections, where the bird was not previously found), Olive-sided Flycatcher at 68 locations (42 novel), and Canada Warbler at 32 locations (15 novel). All field personnel and survey methods were certified under the Dalhousie University Animal Use Protocol 12-031 Mandatory Training for Wildlife.

My detection locations were combined with those from other sources since 2008, including the Maritimes Breeding Bird Atlas, laboratory of Dr. Cindy Staicer (Dalhousie University), and other naturalists and ornithologists. Observations were filtered to remove spatial overlap (observations of the same species in the same location) to identify unique known bird locations.

2.2.3. Habitat surveys

A subset of bird detection locations was selected for vegetation surveys. I used a random stratified design to select locations distributed across ecodistrict and two treatment types: occupancy and harvest condition. For occupancy, sites were either defined as ‘occupied’ or ‘unoccupied’ for a given species (e.g. a site at which only the Rusty Blackbird was located would be ‘occupied’ by Rusty Blackbirds, and ‘unoccupied’ for the other two species). All sites surveyed were occupied by one of the three SAR. Harvest condition was assigned based on 2009-2013 satellite imagery, with ‘harvest matrix’ sites having visible harvesting disturbance within 1 km, and ‘non-harvest matrix’ sites having no visible harvesting activity within 1 km. This was done to capture sites where a harvested condition may occur within the territory of the bird (or larger use area for conspecifics, in the case of Canada Warbler). Due to higher numbers of bird locations in some treatment conditions than others, equal sample sizes were not possible in each group. Vegetation surveys were carried out at 99 sites chosen from bird locations in July and August 2012 and 2013. At each site, a variable-radius forest inventory plot was established using a prism (basal area factor 2, as specified in Nova Scotia forest practices guidelines; McGrath 2013) at the GPS coordinates of the detection (or the most likely nesting habitat within 50 m of the coordinates if detailed location information was unavailable). Trees within the prism plot were classified according to canopy position (dominant, co-dominant, intermediate, or suppressed). Tree species, status (alive or dead), diameter at breast height, height of stem, height of bottom of the canopy, and an index of health were also recorded.

From each inventory plot, two 50-m transects were sampled to capture variation across site. Transects were oriented at a minimum 90° angle from one another, in a randomized direction in potentially usable habitat for the target species (e.g., not directly into the centre of an open wetland or open clearcut). I established vegetation plots at 10-m intervals along each transect, including the centre point, for a total of 11 plots per site.

At each vegetation plot, four concave densiometer measurements were taken in each of the cardinal directions and averaged to provide a measure of canopy cover (Jennings et al. 1999; Parker 2014). To capture structural complexity in the lower strata, percent live leaf cover was estimated for the shrub layer (shrubs and regenerating trees, 0.25 m – 5 m), herbaceous layer (plants <0.25 m), and ground layer (bryophytes, lichens, litter, and substrate). Fern measurements were included in the herbaceous layer. For the shrub layer, species, height and percent cover of all plants occupying >5% of a 4 m^2 quadrat (2 m x 2 m) was recorded. Although Nova Scotia's FEC defines "woody shrubs and regenerating trees usually less than 2-m height, but occasionally taller" (Neily et al. 2011), I used a larger margin to capture regenerating trees suitable for Rusty Blackbird nesting in the shrub layer. For the herbaceous layer, the species and percent cover of all plants occupying at least 5% of a 1 m^2 quadrat was recorded. Finally, all items occupying >5% of the ground layer of the 1 m^2 plot were recorded (e.g. litter, coarse woody debris, mud). Plants were identified to species where possible, though sphagnum, some sedges, some asters, and some graminoids were only identified to genus or family.

2.2.4. Statistical analyses

Measurements for the 11 plots per site were averaged to calculate site means. Standard deviation of the 11 plots was calculated as an indicator of within-site heterogeneity, or habitat patchiness (Sorenson 2002). Standard deviation was used rather than the coefficient of variation, which only characterizes relative heterogeneity, and may not capture structural differences important to passerines (Bleho 2009).

I collected information on the mean and standard deviation of 188 habitat variables (including composite variables, such as ALLFERNS – total fern cover) at each site. The 188 variables were included in two datasets: one including site means, and the other standard deviations for each site. I completed data reduction in three iterative steps: exploratory analysis, multivariate testing, and between-groups hypothesis testing. In the exploratory analysis phase, I reduced the 188 initial variables to eliminate highly correlated variables. I used Indicator Species Analysis (ISA; Dufrene & Legendre 1997) to determine which of the 188 initial variables were significantly associated with a particular bird species or treatment group (occupied vs. unoccupied; harvest matrix vs. non-harvest matrix). ISA generates an index of association with a particular group, termed an indicator value (IV). A perfect indicator for a given treatment would be faithful (always present) and exclusive (not present in other treatments). ISA evaluates variables by the standards of a perfect indicator, assigns an IV, and tests these values for significance by comparing them to IVs generated from randomized subsets of the data (McCune & Grace 2002). Variables that did not emerge as significant from the ISA, or were not deemed biologically important from review of the literature and expert opinion, were removed from analysis or combined into composite classes. For example, percent cover of individual bryophyte species that did not emerge as important (e.g. *Pleurozium schreberi*; *Dicranum polysetum*) were re-classified into the summary variable MOSS, and the original variables for each individual species discarded from analysis. Remaining variables were assessed using factor analysis, and I further removed or reclassified variables with high correlations or low explanatory power.

I retained variables that emerged as statistically important, along with those of known biological importance for the species from review of the literature and interviews with experts. The means and standard deviations of 50 habitat variables were retained for multivariate testing (Table 2.1).

With a reduced suite of 50 variables, I examined multivariate differences between groups using multi-response permutation procedures (MRPP; Berry & Mielke 1984). MRPP is a non-parametric test for multivariate group differences (McCune & Grace 2002). I relativized the data by column total, ensuring both standard units between variables and to maximize the influence of proportions rather than absolute numbers (relative rates of change being more appropriate than absolute rates of change when some variables are observed in much higher abundance than others, McCune & Grace 2002). Using a Sorenson distance measure on relativized data (as Sorenson distance is less sensitive to outliers and performs more evenly across datasets with different levels of underlying diversity; McCune & Grace 2002), I compared means and standard deviations of habitat cover and structure variables across treatments (occupied vs. unoccupied sites for each bird species; harvest matrix vs. non-harvest matrix for each bird species; and pairwise comparison between the three bird species).

I used ISA on the reduced variable set (50 variables; Table 2.1) to identify habitat variables whose abundance and frequency were associated with a particular bird species or treatment. ISAs were conducted using 4999 randomized Monte Carlo runs. To compare means and standard deviations of relativized vegetation cover and habitat structure variables for each treatment, I computed non-metric multi-dimensional (NDMS) scaling (Kruskal 1964; Mather 1976) using Sorensen distance measures (McCune & Grace 2002). A random starting configuration was provided, with 250 runs of real data and 200 runs of randomized data. Ordination output was inspected for visual clustering between labelled groups (species).

Finally, the variable set was further reduced to two final datasets for between-groups analysis: (1) 21 variables for cover and stand density, and (2) 9 tree and shrub heights (Table 2.1, fields marked with an asterisk, with shrub layer variable cover being used in the first dataset, and heights in the second). I retained variables that met any of the following criteria: easily-measurable composites (e.g. total moss cover), identified as significant indicators of occupied sites by ISA, or of known biological importance for one or more bird species. The final variable data set was intended for use in timber cruises and other forest management planning activities.

To develop measurable guidelines for classifying potential habitat on the ground, I used classification and regression trees (CART), which partition treatments by the predominant features of their groups. For each species, the target group was occupied sites, and the independent variables were recursively partitioned using the Gini method to determine the best explanatory tree (McCune & Grace 2002). Cross-validation was applied with 25 sample folds per analysis. Cross-validation was used rather than bootstrapping due to the relatively low sample size. For all three species, model growth was completed with a minimum parent group size of 30 and a minimum child group size of 6. The tree was limited to 4 levels and not pruned. Finally, individual habitat variables were compared between occupied and unoccupied sites for each species, as well as between sites occupied by the three species using Mann-Whitney *U*-tests.

For CART and Mann-Whitney *U*-tests, I used in SPSS 21.0 (IBM Corporation 2012). For ISA and NMDS, I used PC-ORD 5 (McCune & Mefford 2005). Due to the high number of variables and tests used, I set the significance level at $\alpha = 0.01$ to minimize the likelihood of Type I error.

2.3. RESULTS

In 2012 and 2013, I assessed the vegetation of 99 wet forest sites, spanning 5 ecodistricts, occupied by one or more of three landbird species at risk (37 sites occupied by Rusty Blackbird, 45 by Olive-sided Flycatcher, and 38 by Canada Warbler; Table 2.2). Although overall comparisons between ecodistricts of both habitat variable means and standard deviations showed significant differences ($\alpha = 0.01$; Table 2.3), only 4 out of 20 pairwise comparisons revealed significant differences (ecodistrict 720 vs. 740 and 740 vs. 760; Table 2.4). As a result of small sample sizes in each ecodistrict, I judged that ecodistricts were similar enough to be assessed together.

MRPP showed significant differences for both means and standard deviations of habitat variables for all three bird species when comparing sites occupied and those not occupied by a given bird species (Table 2.5). When sites were compared by harvest condition, both means and standard deviations of vegetation responses were significantly different (mean: A = 0.0050, $P = 0.006$; SD: A = 0.0063, $P = 0.002$). However, when comparing sites occupied by each individual species by harvest condition, no differences emerged (Table 2.5).

2.3.1. Species-specific habitat associations

ISA was used to examine the faithfulness and exclusivity of habitat cover and structure variables to occupied and unoccupied treatments for each species. Sites occupied by Rusty Blackbirds were indicated by higher relative frequency and abundance of mean cover of MUD and WATER, whereas high mean cover of DECSHR and SHRTOT was associated with unoccupied sites (Table 2.6). Occupied sites were also indicated by high standard deviation of MUD, WATER, and AQUVEG. When habitat variables (Figure 2.2; Figure 2.3) were compared non-parametrically, the only variable exhibiting a significant difference for Rusty Blackbird was WATER (U = 887.5, P = 0.01), which was higher on occupied sites.

ISA showed that Olive-sided Flycatcher-occupied sites were indicated by TREES<5 m and SNAGS<5 m, while unoccupied sites were indicated by mean CANOPY and ILEVER, as well as standard deviation of MAICAN and ILEVER (Table 2.6). K-W testing of means showed that Olive-sided Flycatcher-occupied sites were associated with lower CANOPY (U = 735, P = 0.002), higher SBA (U = 811, P = 0.005), and lower mean DECSHR height (U = 828, P = 0.009).

Finally, variable means that were significantly indicative of occupied sites for Canada Warbler-occupied were OSMCIN, ALNINC, CANOPY, ILEMUC, and SPHAGNUM. Standard deviations significantly associated with occupied sites included OSMCIN, ALNINC, TOXRAD, and ILEMUC. Unoccupied sites were associated with higher mean and SD of DRYFER, and SD of CANOPY. Canada Warbler-occupied sites had significantly more CANOPY cover (U = 679, P < 0.01), higher mean cover of OSMCIN (U = 684, P <0.01), higher mean cover of ALNINC (U = 641, P < 0.01), and higher mean DECSHRHT (U = 634, P < 0.01).

CART analysis was used to identify site conditions association with occupancy by each species. The model predicted unoccupied sites well for the Rusty Blackbird (95% correct), but only correctly predicted occupied sites in 41% of cases, for an overall success rate of 75%. Rusty Blackbird occupancy was primarily explained with water cover, as all sites with >11% mean cover of WATER were occupied. For sites with a lower mean cover of water, a higher proportion of remaining occupied sites were associated with a lower cover of PICTOT (40% of sites with <5.5% mean cover of PICTOT were occupied, as compared to 6% with >5.5% mean cover of PICTOT).

Occupancy of Olive-sided Flycatcher was associated with site having a mean SBA <= 13 m^2, with 70% of sites exhibiting this feature being occupied. For sites that had a higher stand basal area than this threshold, all sites with >5.2 TREES<5 m were occupied. Unoccupied sites were correctly predicted in 76% of cases, and occupied sites correctly predicted in 78% of cases, with overall model classification success of 75%.

Canada Warbler-occupied sites were associated with OSMCIN cover, as 66% of sites with >7.5% OSMCIN cover were occupied (as compared to only 20% of sites below this threshold). For sites with >7.5% OSMCIN cover, likelihood of occupancy increased with number of deciduous trees >5 m. Of sites with >7.5% and >0.9 DECTREE>5, 80% were occupied by Canada Warbler. The model classified unoccupied sites correctly in 90% of cases, and occupied sites correctly in 63% of cases, for an overall success rate of 80%.

2.3.2. Comparisons between harvest treatments and species

When testing harvest treatments for significant associations using ISA, there were few habitat cover means significantly indicative of harvest condition for any bird species. The exceptions were KALANG mean and standard deviation being significant for Rusty Blackbird-occupied sites in harvest matrices, and SHRTOT and TREES<5 being significant for Canada Warbler-occupied sites in harvest matrices (Table 2.7).

In general, when comparing all sites by harvest treatment using ISA, those in harvest matrices were significantly indicated by means of KALANG, ACERUB, debris, and CON<5, as well as standard deviation of KALANG, DEBRIS, SHROT, ACERUB, DECSHR, TREES<5, CON<5, VIBNUD. No particular variables emerged as significant indicators of sites in non-harvest matrices. When sites occupied by each of the three species were compared to each other using MrPP, significant differences emerged overall for means and standard deviations (Table 2.8; Table 2.9). When compared pairwise, means between Canada Warbler and the other two species significantly differed in mean habitat cover, with Canada Warbler differing from both Rusty Blackbird and Olive-sided Flycatcher in standard deviation of habitat cover. Olive-sided Flycatcher and Rusty Blackbird did not significantly differ.

When sites occupied by three species were compared to one another using ISA, Rusty Blackbird sites were associated with a suite of forest structure variables, whereas Olive-sided Flycatcher sites were significantly indicated by mean cover of GAYBAC (Table 2.10). Canada Warbler-occupied sites were significantly indicated by cover and standard deviation of VIBNUD.

NMDS converged on a 2-dimensional solution, and ordination showed no clear grouping between sites occupied by each of the species (Figure 2.4). The final solution was significantly different than that which could have been obtained by chance for both dimensions (axis 1: data mean = 48.1, randomized mean 51.2, $P < 0.01$; axis 2, data mean = 27.0, randomized mean 33.8, $P < 0.01$).

2.4. DISCUSSION

In general, relative abundances of breeding forest birds are better predicted by forest structure than cover type or size class of trees (e.g. birds in New England forests; DeGraaf et al. 1998). However, in my study, habitat variables reflecting both vegetation and structure emerged as important, including particular plant species as well as structural features such as stand basal area and canopy cover.

Differences emerged between occupied and unoccupied sites for these three SAR in wet forest habitats. Mud and water were important in sites occupied by Rusty Blackbird, which has been documented in other regions (Matsuoka et al. 2010a; Powell et al. 2010a; Avery 2013a). Unlike other studies, coniferous trees in the shrub layer and small conifers in the tree layer did not emerge as significant, and sites with lower total frequency and cover of spruce trees were more likely to be occupied. The latter may have been a product of my forest inventory method (variable radius prism plot), which includes fewer small trees if they are at low density, as well as the effect of sampling across a larger transect rather than focusing only on nest sites. High deciduous shrub cover was associated with unoccupied sites for both Rusty Blackbirds and Olive-sided Flycatchers, results consistent with coniferous forest habitat associations reported in other parts of their range (Altman & Sallabanks 2010; Avery 2013b).

Sallabanks et al. (2006) found canopy cover to be an important proximate structural mechanism driving the distribution and abundance of Olive-sided Flycatchers. In my study, canopy cover was important for both Olive-sided Flycatcher and Canada Warbler, with the former being associated with more open canopies and a higher stand basal area, indicating a patchy, open condition of larger trees, while Canada Warbler-occupied sites had higher canopy coverage. Capturing structural complexity in the lower strata is particularly important for Canada Warblers (Lambert & Faccio 2005; Hallworth et al. 2008b; Reitsma et al. 2013). High shrub stem density is critical for breeding Canada Warblers (Flockhart & Range 2007; Hallworth et al. 2008a), though in Nova Scotia cinnamon fern (*Osmunda cinnamomea*) in conjunction with dense shrubs may provide a similar role, like rhododendrons in the southern extent of their breeding range (Reitsma et al. 2010). Hunt et al. (2015) found higher shrub density in observed locations as compared to unused locations, which was consistent with my results. My results also indicated a mixedwood condition based on the presence of deciduous shrubs and trees.

As my habitat measurements did not differ significantly between occupied sites in harvest vs. non-harvest matrices, structural and vegetation features important for habitat use are retained in the context of forest management. Sites occupied by focal species in harvested landscapes included leave patches and buffers around clearcuts, containing remnant wetland edges and unharvested wet forest habitat strips adjacent to disturbed areas. Other studies have documented the use of both managed and unmanaged areas for these species (Powell et al. 2010b; Hunt et al. 2015). Rusty Blackbirds may equally prefer to nest in managed and unmanaged landscapes (Powell et al. 2010b). Canada Warblers have been documented to be equally abundant in both shelterwood and clearcuts, particularly in a matrix including mature forest (King & DeGraaf 2000). They have also been found in higher densities in post-harvest areas than in post-fire areas, presumably due to affinity for a dense shrub layer (Hobson & Schieck 1999).

To maintain occupancy in managed landscapes, harvesting practices need to ensure maintenance and/or creation of favourable structural habitat conditions. Lambert & Faccio (2005)'s extensive stewardship guidelines for CAWA in northeastern US forests include retaining areas of high shrub density, understory foliage (including ferns), and a structurally complex forest floor. However, for all three species, habitat associations change across their ranges (for region-specific habitat descriptions, see Altman & Sallabanks 2010; Reitsma et al. 2010; Avery 2013), and as such, management prescriptions need to be regionalized.

On a landscape scale, harvested lands can support a broad array of bird species (Becker et al. 2011). As Olive-sided Flycatchers forage from the edges of older stands into open wetlands or clear-cuts, this species may persist in fragmented landscapes where mature forest is juxtaposed with early seral stages (DeGraaf & Yamasaki 2003). In natural conditions, where Rusty Blackbirds use muddy open areas adjacent to wet forest for foraging, identifying and managing the necessary degree of habitat heterogeneity may be an important component of retaining these species on the landscape (Chambers 1999).

In the Nova Scotian context, maintenance of wet forest areas may be preferable to creating early seral stage habitat. In the SNBR, all three species are associated with wet areas and wet habitat features. When habitat variables were considered together, the combined habitat response did not significantly differ between Olive-sided Flycatcher and Rusty Blackbird, and both species use wet coniferous sites. Conserving these species in tandem may be possible as long as key individual habitat needs (e.g. areas of mud and open water for Rusty Blackbird, mature coniferous edges for Olive-sided Flycatcher) are met and prioritized in the management approach.

Horizontal variation in habitat features, as measured by their standard deviation, was frequently important for Canada Warbler, and significantly different from that of the other two species. This suggests more heterogeneous structure across the site. This is likely related to the different territory sizes: Canada Warbler territory sizes are approximately 1 ha, with size depending on habitat quality (Reitsma et al. 2008; Hunt et al. 2015), and the 100-m transect distance across the landscape where I measured habitat characteristics may have exceeded an individual territory, suggesting more heterogeneous patches across the site in areas adjacent to the territory. On the other hand, Olive-sided Flycatchers and Rusty Blackbirds have territories or home ranges 10-20 ha in size (Altman & Sallabanks 2010;

Powell et al. 2010a). As their territories greatly extend beyond a 50 m radius, they will be patchy, and may include smaller mixedwood wet forest components suitable for Canada Warbler.

At present, cutting regulations in Nova Scotia mandate retaining small leave patches (10 trees per hectare cut), clustered near the edge of the cut, and riparian buffers of 20-60 m depending on the width of the watercourse (Province of Nova Scotia 2002). To encompass nesting habitat of all three species at risk, I recommend riparian and wetland buffers be extended to minimum of 100 m around cuts, though 250 m would be preferable to include one or more complete territories, minimize crowding, protect from upland predators, and limit edge effects (Powell et al. 2010b). Wet forest areas are not currently protected by law, but are often poor operating environments for harvesting. Habitat features identified as important for these Rusty Blackbird and Canada Warbler (e.g. mud puddles, open water, cinnamon fern, complex ground structure) could be compromised by the impact of harvesting machinery on soils. Under current buffer regulations, trees and snags identified as important for the Olive-sided Flycatcher would be removed from the landscape in and around wet areas. Existing leave patches would likely not be large enough to retain habitat for these species, particularly the Olive-sided Flycatcher and Rusty Blackbird, who are using predominantly treed areas with openings within a larger forest matrix.

For Canada Warblers in Alberta, preserving riparian buffers is thought to be more important than maintaining residual patches for mitigating effects of forest harvesting (Hunt et al. 2015). Given the similarities in wet forest habitat near clear-cuts for the other two species, this seems likely true for Olive-sided Flycatchers and Rusty Blackbirds in the SNBR. Conserving or managing for the two species with larger territories may in some landscapes capture Canada Warbler habitats within, though ground verification would be needed to assess for habitat features specifically associated with Canada Warbler.

Although my study suggests that occupied sites in managed and protected forest landscapes have few vegetation differences that are important for the three species, this does not mean the habitat is equally suitable. Habitats in managed landscapes may be functionally different in ways that reduce fitness. In New England, Rusty Blackbird nests found in harvested sites (<20 years since cutting) were concentrated in more upland terrain and contained less standing water, which is known to be an important source of invertebrates for feeding (Powell et al. 2010b). Rusty Blackbird nests in harvested areas are more than twice as likely to fail, predominantly due to predation (Powell et al. 2010b). Increased nest predation, as a result of forestry practices, may be a significant factor for bird populations, particularly when it facilitates access by generalist predators (Darveau et al. 1997).

The ecological trap hypothesis posits that organisms experiencing lower success in one habitat type will not perceive differences in success at the time of selection, and preferentially choose the poorer habitat (Villard et al. 2007). A equal-preference version of this hypothesis has been suggested for both Rusty Blackbird and Olive-sided Flycatcher (Powell et al. 2010b; Robertson & Hutto 2013), suggests that nests in proximity to timber harvest are both less productive and less successful. Such effects have been documented in other bird species: forest harvesting can result in higher nest predation rates (Hoover et al. 1995), and increased competition for resources. It can also reduce availability of arthropods (Duguay et al. 2000). In nearby New Brunswick, harvesting has been implicated in longer breeding dispersal distances for Black-throated Blue Warbler (*Dendroica caerulescens*) and Blackburnian Warbler (*Dendroica fusca*) (Betts et al. 2006b). When a forestry-mediated ecological trap hypothesis was explicitly tested for interior species in this region, it was disproved as there were no reductions in productivity for populations in managed areas (Villard et al. 2012). However, the problem may still be salient for the Rusty Blackbird and Olive-sided Flycatcher given their use of edge habitats. Canada Warblers use interiors and edges, and may also experience an ecological trap effect. Males nesting in post-harvest stands have larger range sizes than those in unharvested areas, suggesting they required a larger area to meet foraging requirements (Hunt et al. 2015). However, in Alberta, fledging success did not differ between managed and protected areas (Hunt et al. 2015).

The present study assessed habitat only, and did not locate nests or monitor breeding success. As such, I cannot draw any conclusions about individual fitness in managed or unmanaged habitats. Finally, field study of nests is needed to assess reproductive success in managed and unmanaged habitats in the SNBR, as well as assess the impact of retaining forest buffers on populations on these species. Further study should be given to the effects of habitat fragmentation (Villard & Metzger 2014), as patch size effects are most pronounced for interior species and least pronounced for edge species (Bender et al. 1998). Future work should also include population modeling, including sources and sinks based on field-collected demographic data, to determine if modified habitats serve as ecological traps (Donovan & Thompson 2001).

2.5. TABLES AND FIGURES

Table 2.1 Reduced set of habitat variables measured at sites occupied by one or more of the target species (Rusty Blackbird, Olive-sided Flycatcher, or Canada Warbler) in harvested areas and non-harvested areas in the Southwest Nova Biosphere Reserve, Nova Scotia.

Vertical Layer	Mnemonic	Description
Canopy % Cover	CANOPY*	Cover in the overstory canopy measured by a densiometer
Ground % Cover	DEBRIS*	Total of downed woody material, including fine and coarse woody debris
	MUD*	Mud, or damp soil/bare ground that would become muddy in wet conditions
	ROCK	Exposed bare rock, including boulders and talus
	LICHEN	All lichen species
	WATER*	Open water or puddle
Herbs (<0.25m) % Cover	MOSS	All moss species except HYLSPL, HYPNUM, and SPHAG
	HYLSPL	Stair-step moss (*Hylocomium splendens)*
	HYPNUM	*Hypnum* spp. mosses
	SPHAGN*	*Sphagnum* spp. mosses
	AQUVEG	Aquatic vegetation growing in open water
	OSMCIN*	Cinnamon fern (*Osmunda cinnamomea)*
	PTEAQU	Bracken fern (*Pteridium aquilinum)*
	WOOVIR	Virginia chain fern (*Woodwardia virginica)*
	DRYFER	Ferns associated with mesic to dry habitats, excluding PTEAQU
	WETFER	All ferns of wet habitats, excluding OSMCIN and WOOVIR
	GRASS	Grasses (species in family Poaceae)
	HERBAC*	All herbaceous species, summed
	MAICAN	Wild lily-of-the-valley (*Mainthemum canadense)*
	TOXRAD	Poison ivy (*Toxicodendron radicans)*
	VACTOT	Blueberry spp. (esp. *Vaccinium angustifolium*), summed
	VIOLSP	Violets (*Viola* spp.), summed
	JUNEFF	Common rush (*Juncus effuses)*
	CARTRI	Three-seeded sedge (*Carex trisperma)*
	SEDRUS	Sedge and rush species, summed

Vertical Layer	**Mnemonic**	**Description**
Shrub Layer (0.25-5m) % and Height	CONSHR*	Coniferous trees in the shrub layer, totalled
	ABIBAL	Balsam fir (*Abies balsamifera)*
	PICMAR	Black spruce (*Picea mariana)*
	PICRUB	Red spruce (*Picea rubens)*
	PICTOT*	All spruce (*Picea* spp.), summed
	DECSHR*	Broad-leaved plants in the shrub layer, summed
	ACERUB*	Red maple (*Acer rubrum)*
	ALNINC*	Speckled alder (*Alnus incana rugosa)*
	CHACAL	Leatherleaf (*Chamaedaphne calyculata)*
	GAYBAC	Black huckleberry (*Gaylussacia baccata)*
	ILEMUC*	False holly (*Ilex mucronata)*
	ILEVER	Canada holly (*Ilex verticellata)*
	KALANG	Lambkill (*Kalmia angustifolia)*
	RHOCAN	Rhodora (*Rhododendron canadense)*
	RHOGRO	Bog Labrador tea (*Rhododendron groenlandicum)*
	VIBNUD*	Wild raisin (*Viburnum nudum var. cassinoides)*
	SHRTOT*	All shrub layer plants, summed
Stand Density	TREEHT*	Mean height of all trees in forest inventory plot
	SBA*	Basal area calculated from all prism plots
	CONTREE<5*	Number of softwood trees <5m tall in all prism plots
	CONTREE>5*	Number of softwood trees >5m tall in all prism plots
	DECTREE<5*	Number of hardwood trees <5m tall in all prism plots
	DECTREE>5*	Number of hardwood trees >5m tall in all prism plots
	SNAG<5*	Number of standing dead trees <5m tall in all prism plots
	SNAG>5*	Number of standing dead trees >5m tall in all prism plots

*Variables retained for Kruskal-Wallis and Classification and Regression Tree tests

Table 2.2. Number of sampled sites occupied by Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL) and Canada Warbler (CAWA) in each ecodistrict and treatment class.

Species	Treatment	Sites sampled	Ecodistrict				
			720	**730**	**740**	**750**	**760**
RUBL	Total	37	15	3	13	5	1
	Harvest Matrix	21	12	2	6	1	0
	Non-Harvest Matrix	16	3	1	7	4	1
OSFL	Total	45	17	4	15	3	6
	Harvest Matrix	26	15	2	5	0	4
	Non-Harvest Matrix	19	2	2	10	3	2
CAWA	Total	38	12	5	12	3	6
	Harvest Matrix	18	3	2	11	1	1
	Non-Harvest Matrix	20	9	3	1	2	5
Total	Total	99	34	11	33	10	11
	Harvest Matrix	54	28	7	9	3	7
	Non-Harvest Matrix	45	6	4	24	7	4

Table 2.3: Results of multi-response permutation procedure testing for mean and standard deviation of 53 vegetation response variables across ecodistricts. A = Chance-correct within-group agreement.

Variable Type	Number of samples in ecodistrict					A	*P*
	720	**730**	**740**	**750**	**760**		
Mean	34	33	11	10	11	0.0157	**<0.001**
SD	34	33	11	10	11	0.0199	**<0.001**

Table 2.4: Results of pairwise comparisons from multi-response permutation procedure testing for mean and standard deviation of 53 habitat variables across ecodistricts. A = Chance-correct within-group agreement.

Responses	**Ecodistrict Pairwise Comparisons**	**A**	***P***	**Holm-Bonferroni adjusted *P***
Mean	720 vs. 740	0.0120	<0.001	**0.003**
	740 vs. 760	0.0206	0.001	**0.005**
	750 vs. 760	0.0266	0.006	0.048
	730 vs. 760	0.0218	0.011	0.074
	720 vs. 760	0.0095	0.017	0.101
	720 vs. 750	0.0088	0.018	0.101
	740 vs. 730	0.0036	0.180	0.718
	720 vs. 730	0.0003	0.429	1.000
	740 vs. 750	-0.0011	0.548	1.000
	730 vs. 750	-0.0035	0.627	1.000
SD	720 vs. 740	0.0141	<0.001	**<0.001**
	740 vs. 760	0.0250	<0.001	**<0.001**
	750 vs. 760	0.0309	0.003	0.027
	720 vs. 760	0.0123	0.005	0.032
	730 vs. 760	0.0233	0.007	0.042
	720 vs. 750	0.0107	0.009	0.044
	740 vs. 730	0.0045	0.141	0.563
	740 vs. 750	0.0025	0.255	0.766
	730 vs. 750	0.0040	0.295	0.766
	720 vs. 730	0.0004	0.415	0.766

Table 2.5: Results of multi-response permutation procedure testing for mean and standard deviation of 53 habitat variables for Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA), compared across site conditions of occupancy and harvest matrix. Column title abbreviations: O = Occupied, UO = Unoccupied, A = Chance-correct within-ground agreement, H = Harvest matrix, NH = Non-harvest matrix.

		n				**n**			
Species	**Type**	**O**	**UO**	**A**	***P***	**H**	**NH**	**A**	***P***
RUBL	Mean	37	62	0.0099	**<0.001**	21	16	0.0027	0.235
	SD	37	62	0.0075	**<0.001**	21	16	0.0040	0.159
CAWA	Mean	38	61	0.0131	**<0.001**	20	18	0.0077	0.054
	SD	38	61	0.0124	**<0.001**	20	18	0.0084	0.037
OSFL	Mean	45	54	0.0083	**<0.001**	19	26	-0.0009	0.555
	SD	45	54	0.0067	**0.001**	19	26	0.0004	0.413

Table 2.6: Indicator values (IV) from indicator species analysis (ISA) using the mean and SD of habitat variables measured for sites occupied by the Rusty Blackbird (RUBL; n = 37, occupied, and n = 62, unoccupied), Olive-Sided Flycatcher (OSFL; n = 45, occupied, and n = 54, unoccupied), and Canada Warbler (CAWA; n = 38, occupied, and n = 61, unoccupied) in the Southwest Nova Biosphere Reserve. Group identifies whether sites that were occupied (O) or unoccupied (UO) had the maximum indicator value (IV). Only significant ISA results are shown.

				Observed IV		**Randomized Groups IV**		
Species	**Type**	**Variable**	**Group of Max IV**	**O**	**UO**	**Mean IV**	**SD**	***P***
RUBL	Mean	SHRTOT%	UO	36	64	53.2	2.46	<0.001
		DECSHR%	UO	33	64	52.4	3.01	0.002
		WATER	O	24	1	10	2.91	0.001
		MUD	O	46	13	31.3	4.51	0.009
	SD	MUD	O	50	13	32.9	4.12	0.001
		WATER	O	25	1	11.2	3.01	0.001
		AQUVEG	O	14	0	5.1	2.09	0.006

Species	Type	Variable	Group of Max IV	Observed IV O	Observed IV UO	Randomized Groups IV Mean IV	Randomized Groups IV SD	*P*
OSFL	Mean	Canopy	UO	56	44	51.3	1.21	<0.001
		ILEVER%	UO	23	0	12.1	3.33	0.009
		SNAG<5	O	26	61	47.4	4.17	0.005
		TREES<5	O	34	60	51	3.15	0.007
	SD	MAICAN	UO	32	4	19.4	3.47	0.006
		ILEVER%	UO	26	1	14.3	3.53	0.006
CAWA	Mean	DRYFER	UO	56	15	39.7	4.25	0.004
		OSMCIN	O	12	64	36	4.25	<0.001
		ALNINC%	O	7	54	28.5	4.3	<0.001
		Canopy	O	45	55	51.3	1.24	0.003
		ILEMUC%	O	5	36	21.8	4.13	0.004
		SPHAGN	O	37	59	50.9	2.69	0.007
	SD	CANOPY	UO	60	40	52.4	1.99	0.002
		DRYFER	UO	54	22	42.5	3.67	0.007
		OSMCIN	O	17	58	37.5	3.77	<0.001
		ALNINC%	O	9	52	29.1	3.95	<0.001
		TOXRAD	O	5	30	18	3.58	0.005
		ILEMUC%	O	9	39	24.7	4.02	0.006

Table 2.7: Indicator values (IV) from indicator species analysis (ISA) using the mean and SD of habitat variables measured for sites occupied by Rusty Blackbird (n = 21, harvest, and n = 16, non-harvest), Canada Warbler (n = 20, harvest, and n = 18, non-harvest), and Olive-sided Flycatcher (n = 26, harvest, and n = 19, non-harvest) in the Southwest Nova Biosphere Reserve. Group identifies whether harvested (H) or non-harvested (NH) landscapes had the maximum indicator value (IV). Only significant ISA results are shown.

				Observed IV		Randomized Groups IV		
Species	**Type**	**Variable**	**Group of Max IV**	**H**	**NH**	**Mean**	**SD**	***P***
RUBL	Mean	KALANG%	H	70	9	42.2	6.89	0.001
	SD	KALANG%	H	70	9	42.3	6.69	0.001
CAWA	SD	SHRTOT%	H	39	61	53.1	2.41	0.001
		TREES<5	H	31	69	55.1	3.89	0.002
ALL	Mean	KALANG%	H	62	12	39.3	4.36	<0.001
		ACERUB%	H	64	14	42.7	4.82	<0.001
		Debris	H	63	32	51.2	3.32	0.003
		CON<5	H	56	19	40.7	3.91	0.004
	SD	KALANG%	H	64	12	38.8	3.95	<0.001
		DEBRIS	H	63	34	51.7	2.93	0.001
		SHRTOT%	H	59	41	52.2	1.82	0.001
		ACERUB%	H	58	13	38.1	4.58	0.002
		DECSHR%	H	60	38	51.9	2.32	0.003
		TREES<5	H	60	33	50.1	2.86	0.003
		CON<5	H	54	21	40.5	3.71	0.004
		VIBNUD%	H	36	5	23.3	4.14	0.007

Table 2.8: Results of multi-response permutation procedure tests comparing mean and standard deviation of vegetation variables for sites occupied by Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA).

	n				
Variable Type	**RUBL**	**OSFL**	**CAWA**	**Chance-correct within-group agreement (A)**	***P***
Mean	37	45	38	0.0108	**<0.001**
SD	37	45	38	0.0134	**<0.001**

Table 2.9: Results of pairwise comparisons in multi-response permutation procedure tests comparing mean and standard deviation of habitat variables for sites occupied by Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA).

Pairwise Comparisons	**Variable Type**	**A**	***P***	**Holm-Bonferroni adjusted *P***
RUBL vs CAWA	Mean	0.0133	<0.001	**<0.001**
RUBL vs OSFL	Mean	0.0070	0.006	**0.012**
OSFL vs CAWA	Mean	0.0050	0.025	0.024
RUBL vs CAWA	SD	0.0159	<0.001	**<0.001**
OSFL vs CAWA	SD	0.0090	0.004	**0.008**
RUBL vs OSFL	SD	0.0062	0.027	0.027

Table 2.10: Indicator values (IV) and significant results of indicator species analysis for means and standard deviations of habitat variables when comparing sites occupied by Rusty Blackbird (RUBL, n = 37), Olive-sided Flycatcher (OSFL; n = 45,) and Canada Warbler (CAWA; n = 38) in the Southwest Nova Biosphere Reserve.

		Species of Max	Observed IV			Randomized Groups IV		
Type	**Variable**	**IV**	**RUBL**	**OSFL**	**CAWA**	**MEAN**	**SD**	***P***
Mean	TREES>5	RUBL	46	30	23	36.6	1.94	<0.001
	SBA	RUBL	41	34	24	35.3	1.32	0.001
	SNAG<5	RUBL	51	18	18	34.6	3.76	0.001
	SNAG>5	RUBL	49	22	12	33.8	3.77	0.001
	CON>5	RUBL	43	29	24	35.6	2.01	0.002
	TREES<5	RUBL	44	29	22	36.2	2.62	0.004
	GAYBAC	OSFL	2	29	7	16.6	3.73	0.006
	VIBNUD	CAWA	4	1	35	14.6	3.63	<0.001
SD	SNAG<5	RUBL	45	20	22	33.4	3.01	0.004
	VIBNUD	CAWA	5	2	40	17.3	3.65	<0.001

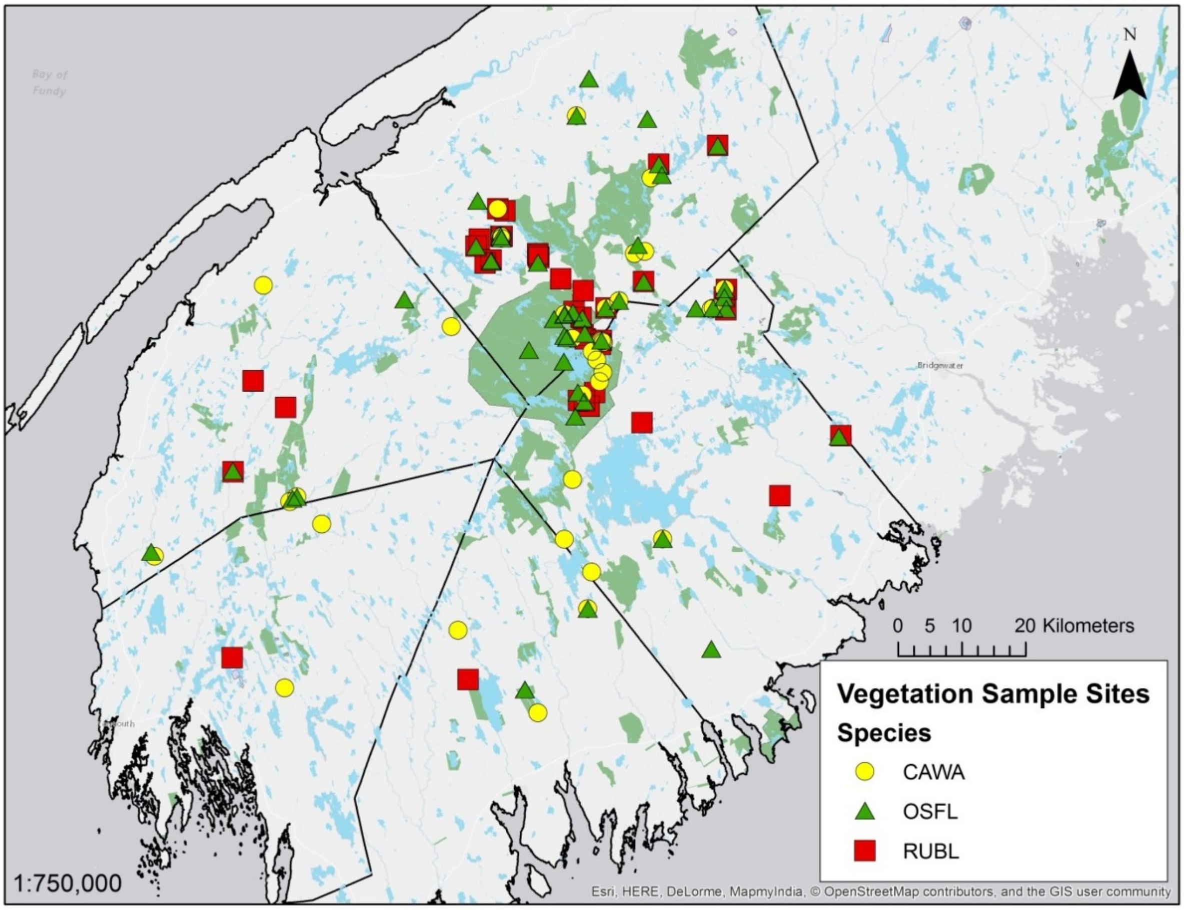

Figure 2.1: The five counties of the Southwest Nova Biosphere Reserve (outlined in black), with protected areas shaded in green. Indicated by symbols are sites sampled for vegetation composition and structure in known locations of Rusty Blackbird (RUBL; red squares), Olive-sided Flycatcher (OSFL; green triangles), and Canada Warbler (CAWA; yellow circles).

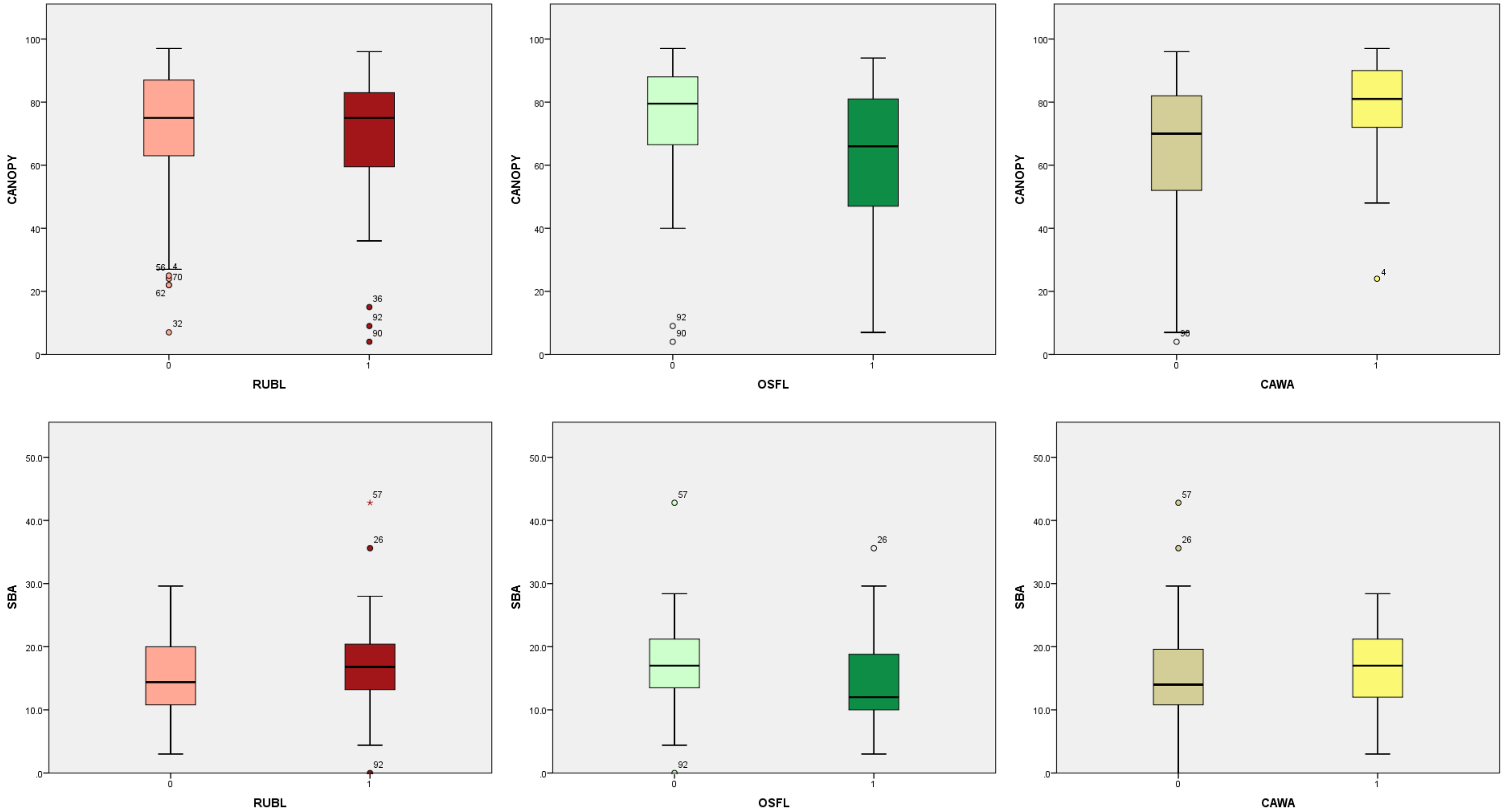

Figure 2.2: Boxplots showing distribution of mean canopy cover (CANOPY, top row) and mean stand basal area (SBA, bottom row) in 99 sites unoccupied (group = 0) and occupied by (group = 1) the Rusty Blackbird (RUBL; red), Olive-sided Flycatcher (OSFL; green), and Canada Warbler (CAWA; yellow) in the Southwest Nova Biosphere Reserve.

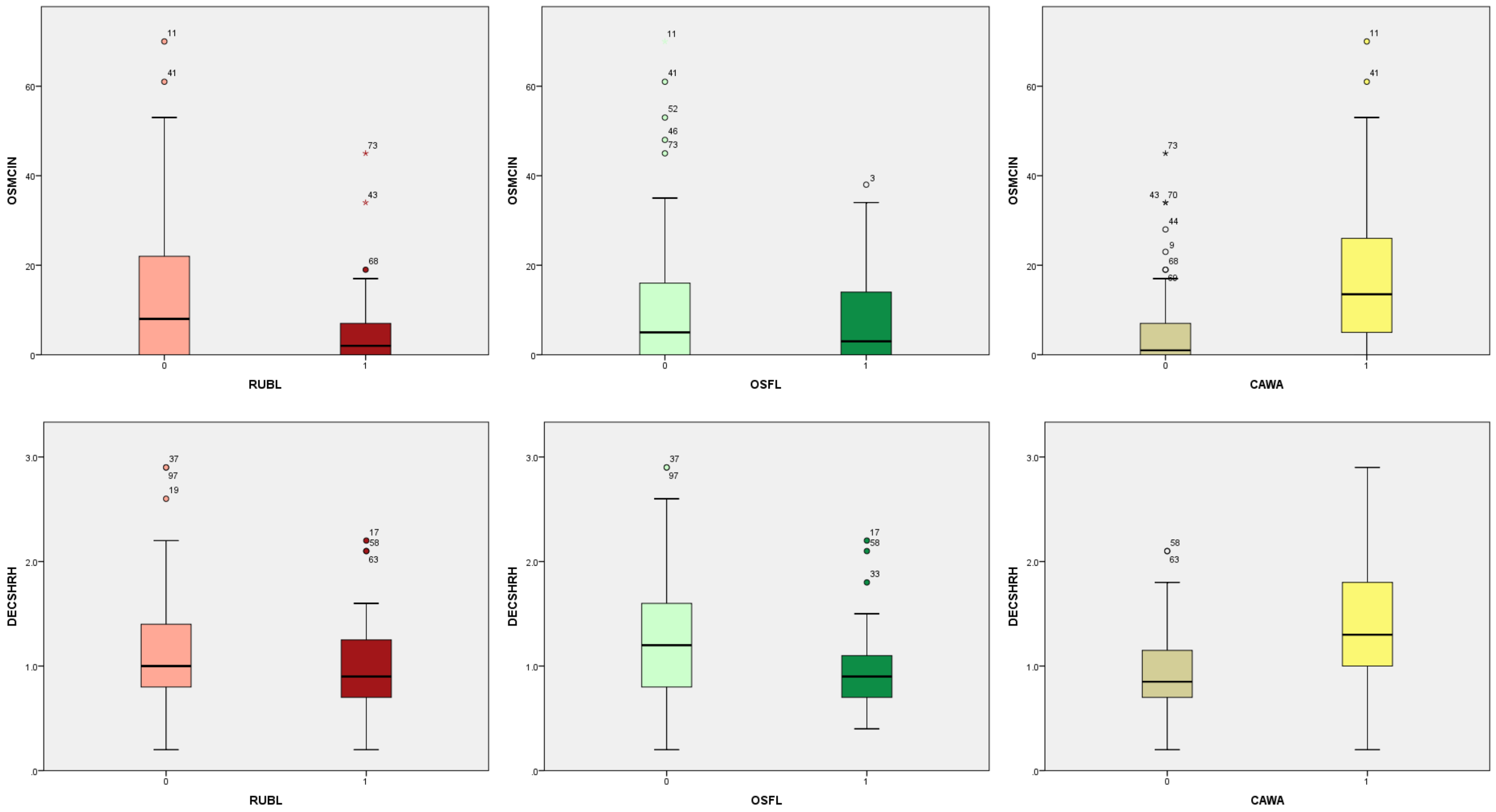

Figure 2.3: Boxplots showing distribution of mean cover of *Osmunda cinnamomea* (OSMCIN, top row) and mean height of deciduous shrubs (DECSHR, bottom row) in 99 sites unoccupied (group = 0) and occupied by (group = 1) the Rusty Blackbird (RUBL, red), Olive-sided Flycatcher (OSFL, green), and Canada Warbler (CAWA, yellow) in the Southwest Nova Biosphere Reserve

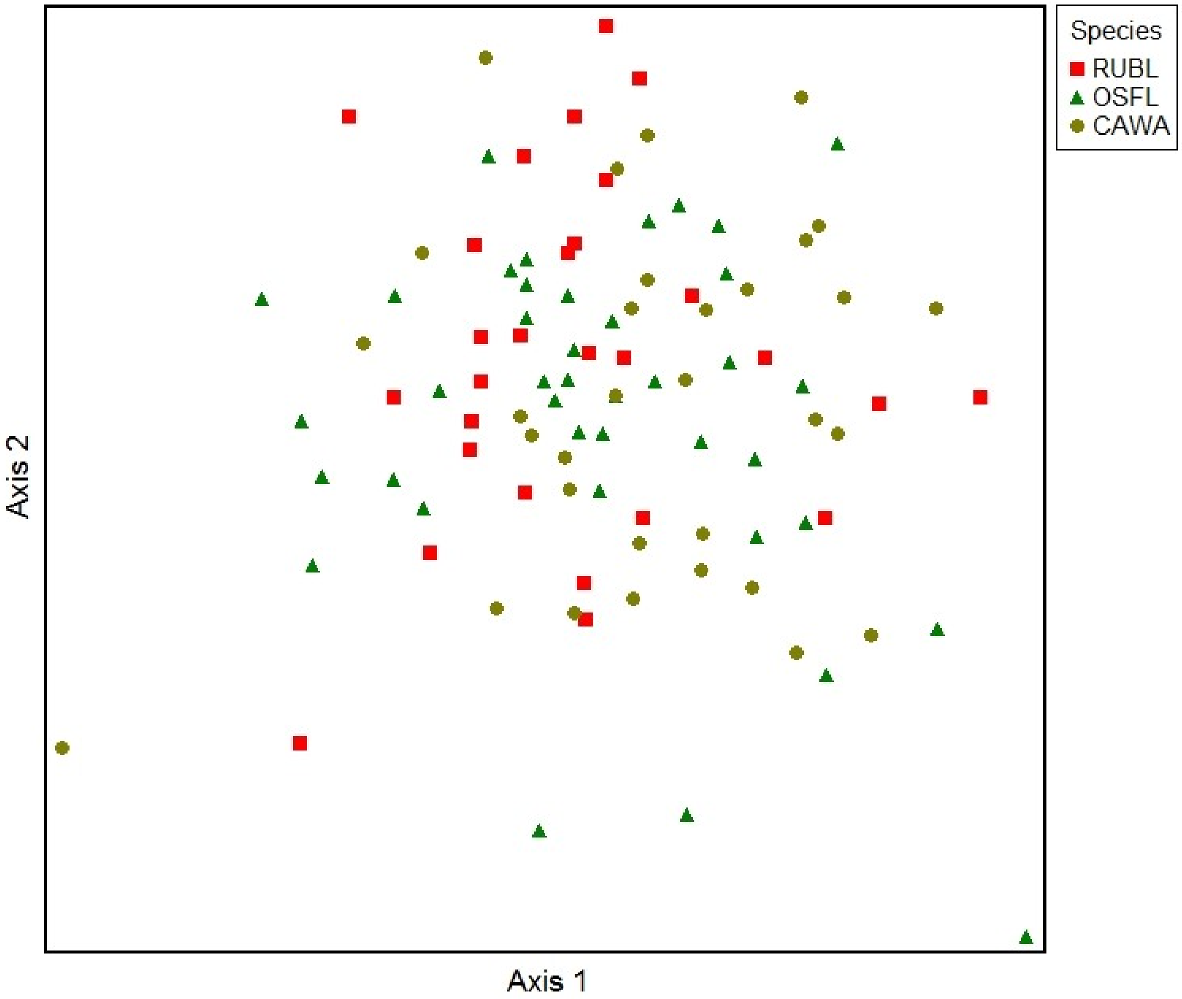

Figure 2.4: Ordination of final solution generated for means of habitat variables in sites occupied by Rusty Blackbird (n = 37, red squares), Olive-sided Flycatcher (n = 45, green triangles) and Canada Warbler (n = 38, yellow circles) in the Southwest Nova Biosphere Reserve. Solution generated by non-metric multidimensional scaling using 250 runs from random seed.

CHAPTER 3 GIS AND FOREST ECOSYSTEM CLASSIFICATION FOR MANAGEMENT PLANNING

3.1. INTRODUCTION

Forest managers often strive to conserve for wildlife values as part of sustainable forest management. This is particularly true for SAR, whose habitats or breeding sites may be legally protected. Typically, timber cutting operations are planned at using information at the scale of individual forest stands (1-10 ha), characterized by forest cover contiguous in species and age, subject to the same forest processes of growth, mortality, and competition (Neily et al. 2011; Wang et al. 2014), using GIS layers describing forest cover and disturbance. It is common for stand type to be field-verified before cutting, which typically includes on-the-ground timber cruises and forest ecosystem classification (FEC). Forest management plans that seek to mitigate impacts on SAR typically use GIS modeling of habitat or direct field surveys, assuming that SAR habitat can be adequately identified by classification tools used for stand-scale management.

In Nova Scotia, Canada, conservation planning is ongoing for three federally-listed landbird SAR that rely on wet forest habitat during the breeding season (Rusty Blackbird, Olive-Sided Flycatcher, and Canada Warbler; COSEWIC 2006, 2007, 2008; Government of Canada 2011). These species occupy areas that are protected as well as managed, including lands in and adjacent to recent forest harvesting. In the Maritimes, all three species commonly nest in or near wet forests to meet their insectivorous foraging requirements (Altman & Sallabanks 2010; Reitsma et al. 2010; Avery 2013).

Commonly employed in both forest management planning and conservation ecology, GIS analyses are used for assessing land cover (e.g. Rooney et al. 2012), predicting species distributions (e.g. Cumming et al. 2010; Barker et al. 2014), and designing management plans for species at risk (e.g. Akçakaya 2001; Beazley et al. 2005). GIS layers that classify forest characteristics can be used to describe habitat preferences for species, which are one the best ways to predict presence and abundance of bird species (Riffell et al. 2006). In Nova Scotia, GIS layers describing forest cover and Ecological Land Classification (ELC) have been used for SAR conservation planning (Beazley et al. 2005; Cameron & Neily 2008), including for these three SAR (Ferrari 2014; Westwood et al. 2015; Bale et al. *in prep*). However, before engaging in conservation activities based on GIS-derived models, it is important to understand potential sources of error governing their predictive inputs (Rooney et al. 2012), and how well they can describe habitat features for species under consideration. Furthermore, as different taxa interact with their environments at different spatial extents (Addicott et al. 1987), predictive relationships may be scale-dependent. Suitable GIS layers may not be available, or lack sufficient accuracy, to capture habitat features at the required scale.

3.1.1. Sources of error in GIS data for forest management

Despite their common use, GIS data are vulnerable to unreliability due to high levels of error (Bruce et al. 1997). When using these tools for management or conservation, it is important to know if available spatial data layers are accurate at capturing habitat features for SAR. At large scales, ecosystem mapping and classification often rely on remote sensing or photointerpretation. However, the best methods of classification only yield an average accuracy of approximately 80% (Johansen et al. 2007), commonly due to interpreter error or lack of definition in the images.

For the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in particular, characterizing wet forest types accurately is important. These are often poorly represented in GIS data (Klemas 2011; Kreakie et al. 2012) and their accuracy can fluctuate widely due to the ephemeral nature of many types of wetland (Gómez-Rodríguez et al. 2008; Skagen et al. 2008). Identifying wet forested areas using remote sensing is challenging because they tend to be small and patchy (Klemas 2011), and difficult to differentiate from upland forest (Riffell et al. 2006). Particularly for species using wet forest habitats, it is important to verify the accuracy of relevant spatial data layers before using models or mapped conservation products based on these layers.

3.1.2. A field-based verification and conservation tool

FEC is a tool originally developed for use by woodlot owners and forest managers to describe forest conditions, by field based stand-level categorization of forest ecosystems into coherent groups. Nova Scotia's FEC system uses dichotomous keys to allow a user to classify vegetation type and soil type for a field site, which is then used as a proxy for nutrient and moisture regime (Neily et al. 2011). These groups are used to inform harvesting and silvicultural management (e.g. Keefe & Mcgrath 2006; McGrath 2011). FEC has been applied to other ecological uses, such as forest fire and disease management (McRae 1996; Wiensczyk et al. 1996), but rarely to wildlife management (but see Bowman et al. 1996; Malcom et al. 2004; Aldridge & Boyce 2007).

Nova Scotia's FEC is unique compared to that of other jurisdictions in that it describes broad forest communities, including understory vegetation, cryptograms, and wildlife, as well as integrates directly into Canada's Ecological Land Classification (ELC) framework. ELC categorizes ecosystems based on climate and vegetation at a variety of scales, ranging from the regional extent (ecozones) down to the stand level (ecosections and ecosites; Ecological Stratification Working Group 1995). At the stand scale, management applications include forest planning, wood supply modeling, and silvicultural planning, among others (Neily et al. 2003). Nova Scotia's FEC, as part of the ELC, is currently used in forest management prescriptions on both public and private lands (Stewart & Neily 2009; McGrath 2011). However, the capacity of FEC to characterize and manage wildlife habitat has not been formally investigated.

Additionally, as part of the ELC system, Nova Scotia's FEC can be used to collect reference data on forest cover and soil characteristics. This information can be used as reference data to ground-verify GIS layers for ELC and forest cover (derived from the provincial Forest Inventory Database; FID). ELC has been mapped in Nova Scotia down to the level of ecosection (Neily et al. 2003), which includes soil texture and drainage. If FEC categories can be directly correlated to habitats for species at risk, they could also be used as an on-the-ground conservation tool by managers already engaging in FEC classification for forestry purposes.

My objectives were to (1) determine if habitat occupied by three landbird species at risk was associated with particular FEC forest groups, vegetation types, soil types, and ecosites; (2) investigate the accuracy rate of spatial datasets commonly used for forestry and conservation planning in habitats occupied by these species at risk through comparison of GIS datasets to field-collected FEC information; and (3) evaluate the potential of Nova Scotia's FEC system as a descriptor of habitat for these species, and assess management implications in a context of spatially inaccurate GIS layers.

3.2. METHODS

Field data were collected in the SNBR (1,546,374 ha, 65°24'7" W, 44°13'58 N). The SNBR is in the western ecoregion of Nova Scotia, characterized by a Maritime climate, and predominantly coniferous forest with associations of pine, spruce, and hemlock (Neily et al. 2008). The disturbance regime is characterized by small gaps created through windthrow, often due to the influence of hurricanes. On drier, richer soils, forest cover is characterized by sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghensis*) in combination with other tolerant hardwoods (Rowe 1972). Forests on moist sites across the SNBR are dominated by red maple (*Acer rubrum*) and black spruce (*Picea mariana*). On mesic, poorer sites, associations of eastern hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), and white pine (*Pinus strobus)* occur (Neily et al. 2008). Timber harvesting and land clearing has been occurring in this region for 300-400 years (Mosseler et al. 2003), and at present, large public and private land holdings devoted to forest harvesting exist in this area, as do small private woodlots. In addition, there are large protected areas under federal and provincial control.

In 2012-2013, I conducted FEC surveys at 98 locations in the SNBR known to be occupied by one or more of the three species of SAR (Figure 3.1). At each location, I established site centre at the GPS coordinates of known sighting (or the most likely nesting habitat within 50 m of the coordinates when detailed sighting information was unavailable). Three FEC plots were captured at each site: one ate the centre (centre plot), and at the ends of two 50-m transects (end plots). Transects were oriented a minimum of 90° from one another, in directions of potentially usable nesting habitat for the target species (e.g. if a centre plot was at a clear-cut edge, transects were not directed across the middle of the clear-cut). At each of the three FEC plots, I recorded the location in UTM coordinates with a handheld GPS unit, and classified the site into one of 14 forest groups (F-groups), 88 vegetation types (V-types), 19 soil types (S-types), and 16 ecosite types (Ecosites) using the Nova Scotia Department of Natural Resources FEC System (Keys et al. 2011a, 2011b; Neily et al. 2011). FEC information was recorded at centre plots in both 2012-2013, but only at end plots at sites sampled in 2013. Where possible, sites sampled in 2012 were revisited to gather FEC end-plot information. In total, end plot FEC information was collected for 70 of 98 sites. Twelve of 98 centre plots and 20 of 140 end plots received no V-type or Ecosite classification, due to being in an open condition (e.g. wetlands, clearcuts)I also surveyed forest and understory vegetation at plots established at 10-m intervals along each transect for investigation of the habitat associations of these three landbird species (see CHAPTER 2).

V-type, S-type and ecosite information was assessed for each bird species as frequencies and proportions of each category. Frequencies were cross-tabulated to assess if species used FEC units in proportion to their availability. I tested for strength of association using Phi (a chi-square-based measure) and contingency coefficients (cc; indicates proportional reduction in error when values of one variable are used to predict values of another). Analyses were only completed for forest group and ecosite type, as expected frequencies per category were too small for V-type and S-type. Statistical analyses were completed in SPSS 21 (IBM Corporation 2012), and the significance level was set at $\alpha = 0.05$. Sample sizes varied by test as a site occupied by more than one species could be included in the test more than once.

3.1.1. Error validation of spatial datasets

I used my field-collected vegetation and wetness data to verify two GIS landcover layers commonly used in provincial management planning for industry as well as species at risk conservation: the Forest Inventory Database (FID), and the ELC (Table 3.1). Based on orthorectified aerial photography, the FID layer classifies all provincial lands into one or more of 21 forest types and 18 non-forest types in polygons (non-forest types include catergories such as barrens, agricultural lands, etc.; NSDNR 2006). Forested areas are delineated into stands based on species, crown closure, and height, with a maximum coverage of four tree species recorded. ELC classifies polygons based on infrared photography into ecoregion, ecodistrict, and ecosection, and includes a description of soil moisture and texture at the ecosection level (1:10 000 scale; Neily et al. 2003).

FEC field data were integrated into a digital format to be compared to GIS data. I mapped the locations of the FEC plots as point data, and created circular buffers around each point at radii of 50 m and 100 m to assess scale-based differences in classification accuracy. FEC V-type and S-type were compared against FID cover type and ELC soil moisture and texture using a confusion matrix (also known as an error matrix or misclassification matrix). This generic method to assess the accuracy of nominal GIS datasets (Congalton & Mead 1983; Cihlar et al. 2003; Skirvin et al. 2004) is commonly used to compare categorical datasets based on remote sensing imagery with reference data collected on the ground to determine the level of error (Naesset 1995; Foody 2005; Johansen et al. 2007; Hart 2014).

I constructed nine confusion matrices, one at each buffer size for three variables: soil texture, soil moisture, and forest cover (Table 3.2). To complete the confusion matrices, I re-classified FEC F-group, V-type and S-type into congruent categories, and only included categories that were observed in the field (Table 3.3; Table 3.4; Neily et al. 2011). For V-types with two equally dominant species, I referred to field-collected habitat survey data (Chapter 2) to determine which species occurred more frequently at the plot in question, and reclassified the plot accordingly.

FEC points and buffer polygons were intersected with the FID and ELC layers, and corresponding FID categories for primary and secondary species recorded, as well as ELC soil texture and soil moisture. I used ArcGIS 10.2.2 (Esri Inc. 2014), with all map layers projected in NAD1983 UTM Zone 20N. I cross-tabulated reference data (field observations, columns) with classified data (mapped information, rows) in confusion matrices for each buffer size for each GIS layer-derived variable. For all three matrices, it was possible for more than one mapped class to be assigned to each plot, given multiple intersecting polygons within the buffer. In these cases, the category that was considered a 'match' for that FEC point was chosen (i.e. if the FEC point was assigned as RM – red maple, and the corresponding mapped categories were red maple and black spruce, the value was entered as RM in the confusion matrix). Both primary and secondary species were intersected from the FID layer. If no intersecting categories were a match, the buffer was assigned the category of the primary species of the polygon with highest percent cover. This was done to reflect accuracy relevant to a user searching for a desired category (for example, a user searching RM would locate all stands with a significant proportion of the species, rather than only where it was dominant).

For all matrices, the level of congruence between classified and reference data was quantified by calculating accuracy. For each variable category, producer's and user's accuracy was calculated by dividing the number of correctly classified samples by the total number of samples in that mapped class or field category (Story & Congalton 1986; Naesset 1995). Accuracy was the percent of samples that were correctly classified.

Cohen's Kappa (Cohen 1960) coefficient (k) is a commonly used tool for testing correctness in photointerpretation (Congalton & Mead 1983), and measures the relationship of expected disagreement to agreement beyond chance, incorporating both accuracy for individual categories and overall map accuracy. Kappa is calculated using the formula:

$$K = \frac{(d - q)}{(N - q)}$$

where *d* is the relative observed agreement (on the diagonal of the matrix), *q* is the proportion of values that are in agreement due to chance (the sum of the proportion of observed values in each class), and N is the total number of objects recorded in the matrix (Cohen 1960). Although *K* was calculated for all variables, coefficients for soil variables should be interpreted with caution, as categories were not necessarily exclusive (some soil types could have membership in more than one category). Sample size differed between variables due to inability to classify some plots.

3.3. RESULTS

In 2012 and 2013, I sampled 238 FEC plots at 98 locations in the SNBR, including 37 occupied by Rusty Blackbirds, 45 by Olive-sided Flycatchers, and 38 by Canada Warblers. Complete FEC information (including V-type, S-type, and ecosite) was gathered at 86 centre plots and 120 end plots.

3.2.1. Species-specific FEC associations

Eight of 14 possible forest groups were observed at sites occupied by these landbird at risk species. When considering all FEC plots, for all three species, forest group was most commonly classified as either wet deciduous (Rusty Blackbird = 28%, Olive-sided Flycatcher = 20%, Canada Warbler = 40%), spruce-pine (Rusty Blackbird = 25%, Olive-sided Flycatcher = 36%, Canada Warbler = 13%), or wet coniferous (Rusty Blackbird = 21%, Olive-sided Flycatcher = 34%, Canada Warbler = 36%). For centre plots only, proportions of the three categories used by Rusty Blackbird were similar, whereas Olive-sided Flycatchers and Canada Warblers were concentrated more strongly into both the wet coniferous and wet deciduous forest groups (70% of Olive-sided Flycatcher centre plots in these two types, and 83% of Canada Warbler centre plots; Figure 3.2). When looking at all centre and edge plots for individual V-types, Rusty Blackbirds and Olive-sided Flycatchers had ≤ 13% of samples in a single category, whereas Canada Warblers showed much higher frequency in two categories than any others: 24% of sites were classified as Red

Maple/Cinnamon Fern/Sphagnum (WD2, n = 20) and 21% as Black Spruce/Cinnamon Fern/Sphagnum (WC1 n = 21). Overall distribution of forest group for all plots significantly differed from that expected by chance (n = 241, Phi = .373, cc = 0.350, P = 0.002). However, when looking at centre plots only, F-group proportion did not differ from chance (n = 101, Phi = .373, cc = 0.424, P = 0.002).

Soil type was characterized as Organic at the largest proportion of all plots for all species (ST14, 50% of Rusty Blackbird sites, 51% of Olive-sided Flycatcher sites, and 73% of Canada Warbler sites; Figure 3.3). Other frequently observed soil types included Fresh – Medium to Coarse Textured (ST2; Rusty Blackbird = 11.4%, Olive-sided Flycatcher = 2%, Canada Warbler = 3%) and Moist – Medium to Coarse Textured (ST3; Rusty Blackbird = 5%, Olive-sided Flycatcher = 11%, Canada Warbler = 6%).

For all species, observed ecosites were prominently categorized as having high moisture and poor nutrient content (Figure 3.4). When all plots were considered, the highest proportion of plots for all species fell into two classifications: either Wet – Very Poor/Black spruce – Tamarack (AC4; Rusty Blackbird = 12%, Olive-sided Flycatcher = 21%, Canada Warbler = 32%) or Wet – Poor/Spruce – Fir – Red Maple (AC8; Rusty Blackbird = 17%, Olive-sided Flycatcher = 25%, Canada Warbler = 26%). Observed ecosite categories measured at centre-plots only did not differ from expected (n = 101, Phi = .481, cc = 0.396, P = 0.280), however, a significant difference was found when all plots were included (n = 241, Phi = .397, cc = 0.369, P = 0.019).

3.2.2. Classification error for GIS layers

When field-verified using the V-type and S-type component of FEC information, accuracy of GIS layers was poor overall. Total accuracy of soil drainage at FEC points when compared to ELC classification ranged from 28-32% (Table 3.5). When corrected for chance agreement using pseudo-categories, Kappa was reported as in the range of slight agreement at all buffer sizes (Table 3.6). Similar results were observed for soil texture (Table 3.7). Organic soils in particular were poorly captured by the GIS layer, and classified with only 17% accuracy at the FEC point, increasing to only 26% at the 100-m buffer. Removing organic soil categories from the analysis yielded a dramatic increase in accuracy and agreement, increasing Kappa agreement to fair-moderate for soil drainage, and to fair-substantial for soil texture (Table 3.8). Few samples were classified as ‘fine’ soils by FEC or ELC, resulting in a very low sample size for that category. Other than organic soils, drainage of FEC soil types frequently associated with the three target species at risk were generally well captured (ST3, 85-100% accuracy; ST2, 100%; ST15/G, 57-100%; ST16/G, 69-75%). Texture was well-captured for ST2, ST15, and ST16 (85-100% accuracy for all types across all buffers), but poorly for ST3 (40-45%).

Forest cover accuracy, measured by comparing dominant species classified by FID and FEC, was relatively high overall (Table 3.8). At the 0-m range, overall accuracy was 40% with a fair level of agreement (n = 209, $K = 0.29$). This increased to 55% at the 50-m range (n = 209, $K = 0.45$, moderate agreement) and 62% at the 100-m range (n = 209, $K = 0.53$, substantial agreement). The V-groups most commonly associated with sites occupied by Rusty Blackbirds, Olive-sided Flycatchers, and Canada Warblers were dominated by Black spruce, Red spruce, Balsam fir, Tamarack, and Red maple. Black spruce (n = 75) was identified by the FID in 47% of cases at 0 m, extending to 73% of cases at 100 m. Red spruce (n = 24) accuracy was 50% at all buffer sizes, while Red maple ranged from 37-60% accuracy (n = 63).

3.4. DISCUSSION

Nova Scotia’s FEC system was a useful descriptor of habitat relationships for these three landbird species, as it characterized occupied sites into existing vegetation, soil, and ecosite classifications. The Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler showed fidelity to a small proportion of the total available F-groups, S-types, and ecosites, with all species predominantly occupying habitat described by wet, poor conditions. Sites were characterized by organic soils and overstory species such as black spruce and red maple. Particularly since all three species consistently occurred in ecosites 4, 8, and 12 with high frequency, it may be possible to manage for all three species in concert in forested landscapes. Furthermore, they could potentially be used as focal species (Lambeck 1997) to conserve for broader ecological characteristics captured within these ecosite types.

Although habitat requirements of the three species overlap in Nova Scotia (Chapter 2), the territory size of the Rusty Blackbird and Olive-sided Flycatcher is much larger than that of the Canada Warbler. Canada Warbler sites were concentrated into fewer F-groups, S-types, and ecosites than the other species, suggesting greater homogeneity of habitat, which was corroborated by findings for vegetation variables measured in Chapter 2. For both the Rusty Blackbird and Olive-sided Flycatcher, examining centre plots only reduced the diversity of FEC categories observed, and may be useful for identifying potential areas used for the species for nesting, perching, or foraging. When end plots were taken into consideration, this provided insight to some of the site conditions occurring within territories, although it should be cautioned that true independence of end plots cannot be assumed due to the likelihood of spatial autocorrelation.

As evidenced by generally low classification accuracy overall, habitat types for these species are poorly captured at the stand level by Nova Scotia’s commonly-used GIS layers for forestry and conservation planning. However, reference data (in my case, FEC points) are generally considered 100% accurate (Stehman 1996). This may not have been true due to difficulties classifying the V-type of forest-wetland transitions, open wetlands or open clearcuts, and forests with co-dominant overstory species. Most of this error affected V-type classification, but would be unlikely to affect results for ecosites, which are more dependent on accuracy of F-group and S-type.

In my study, I relaxed the rules of correspondence and added greater search distances to maximize the possibility of assigning a match between classified and reference data. Although accuracy did increase with larger buffer sizes, the difference in accuracy between point level and a 100-m search distance was only large for forest cover (a 20% difference, compared with 6-10% for soil classification). Error was likely attributional in nature, from outdated imagery used for classification.

ELC did not capture organic soils well, and modifications to its classification method should be considered to better represent these features. ELC classifications would benefit from incorporating classification by hyperspectral imagery, which is a commonly-used method for estimating organic content in soils and allows for more accurate delineation of organic soil types (Lagacherie et al. 2006; Anne et al. 2014).

There is much interest in using remote sensing products as a surrogate for ecological system assessment, rather than more intensive methods that require site visits (Rooney et al. 2012). Bergeron et al. (2012) have asserted that biodiversity conservation in general is only feasible with the use of such surrogates. Vegetation cover is often used as the main explanatory covariate for stand and regional-scale species distribution modeling (e.g. Bustamante & Seoane 2004; Atamian et al. 2010). I believe there is a need to verify spatial products in individual jurisdictions before engaging in conservation planning, to appropriately assess the amount of uncertainty in modelled and mapped products. In some jurisdictions, using spatial layers as surrogates for biodiversity information has produced relatively little error (Rooney et al. 2012), though this was scale dependent, with bird diversity best predicted at a 500-m scale, and plant diversity best predicted at 100-m scale (which can be above stand-scale, which is as low as 1 ha resolution; Dickinson 2014). In Manitoba, verification of FID layers with FEC field data showed extremely poor agreement (Van de Vooren 2002). Nova Scotia's FID layer only showed good levels of agreement at the largest buffer size (100 m, 3.1 ha), which is larger than the territory size of the Canada Warbler. Given the variety of GIS products available from region to region, verifying the accuracy of spatial layers with respect to habitat requirements of the wildlife species under consideration will allow for better-informed management. In southwestern Nova Scotia, FEC ecosites are a promising tool for characterizing habitat for these SAR, whereas GIS layers used to capture these habitat features suffer from relatively poor accuracy, especially at smaller buffer sizes.

The potential for FEC to be used in disciplines beyond forest management is drastically understudied (McRae 1996). Once ecosite can be successfully and accurately mapped by GIS, or existing FIDs and ELC layers improve in accuracy, there is great potential to use

FEC associations for habitat management planning. Given that FEC is in daily use by forester professoinals, it also offers a simple tool that can immediately be used to incorporate habitat for SAR into integrated forest management systems. As the quality of spatial data improves with tools such as LiDAR (Wulder et al. 2014), it may be possible in future to accurately map ecosite or other FEC components. Until that time, GIS-based management planning for these SAR should be augmented with FEC-based habitat assessment in the field to identify potential breeding habitat and prevent its destruction by forest operations.

3.5. TABLES AND FIGURES

Table 3.1: Geographic Information System layers classifying forest vegetation cover and soil texture and moisture.

GIS Layer	Mne-monic	Description	Data Year	Scale	Rights	Citations
Forest Ecosystem Classification Plots	FEC	Field-collected forest ecosystem classification information, including vegetation type, soil type, and ecosite type. Georeferenced with handheld GPS unit.	2012-2013	N/A	Lab of Dr. Cindy Staicer, Dalhousie University	N/A
Ecological Land Classification	ELC	Land systems mapped from infrared aerial photography. Data used includes soil texture and moisture content.	1982-1999	1:50 000	Nova Scotia Department of Natural Resources - Forestry Division	NSDNR 2003
Nova Scotia Inventory Database	FID	Forest cover mapped from aerial photography. Data used includes primary and secondary overstory tree species.	1987-2006	1:50 000	Nova Scotia Department of Natural Resources - Forestry Division	NSDNR 2007

Table 3.2 : Variables compared between field-collected reference data and classified data to determine accuracy of GIS data layers.

			Data Origin	
Variable	**Mnemonic**	**GIS Data Layer**	**Classified (Mapped)**	**Reference (Verification)**
Soil moisture	SOILMOIS	Ecological Land Classification	Soil moisture category classified according to ecosection delineation from aerial photography	FEC S-type field classified using dichotomous key, moisture categorized by the presence of saturation features (oxidation and reduction)
Soil texture	SOILTEXT	Ecological Land Classification	Soil texture category classified according to ecosection delineation from aerial photography	FEC S-type field-classified using dichotomous key, texture categorized according to particle size classes
Tree species cover	TREECOV	Nova Scotia Forest Inventory Database	Tree species cover classified according to photointerpretation	FEC V-type classified using dichotomous key based on dominant overstory species; dominant overstory species indicated for that V-type

Table 3.3: Equivalency table for soil drainage and soil texture categories classified by the Nova Scotia Forest Ecosystem Classification (FEC) and Nova Scotia Ecological Land Classification (ELC).

Soil Drainage		
Code	**Description**	**Equivalent FEC Soil Types**
P	Poorly drained	ST4, ST7, ST10, ST13, ST14
I	Imperfectly drained	ST3, ST6, ST9, ST12, ST16, ST18
W	Well drained	ST1, ST2, ST5, ST8, ST11, ST15, ST17
X	Variable	ST19

Soil Texture		
Code	**Description**	**Equivalent FEC Soil Types**
C	Coarse textured - sands and loamy sands	ST1, ST2, ST8-C, ST9-C, ST10, ST15, ST16, ST17, ST18
M	Medium textured - sandy loams, loams, and silt loams	ST2, ST3, ST4, ST5, ST6, ST7, ST8, ST9, ST10, ST11, ST12, ST15, ST16, ST17, ST18
F	Fine textured - sandy clay loams, clay loams, and clay	ST5, ST6, ST7, ST11, ST12, ST13
X	Organic	ST14, ST19

Table 3.4 : Equivalency table for forest cover classified by the Nova Scotia Forest Ecosystem Classification (FEC) and Nova Scotia Forest Inventory Database (FID) in sites occupied by three landbird species at risk.

FEC V-Type Species			**FID Species**	
Code	**Name**	**Mean Cover of Primary & Secondary**	**Code**	**Name**
CE1	Eastern white cedar/Speckled alder/Cinnamon fern/Sphagnum	Eastern white cedar (50%) Red maple (10%)	EC	Eastern white cedar
IH1	Large-tooth aspen/Lambkill/Bracken	Large-tooth aspen (66%) Red maple (14%)	TA	Aspen (large-toothed, trembling)
IH2	Red oak - Red maple/Witch hazel	Red oak (33%) Red maple (33%)	RO/RM	Red maple/Red oak
IH7	Red maple/Hay-scented fern - Wood sorrel	Red maple (66%) Sugar maple (18%)	RM	Red maple
MW2	Red spruce - Red maple - White Birch/Goldthread	Red spruce (32%) Red maple (24%)	RS/RM	Red spruce/Red maple
MW2a	Red spruce - Red maple - White Birch/Goldthread, Aspen variant	Red spruce (34%) Large-toothed aspen (33%)	RS/TA	Red spruce/Aspen
MW4	Balsam fir - Red maple/Wood sorrel - Goldthread	Red maple (30%) Balsam fir (36%)	RM/BF	Red maple/Balsam fir
SH1	Hemlock/Pin cushion moss/Needle carpet	Hemlock (74%) Red spruce (9%)	EH	Eastern hemlock
SH2	Hemlock/White pine/Sarsaparilla	Hemlock (44%) White pine (26%)	EH	Eastern hemlock
SH3	Red spruce - Hemlock/Wild lily-of-the-valley	Red spruce (35%) Hemlock (31%)	RS/EH	Red spruce/Eastern hemlock
SH4a	Red spruce - White pine/Lambkill/Bracken, Red spruce variant	Red spruce (52%) Black spruce (23%)	RS	Red spruce
SH5	Red spruce - Balsam fir/Schreber's moss	Red spruce (63%) Balsam fir (13%)	RS	Red spruce
SH6	Red spruce - Balsam fir/Stair-step moss - Sphagnum	Red spruce (54%) Balsam fir (17%)	RS	Red spruce

FEC V-Type Species			FID Species	
Code	Name	Mean Cover of Primary & Secondary	Code	Name
SP3a	Red pine - White pine/Bracken - Mayflower, Black spruce variant	Black spruce (31%) Red pine (15%)	BS	Black spruce
SP4	White pine/Blueberry/Bracken	White pine (59%) Balsam fir (14%)	WP	White pine
SP4a	White pine/Blueberry/Bracken, Black spruce variant	Black spruce (36%) Red spruce (19%)	BS	Black spruce
SP4b	White pine/Blueberry/Bracken, Huckleberry variant	White pine (37%) Balsam fir (15%)	WP	White pine
SP5	Black spruce/Lambkill/Bracken	Black spruce (51%) Balsam fir (16%)	BS	Black spruce
SP6	Black spruce - Red maple/Bracken - Sarsaparilla	Black spruce (34%) Red maple (20%)	BS/RM	Black spruce/Red maple
SP7	Black spruce/False holly/Ladies' tresses sphagnum	Black spruce (52%) Balsam fir (11%)	BS	Black spruce
SP9	Red oak - White pine/Teaberry	White pine (24%) Red oak (24%)	WP/RO	White pine/Red oak
TH5	Beech/Sarsaparilla/Leaf litter	Beech (58%) Yellow birch (14%)	BE	Beech
WC1	Black spruce/Cinnamon fern/Sphagnum	Black spruce (44%) Balsam fir (9%)	BS	Black spruce
WC2	Black spruce/Lambkill - Labrador tea/Sphagnum	Black/hybrid spruce (42-65%) Balsam fir (6%)	BS	Black spruce
WC2a	Black spruce/Lambkill - Labrador tea/Sphagnum, Huckleberry-Inkberry variant	Black/hybrid spruce (28-40%) Red maple (13%)	BS	Black spruce
WC5	Red spruce - Balsam fir/Cinnamon fern/Sphagnum	Red spruce (49% Balsam fir (19%)	RS	Red spruce
WC6	Balsam fir/Cinnamon fern - Three seeded sedge/Sphagnum	Balsam fir (42% Black spruce (12%)	BF	Balsam fir

FEC V-Type Species			FID Species	
Code	**Name**	**Mean Cover of Primary & Secondary**	**Code**	**Name**
WC7	Tamarack - Black spruce/Lambkill/Sphagnum	Tamarack (41%) Black spruce (20%)	TL	Tamarack
WC7a	Tamarack - Black spruce/Lambkill/Sphagnum, Huckleberry-Inkberry variant	Tamarack (32%) Black spruce (22%)	TL/BS	Tamarack/Black spruce
WD2	Red maple/Cinnamon fern/Sphagnum	Red maple (49%) White birch (20%)	RM	Red maple
WD3	Red maple/Sensitive fern - Lady fern/Sphagnum	Red maple (50%) Red spruce (14%)	RM	Red maple
WD4	Red maple/Poison ivy/Sphagnum	Red maple (42%) Black spruce (13%)	RM	Red maple
WD4a	Red maple/Poison ivy/Sphagnum, Huckleberry-inkberry variant	Red maple (42%) White ash (16%)	RM	Red maple
WD6	Red maple - Balsam fir/Wood aster/Sphagnum	Red maple (37%) Balsam fir (27%)	RM/BF	Red maple/Balsam fir
WD7	Balsam fir - White ash/Cinnamon fern - New York fern/Sphagnum	Balsam fir (19%) White ash (11%)	BF/RM	Balsam fir/Red maple
WD8	Red spruce - Red maple/Wood sorrel - Sensitive fern/Sphagnum	Red spruce (38%) Red maple (17%)	RS/RM	Red spruce/Red maple

Table 3.5: Classification accuracy and Kappa coefficients for soil texture and drainage from field-collected data as compared to data classified by the Nova Scotia Ecological Land Classification digital layer.

	Soil Drainage				**Soil Texture**			
	All soils (n = 246)		**Mineral only (n = 100)**		**All soils (n = 246)**		**Mineral only (n = 102)**	
Buffer size	**Acc**	***K***	**Acc**	***K***	**Acc**	***K***	**Acc**	***K***
0 m	28%	0.11	62%	0.36	39%	0.20	79%	0.60
50 m/0.8 ha	30%	0.12	66%	0.41	46%	0.27	80%	0.61
100 m/3.1 ha	34%	0.16	75%	0.57	49%	0.32	81%	0.85

*Interpretation of Kappa coefficients (Cohen 1960): < 0.0 = less than chance agreement, 0.01-0.20 = slight agreement, 0.21-0.40 = fair agreement, 0.41-0.60 = moderate agreement, 0.61-0.80 = substantial agreement, 0.81-0.99 = almost perfect agreement.

Table 3.6: Confusion matrices comparing soil drainage classified at 235 plots using Forest Ecosystem Classification (FEC) in the Southwest Nova Biosphere Reserve with soil drainage classified from photointerpretation in the Nova Scotia Ecological Land Classification (ELC) digital layer. FEC classifications were grouped into three pseudo-categories for calculating Kappa statistics: Poorly Drained (n = 152), Imperfectly Drained (n = 60), and Well Drained (n = 23).

Drainage Class	**Soil Type**																
No buffer	**ST4**	**ST7**	**ST10**	**ST13**	**ST14**	**ST3**	**ST6**	**ST12**	**ST16**	**ST2**	**ST1**	**ST5**	**ST8**	**ST15**	**Row Total**	**User Accuracy**	**Kappa**
Poorly drained					3	2									5	1.00	*d* = 65
Imperfectly drained	2			1	66	15	1		11	10	3		1	6	116	0.32	*q* = 44
Well drained	9	1	2	1	65	3	1	2	4	10	2	1	2	8	111	0.21	*n* = 235
Not applicable				1	1				1						3		
Column Total	11	1	2	3	135	20	2	2	16	20	5	1	3	14	235	Total Accuracy	
Producer Accuracy	0.00	0.00	0.00	0.00	0.02	0.85	0.50	0.00	0.69	1.00	0.40	1.00	0.67	0.57		0.28	*K* = 0.11

50m buffer	**ST4**	**ST7**	**ST10**	**ST13**	**ST14**	**ST3**	**ST6**	**ST12**	**ST16**	**ST2**	**ST1**	**ST5**	**ST8**	**ST15**	**Row Total**	**User Accuracy**	**Kappa**
Poorly drained					4	2									6	1.00	*d* = 70
Imperfectly drained	4			1	83	16	1		12	10	3		1	4	135	0.29	*q* = 48
Well drained	7	1	2	2	48	2	1	2	4	10	2	1	2	10	94	0.27	*n* = 235
Not applicable															0		
Column Total	11	1	2	3	135	20	2	2	16	20	5	1	3	14	235	Total Accuracy	
Producer Accuracy	0.00	0.00	0.00	0.00	0.03	0.90	0.50	0.00	0.75	1.00	0.40	1.00	0.67	0.71		0.30	*K* = 0.12

100m buffer	**ST4**	**ST7**	**ST10**	**ST13**	**ST14**	**ST3**	**ST6**	**ST12**	**ST16**	**ST2**	**ST1**	**ST5**	**ST8**	**ST15**	**Row Total**	**User Accuracy**	**Kappa**
Poorly drained					4	2									6	**1.00**	*d* = 79
Imperfectly drained	5		2	1	100	18	1		12	10			1		150	**0.27**	*q* = 50
Well drained	6	1		2	31		1	2	4	10	5	1	2	14	79	**0.41**	*n* = 235
Not applicable															0		
Column Total	11	1	2	3	135	20	2	2	16	20	5	1	3	14	235	Total Accuracy	
Producer Accuracy	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**1.00**	**0.50**	**0.00**	**0.75**	**1.00**	**1.00**	**1.00**	**0.67**	**1.00**		0.34	*K* = 0.16

Table 3.7: Confusion matrices comparing soil texture classified at 246 field locations using Forest Ecosystem Classification (FEC) in the Southwest Nova Biosphere Reserve with soil drainage classified from photointerpretation in the Nova Scotia Ecological Land Classification digital layer. FEC classifications were grouped into three pseudo-categories for calculating Kappa statistics: Fine (n = 3), Medium (n = 37), Coarse (n = 62), and Organic (n = 144).

	Soil Texture														Row		
No buffer	**ST13**	**ST5**	**ST6**	**ST7**	**ST12**	**ST3**	**ST4**	**ST1**	**ST2**	**ST8**	**ST10**	**ST15**	**ST16**	**ST14**	**Total**	User Accuracy	**Kappa**
fine (F)															0		*d* = 97
med (M)	1	1	2	1	2	8	2	1	8	2	4	3	11	83	129	0.35	*q* = 60
coarse (C)						12	5	3	11			9	5	36	81	0.35	*n* = 246
organic (T)	1						4	1	1	1		2		24	34	0.71	
Not applicable (X)	1													1	2		
Column Total	3	1	2	1	2	20	11	5	20	3	4	14	16	144	246	**Total Accuracy**	
Producer Accuracy	0.33	1.00	1.00	1.00	1.00	0.60	0.45	0.80	0.60	0.33	0.00	0.79	0.31	0.01		**0.39**	***K* = 0.20**

50m buffer	**ST13**	**ST5**	**ST6**	**ST7**	**ST12**	**ST3**	**ST4**	**ST1**	**ST2**	**ST8**	**ST10**	**ST15**	**ST16**	**ST14**	**Row Total**	**User Accuracy**	**Kappa**
fine (F)															0		*d* = 113
med (M)	2	1	2	1	2	8	4	1	7	2	4	3	11	76	124	0.37	*q* = 64
coarse (C)						12	5	3	13			9	5	31	78	0.38	*n* = 246
organic (T)	1						2	1		1		2		37	44	0.84	
Column Total	3	1	2	1	2	20	11	5	20	3	4	14	16	144	246	**Total Accuracy**	
Producer Accuracy	0.00	1.00	1.00	1.00	1.00	0.40	0.36	0.80	1.00	0.67	1.00	0.86	1.00	0.26		**0.39**	***K* = 0.27**

100m buffer	**ST13**	**ST5**	**ST6**	**ST7**	**ST12**	**ST3**	**ST4**	**ST1**	**ST2**	**ST8**	**ST10**	**ST15**	**ST16**	**ST14**	**Row Total**	**User Accuracy**	**Kappa**
fine (F)															0		*d* = 120
med (M)	3	1	2	1	2	9	6	2	9	3	4	6	11	76	135	0.41	*q* = 61
coarse (C)						11	5	3	11			8	5	31	74	0.36	*n* = 246
organic (T)														37	37	1.00	
Column Total	3	1	2	1	2	20	11	5	20	3	4	14	16	144	246	**Total Accuracy**	
Producer Accuracy	0.00	1.00	1.00	1.00	1.00	0.45	0.55	1.00	1.00	1.00	1.00	1.00	1.00	0.26		**0.42**	***K* = 0.32**

Table 3.8: Confusion matrices comparing species of dominant forest cover classified at 209 field locations in the Southwest Nova Biosphere Reserve with species of dominant forest cover classified from photointerpretation in the Nova Scotia Forest Inventory Database digital layer. See Table 3.4 for description of species codes.

No Buffer	**BE**	**BF**	**BS**	**EC**	**EH**	**RM**	**RO**	**RS**	**TA**	**TL**	**WP**	**Other**	**Row Total**	**User Accuracy**	**Kappa**
BE													0	1.00	*d* = 81
BF		1								1			2	0.50	*q* = 30
BS			35			10		3			1		49	0.71	*n* = 209
EC				3									3	1.00	
EH					2	2							4	0.50	
RM			4			23		2					29	0.79	
RO						1					1		2	0.00	
RS			4					10			1		15	0.67	
TA									1				1	1.00	
TL										3			3	1.00	
WP			2		4	5		1			3		15	0.20	
Other	1	1	30		3	22	1	8	1	9	10		86	1.00	
Column Total	1	2	75	3	9	63	1	24	2	13	16	0	209	**Total Accuracy**	
Producer Accuracy	0.00	0.50	0.47	1.00	0.22	0.37	0.00	0.42	0.50	0.23	0.19	1.00		**0.39**	***K* = 0.29**

50m Buffer	**BE**	**BF**	**BS**	**EC**	**EH**	**RM**	**RO**	**RS**	**TA**	**TL**	**WP**	**Other**	**Row Total**	**User Accuracy**	**Kappa**
BE													0	N/A	*d* = 114
BF		1								1			2	0.50	*q* = 37
BS			51			5		3			1		60	0.85	*n* = 209
EC				3									3	1.00	
EH			1		4	1							6	0.67	
RM			4			32		3					39	0.82	
RO						2					1		3	0.00	
RS			2			1		12					15	0.80	
TA									1				1	1.00	
TL										5			5	1.00	
WP			2		3	5					5		15	0.33	
Other	1	1	15		2	17	1	6	1	7	9		60	N/A	
Column Total	1	2	75	3	9	63	1	24	2	13	16	0	209	**Total Accuracy**	
Producer Accuracy	0.00	0.50	0.68	1.00	0.44	0.51	0.00	0.50	0.50	0.38	0.31	N/A		**0.55**	***K* = 0.45**

100m Buffer	**BE**	**BF**	**BS**	**EC**	**EH**	**RM**	**RO**	**RS**	**TA**	**TL**	**WP**	**Other**	**Row Total**	**User Accuracy**	**Kappa**
BE													0	N/A	*d* = 129
BF		2								1			3	0.67	*q* = 39
BS			55			4		3		1	1		64	0.86	*n* = 209
EC				3									3	1.00	
EH			4		5								9	0.56	
RM			1			38		2					41	0.93	
RO						2					1		3	0.00	
RS			2			1		12					15	0.80	
TA									1				1	1.00	
TL										6			6	1.00	
WP			1			3					7		11	0.64	
Other	1		12		4	15	1	7	1	5	7		53	N/A	
Column Total	1	2	75	3	9	63	1	24	2	13	16	0	209	**Total Accuracy**	
Producer Accuracy	0.00	1.00	0.73	1.00	0.56	0.60	0.00	0.50	0.50	0.46	0.44	N/A		**0.62**	***K* = 0.53**

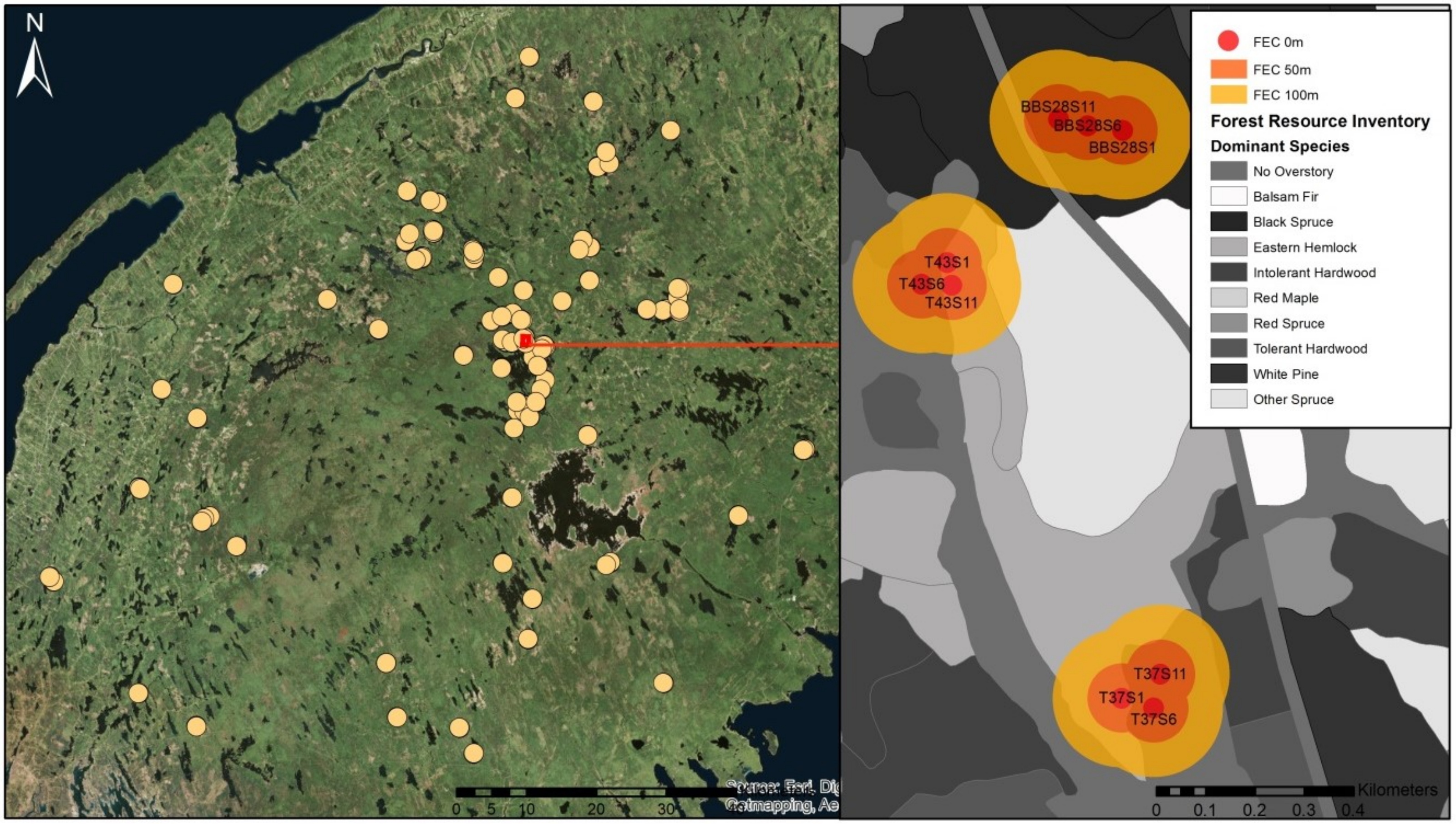

Figure 3.1: Study area showing 265 FEC plots sampled at 99 locations in the Southwest Nova Biosphere Reserve (gold circles, left inset) and buffer sizes around 9 FEC sample plod contrasted with provincial Forest Inventory Database forest cover data (right inset).

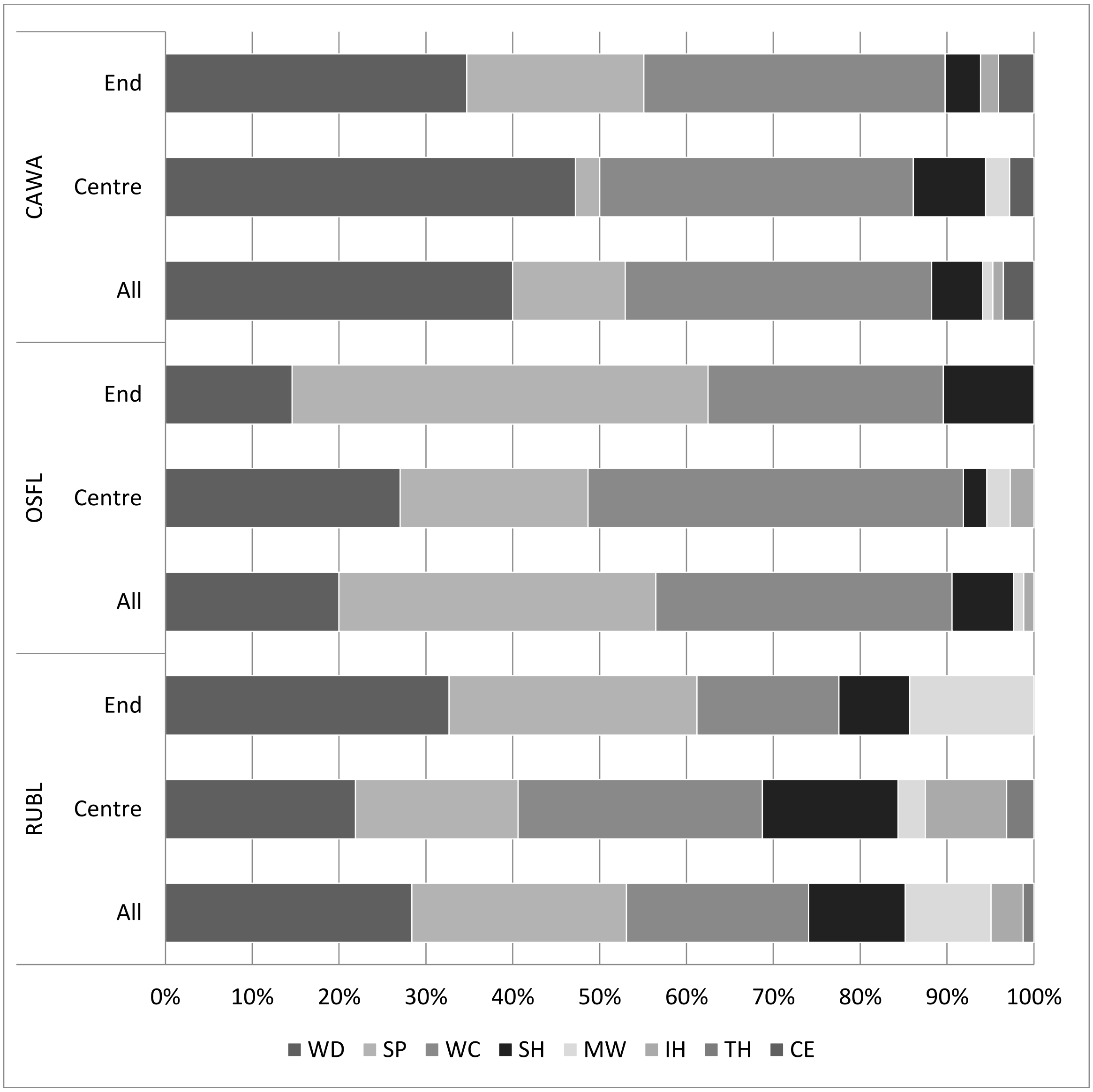

Figure 3.2: Percentage of forest groups classified at plots occupied by the Rusty Blackbird (RUBL; all plots n = 81, centre plots n = 32), Olive-sided Flycatcher (OSFL; all plots n = 85, centre plots n = 37), and/or Canada Warbler (CAWA; all plots n = 85, centre plots n = 36) in the Southwest Nova Biosphere Reserve. Classified forest groups include wet deciduous (WD), spruce-pine (SP), wet coniferous (WC), spruce-hemlock (SH), mixedwood (MW), intolerant hardwood (IH), tolerant hardwood (TH), and cedar (CE).

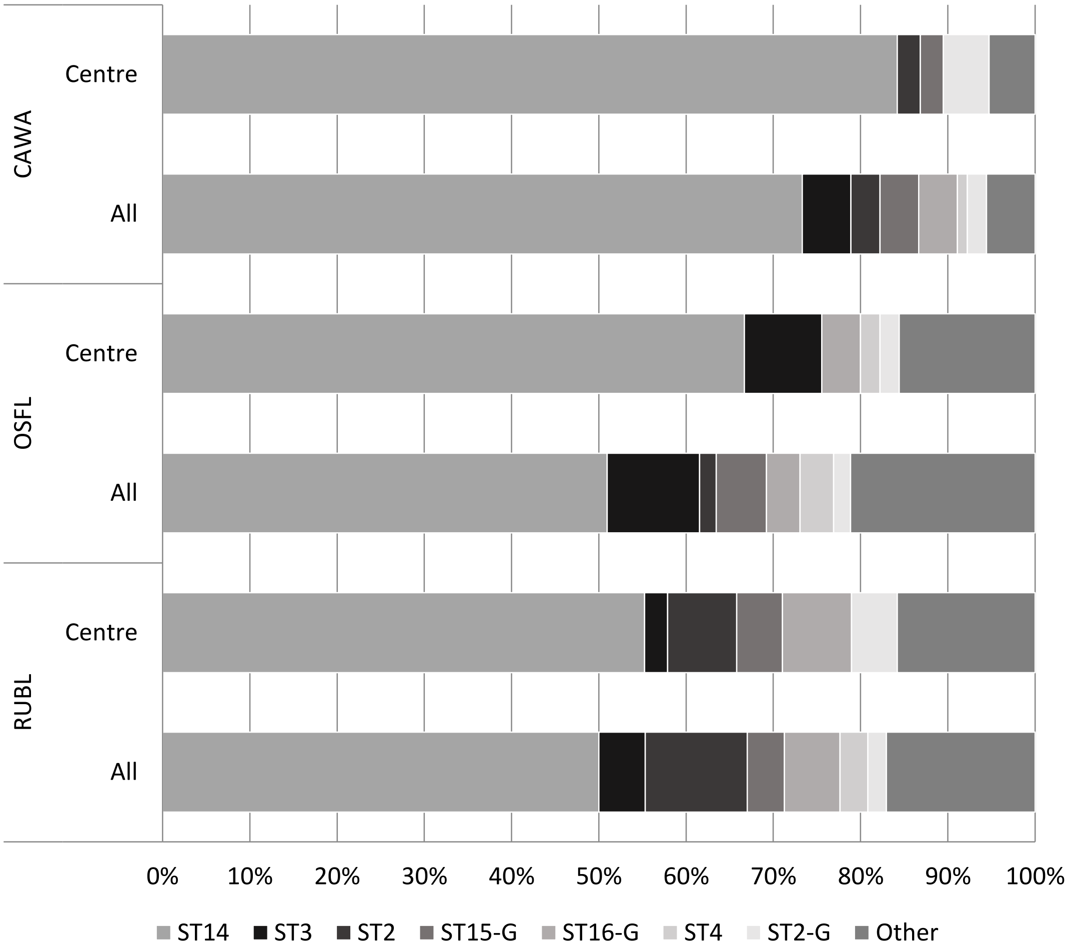

Figure 3.3 : Percentage of soil types classified at plots occupied by the Rusty Blackbird (RUBL; all plots n = 94, centre plots n = 38), Olive-sided Flycatcher (OSFL; all plots n = 104, centre plots n = 45), and/or Canada Warbler (CAWA; all plots n = 90, centre plots n = 38) in the Southwest Nova Biosphere Reserve. Classified soil types included organic (ST14), moist-medium to coarse textured (ST3), fresh-medium to coarse textured (ST2 and granitic phase, ST2-G), dry shallow-medium to coarse textured, granitic phase (ST15-G), moist shallow-medium to coarse textured, granitic phase (ST16-G), wet-medium to coarse textured (ST4), and other types.

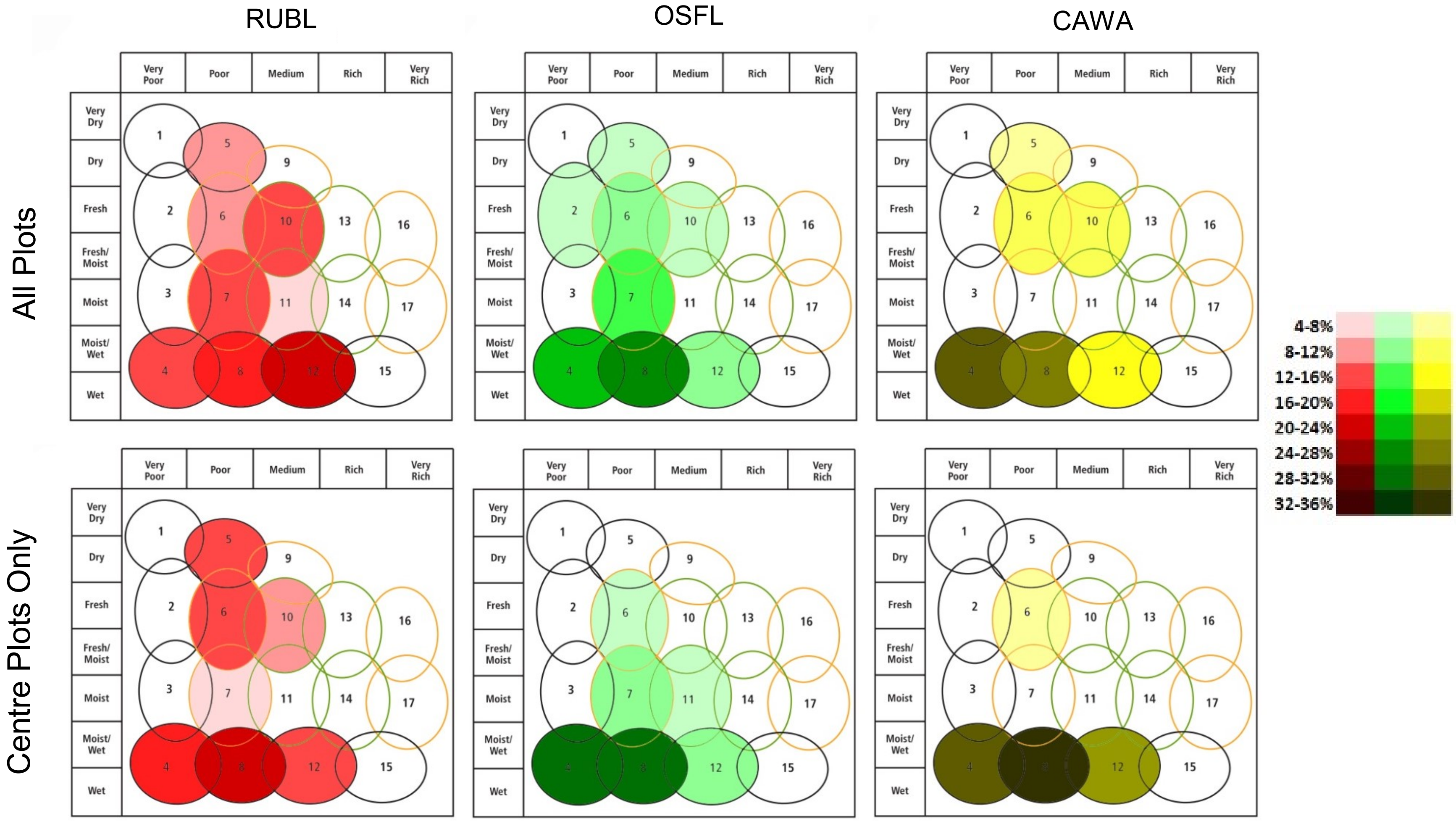

Figure 3.4: Ecosites classified at plots occupied by Rusty Blackbird (RUBL; all plots n = 75, centre plots n = 30), Olive-sided Flycatcher (OSFL; all plots n = 81, centre plots n = 35), and/or Canada Warbler (CAWA; all plots n = 85, centre plots n = 36) in the Southwest Nova Biosphere Reserve. Ecosites are organized by moisture and richness (nutrient availability) along edatopic grids (Keys et al. 2011b).

CHAPTER 4 CHOOSING A SPECIES DISTRIBUTION MODEL FOR CONSERVATION

4.1. INTRODUCTION

Correlative models are widely used to describe patterns and make quantitative predictions about species distributions and the environment. Species distribution models (SDMs) include a suite of empirical and mechanistic models, encompassing numerous techniques that make a spatial prediction about species distribution, abundance, or occurrence. The function of all SDMs is twofold: to provide ecological explanations for observed spatial patterns, and to predict conditions or distributions in unsampled locations or times.

SDMs have become commonplace in many disciplines, including conservation biology, ecology, biogeography, and wildlife management (for key summaries of SDM techniques and applications, see Guisan & Zimmermann 2000; Segurado & Araújo 2004; Guisan & Thuiller 2005; Pearson 2007; Franklin 2009, 2013). SDMs have been used to tackle conservation problems and to support decision-making about wildlife and resource management, such as identifying areas of high-value habitat, estimating population size, and projecting shifts in species distributions in relation to climate change, among many others (e.g. Larson et al. 2003; Macdonald & Rushton 2003; Cumming et al. 2013).

SDMs can be divided into two broad categories of models: empirical (or correlative) and mechanistic (Kearney & Porter 2009). The former uses known distributions to predict habitat suitability or likelihood of species occurrence, abundance, or occupancy, whereas the latter uses information about species physiology and demography to predict functional connectivity, breeding success, and other responses (Murphy & Evans 2011). Models in each category use different types of information, and predict distributions according to different metrics. For the most part, authors that explicitly use the term 'SDM' are referring to empirical models only when they do so, as mechanistic models are much less commonly used. However, both kinds of models are important: each is grounded in different aspects of ecological theory, and is only suitable for making certain kinds of predictions.

Depending on the expertise of the modeler and the size of the dataset, successfully assembling one or more SDMs to guide conservation decisions can be a complicated process. SDM construction can require a great deal of time and intensive use of computational resources. Choosing an SDM should be done strategically, with thought given to how the model can inform a chosen conservation objective. This entails taking into account available data, the experience of the user, and possible prediction metrics, among other concerns.

A number of excellent reviews are available to help users compare SDM(s) based on data type and model performance (see Guisan & Zimmermann 2000; Pearson 2007; Elith & Leathwick 2009a, 2009b; Franklin 2009; Guisan et al. 2013). However, these reviews make few clear connections with conservation applications, and either ignore mechanistic SDMs or give them only passing mention. Guisan & Zimmermann (2000) recognized that it is essential to select a model based on the goal of the study, yet no guides exist to help a user select a SDM specifically for conservation objectives.

Managers typically use SDMs to meet objectives of species conservation or recovery, such as designing protected areas, identifying critical habitat, or anticipating the effects of climate change. Rather than building a model and then attempting to apply the outcome to the objective, consideration of the final intent at the outset is needed. By selecting a model with the conservation objective in mind, it will be possible the refine the model to meet scientific and practical needs.

An easily-interpretable framework is needed to aid managers and researchers in selecting a model that is suitable for their conservation objectives. In this chapter, I develop such a framework using previously published documentation of best practices from experts in the field, and survey existing SDMs that have been constructed for specific conservation objectives.

Objectives of this chapter include (1) contextualizing SDM in ecological theory to determine which prediction metrics are ecologically appropriate for empirical and mechanistic SDMs, (2) evaluating recently published academic and gray literature SDMs for landbirds to determine if prediction metrics were reported with the correct measure and amount of uncertainty for model and data type, and (3) use lessons learned to develop a framework for selecting an appropriate SDM based on data type, conservation objective, data quality, and model performance.

4.2. CONTEXTUALIZING SPECIES DISTRIBUTION MODELING IN ECOLOGICAL THEORY

Increasing availability of GIS data products and computer packages for model algorithms, as well as open-source modeling software, has enabled proliferation of many different types of SDMs in recent years. Over time, various names in modeling lexicon have become synonymous with SDM, such as ‘species niche models’, ‘bioclimatic envelope models’ and ‘spatially-explicit habitat models’. For the purpose of this chapter, SDM will be the preferred term, in accordance with Franklin (2009). Furthermore, I will consider SDMs to include only spatially-explicit models, which are models that make a distributional prediction in geographic space (as opposed to, for example, niche space).

The main two categories of SDM considered in this chapter are: (1) Empirical models, which generally use known species locations and environmental covariates to predict species occurrence, abundance, or occupancy, and (2) mechanistic models which use biophysical constraints and demographic information for the organism along with environmental factors to predict occupancy, fitness, breeding success, or other life history traits. Models can either be static (prediction in one time frame) or dynamic (predictions changing through time). Empirical SDMs will be given a more detailed treatment because they are more commonly used, tend to be designed to provide a spatial output, are suited to a variety of spatial scales, and have relatively easy application to conservation planning. Mechanistic SDMs require intensive data acquisition that is not possible in many conservation and management scenarios, typically confined to local or sub-regional areas, and can be much more difficult to project as spatial maps. An overview and recommendations for use will be given for mechanistic SDMs as well as empirical ones, but specific algorithms for mechanistic models will not be examined in depth. At present, there are no known comprehensive reviews of mechanistic models, and each model type must be assessed for use on a case-by-case basis.

4.2.1. Ecological theory and model limitations

Ecological models involve taking ecological concepts from niche theory, or how an organism responds to resources and competitors, and embedding them into an algorithmic framework (Brown et al. 1996; Franklin 2009). Organisms are limited regarding what environments they can occupy, and the factors driving these limits are many: e.g. physiological limitations (such as thermal tolerance), biotic interactions, or competitive exclusion. SDMs can be used for interpolation (predicting values in unsampled sites within a region that contains samples) or extrapolation (predicting values in unsampled geographic domains, as well as past or future climates; Elith & Leathwick 2009c).

All SDMs have limitations, based on model assumptions and covariates. They also are generally limited by issues related to sample distribution and variable uncertainty. In many cases, the SDMs that are employed are not based on sound ecological theory, limiting the realism of their predictions (Elith & Leathwick 2009c). Different SDMs have different explanatory abilities, however, all have some level of model uncertainty that must be accepted. The consequence of theoretical limitations differs for each individual SDM. For certain models in certain situations, the amount of uncertainty or the scientific limitations may outweigh the usefulness of model outputs, or the model's ecological assumptions may make it unsuitable for the desired objective (Drew et al. 2011; Guillera-Arroita et al. 2015). Thus, it is important to navigate model selection being fully aware of the strengths and limitations of model algorithms.

4.2.1.1. Empirical algorithms

Empirical SDMs relate georeferenced data about species locations with information on the environmental characteristics of those locations (Elith & Leathwick 2009b). In their simplest forms, empirical SDMs can be constructed even without georeferenced location data: expert opinion is used to generate hypotheses about occurrence based on environmental covariates known or thought to be relevant to the organism. The least sophisticated empirical SDMs that use geo-referenced organism location data are purely geographic in nature (e.g. kernel density estimators, range maps; Bateman et al. 2013). However, most evidence suggests that the inclusion of both spatially geo-referenced species data and environmental information at these locations is essential for good model performance (Elith & Leathwick 2009c).

Modern empirical SDMs, which relate georeferenced species and environment data, grew from generalized linear modeling (GLM) techniques, becoming more common in the 1990s. GLM structural features are still part of many current methods (Phillips et al. 2006), whereby a prediction metric (the response variable, or the aspect of species distribution being estimated) is related to a series of environmental covariates. The development of GIS has allowed for increasingly complex digital models of environmental data, and methods to relate these to species location data have subsequently been developed. SDMs are now commonly used for prediction of distributions, spurred in part by demands for mapped products for conservation and land management (Elith & Leathwick 2009c).

At present, there are dozens of empirical SDM algorithms in use. Elith & Leathwick (2009a) and Franklin (2009) summarize SDMs into model types and algorithm families and in this chapter, I adapt these family groups to classify different types of SDMs. I have not endeavored to include an exhaustive review of all empirical SDMs in past or present use, but many common methods within each algorithm family are included. Table 4.1 describes algorithm families and lists common algorithm types. For lists and descriptions of many of these individual model algorithms, see Elith & Leathwick (2009a) and Franklin (2009).

I separate models by general methodological approach, into five families: (1) expert-based, where expert-defined rules are used to determine relationships between covariates and species occurrences, (2) envelope and similarity, which quantify ranges, means, and other descriptors of covariates in bounds around species locations, (3) statistical, which use statistical methods in ecology to derive covariate distributions, (4) machine learning, which apply iterative rule-based processes to achieve model parsimony, and (5) occupancy algorithms, which use information about detectability from repeated measures to predict probability of habitat occupancy.

The overarching limitation of most empirical SDMs is that they are imperfect in their ability to explain the occupied conditions (i.e. the realized niche) versus the potential distribution (i.e. the fundamental niche) of the species (Guisan & Zimmermann 2000; Pearson 2007). Empirical SDMs can only explain the fundamental niche from covariates (predictor variables or dimensions) that are entered by the user, which are typically based on known distributions. Factors that determine the realized niche, such as predation and competition, are rarely explicitly modeled by empirical SDMs.

The prediction is limited by what can possibly be modeled from available covariates. There will be unknown contributing factors: ‘known unknowns’ (such as environmental variables that are known to be influential but cannot be modeled from available data, e.g. competitive interaction by another species for whom occurrence records are not available, or information about understory plant coverage that is not captured in GIS layers), or ‘unknown unknowns’ (important covariates that have not been, or cannot be, measured, e.g. an anthropogenic disturbance that is not anticipated). Due to these unknowns, it is also important to be skeptical about which components of the fundamental niche are represented by SDM predictions, as noted by Elith & Leathwick (2009b). In an empirical SDM, only a limited number of covariates are included, and they are related to occurrence samples that do not completely represent a given population. Depending on the amount and importance of these unknowns, the ability to realistically predict the fundamental niche can be limited.

When applying empirical SDMs to conservation objectives, a user's foremost consideration should be whether the model's predictions can accomplish their conservation objective. Model predictions, or the parameter they are able to estimate, are dependent on data type (Table 4.1). Empirical SDMs use five types of species data (adapted from Guillera-Arroita et al. 2015): species biology (SB), presence-only (PO), presence-absence (PA), abundance-absence (AA), and occupancy-detection (DET). SB data include information about a species' biology and ecology that is used *a priori* by experts to determine suitable habitat features. PO data use spatially georeferenced locations where a species has been documented to occur. Depending on the modeling method used, PO data can be converted to presence-background (PB) data, by pseudo-absence data from unsampled sites that are presumed to be 'available'. PO and PB models have increased in popularity, as they can use telemetry data, museum records, and citizen science. PA data is a measure of occurrence, with both species presence and absence documented for each site. AA data are similar to PA data, but include numerical counts at presence sites, and AA data can be used to derive population density if detectability is taken into account. Finally, DET data estimate the detectability of an organism or population and can be measured with repeat visits, mark-recapture techniques, or estimated using statistical offsets (MacKenzie et al. 2006; Sólymos et al. 2013).

Where a species *breeds successfully,* where it *occupies*, where it *can occur*, or where it is *likely to be observed* are all very different predictions. Empirical SDMs can only accomplish some of these, and which are sacrificed depends on the type of data input. Generally, SB data in empirical models can only rank a relative probability of species occurrence in a given habitat (though they can serve other functions in mechanistic algorithms). SB-based model outputs typically give an index of habitat suitability, whereby some habitats can be ranked as relatively higher or lower than others. Barry et al. (2006) cautioned that expert-led models should not be used as representations of species or community presence, but rather, only for their ability to measure changes in habitats over time. Models using PO data can only rank likelihood of occurrence. Algorithms that convert PO data to a PB condition can predict relative likelihood of occurrence under certain conditions, whereas PA can predict relative likelihood of occurrence. Models using

PA data are advantageous because they yield more accurate predictions (Brotons et al. 2004), contain valuable information about survey locations that can be used to analyze bias, and can give a measure of prevalence for calibration when calculating probability of occurrence (Franklin 2013). AA data can predict expected abundance. If AA data are corrected for detectability (see Bayne et al. 2011; Sólymos et al. 2013), they can be used to calculate expected population density (e.g. (Stralberg et al. 2014). When predictions of abundance or occurrence are constrained using detection probability, DET data can be used to predict likelihood of occupancy (MacKenzie et al. 2006).

Though often overlooked by users, predictions are linked to survey methodology. The methods that were used in the collection of the data must be taken into account when applying the outcome of the model to the real world. Take, for example, a model generated with PA data from point counts surveying for 10mins with a 100-m detection radius. The resulting map will be the relative likelihood of observing during the species during a 10-min point count survey within a 100-m radius—not the absolute likelihood of observing it in that location.

Despite these drawbacks, empirical SDMs have many advantages: they offer powerful tools to assess the likelihood of species occurrence, and potentially abundance. From this, one can infer habitat suitability on a landscape. They can implicitly incorporate any process associated with covariates, be tailored to fit commonly available data, have high precision for local analysis, are less likely to overestimate range, and provide a relatively simple output. They are good for large spatial scales. They are particularly useful for poorly-studied taxa as inferences can be made from relatively few observations (or purely from expert knowledge), and tend to be highly generalizable (Kearney & Porter 2009). Empirical SDMs can predict where a species is *likely to be observed*, or, where it *can occur*, and if detectability information is included, locations it is *likely to occupy*.

However, empirical SDMs have some unavoidable theoretical limitations. They assume equilibrium or pseudo-equilibrium between observed species patterns and the environment, for example, assuming that abundance at a location can be reliably estimated from a given sample. However, for most species, assumptions of equilibrium are rarely valid as environmental conditions, biotic interactions, and other factors are in constant flux (Alley 1982; Vallecillo et al. 2009; Crawford & Hoagland 2010). Most SDMs, with known locations corrected for detectability, can only predict species occurrence and not which habitats are occupied. It is important to note that although empirical SDMs can infer relative suitability, they cannot identify which patches of habitat are truly suitable from a fitness perspective without including physiological or demographic parameters relating to these different environments. Abundance data may be able to infer reproductive success (Carl & Jones 2004), but AA data is much less commonly available than PO or PA. Absence or pseudo-absence data do not necessarily indicate an unsuitable environment, but simply one where the species is not known to occur. The capacity of empirical SDMs to make accurate predictions in climate change scenarios has been criticized (Araújo et al. 2005), particularly given their lack of inclusion of mechanistic or evolutionary processes (Dormann 2007). For these reasons, empirical SDMs are by nature less effective in unsaturated habitats, with organisms that are very difficult to detect, in a changing environment (Guisan & Zimmermann 2000), or when sampling is not accounted for (Kearney & Porter 2009).

4.2.1.2. Mechanistic algorithms

Physiological limitations constrain the environments which organisms can inhabit, and their abundance. In a mechanistic model, the organism is entered into the model not as merely an observation, but a set of behavioral, morphological, and physiological traits (Kearney & Porter 2009). This allows for the incorporation of biological responses that limit the range of a species, which are important for assessing what habitat is possible to occupy. Mechanistic SDMs, depending on the data type, can predict where a species *occupies*, or where it can *breed successfully* (or has success for some other life history trait). Whereas empirical SDMs are best suited to predict distribution, mechanistic SDMs are suited to predicting populations’ responses to changing conditions.

Mechanistic SDMs (also known as ‘physiologically-based’, ‘process-based’, or ‘dynamic simulation’ models) begin from a process-based view of the fundamental niche of an organism, and map this information on to the landscape to understand range constraints (Kearney & Porter 2009). They do not begin by analyzing the known distribution of a species (as empirical SDMs do), but rather, with the biology and ecology of the organism itself (by characterizing physiological tolerance or demography, expressed as rates of mortality, fecundity, carrying capacity, etc.). The output of mechanistic models varies depending on the type of model. Typically, they can give spatial predictions of population growth or fecudnity in different habitat conditions. The exceptions are metapopulation models, which use information about population demographics as well as occupancy to predict population density or probability of habitat occupancy (the likelihood that a given patch of habitat will be occupied by a given species; Araújo 2009).

I group mechanistic models into three general types (Table 4.2): (1) spatial population viability analysis (SPVA), which uses population ecology and demography to predict parameters like fecundity, colonization, and extinction (Akçakaya 2000), (2) spatially-explicit mechanistic niche models, which model traits governing the fundamental niche, such as thermal tolerance (for fundamental literature, see Root 1988, for an example using trees, see Morin et al. 2007), and (3) occupancy models that incorporate mechanistic processes. The list of models provided in Table 4.2 is certainly non-exhaustive. Within these broad types, I have sorted models into categories based on the type of information they use to generate a prediction.

Data inputs for mechanistic SDMs models vary, but typically involve some kind of population viability (PV) data such as genetic markers, physiological tolerance, fecundity, or survival. Physiological limits can be derived from laboratory testing. Mark-recapture studies can be used to gather detectability data from repeat measures (DET), which is useful for occupancy models and SPVA analysis. Model estimation parameters depend on the type of data input (Table 4.2). Estimation parameters include probability of occurrence, probability of occupancy, and viability (I use ‘viability’ to be inclusive of functional parameters like fecundity, colonization, breeding success, survival, carrying capacity, population growth rates, dispersal, and others). As with any model, the data used as input determine what the model is capable of estimating.

Mechanistic models are advantageous over empirical models in that they function in non-equilibrium conditions or novel circumstances, and have high transferability (Kearney & Porter 2009). Increasingly widespread availability of genetic information has allowed for powerful new tools to model landscape genetics (Murphy & Evans 2011). Mechanistic models are explicitly biologically grounded, and thus their assumptions are independent of the specific occurrence or abundance data added to the model to aid in spatial prediction.

Mechanistic modeling requires detailed knowledge of the species being modeled (Guisan & Zimmermann 2000), such as genetic information, thermal tolerance, dispersal, fecundity, and many other types of demographic or biological knowledge (Bateman et al. 2013). SPVA often lacks in spatial detail (Carroll et al. 2003), and takes more time, effort, resources, and data to construct and validate (Kearney & Porter 2009). Mechanistic models using collected biological data from specific populations are typically confined to small geographical areas, due to the fine resolution of these data. On the other hand, mechanistic models using thermal tolerance, dispersal distance, or other traits modeled at a large scale will be restricted to extremely coarse-filter projections (e.g Saracco et al. 2008). In general, though mechanistic models provide outputs that are ecologically interpretable, they require considerable effort and combination with GIS techniques to generate mapped outputs. In contrast, many empirical SDMs lend themselves relatively simply to projection in a GIS environment, whereas representing mechanistic SDMs outputs spatially can be challenging for some algorithms (Kearney & Porter 2009).

There have been attempts at convergence in recent years, where empirical SDMs include covariates or constraints based on mechanistic principles. Though rarely employed, these techniques vary: for example, integrating estimates of dispersal from previous field studies into empirical projections (Zozaya et al. 2011), constraining prediction by minimum viable population requirements (Larson & Sengupta 2004), and including thermal tolerance limits into distribution projections for climate change scenarios (Monahan 2009).

4.3. CONSERVATION OBJECTIVES AND APPROPRIATE USE

The mapped outputs of SDMs, whether empirical or mechanistic, aid in choosing locations to apply conservation measures or evaluating threats, and can be integrated with other kinds of management planning. Some conservation objectives are aspatial (e.g. reducing a generalized threat), but most can be represented spatially (e.g. by localizing areas of highest threat). It is up to the practitioner to choose an objective—this cannot be determined by an SDM (for assistance with objective-setting, see Tear et al. 2005). All conservation objectives can be informed by metrics specifically selected to predict the most ecologically relevant information for decision-making.

For every conservation objective, there will be predicted metrics of species response that are ideal (metrics well-grounded in ecological theory), or metrics that could be used as plausible surrogates for ecological responses if there is a paucity of information. Detailed consideration of appropriate prediction metrics for a given objective should precede modeling. For example, if the goal is to identify critical habitat, it is essential to know not only if habitat is suitable, but whether it can support a viable population. The ultimate goal of species recovery is typically to maintain or increase population levels towards some pre-decline benchmark (Sanderson 2006; Westwood et al. 2014). To achieve this, it is necessary to have detailed life history and population status information, which is not incorporated in most empirical SDMs. Typically, conservation planning methods forgo explicit measures of population viability for surrogates such as amount of habitat, population size, or other metrics. This does not always have a sound basis in ecological theory (Nicholson & Ovaskainen 2009), but may be the only option given available data.

SDMs, if applied without adequate consideration of the use of the metric they are predicting, result in poor inference and sub-optimal management outcomes (Guillera-Arroita et al. 2015). Where a species *reproduces successfully,* where it *occupies*, where it *can occur*, or where it is *likely to be observed* are all very different predictions. It is important to distinguish between these metrics when trying to meet conservation objectives. It is critical that, prior to model selection, users be aware of what metrics a given model is capable of estimating (Guillera-Arroita et al. 2015).

4.3.1. Surveying appropriateness of existing SDMs for conservation applications

4.3.1.1. Methods

Given the increasingly common application of SDMs to conservation objectives, I assessed how users have applied their models, and whether they reported the response metric correctly for the type of data and model used. To do so, I surveyed peer-reviewed publications as well as gray literature from NGOs and government departments worldwide. I limited the evaluative portion of the review to SDMs for landbird species, to reduce the scope to broadly similar ecological contexts.

I used the Dalhousie University NovaNet database to search the entire catalogue from 2004-2015 using the terms “bird + species distribution model”, “bird + mechanistic niche model”, “bird + occupancy model” and “bird + predictive habitat model.” I also used a Google search with the terms “species distribution + bird + gov” to locate gray literature, which is not included in NovaNet’s catalogue (particularly government department reports). I also sent out an email request for gray literature amongst listservs associated with bird research in North America and worldwide. When I found relevant titles, I examined their references for additional titles to investigate. Only papers and reports in English and French were considered. To be included in my analysis, papers, reports, and documents needed to fulfill all of the following criteria:

a) Develop a spatially-explicit species distribution model, whereby the model output was mapped onto the land surface;
b) Predict species occurrence, abundance, population density, occupancy, or a parameter of viability in a continuous or categorical manner; and
c) Include at least one landbird species in the model.

Articles chosen for further analysis presented original research that developed and applied at least one spatially-explicit predictive distribution model to one or more landbird species anywhere in the world. I evaluated 128 unique SDM algorithms from 20 reports and 56 academic papers, as many authors used more than one model algorithm. Effort was put into locating as much gray literature as possible (21 models in 20 reports, comprising 16% of models and 28% of literature surveyed).

Each paper used one or more models, with a single model being defined as the output produced by a given modeling algorithm. When final map outputs were constructed from 'stacked' or 'ensemble' methods (aggregating outputs of algorithms), each algorithm was counted uniquely as a model. For each model, I recorded the authors, year, paper type, algorithm family, specific algorithm used, data type, prediction metric (reported), the correct prediction metric for that paper's data type, and conservation aim.

I compared prediction metrics reported by authors to the prediction metric appropriate for that data type (Table 4.3). The reported prediction metrics were assessed as 'correctly reported', 'partially correctly reported', or 'incorrectly reported'. A model was reported correctly when the metric was correct for the data type with the appropriate amount of uncertainty expressed. A 'partially correctly reported' prediction metric expressed the correct type of prediction, but did not include uncertainty correctly (e.g. 'species occurrence' reported for PO data, which should be reported as 'rank likelihood of species occurrence'). Finally, an incorrectly reported model gave the wrong prediction for a given data type (e.g. 'occupancy' reported for AA data, which should yield 'relative abundance').

I also assigned a binary value for each model to each of four conservation aims: 1) spatial conservation prioritization; 2) predicting species assemblages or richness; 3) mapping current range; 4) predicting responses to climate change, and 5) predicting population viability. I also recorded when an express aim of the paper was to test or improve SDM modeling theory. For each model, conservation aim was derived from the paper's objectives or discussion section. Models could be assigned a value for more than one conservation aim.

4.3.1.2. Results and discussion

Of the 128 models evaluated, 111 were empirical, 4 mechanistic, and 13 used mixed empirical-mechanistic approaches. The most common algorithm families were regression-based (45 models), followed by decision trees (22 models) and maximum entropy (15 models; Table 4.4). This is consistent with Wiersma (2011) who examined the proportion of model types used from 1998-2007 and found that, overwhelmingly, regression-based methods were most common. As modelling has evolved, newer methods such as machine learning and maximum entropy have come to be favoured over regression-based in some cases. Visualization of publication by year (Figure 4.1) indicates that some algorithm families, such as envelope and niche models and expert-led models, were more popular in the earlier portion of the last decade, with maximum entropy and decision trees gaining in recent years.

The prediction metric for models was reported correctly (with an appropriate expression of uncertainty) 10 cases (7.8%), partially correct (without an appropriate expression of uncertainty) in 88 cases (68.8%), and incorrectly (reported prediction metric incompatible with data type used) in 30 cases (23.4%). Entirely correct reporting only occurred for models using regression-based, neural networks, maximum entropy, or decision-tree algorithms. Regression-based algorithms, decision trees, spread models, and expert-led models were most likely to report an incorrect prediction metric for the type of data used (Figure 4.2). Accuracy of reporting did not vary greatly by the aim of the model (Figure 4.3). Of the 107 models algorithms analyzed in academic publications, prediction metrics were reported correctly in 23.4% of models, partially correctly in 70.1%, and incorrectly in 6.5%. The gray literature model algorithms (21) reported prediction metrics correctly in 23.8% of cases, partially correct in 62% of cases, and incorrectly in 14.3%. Models from the gray literature were confined to six algorithm families: decision tree (3), expert-led (6), genetic (1), maximum entropy (5), neural networks (1), and regression-based (5). Only one paper from gray literature used more than one model algorithm in their report, and none used ensemble methods, mechanistic models, or mixed methods (mechanistic components in empirical algorithms).

Though these 128 model algorithms represent a non-systematic sample, the high proportion of model results that reported prediction metrics without an appropriate description of uncertainty is concerning. Much of the incorrect reporting seemed to arise from misinterpretation by the authors regarding the limitations of their input species data. These mistakes are extremely common: in a literature survey of over 100 academic papers that used Maxent, Yackulic et al. (2013) found that over half incorrectly interpreted the output as actual probability of occurrence, rather than relative probability of occurrence (being relative to bias, detectability, and other sampling constraints). Such misreporting could lead both investigators and managers to be over-confident in the capacity of their models to make accurate predictions, or not adequately consider their constraints. This is particularly true for models non-mechanistic projecting into the future or unsampled locations, which may overestimate species presence (Merow et al. 2011).

This may be particularly relevant outside of academic spheres, as it may be difficult for managers to stay abreast of up-to-date modeling theory, especially given how quickly the discipline changes. Managers may also lack the training to select models appropriately, or be unaware of alternative methods. Although much caution has been raised regarding the use of HSI models (Brooks 1997), the gray literature here and personal communication with government scientists and environmental consultants suggests that this older technique is still in widespread use, and is the preferred technique for many. The lack of mechanistic, ensemble, or mixed methods modeling in the gray literature surveyed here may be symptomatic of a divide between model developers and conservation managers.

4.4. SELECTING AN SDM STRATEGY BASED ON CONSERVATION OBJECTIVE

4.4.1. A new guide for model selection

An obvious need exists for managers to use SDMs, particularly robust ones, in conservation planning. Prospective users must be able to simply and quickly evaluate what modeling methods are appropriate for their data and conservation objectives. Based on prior review of ecological limitations and use of existing SDMs in the literature, I propose a framework to assist in the selection of a modeling strategy based on conservation objective, which is intended to produce mapped outputs of species distribution to inform management decisions. This framework includes four steps:

1. Consider the data available in your study area. Follow Flow Chart 1 (Figure 4.4) to determine which prediction metric(s) can be modeled from your data.
2. Select a conservation objective from those listed in Table 4.5. Follow the indicated flow chart(s) to select the appropriate SDM methodology based on data type and availability (Flow Charts 4.2-4.5).
3. Independently research the selected modeling approach(es) to determine if they are a) suitable for the objective and b) feasible for the data and experience of the user.
4. Build the selected SDM(s) according to best practices (see next section).

Although this framework is intended to guide selection of one or more modeling approaches, it is, of course, the responsibility of users to ensure they independently assess modeling options, understand their function and limitations, and have data that meets requirements. Elith & Leathwick (2009b) as well as Jakeman et al. (2006) provide lists of key steps in good modeling practice.

Users should familiarize themselves with the limitations of their prediction metrics based on data type (Table 4.3) to ensure they correctly report uncertainty. For example, users should note that calculation of population density requires detection probability to be accounted for, which can include a measure of temporary emigration, or use standardized indices (Bayne et al. 2011; Chandler et al. 2011; Sólymos et al. 2013). PO or PB data can only predict relative likelihood of presence (Table 4.1), and this prediction is relative to bias, survey effort, and detectability. Some PO or PB model types can account for survey effort or bias, making predictions more realistic. At present, empirical SDMs based on PO or PB data can only predict relative occurrence (and thus relative habitat suitability) on the landscape. More information may soon be available from new methods that are able to incorporate measures of detectability (Dorazio 2014), and indeed, has begun in some spheres (Sólymos et al. 2013). The user should keep these considerations in mind when navigating this framework to generate a prediction appropriate for their conservation objective.

4.4.2. Examples of use

4.4.2.1. Scenario 1

A district manager for a nature conservancy group is tasked with purchasing a new land holding to conserve the habitat of Sage Grouse (*Centrocercus urophasianus* Bonaparte) in a small portion of southern Alberta, Canada. She examines the data she has available: literature on sage grouse biology, as well as location data and a measure of detectability from a mark-recapture study on sage grouse in her province. She consults Flow Chart 1 (Figure 4.4) to identify which prediction metric she can calculate. She reads the first question, ‘Do you have spatially geo-referenced extinction, colonization, survival, fecundity, genetic similar, and/or other demographic and physiological parameters for populations in your study area?’. She does not, so she answers ‘no’. The next question asks if she has estimates of detectability from repeated measures, to which she answers yes. She can calculate occupancy.

Next, she visits Table 4.5 and chooses a conservation objective. She chooses ‘select habitat for inclusion in reserve system (single species)’. Since she has data to engage in occupancy modeling, she follows directions to visit Flow Chart 3 (Figure 4.6). Starting from the top of the chart, she follows the instructions and concludes that she will model occupancy and abundance, using Unmarked Populations for the algorithm family.

She researches unmarked occupancy models (Fiske & Chandler 2011), and builds her model using the statistical package *unmarked* (Fiske & Chandler 2011) based on the data from the detectability study. She projects the output using environmental covariates in GIS to generate a spatial prediction of Sage Grouse occupancy on the landscape. After this point, she can decide to employ other methods, such as cost analysis (e.g. Moilanen et al. 2009) to prioritize which land to pursue purchasing.

4.4.2.2. Scenario 2

A government biologist has been assigned to the recovery team for the Canada Warbler (*Cardellina canadensis* L.) and tasked with identifying critical habitat for conservation nationwide. His data include point counts from breeding bird atlas surveys, but he also has opportunistic observations captured by citizen science as well as museum records. He has a total of 200 location records in his study area. He has abundance information from the atlas surveys, but not the other data, so when following Flow Chart 1 (Figure 4.4) he is forced to answer 'no' to "Does your dataset include abundance information in the form counts? (AA)", and chooses occurrence as his prediction metric.

At this stage he also evaluates his potential environmental covariates, and a literature survey on the biology and habitat requirements of Canada Warblers, he identifies four covariates for which have GIS layers. He visits Table 4.5 and at first selects "Identify critical habitat" as his conservation objective. However, he does not have the data to predict occupancy or population viability, so instead, he chooses "increase or stabilize population numbers". He visits Flow Chart 2 (Figure 4.5) to select an algorithm family.

Beginning at the top of the flow chart, he determines he has enough presence observations to proceed. He has not controlled for autocorrelation (see *Best practices*), so he filters his data to ensure each presence point is a minimum distance apart. His species data is PO. The flow chart then asks if he can generate a mapped estimate of sampling bias. He creates a GIS mask that incorporates an index of survey effort available from breeding bird atlas data, as well as a measure of the spatial clustering around towns and cities from the occurrence data contributed by citizen scientists. The flow chart directs him to use a type of machine learning model: maximum entropy. He uses the program Maxent (Phillips & Dudik 2008; Elith et al. 2011) to construct a model using the Canada Warbler occurrence data, the sampling bias mask, and his environmental covariates. The output is a colour-coded map of relative probability of occurrence of Canada Warblers on the landscape. He includes the output in his report, but is careful to note that critical habitat, legally speaking, could not be modelled. Identifying critical habitat would require predicting occupancy or population viability, which was not possible with the available data.

4.4.2.3. Scenario 3

A sophisticated research team is engaged in continental-scale project to identify potential climate refugia for dozens of vertebrate species. For avifauna, they have count data from large long-term monitoring projects. They also have a series of standardized indices to correct their abundance information for detectability (AA + DET). Using Flow Chart 1 (Figure 4.4), they determine that they can calculate population density.

When examining conservation objectives (Table 4.5), they decide to choose both 'Assess effects of climate change' and 'Select habitat for inclusion in a reserve system (Multi-species)'. As directed, they review Flow Chart 4 (Figure 4.7), which instructs them to visit Flow Chart 2 (Figure 4.5). They decide to construct an SDM to predict population density for each species, and stack their outputs. However, they do not have data on interspecies interactions, so they cannot include this information as a model covariate. Though they are instructed to visit Flow Chart 2, as they also wish make a dynamic model, they first consult Flow Chart 5 (Figure 4.8). After reviewing the chart, they research mechanistic life-history information for all of their species, and conclude they can include dispersal distance constraints as a model covariate. Finally, they visit Flow Chart 2 (Figure 4.5) to select an algorithm family.

Based on their presence-absence data and their advanced modeling knowledge, they conclude that they will develop the models using artificial neural networks. However, they wish to compare projections calculated by different methods, and thus also choose to apply an ensemble method that 'stacks' the outcome of their neural networks along with other methods, such as boosted regression trees, Bayesian methods, and random forests. Using their detectability corrected-data, they produce aggregated climate refugia models for many landbird species based on multiple algorithms, and then 'stack' the models for each species to identify general priority conservation areas.

4.5. BEST PRACTICES

A number of best practices as well as rules of thumb have emerged out of general consensus in the SDM literature, and these should be followed during modeling. In order to construct an SDM using occurrence data, there must be at least 10 ‘presence’ locations of the species for each covariate used (Harrell 2001). Too many covariates (or too few species occurrences) will lead to model overfitting, where the covariates are fit not only to the data, but the noise as well, increasing explanation power for training data but greatly reducing the ability to make realistic predictions (McGill 2013). Regardless of model type, modeling should *always* include a validation procedure, which is commonly done using statistical model selection criteria (Guisan & Zimmermann 2000; Johnson & Omland 2004). In general, it may be best to choose more conservative models to avoid overfitting, as giving inaccurate estimates of suitable, available, or occupied habitat may mislead conservation planners (Crawford & Hoagland 2010). Overfitting also reduces model transferability to new locations or times (Wenger & Olden 2012)

Ensemble modeling is a relatively recent technique of combining predictions of species distributions that are produced using multiple algorithms to hone prediction accuracy (Brotons et al. 2004). Ensemble modeling has come to be recognized as a best practice among SDM experts (Araújo & New 2007; Marmion et al. 2009; Meller et al. 2014). Given that each SDM technique has its own uncertainties and limitations, combining outcomes from multiple models is thought to reduce a major source of variability, or, at the very least, give estimates of important sources of uncertainty (Meller et al. 2014). In an ensemble, models can be combined through an averaging, ordination, or other synthetic technique, or weighted according to model fit using, for example, Bayesian algorithms (Franklin 2009; Coetzee et al. 2009).

Spatial autocorrelation violates an assumption of independence among samples in models, and is rarely addressed by modelers (Franklin 2009). Spatial autocorrelation is the degree of clustering or dispersion, by which neighbouring samples tend to be more similar than those far apart. The effects of spatial autocorrelation may be more problematic when trying to capture the influence of covariates than when making spatial predictions (Franklin

2009). Best practices requires spatial autocorrelation to be addressed either before modeling using spatial filtering, during modeling by using an autoregressive or autologistic algorithm, or after modeling by comparing a spatial method with a non-spatial one (Carroll & Johnson 2008; Franklin 2009). It is important during this phase to consider factors of conspecific attraction that could be incorporated as mechanistic processes in models.

Ultimately, users must choose models for which they have (or can gather) data, but must keep in mind error arising from overlooking aspects of population dynamics (Pearson 2007). Although habitat suitability and fitness parameters are correlated, users should be careful not to mistake a prediction of habitat suitability as being a representative surrogate for physiological parameters such as fecundity (e.g. Brambilla & Ficetola 2012). For this reason, many modelers (Dormann 2007; Araújo 2009; Fordham et al. 2012; Bateman et al. 2013) suggest that it may almost never be appropriate to ignore the importance of ecological processes such as biotic interactions, dispersal, and movement when projecting future distributions. Predictions of species distribution are powerful tools, but no substitute for long-term datasets on abundance that can be analyzed for trend information.

Extrapolation remains a challenge for empirical SDMs. Franklin (2010, 2013) suggests three approaches for creating more realistic extrapolations: (1) Incorporating information about species biology and ecological limitations during the conceptual formulation of empirical models; (2) Using the output from a mechanistic SDM as an input to an empirical SDM, or vice versa (termed ‘linked’ modeling); and (3) Comparing empirical and mechanistic predictions. Few investigations have been done into model transferability, and accuracy of extrapolation can vary by model algorithm (see Wenger & Olden 2012 for an assessment of transferability of four common algorithms). These methods do not only apply to extrapolation. Arguably, many (if not all) conservation objectives could benefit by the increased realism of prediction that arises from having a spatial representation of habitat suitability that is informed by mechanistically-derived information about population dynamics, rather than just correlative relationships with environmental covariates. In reality, this information is difficult and expensive to capture, although it is increasingly available.

Mechanistic models offer the capacity to include measurements of fecundity and demography into estimations of species niche, allowing for much more realistic and powerful predictions. For example, a combination of habitat suitability and connectivity can potentially be used as a surrogate for probability of persistence (Nicholson & Ovaskainen 2009). SPVA can be used to assess habitat occupancy based on age and stage of the organism, as well as include genetic factors (McCarthy 2009), and enables optimizing selection of reserve area and estimating extinction risk. If genetic differentiation is observable on the scale being studied, samples of genetic information from different populations offers new ways of estimating dispersal and fecundity with effort that is constantly decreasing due to technological advancements (Sunnucks 2011).

However, empirical SDMs are often used in place of mechanistic SDMs and generalized to make population predictions, because data on dispersal, competitive effects, connectivity, and other assessments of constraints on population are lacking (Elith & Leathwick 2009b), especially at large scales. Although it is recommended that outputs of empirical and mechanistic SDM be compared to better understand the ecology of the species and refine predictions (Kearney & Porter 2009), this is often impossible. At larger scales, the theoretical drawbacks of empirical SDMs (being only able to model realized niche) may not be as pronounced (Hirzel & Lay 2008), especially if dispersal limitations and habitat heterogeneity are accounted for (Pulliam 2000).

Finally, most single-species models do not include the possibility of species interactions and community level effects (e.g. predation, competition) due to lack of data and increased model complexity. Single-species empirical SDMs are generally biased to over-predict the amount of used and available habitat (Laurent et al. 2011). Thus, interactions at the community-level should be included where possible, though this is largely dependent on spatial scale and available data. Particularly if conservation objectives are aimed at more than one species, multi-species modeling should be considered. Multispecies SDMs are becoming more accessible to produce mapped outputs for assemblages of species, and some allow for explicit modeling of interactions between species (Kissling et al. 2012).

4.6. RECOMMENDATIONS AND FUTURE DIRECTIONS

Species distribution modeling has advanced quickly in recent decades, and the pace of improvement and proliferation of new techniques will almost certainly continue. The framework presented here is intended to help lead prospective users through the morass of the many different SDMs to select an appropriate modeling approach. Although many of the modeling methods mentioned in this review have been directly compared to one another to evaluate performance, many have not. Araújo & Guisan (2006) identified the need to investigate conceptual and algorithmic uncertainties in models, and more thoroughly evaluate the strengths and limitations of each of the (many) current approaches. It should be noted, though, that the differences in performance between model types are typically smaller than differences among species being modelled (Franklin 2009).

Overall, it is imperative that users understand the limitations of model prediction to avoid misuse (Araújo & Peterson 2012). An ongoing challenge for SDMs, particularly extrapolative ones, is including biotic interactions such as competition, mutualism, and others (Elith & Leathwick 2009c). Many of these issues have been pointed out *ad nauseum* throughout the development of SDMs, with many authors calling for integrated empirical-mechanistic models (Larson et al. 2004; Guisan & Thuiller 2005; Phillips et al. 2009; Huntley et al. 2010; Higgins et al. 2012) and greater collaboration between theoretical and functional ecologists (Guisan et al. 2006).

These sought-after integrated models have yet to appear, but the beginnings of a convergence are evident: empirical models incorporating detectability estimates and survey bias (Sólymos et al. 2013; Dorazio 2014), and models combining empirical and dynamic elements (Peterman et al. 2013; Merow et al. 2014). However, these early attempts are computationally and theoretically intensive, lack consensus, and are not yet ‘packaged’ for wider adoption. Given that in the present investigation, only 17 of 128 modeling algorithms incorporated mechanistic elements, there is a need for clear methods, grounded in ecological theory, to integrate mechanistic and empirical SDMs.

Ultimately, a greater dialogue is needed between conservation practitioners and modelers to meet conservation needs more effectively (Guisan et al. 2013). SDMs provide powerful tools for conservation planning, but more attention must be paid to designing SDMs for direct use and interpretation by conservation managers. All modeling approaches need clear documentation and to be available in customizable packages (such as add-ins to common statistical programs or stand-alone graphical user interfaces (GUI)). Robust user groups need to be available to help develop user guides and support through troubleshooting. This may require a ‘paring down’ of the many multitudes of SDMs to focus on developing easy-to-use packages for algorithms that perform well, as well as a specific focus on integrating mechanistic SDMs with empirical ones. Until such approaches are widely available, the framework presented here can help guide the user through selection of both empirical and mechanistic models. By following the steps outlined in this review (Table 4.5), the user can use best practices to select the most appropriate and powerful tools to manage for the conservation objectives at hand.

4.7. TABLES AND FIGURES

Table 4.1: Empirical species distribution models in common use, organized by model type and algorithm family.

Model Family	Algorithm Type	Description	Data Type*	Common Models	Advantages	Drawbacks	Model estimation parameter
Envelope and Similarity	Envelope and Niche	Bounds species presence; predicts habitat suitability based on meeting habitat profiles within the bounded area(s)	PO	BIOCLIM; Environmental Niche Factor Analysis (ENFA)	Works in data-poor situations; can be modified to include mechanistic processes	Typically outperformed by other methods	Ranks likelihood of occurrence
Envelope and Similarity	Kernel	Infers species range spatially, often with telemetry data. Does not typically include environmental covariates	PO	Kernel Estimation	Useful for basic range delineation	Not appropriate for prediction	Ranks likelihood of occurrence
Envelope and Similarity	Distance and Similarity	Assess multivariate distance measures to describe mean vector of covariates with relation to the response variable	PO	DOMAIN; General Dissimilarity Modeling; Distance Measures (Mahlanobis, Euclidean, etc.)	Works in relatively simple situations with few interactions	Not ideal when data is limited/ habitat variables are dynamic. Linear relationships only, requires continuous covariates. Less robust compared to machine learning	Ranks likelihood of occurrence

Model Family	Algorithm Type	Description	Data Type*	Common Models	Advantages	Drawbacks	Model estimation parameter
Expert-based	Expert-led	Expert knowledge of species biology and ecology is used to select parameters thought to be of high value	SB	Convex or alpha hulls; GIS overlays; Habitat Suitability Index (HSI) Modeling	Can be used in situations with little or no PO or PA data.	Typically outperformed by other methods when PO or PA data are available	Ranks relative probability of occurrence
Machine Learning	Decision Tree	Decision trees classify responses according to monothetic hierarchies. Typically, many decision trees will be generated and then averaged or combined according to model specifications	PA/AA	Boosted Regression Trees (BRT); Classification and Regression trees (CART); Classification Tree Analysis (CTA); Mixture Discriminant Analysis (MDA); Random Forest (RF)	Works with categorical and nonlinear covariates. Copes with unknown covariate interactions, missing data, and poorly-known species ecology. Typically better than single classification trees or parametric methods. No need for prior data transformation or elimination of outliers.	Not ideal when species response is expected to be linear or smooth. Rare classes need to be sufficiently represented, though this is corrected for in boosting methods like BRT/RF	Predicts probability of occurrence (if detection bias is controlled for, otherwise relative likelihood)
Machine Learning	Genetic Algorithm	Classification rules "evolve", based on random mutations and "fitness", until an optimal solution is reached	PO	Genetic Algorithm for Ruleset Production (GARP)	Can be used to predict species distribution or to select between models in an ensemble.	Performs poorly compared to regression-based, machine learning, and neural network methods	Ranks likelihood of occurrence

Model Family	**Algorithm Type**	**Description**	**Data Type***	**Common Models**	**Advantages**	**Drawbacks**	**Model estimation parameter**
Machine Learning	Maximum Entropy	Estimates the most uniform distribution (or maximum entropy) of sampling points compared to background locations, using constraints derived from data	PB	MaxEnt	Good for data-poor situations. Relatively easy to implement.	Requires measures of survey bias to be robust. Often considered inappropriate for forecasting	Predicts relative likelihood of occurrence (if sampling bias is controlled for, otherwise ranks likelihood)
Machine Learning	Neural Networks	Derives nonlinear composite variables and models response as a function of these features	PA/AA	Artificial Neural Networks (ANN)	Have outperformed other methods in comparative studies.	Extremely complex.	Predicts probability of occurrence (if detection bias is controlled, or relative likelihood)
Occupancy	Unmarked Populations	Model spatial variation in density by incorporating measures of detection probability across repeated measures of organisms	DET	N-Mixture; PRESENCE; unmarkedR; Hierarchical Bayesian; single season; multi-season	Can provide a more accurate picture of organism distribution.	Requires multiple-visit estimates of detectability, usually small scale.	Probability of occupancy; probability of population density; probability of abundance
Statistical	Ordination	Orients species distributions in environmental space.	PA/AA	Canonical Correspondence Analysis (CCA); Redundancy Analysis (RDA)	Useful for community modeling.	Few comparisons exist with other methods. More difficult to generate mapped spatial map.	Predicts relative likelihood of occurrence

Model Family	Algorithm Type	Description	Data Type*	Common Models	Advantages	Drawbacks	Model estimation parameter
Statistical	Regression-based	Predicts response variable from covariates based on their observed importance. Variations extend linear models that can accommodate non-normal response variables.	PB/PA/AA	Generalized Additive Models (GAM); General Estimating Equations (GEE); Generalized Linear Mixed Models (GLMMs); Geographically Weighted Regression (GWR); Logistic/auto-logistic models; Multivariate Adaptive Regression Splines (MARS); Resource Selection Functions (RSF)	MARS can account for local variable interactions (varying across distribution). Locally-weighted approaches, such as GWR and GLMMs, can be used to identify scale dependency and can outperform other methods in some cases.	Not ideal with non-binary categorical variables. Covariate interactions must generally be known in advance. GAMs are not well suited for extrapolation. GEEs are not robust for spatial prediction. RSFs are useful for highly mobile species.	Predicts probability of occurrence (if detection bias is controlled for, otherwise relative likelihood)

*Data Types: SB – information about species biology and ecology derived *a priori*; PO – presence only, with georeferenced locations of species occurrence; PB – presence background, with georeferenced locations of species occurrence and pseudo-absence data from sites presumed ‘available’; PA – presence-absence, with georeferenced locations of occurrence or abundance data at sites where species are documented to be present and absent. AA – similar to PA, but includes numerical counts at presence sites, and can be used to derive population density if abundance is corrected for detectability; and DET – derived from sampling where detectability is measured using repeat visits, mark-recapture techniques, or estimated using statistical offsets.

Table 4.2: Mechanistic species distribution models in common use, organized by model type and input data category.

Model Type	Category	Description	Data Type*	Common Model or Model Suites	Model estimation parameters**
Occupancy	Marked Populations	Models viability and/or spatial variation in density by marking and recapturing/re-sighting organisms	PV/DET	DISTANCE; CAPTURE; MARK	Probability of occupancy; population density; abundance; viability
Mechanistic Niche Model		Models traits governing the fundamental niche, such as thermal tolerance	PV	Custom; PHENOFIT (trees)	Probability of occurrence; viability
Spatial Population Viability Analysis	Evolutionary Trait Models	Uses information on the evolutionary relationships of organism to predict traits. Can be applied to empirical SDMs to assess habitat constraints.	PV	Phylogenetic Generalized Least Squares (PGLS)	Probability of occurrence; viability
Spatial Population Viability Analysis	Landscape Genetics	Evaluates functional connectivity using all possible paths through a landscape	PV	Isolation-by-resistance; Least cost path; Genetic distance; Graph theory; Circuit theory	Probability of occurrence; viability
Spatial Population Viability Analysis	Metapopulation	Assumes a patchy distribution of species across habitats, and uses unique information from populations/subpopulations to model features of the metapopulation.	PV/DET	Structured Patch Occupancy Metapopulation Models (SPOM); Structured metapopulation models; Spatial simulation models; Population matrix models; RAMAS GIS	Probability of occupancy; population density; abundance; viability

Model Type	Category	Description	Data Type*	Common Model or Model Suites	Model estimation parameters**
Spatial Population Viability Analysis	Spread models	Includes species-specific constraints related to dispersal. Can be applied to projections of empirical SDMs	PV	MigCLIM; SHIFT; grid-based models	Probability of occurrence; viability

*Data Types: SB – information about species biology and ecology derived *a priori*; DET – derived from sampling where detectability is measured using repeat visits or mark-recapture techniques, or estimated using statistical offsets.

**The parameter 'viability' is inclusive of parameters like fecundity, colonization, breeding success, carrying capacity, population growth rates, and others.

Table 4.3: Prediction metrics for species distribution models based on data type.

Model Type	Data Type	Acronym	Prediction metric
Empirical	Species biology (*a priori*)	SB	Rank relative probability of occurrence/habitat suitability
	Presence-only	PO	Rank likelihood of occurrence
	Presence-background	PB	Relative likelihood of occurrence constrained by condition
	Presence-absence	PA	Relative likelihood of occurrence
	Abundance-only	AO	Rank likelihood of abundance
	Abundance-absence	AA	Relative abundance
	Detectability-corrected abundance-absence	AA + DET	Predicted abundance/Population density
	Detectability-corrected presence-absence	PA + DET	Likelihood of occupancy
Mechanistic	Viability	PV	Viability (e.g. breeding success, survival, fecundity, etc.)
	Viability (Physiological tolerance)	PV + SB	Predicted range
	Detection-corrected viability	PV + DET	Likelihood of occupancy
Mixed	Presence-only and viability	PO + PV	Rank likelihood of occupancy/viability
	Presence-absence and viability	PA + PV	Likelihood of occupancy/viability

Table 4.4: Reported prediction metrics of 100 evaluated species distribution models by algorithm type. Column headers: M = model type, AF = Algorithm family, n = number of models evaluated, SCP = Spatial conservation prioritization, SA = Species assemblages/richness, RM = range mapping, CC = Responses to climate change, PV = Population viability, SDM = Theoretical contribution to SDM development.

M	AF	n	SCP	SA	RM	CC	PV	SDM	Included publications
Empirical	Envelope and Niche Models	7	4	1		1		5	Atamian et al. 2010; Brotons et al. 2004; Elith et al. 2006; Levinsky et al. 2013; Titeux et al. 2007; Wisz et al. 2008
	Kernel	2			2				Auer 2008; Hamel & Ozdenerol 2009
	Distance & Similarity	6	2	2		2		4	Elith et al. 2006; Levinsky et al. 2013; Wisz et al. 2008
	Expert-led	11	11			1		1	Beaudry et al. 2010; Beazley et al. 2005; Glennon 2009; Government of Victoria 2013; Holmes et al. 2008; Jetz et al. 2007; Jobin et al. 2005; McCorkle et al. 2006; Rittenhouse et al. 2008; Tirpak et al. 2009; Westwood 2012
	Decision Tree	22	8	7		10	2	5	Barbet-Massin et al. 2012; Barket et al. 2014; Coetzee et al. 2009; Cumming et al. 2013; Distler et al. 2015; Elith et al. 2006; Goetz et al. 2010; Haché et al. 2014; Kreakie et al. 2012; Liu et al. 2011; Matthews et al. 2004; Schuetz et al. Shirley et al. 2013; Vallecillo et al. 2009; Wisz et al. 2008
	Genetic	4	2	1		1		2	Duffe et al. 2008; Elith et al. 2006; Levinsky et al. 2013; Wisz et al. 2008
	Maximum Entropy	15	8	2	1	3		4	Buermann et al. 2008; Burnett et al. 2008; Cardador et al. 2015; Duffe et al. 2008; Elith et al. 2006; Ferrari 2014; Geupal et al. 2007; Kreakie et al.

M	AF	n	SCP	SA	RM	CC	PV	SDM	Included publications
									2012; Levinsky et al. 2013; Randall 2013; Sohl 2014; Velásquez-Tibatá et al 2013; Wisz et al. 2008; Yost et al. 2008
	Neural Networks	4	1	3		2		1	Barbet-Massin et al. 2012; Coetzee et al. 2009; Cumming et al. 2013; Foody 2005
	Unmarked Populations	5	3	1				1	Collier et al. 2012; De wan et al. 2009; Kéry and Royl 2008; Royle et al. 2008; Vierling et al. 2013
	Regression-based	45	20	14		12	4	20	Alridge & Boyce 2007; Bacaro et al. 2011; Barbet-Massin et al. 2012; Bellis et al. 2008; Betts et al. 2006; Brotons et al. 2004; Bustamante & Seoane 2004; Carroll & Johnson 2008; Carroll et al. 2006; Coetzee et al. 2009; Elith et al. 2006; Fisichelli et al. 2012; Foody 2005; Gibson et al. 2004; Giordano et al. 2010; Heikkinen et al. 2007; Huntley et al. 2006; La Sorte & Thompson 2007; McPherson & Jetz 2007; Mitchell et al. 2006; Nielsen 2007; Parons et al. 2009; Stralberg & Gardali 2007; Stralberg et al. 2006; Vallecillo et al. 2009; van Riper et al. 2014; Vernier et al. 2008; Voegeler et al. 2011; Wisz et a. 2011
Mechanistic	Evolutionary Trait	1				1			Bradshaw et al. 2014
	Meta-population	1					1		Aldridge and Boyce 2007
	Spread models	4	3				2	2	Larson and Sengupta 2013; Merow et al. 2011; Shanahan and Possingham 2009; Zozaya et al. 2011

Table 4.5: Steps for selecting a species distribution modelling method to inform management decisions for common conservation objectives.

Example Conservation Objective	**Steps to follow**
Assess biodiversity metrics	Flow Chart 4: Approaches for developing community-level distribution models (Figure 4.7)
Assess effects of climate change	Flow Chart 5: Approaches for developing climate projection models (Figure 4.8)
Estimate historical distribution	Flow Chart 5: Approaches for developing climate projection models (Figure 4.8)
Identify critical habitat	Flow Chart 3: Selecting a model for predicting occupancy and/or population viability (Figure 4.6)
Increase or stabilize population numbers	Flow Chart 2: Selecting a model for predicting occurrence, abundance, and/or population density (Figure 4.5) **OR** Flow Chart 3: Selecting a model for predicting occupancy and/or population viability (Figure 4.6)
Reintroduction/Translocation	Flow Chart 3: Selecting a model for predicting occupancy and/or population viability (Figure 4.6)
Select habitat for inclusion in reserve system (single species)	Flow Chart 2: Selecting a model for predicting occurrence, abundance, and/or population density (Figure 4.5) **OR** Flow Chart 3: Selecting a model for predicting occupancy and/or population viability (Figure 4.6)
Select habitat for inclusion in reserve system (multi-species)	Flow Chart 4: Approaches for developing community-level distribution models (Figure 4.7)
Predicting spread of invasive species	Flow Chart 3: Selecting a model for predicting occupancy and/or population viability (Figure 4.6)

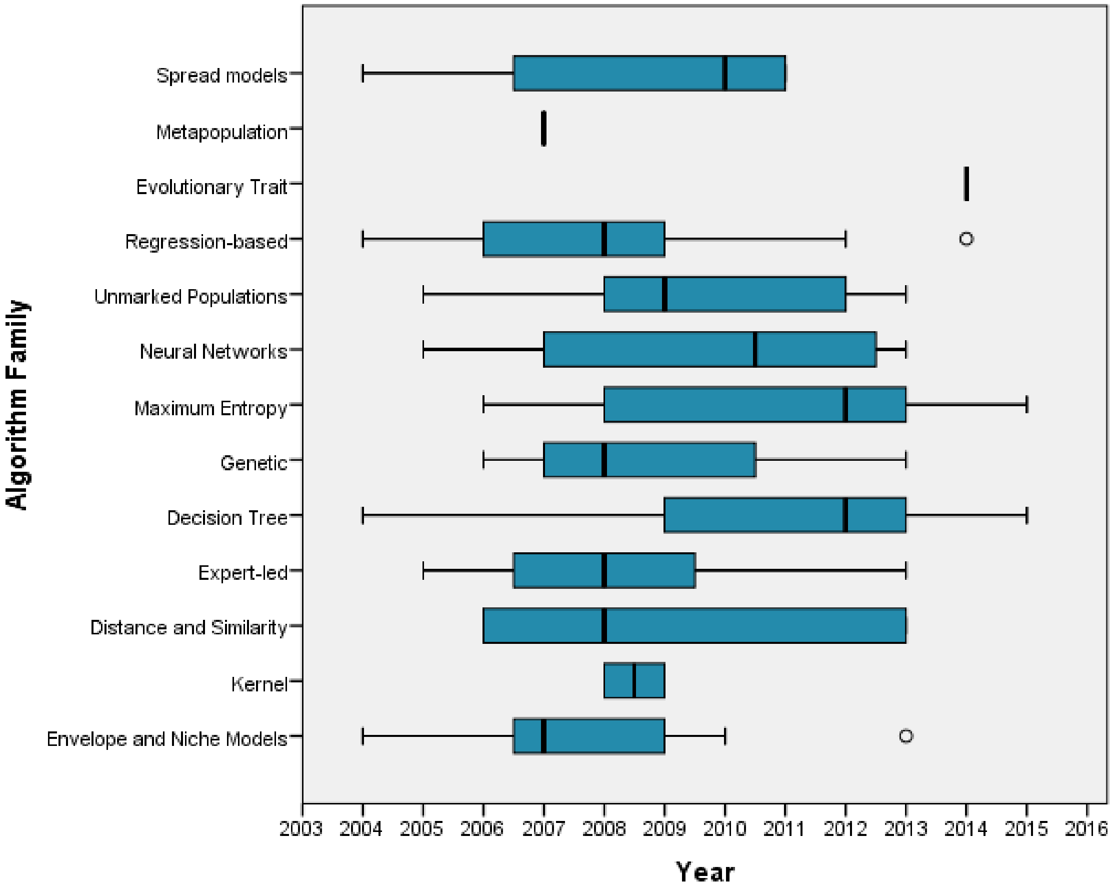

Figure 4.1: Boxplots showing year of publication for 128 landbird species distribution models categorized by algorithm family, with error bars showing 95% confidence interval.

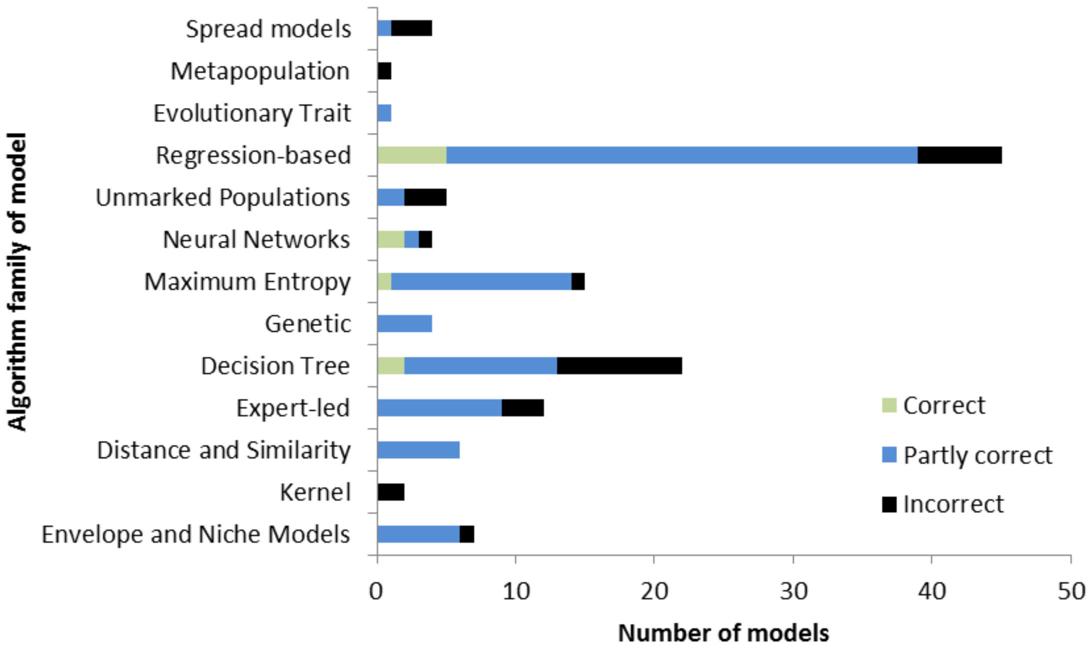

Figure 4.2: Accuracy of reported prediction metrics for 128 landbird species distribution models categorized by algorithm family. ‘Correct’ models reported both appropriate prediction metric and expressed uncertainty by data type. ‘Partly correct’ models indicated correct prediction type, but inaccurately defined uncertainty. ‘Incorrect’ models reported the wrong prediction metric by data type.

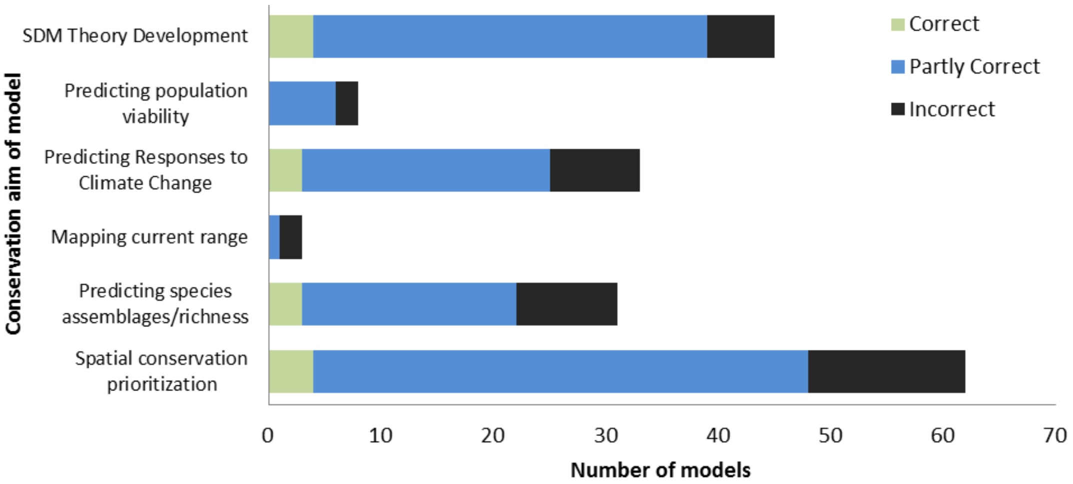

Figure 4.3: Accuracy of reported prediction metrics for 128 landbird species distribution models categorized by stated conservation goal. ‘Correct’ models reported both appropriate prediction metric and expressed uncertainty by data type. ‘Partly correct’ models indicated correct prediction type, but inaccurately defined uncertainty. ‘Incorrect’ models reported the wrong prediction metric by data type.

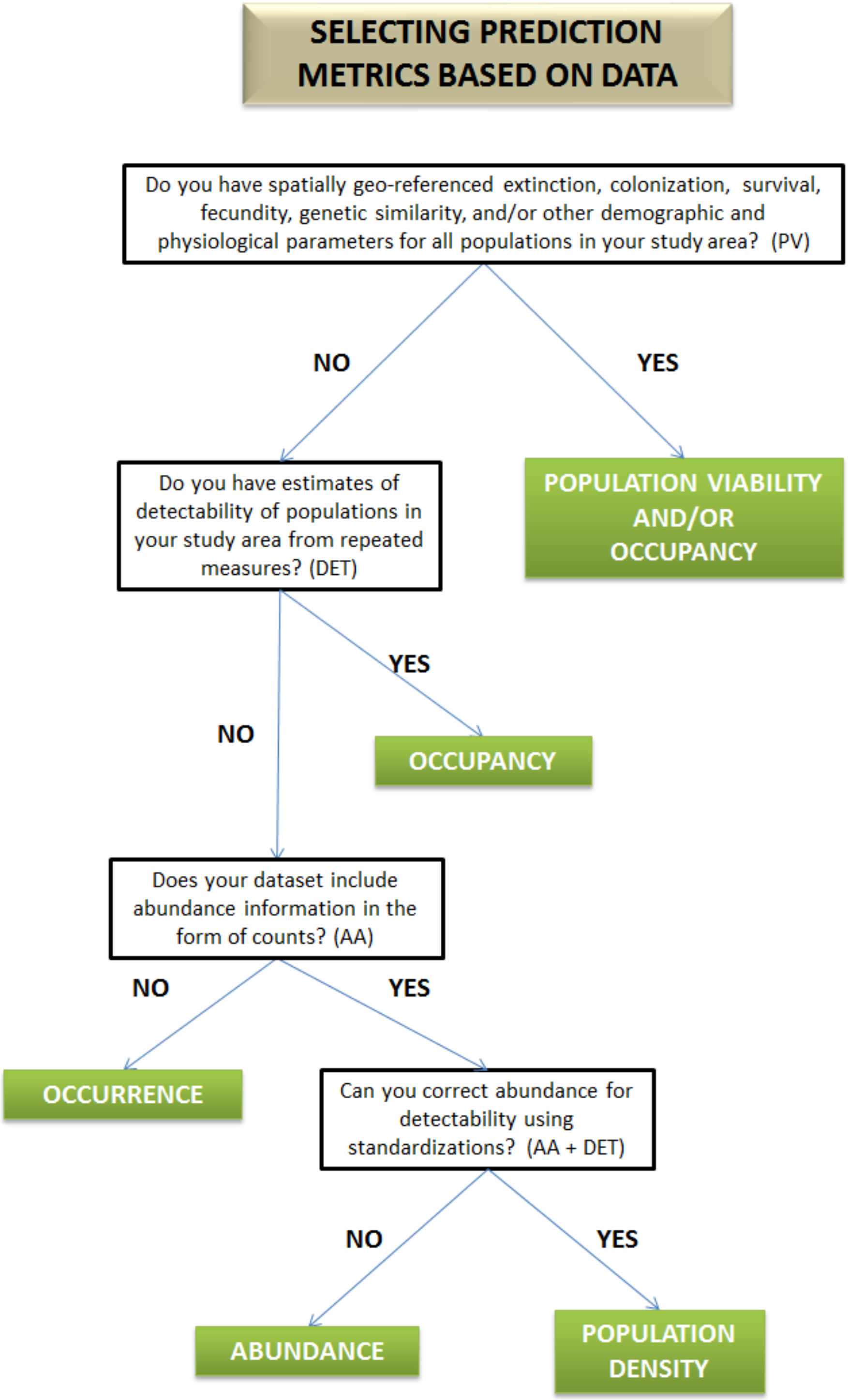

Figure 4.4: Flow Chart 1, Steps to identify possible prediction metrics based on available data for species in a given study area.

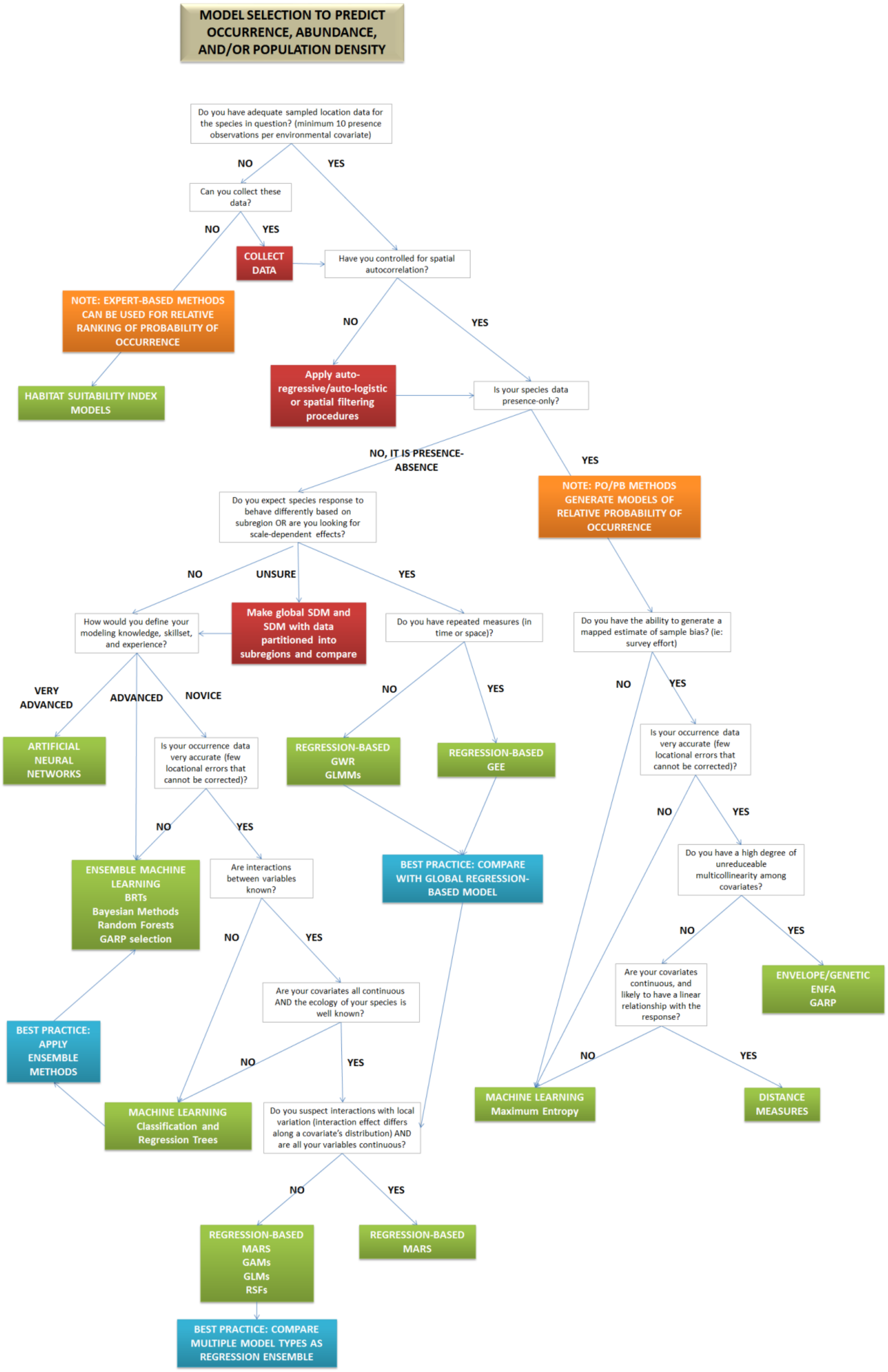

Figure 4.5: Flow Chart 2, Selecting a model for predicting occurrence, abundance, and/or population density.

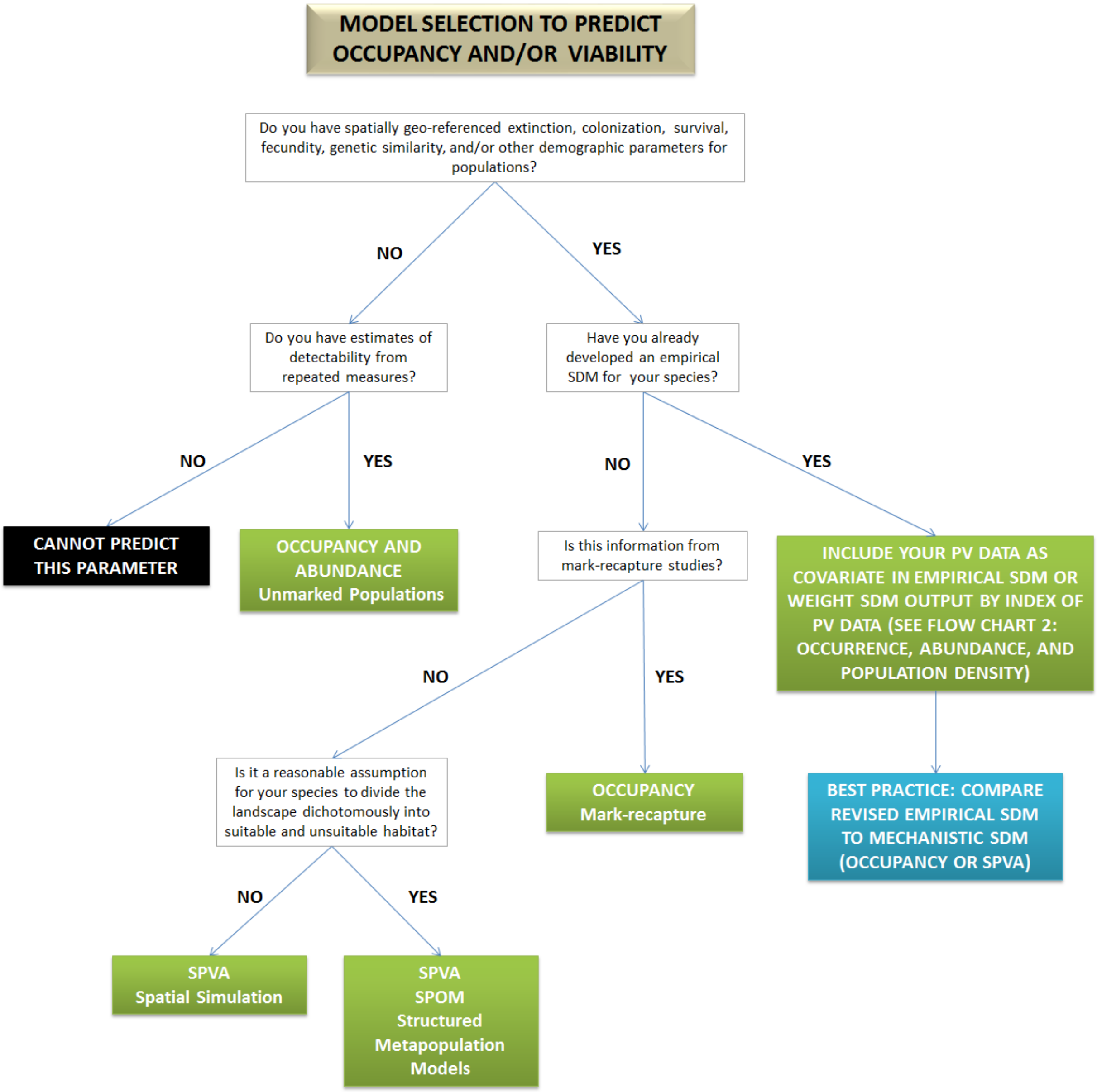

Figure 4.6: Flow Chart 3, Selecting a model for predicting occupancy and/or population viability.

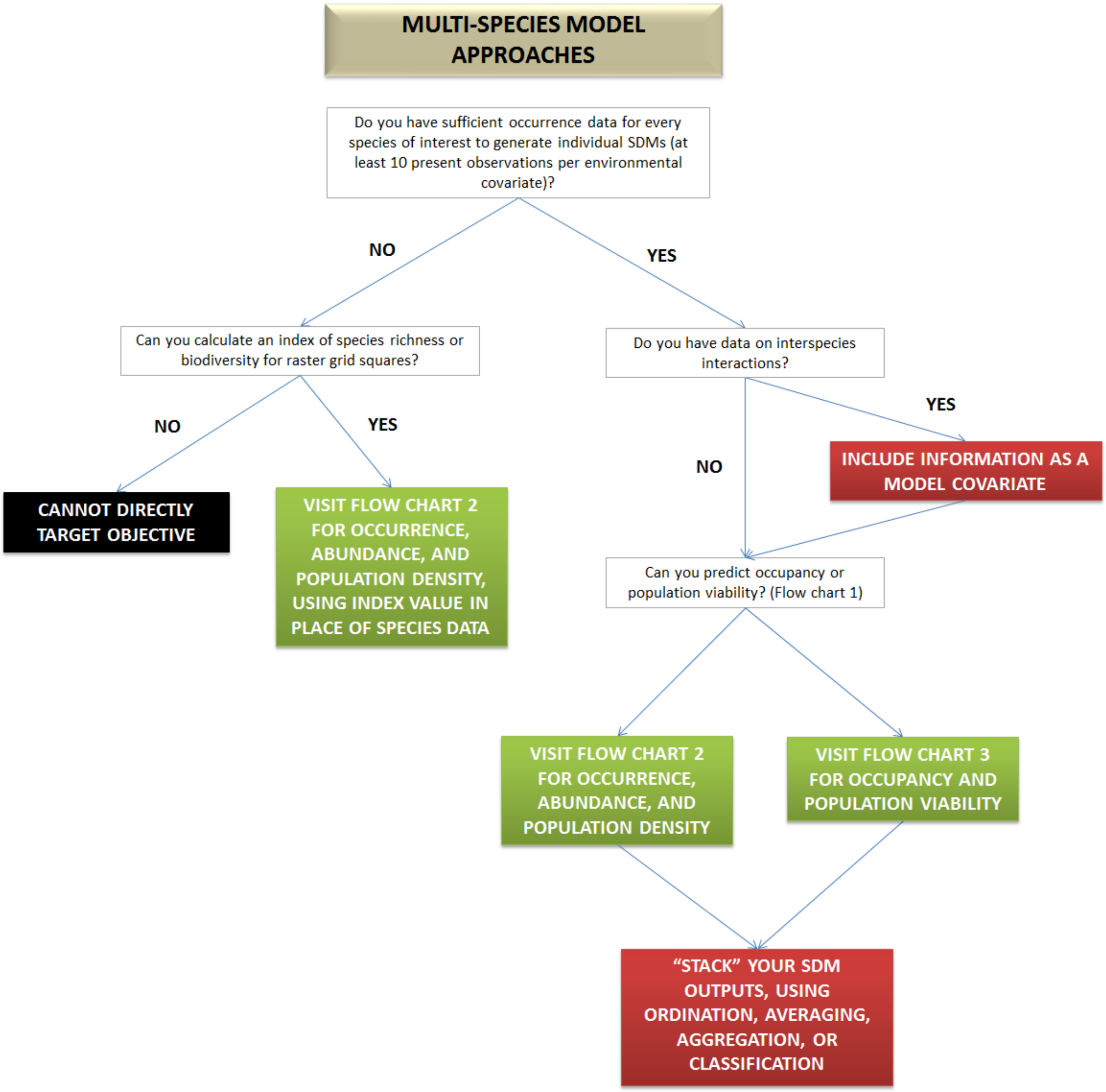

Figure 4.7: Flow Chart 4, Approaches for developing community-level distribution models.

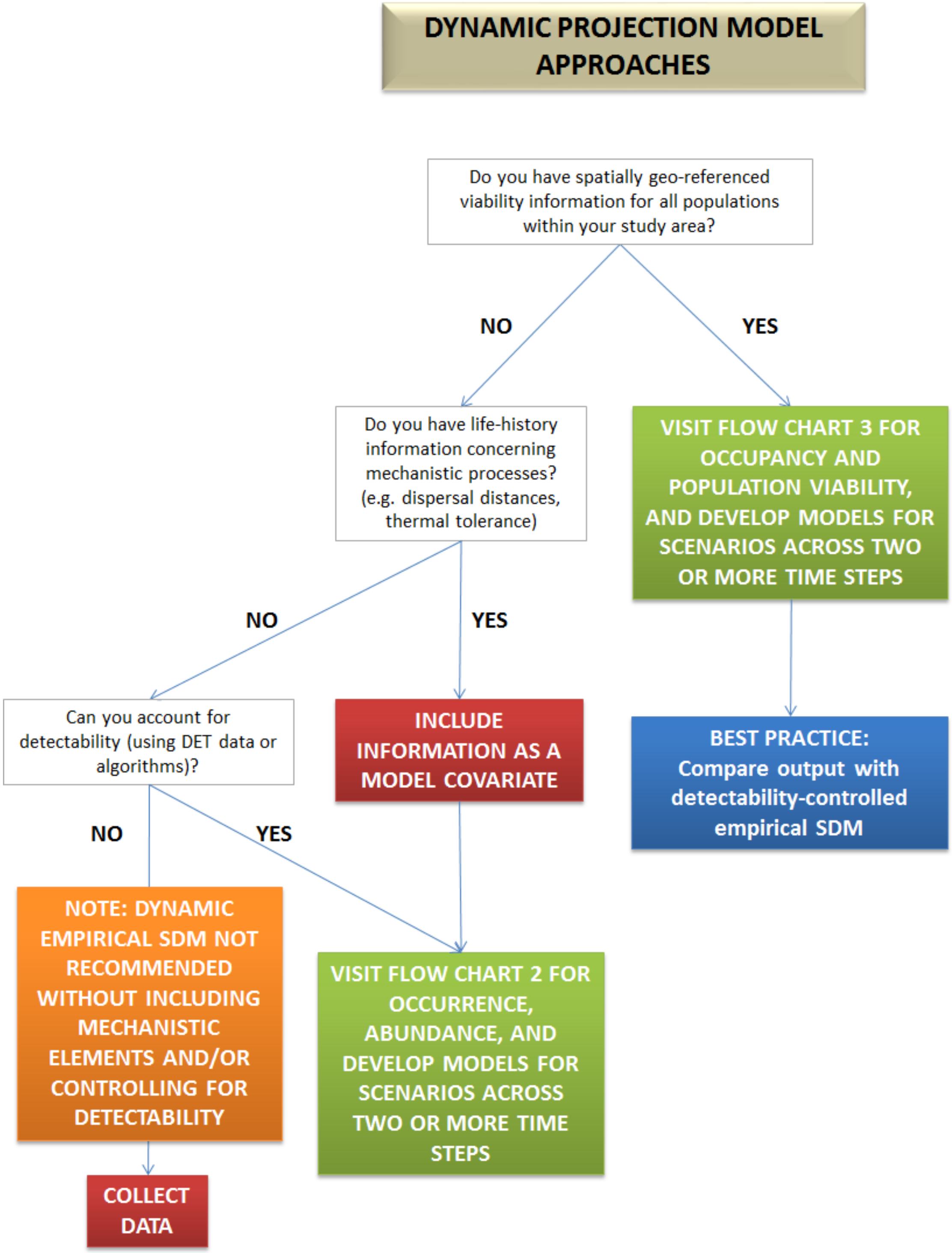

Figure 4.8: Flow Chart 5, Approaches for developing climate projection models.

CHAPTER 5 SPECIES DISTRIBUTION MODELING IN MARITIME NATIONAL PARKS

Westwood, A., Solymos, P., Fontaine, T., Bayne, E. 2015. Estimating population density of the Rusty Blackbird (*Euphagus carolinus*), Olive-Sided Flycatcher (*Contopus cooperi*), and Canada Warbler (*Cardellina canadensis*) in national parks in New Brunswick and Nova Scotia. Report prepared for Parks Canada on behalf of the Boreal Avian Modelling Project, University of Alberta: Edmonton. 63pp.

5.1. INTRODUCTION

The Rusty Blackbird, Olive-Sided Flycatcher, and Canada Warbler have experienced steep population declines (COSEWIC 2006, 2007, 2008), and are federally-listed species at risk (SAR; Government of Canada 2011). Particularly for Rusty Blackbird and Canada Warbler, annual rates of decline have been among the highest in the eastern portion of their Canadian breeding range (Environment Canada 2014a). A unique subspecies of Rusty Blackbird, *E. c. nigrans*, breeds in Nova Scotia. Both nationally and in Maritimes, these SAR occupy federally, provincially, and privately protected lands, outside of which forest and wetland areas are undergoing harvesting, resource extraction, recreation, and other managed uses.

Protected areas are a tool used to achieve biodiversity conservation by limiting human intervention in an area. In Canada, Parks Canada's mandate includes ensuring the ecological integrity of its lands (Parks Canada 2011), which includes the stewardship of species at risk within its lands. Under the National Accord for the Protection of Species at Risk, Parks Canada is involved with the development and support of recovery strategies and implementation of recovery actions, and also engages in other monitoring and management activities.

Protected areas contribute to biodiversity and community well-being, but their effectiveness can vary depending on regional and management objectives (Leverington et al. 2010). Forested areas of New Brunswick have undergone substantial fragmentation in recent years (Betts et al. 2003). The total proportion of forest dominated by mixedwood stands in New Brunswick has decreased over the past half-century because of altered disturbance regimes and forest harvesting (Amos-Binks et al. 2010). In Nova Scotia, only 32.5% of the province's "natural landscape types" were considered adequately represented within the protected areas system in 1994 (NSDNR 1994). More recent estimates suggest that 48% of "natural landscape types" are represented at a satisfactory or near-satisfactory level in Nova Scotia (David MacKinnon, pers. comm.). Though protected areas holdings continue to expand (Province of Nova Scotia 2013), expansions were not completed in a fashion that prioritized protection of suitable habitat for Olive-sided Flycatcher, Canada Warbler, and Rusty Blackbird, or the wet forest ecosystems they occupy. As available forest outside of park boundaries continues to be developed, it is important to know the potential for existing protected areas to protect suitable habitat, and to assess if birds are more or less likely to be found in protected areas than other areas in the same region. Additionally, estimates of population size in local areas can allow for evaluation of population viability.

In national parks in New Brunswick and Nova Scotia, the status of Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler populations has been assessed as unrankable due to a lack of information (Parks Canada Agency 2011a, 2011b, 2011c). At present, population sizes for these species cannot be estimated from data collected within the parks themselves due to low sample sizes. Conservation of these species within these areas requires detailed information on habitat distribution and quality, which is presently not available at a scale suitable for management. The paucity of information requires that predictive modelling be used to estimate population sizes based on regional knowledge about species-habitat relationships. Despite potential sources of uncertainty in the estimation process, mapped regional estimates of species distribution are essential to guide conservation planning (Sanderson et al. 2002). For spatial conservation, datasets at a scale of 1 km^2 or greater are of limited value for land use planning at the watershed or municipal level (Woolmer et al. 2008). To inform reserve design and land management, predictions are needed as close as possible to those of the resolution of individual forest stands (Betts et al. 2006a).

5.1.1. Modelling species associated with wet forest habitats

Recent reviews of the breeding ecology of all three species have been provided by the Birds of North America Online (Altman & Sallabanks 2010; Reitsma et al. 2010; Avery 2013a). Rusty Blackbird predominantly nest in small conifers near wet areas (Matsuoka et al. 2010). Olive-sided Flycatcher predominantly occupy coniferous forest sites near patches of early seral vegetation, including both the edges of bogs and burns in natural habitats, and clearcut edges in disturbed areas (Altman & Sallabanks 2010). Canada Warbler require a well-developed shrub layer and a complex forest floor (Reitsma et al. 2010), and can also be locally abundant in regenerating forests (i.e., 6–30 years post-disturbance) following anthropogenic or natural disturbances (Lambert & Faccio 2005). Though found in a variety of forest types, Canada Warbler is most common in wet mixed forest. Rusty Blackbird and Olive-sided Flycatcher have large territories (10-20 ha), with habitat immediately around the nest site comprising only a small area within a heterogeneous matrix. Canada Warbler have small territories, whose composition is more homogenous, and in southwestern Nova Scotia are almost exclusively confined to wet forest habitat (CHAPTER 2).

Depressional forest wetlands, determined by run-off or groundwater processes, are recognized as important breeding bird habitat for many species (Riffell et al. 2006), though they have not been studied for these species in particular. In the U.S., forested wetlands have been decreasing at faster rates than other types of forests (Abernathy & Turner 1987). However, high-quality spatial reference data for these ecosystems are scarce, making them difficult to represent in species distribution models. Aerial delineation of wet forest areas is difficult, as the canopy over wet areas is often continuous with canopy of upland forest (Riffell et al. 2006).

Because of these issues, wetland habitat types can be poorly recorded, and where they are recorded, accuracy can fluctuate widely due to the ephemeral nature of many types of wetland (Gómez-Rodríguez et al. 2008; Skagen et al. 2008). Species distribution models (SDMs) for species reliant on GIS layers describing wetlands have, at least in some cases, performed poorly (Kreakie et al. 2012). For these reasons, it is common to use proxy data to predict the locations and types wetlands in models, such as depth to water table or soil wetness index. Particularly for species associated with wet forest areas, it is important to test various approaches to modelling wet areas. Accuracy can be gauged by assessing model fit, to help select the most effective representation of wet areas.

SDMs predicting species distribution across the landscape are particularly useful for conservation (CHAPTER 4), as they generate an easily-interpretable mapped product that can be used to assess critical areas for management. SDMs associate species observations and environmental covariates to describe species distributions on the landscape (Franklin 2009; Elith & Leathwick 2009c). They give insight into both ecological relationships for the species, as well as maps of habitat species occurrence, occupancy, abundance, or population density that can be used to inform conservation strategies (Elith & Leathwick 2009b; Franklin 2009; Moilanen et al. 2009). For species at risk, it is important to uncover habitat preferences and develop spatially-explicit predictions of population distribution on the landscape to inform conservation.

The Boreal Avian Modeling (BAM) project has generated national-scale species distribution models for Olive-sided Flycatcher and Canada Warbler, with models based on landcover (Hache et al. in prep) and climate space (Lefevre et al. n.d.; Cumming et al. 2013). Using count data for birds in models allows for prediction of population sizes and distributions (Elith & Leathwick 2009c). However, national models based on coarse resolution data (1-10 km^2 or greater) are not designed to describe local variation in habitat suitability, or to engage in stand-level planning. Additionally, national-scale models develop their habitat based on habitat preferences determined from point counts across the range. This is particularly relevant for these SAR, which exhibit different habitat preferences across their range. Using regional abundance data combined with finer scale covariates, constrained regionally to reflect the local ecology of the species, may improve SDM estimates. The resulting information about the availability, quality, and distribution of breeding habitat can be used for on-the-ground management, as well as to understand ecological associations of these species at the easternmost extreme of their range.

This chapter included five main objectives: (1) Generate predictive models and maps of bird density for Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler and evaluate the contribution of different covariates, (2) Estimate population sizes in 4 national parks in Nova Scotia and New Brunswick for these three species, (3) Map predicted density estimates and their uncertainty, (4) Compare model selection across subsets representing wet habitat using three different methods (wetland delineation, depth to water table, and the interaction of depth to water table with forest cover), (5) Compare estimates between national parks and replicate areas in corresponding ecoregions to evaluate the contribution of national parks to species conservation.

I used the BAM point count dataset to develop high-resolution predictive SDMs for Olive-sided Flycatcher, Canada Warbler, and Rusty Blackbird in Maritime national parks, using a library of high-resolution ecological covariates selected *a priori* based on known species-habitat relationships. The modeling method used was Poisson log-linear, with corrections for detectability and variation in sampling effort across study protocols (Sólymos et al. 2013). A branching forward stepwise variable selection process with bootstrapping was used to minimize bias in covariate selection. The density predictions allow for evaluation and comparison of habitats within parks to guide SAR planning and management.

5.2. **METHODS**

5.2.1. Study area

The four national parks under consideration (Kouchibouguac, Fundy, Cape Breton Highlands, Kejimkujik) are within the eastern Canadian provinces of New Brunswick (NB) and Nova Scotia (NS). Prince Edward Island National Park was excluded as the geospatial layers necessary for analysis were not available in the province. Kejimkujik National Park and Historic Site is divided into a mainland park and seaside adjunct, the latter of which was excluded from this analysis due to its small size and predominantly coastal ecosystem. All parks in this analysis have a coastal component except Kejimkujik (Mainland), which is located in the centre of southwest Nova Scotia. Coastal areas of parks were also included in analysis. New Brunswick encompasses 7.5 million ha, and borders Québec and Maine.

NS is peninsular, and encompasses 5.8 million ha, and is connected to the remainder of North America through a 24 km wide isthmus. NS and NB represent the extreme eastern extent of the breeding range for all three species.

Nova Scotia includes 9 distinct ecoregions, and its ecosites have been divided into two main groups: Acadian and Maritime Boreal (Keys et al. 2011b). NB is similar, with 7 unique ecoregions and high forest heterogeneity across the landscape (NBDNR 2007). Much of both provinces are forested, though fragmented by forest harvesting operations. Non-forested areas tend to comprise a patchwork of urbanization and agriculture, as well as coastal and highlands environments. In addition to the national parks, there are many provincially protected areas, totaling 1.2 million ha. As of 2013, 9% of the total land base consisted of protected areas, whereas national parks accounted for 1.4% of the total study area. Sixteen ecoregions occur in New Brunswick and Nova Scotia, and of these, national parks in the region capture seven within their borders (Ecological Stratification Working Group 1995).

5.2.2. Avian dataset

BAM has compiled avian point count data in the boreal and hemi-boreal region from Canada and the U.S. (Cumming et al. 2010b, borealbirds.ca), including areas of forested and non-forested habitat. It currently comprises over 1.5 million avian point count records conducted between 1990 and 2014, from over 125 000 locations in North America. This dataset also includes long term projects such as provincial Breeding Bird Atlases and the Breeding Bird Survey, as well as contributions from universities, governments, and industrial partners. Varying point count methodologies are harmonized, allowing for quantitative density estimation (Barker et al. 2015) and the coverage of the dataset helps to account for potential roadside survey bias. Density is corrected for detectability and variable survey methodologies using the QPAD method (Sólymos et al. 2013). Count harmonization includes estimating singing rates and effective detection radius, while controlling for effects of survey protocol and environmental and temporal covariates on detection probability. Of BAM's point count locations, 15 021 occur in the study area

(Figure 5.1), with years ranging from 1996 to 2013. At least one Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler were observed at 77, 801, and 658 point count locations, respectively (Table 5.2).

Songbirds have a local breeding site embedded in a much larger home range used for foraging or extra-pair copulation (Taylor & Krawchuk 2005). Two buffer sizes were established around each point. A small buffer was chosen to reflect the local area around the bird location (termed local buffer), which was 50 m (0.8 ha) for Canada Warbler and Rusty Blackbird, and 100 m for Olive-sided Flycatcher. A 250 m (19.6 ha) buffer (termed territory buffer) was created to incorporate information about habitat attributes at the territory size of an Olive-sided Flycatcher and Rusty Blackbird, which have been documented as ranging from 10-45 ha (COSEWIC 2006, 2007) with a mean range size of 15 ha for Rusty Blackbird (Powell et al. 2010a). Canada Warblers have much smaller territories, ranging from 0.4 ha to 0.75 ha (COSEWIC 2006). As Canada Warbler territories often occur in clusters, potentially indicating conspecific attraction, the larger buffer includes neighbouring habitat features that may be important for suitability (Dr. Leonard Reitsma, Plymouth University, pers. comm.). These buffer sizes are consistent with other studies of scale (Taylor & Krawchuk 2005).

5.2.3. Models

In accordance with Haché et al. (2014), Poisson log-linear models were generated using a branching hierarchy model-building process (a forward stepwise variable selection approach). Bootstrap smoothing procedures were applied to address model uncertainty.

The modeling method used a nesting hierarchy to evaluate the importance of covariates, which I divided into 8 'stages' based on *a priori* assumptions (Figure 5.3). Stages were numbered 1-8, and variables associated with earlier stages thought to be more proximate to the birds' mechanisms of habitat selection. The 8 stages included 1) wetness; 2) forest cover; 3) forest structure; 4) landscape complexity, 5) anthropogenic disturbance; 6) distance from roads; 7) landscape connectivity; and 8) protection status.

I evaluated three different ways of defining wet forest habitat by running different model subsets, and changing the geospatial layers used to describe wetness as well as the presence/absence of an interaction term between forest cover and wetness. The variables used to describe forest cover were consistent between subsets. The resulting three subsets were WETLANDS, WETNESS, and WETNESS x Forest (hereafter WETxFOR). Each model included the same candidate variables for model stages 3-8, but differed in candidate variables for stages 1 and 2. For the WETxFOR subset, stages 1 and 2 were merged into a single step representing an interaction between the two variable types. To allow for direct comparison against the WETxFOR subset, stages 1 and 2 were run as a single step in the other subsets.

These steps were designed to approximate those used in the national SAR models by Haché et al. (in prep), but were adapted based on availability of finer scale covariate data. Furthermore, I did not control for temporal variation or spatial variation given the relatively limited extent of the study area and dataset. All R scripts for offsets and models are available at https://github.com/psolymos/bamanalytics

5.2.3.1. *Extraction of spatial covariates*

Spatial covariates were extracted at all BAM point count locations in the study area. All GIS layers were projected in NAD83 (CSRS), the official reference system for coordinates in New Brunswick and recommended for Nova Scotia (New Brunswick 2011; Seely 2011). Covariates were extracted from GIS layers using ESRI ArcGIS 10.2.2 (Esri Inc. 2014), PostGIS (Obe & Hsu 2011), R (R Core Team 2015), and/or Geospatial Modelling Environment (Beyer 2012). In total, 61 covariates (Table 5.4) were extracted from 19 source GIS layers (Table 5.5), with vector data having a minimum mapping unit of <50 m, and raster data having a minimum resolution of 10 m and a maximum of 90 m.

5.2.3.2. Wetness

The first model stage included covariates expressing the moisture regime of the bird location and surrounding area. The WETLANDS subset used wetlands layers classified from aerial photography were collected at the provincial level for NS and NB, and the wetland classes harmonized using vegetation cover equivalencies within the Canadian Wetlands Classification System (National Wetlands Working Group 1997; Table 5.6). Coastal wetlands (e.g. salt marshes) were excluded from the analysis. The dominant harmonized wetland vegetation class at each point count was determined within the local buffer for each species (as the wetland class which occupied a greater proportion of the buffer). Stream length and wet areas perimeter (including wetlands) within the territory buffer was totaled, as well as the proportion of territory buffer classified as wetland. These covariates were used in the WETLANDS model subset (Table 5.3).

The remaining model subsets, DTW and DTWxFor, used measures of depth to water table obtained from wet areas mapping (Forest Watershed Research Centre n.d.; Murphy et al. 2007). Wet areas mapping derived from LiDAR-based point cloud data or a digital elevation model data allows for delineation of flow channels, wet areas, and an estimate of the depth to water table (DTW) from soil surface (White et al. 2012). DTW is more closely related to soil and vegetation type than the commonly-used terrain wetness index (Murphy et al. 2009). DTW ≤ 1 m has been used to capture wet areas, has good correspondence with field-mapped wetlands, and performs better than soil wetness index (Murphy et al. 2007, 2009; White et al. 2012). For these two model subsets, the proportion of territory buffer with DTW ≤ 1 m was extracted (Figure 5.2), as well as the standard deviation of DTW across the territory buffer.

5.2.3.3. Forest cover and structure

Forest cover information was derived from the Common Attribute Schema for Forest Resource Inventories (CASFRI; Cumming et al. 2010a; Cosco 2011) which combines provincial forest resource inventory databases into a comprehensive classification of the most common attributes present across jurisdictions. CASFRI includes data regarding stand species composition, canopy height, closure, and other characteristics. CASFRI data was extracted within local and territory buffers, with many polygons occurring within a single buffer area. Due to the proprietary nature of some of the data, CASFRI information was not available across the entirety of the study region, limiting prediction ability in some areas of New Brunswick.

Forest cover and structure variables were used in all subsets. Tree species composition at the stand level was calculated by converting the percent cover of each tree species into area coverage within both local and territory buffers. As there were generally multiple polygons within each buffer, areal coverages were summed to give the m^2 occupied by each tree species within the buffer. Mean and standard deviation of canopy closure and height were calculated for both buffer sizes.

5.2.3.4. Disturbance

Disturbance information was acquired from both the CASFRI and Human Footprint (HF) mapping. The HF uses four types of data as proxies for human influence: population density, land transformation, accessibility, and electrical infrastructure (Sanderson et al. 2002). Datasets representing these influences were standardized and scored according to percent influence, then combined as an index. Woolmer et al. (2008) mapped HF at 90 m resolution for the Northern Appalachian/Acadian ecoregion of North America. Forest-specific disturbances were documented by the CASFRI, including burns, cuts, partial cuts, slides, windfalls, and other unspecified disturbances. The proportion of territory buffer disturbed was calculated by dividing CASFRI disturbance polygon areas within buffers by the total area of the buffer. Disturbance was not coupled temporally with point counts.

5.2.3.5. Complexity, connectedness, and roads

Landscape complexity was characterized by Anderson et al. (2012) as the variety of microclimates present in a site, measured as a function of topography, elevation range, and moisture gradients. They calculated the number of landforms in an area and modified this total by elevation range and wetland density. Wetland density was used to give a measure of micro-topographical variation in flat landscapes (Anderson et al. 2012). Landscape complexity was calculated in units of 1000 ha hexagons across the landscape, and categorized as below mean, mean, or above mean for the North Appalachian/Acadian ecoregion (Figure 5.3). I extracted mean complexity class within each territory buffer.

Mean index of local connectedness was also extracted for each territory buffer. Local connectedness measures the strength of structural connections between natural ecosystems on a local landscape (Anderson & Clark 2012). Connectedness measures the outward permeability of ecological flows, based on land cover and land use types, from one cell to its neighbours as predicted using resistant kernel analysis.

Distance to roads was calculated as distance from the BAM point count location to the nearest road feature from the National Road Network (Government of Canada 2014; Figure 5.4). Finally, all BAM point counts were intersected with layers of parks and protected areas (including federal, provincial, and municipal protected areas) and classified as being either in unprotected or protected lands.

5.2.3.6. Pre-processing and modelling

The BAM data system consists of projects that were collected using heterogeneous protocols (Barker et al. 2015), and corrects for this heterogeneity through the application of statistically calculated offsets (Sólymos et al. 2013). Avian abundance data were corrected based on metrics that control for the effects of survey protocols on detectability of each species, based on time of day, time of year, and duration and radius of survey. Species-specific offsets (including singing rate) are combined with satellite-derived habitat information to estimate densities of territorial males. Offsets are applied to recorded abundance for each species at each point, and the resulting estimates used in the models.

All covariates were standardized, and CASFRI tree species were re-classed into genus (see https://github.com/psolymos/bamanalytics/blob/master/R/maritimes.R for model code and standardization specifics). At each stage, covariates at varying scale were available for selection. A bootstrap procedure was generated 240 times in an iterative approach using consistent AIC (CAIC = 0.5 AIC + 0.5 BIC) to determine the frequency with which a particular predictor variable was selected (Burnham & Anderson 2002; Table 5.3). This reduced overfitting and variance in predictions. Between model subsets, selection frequency was used to determine, out of the 240 iterations, how often a particular subset was selected. Subsets which are selected more frequently are expected to have higher explanatory power. Within model subsets, selection frequency was used to estimate the contribution of a given variable to explaining variance at each stage, which variables having high selection frequency contributing more strongly to the model.

Variables were ranked by selection frequency at each stage, which the most-selected variable receiving the top rank. At each stage, the top-ranked variable was selected, and added to variables in the next stage (therefore meaning the 'null' model for a subsequent stage represented the top variables selected at the previous stages). This bootstrap procedures and selection process also allows for measures of model validation and prediction uncertainty (Haché et al. 2014), as determined by the distribution of variable selection. For example, if many variables are selected in equal proportions at a given stage, this is a more uncertain model than if a single variable is selected at a very high proportion.

5.2.3.7. Spatial predictions of density

To predict density of each species across the study area as well as estimate population sizes, the surface of NB and NS was covered with a net of points, located at the centre of a grid of 250 m by 250 m cells. The resulting 2.12 million points were buffered at the local and territory sizes for the three species. At each point, all model covariates were extracted using the same process as the avian data layers.

I used the habitat models to generate density estimates at each point. Population sizes within national parks were calculated by summing converted density estimates from points within national parks. Though available covariates made it possible to predict at finer spatial resolution, computational limitations restricted predictions to the grid size used here. For each species, I used mean predicted density at prediction points to produce a digital raster at 250 m for each national park, showing spatial resolution of density and coefficient of variation.

5.2.4. Comparison of National Parks to other lands

Of the 2.1 million prediction points in NS and NB, 28 880 were within the area covered by the four national parks: Cape Breton (15 447 points), Kouchibouguac (3 410 points), Fundy (3 367 points), Kejimkujik Mainland (6 358 points), and Kejimkujik Seaside (298 points). A 5 km x 5 km grid was superimposed over the study area, with each grid square numbered. Grid squares were further divided by ecoregion. Within each National Park, the number of grid squares falling into each ecoregion was tallied, as well as the number of prediction points within the grid square. Each grid square was considered a replicate, and prediction point within that replicate considered a sample. Kejimkujik Seaside was excluded from analysis due to the low number of grid squares containing samples. Replicates could contain up to 400 samples, and only replicates with less than 30 samples were omitted from analysis. The number of replicates per park, separated by ecoregion, ranged from 7 (Fundy, ecoregion 123) to 38 (Cape Breton Highlands, ecoregion 129; Table 5.7).

For comparison between predictions of species density between national parks and non-park lands in the same ecoregion, sampling was replicated in random grid squares. All non-park grid squares within the ecoregion were assigned random numbers from 1 to 1000 using a python code, and arranged from smallest random number to largest. Grid squares in an ecoregion were selected to be replicates sequentially until matching the number of replicates for the corresponding national park in that ecoregion. This randomization and selection process was repeated for samples within each replicate. For example, consider a grid square that the park boundary passes through, and part of the square is contained within the park, and the remainder is outside. Out of the possible 400 sample points in that square, 350 are within the park boundary and included for analysis. In the matching grid square for that ecoregion (replicate), only 350 randomly selected samples were included out of the potential maximum of 400. If a replicate did not contain enough prediction points to meet the necessary samples (for example, the ecoregion boundary was placed such that only 200 of 400 prediction points fell within the ecoregion, although 350 samples were necessary), that replicate was excluded and the next random grid square chosen. A total of 123 grid squares were chosen as comparison replicates to match the 123 grid squares falling within park boundaries (Figure 5.5).

For Olive-sided Flycatcher and Canada Warbler, predicted mean number of territorial males/ha at the replicate level was compared between the protected areas and remainder of the ecoregion using t-tests. Rusty Blackbird was excluded from testing for not meeting distributional assumptions of normality and homoscedacity.

5.3. RESULTS

5.3.1. Variable selection

For each species, I compared all of the models across all bootstrapped runs to determine overall selection frequency between the subsets. In the Rusty Blackbird and Canada Warbler models, WETNESS was the most-selected subset at all stages. In Olive-sided Flycatcher models, WETxFOR was the most-selected subset at all stages. At each stage, up to 14 variables were selected at least once, though in all cases, the two most-selected variables accounted for at least 62.5% of the total selection at that stage, with a mean of 83% of selection.

As only stages 1&2 differed amongst the three subsets, this stage was the point of divergence for selection. At the first stage of selection (grouped between stages 1&2), Rusty Blackbird was somewhat divided, with WETNESS, WETLANDS, and WETxFOR selected 56.6%, 37.8%, and 4.2% of the total, respectively (Table 5.10). For Olive-sided Flycatcher, at initial stages WETxFOR was selected in 91% of cases, followed by

WETLANDS and WETNESS at 7% and 2% of cases, respectively (Table 5.17;Table 5.11). The Canada Warbler model selected WETNESS almost exclusively, at 99.2% of the total selection (Figure 5.20), and WETLANDS was not selected at all. Within each model subset, the covariates with the highest selection frequency at each stage were chosen for inclusion in the final models (Table 5.8). Variable selection paths show relative selection frequency of each variable within each subset, allowing for a visual estimate of uncertainty (Figure 5.6).

5.3.1.1. Rusty Blackbird

For the Rusty Blackbird, out of the 240 bootstrapped runs, the WETNESS model subset had the most runs with the lowest AIC (136 runs), followed by WETLANDS (94 runs) and WETxFOR (10 runs). The spread of selection between models is indicative of poor agreement. Variables consistently selected among model subsets were considered to be the most important predictors of variation on density. In the first and second stages of the WETNESS subset, DTW_STD and CASFRI territory were the most selected variables by a large margin (Table 5.12). At the first stage in the WETLANDS subset, WET_VEG local was the most selected as well as CASFRI territory in the second stage, though by a smaller margin. For the remainder of the model, the best predictors of Rusty Blackbird abundance included CANCL_AV territory, FOOTPRINT territory, and PROTECT local. The most-selected variable was consistent across subsets for most stages (Figure 5.13; Figure 5.6 Rusty Blackbird).

In the first and second stages of the WETNESS subset, DTW_STD and CASFRI territory were the most selected variables (Table 5.12). At the first stage in the WETLANDS subset, WET_VEG local was most selected as well as CASFRI ter in the second stage, though by a smaller margin. For the remainder of the model, the best predictors of Rusty Blackbird abundance included CANCL_AV ter, FOOTPRINT ter, and PROTECT, local. The most-selected variable was consistent across subsets for most stages (Table 5.13). Densities were generally higher where dominant forest cover consisted of *Abies spp.* and *Picea spp.* at both buffer sizes, and were lower when other forest cover categories dominated

(Figure 5.7; Figure 5.8). Rusty Blackbird density showed no clear pattern with DTW_STD or WET_PROP across the territory (Figure 5.9). Neither did patterns emerge relating to any structural variables or landscape complexity (Figure 5.11; Figure 5.12) Human footprint (Figure 5.13) and on-road condition (Figure 5.14) was associated with a decrease in density. while connectedness was associated with an increase (Figure 5.15). A slight increase in density was associated with areas that had been disturbed by forest harvesting (Figure 5.16) as well as unprotected sites (Figure 5.17).

5.3.1.2. *Olive-sided Flycatcher*

Amongst the 240 Olive-sided Flycatcher bootstrapped runs, the subset WETxFOR had the lowest AIC in 218 runs, whereas WETLANDS had the lowest AIC in 16 runs and WETNESS had the lowest AIC in 6 runs. For the WETxFOR subset, the variable CASFRIxDTW_PROP territory was selected in 100% of the runs, whereas in the WETLANDS subset, WET_LENGTH territory was the most-selected variable (Figure 5.17). Variables best explaining Olive-sided Flycatcher abundance included HT_STD territory, COMPLEXITY territory, FOOTPRINT territory, and CONNECT territory (Figure 5.18). The most-selected variable was the same for each stage across all three subsets (Figure 5.6 OSFL).

Olive-sided Flycatcher showed highest densities in forests dominated by *Picea* spp. (but not *Picea glauca)*, *Picea mariana,* and *Abies* spp., and the lowest in forests dominated by *Pinus* and deciduous (Figure 5.7). Density of males per hectare increased slightly with increasing DTW_PROP at the local level, with a much more dramatic increase at the territory level (Figure 5.18). When leading species was interacted with the proportion of 250 m buffer classified as wet (depth to water table <= 1m), tree species associated with higher Olive-sided Flycatcher density followed a similar pattern as when tree cover was considered in isolation. For all tree cover types except *Alnus* spp., Olive-sided Flycatcher density increased with a greater proportion of buffer classified as wet (Figure 5.8).

At the local level, higher Olive-sided Flycatcher density was associated with lower mean canopy closure and standard deviation (Figure 5.10), as well as lower mean height (Figure 5.11). When considering the range of standard deviation across the territory, higher densities were associated with values closer to the median. Human footprint had a negative effect on density (Figure 5.13), as did being on-road (Figure 5.14). Olive-sided Flycatcher density increased with greater landscape complexity and connectedness (Figure 5.12; Figure 5.15). Protected sites showed slightly higher Olive-sided Flycatcher densities than unprotected sites (Figure 5.17).

5.3.1.3. Canada Warbler

When examining model selection between subsets, the subset WETNESS was chosen in all of the 240 runs based on having the lowest AIC value. Within that subset, the variable DTW_STD territory was selected in all 240 runs (Figure 5.9). CASFRI territory was the forest cover variable best explaining Canada Warbler abundance. Across the remaining model stages, highly selected variables included CANCL_STD local, COMPLEXITY territory, FOOTPRINT territory, and CONNECTIVITY (Figure 5.6 CAWA).

In the WETNESS subset, higher densities of Canada Warbler males at both scales corresponded with forest stands with high proportions of *Abies* spp., *Alnus* spp., *Picea* spp., *Picea mariana*, and lower densities were predicted in stands dominated by *Acer* spp., *Larix* spp., *Picea glauca*, and *Pinus* spp. (Figure 5.7). This was consistent across both scales, with the higher proportions of *Abies* spp. markedly increasing density predictions at the territory scale. Higher DTW_PROP were associated with higher densities of Canada Warbler, with the effect more pronounced at the territory scale (250 m) (Figure 5.18). For forest structure variables, densities peaked just below the median for CANCL_STD at both scales, as well as HT_STD and HT_AV (Figure 5.10; Figure 5.11). Landscapes with mean to above mean complexity were predicted to have higher densities, as did areas with higher connectivity (Figure 5.12, Figure 5.15).

With regard to disturbance, densities were reduced in areas with a high human footprint (Figure 5.13), however, cuts showed higher densities than undisturbed areas, with a small positive association. Burned areas showed very low density predictions (Figure 5.16). Off-road conditions resulted in higher density predictions (Figure 5.14), and site protection status did not have a notable impact (Figure 5.17).

5.3.2. Predictions and population sizes

I produced estimates of mean density of territorial males in National Parks in New Brunswick and Nova Scotia for Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler for four Maritime national parks (Figures 19-23). Coefficient of variation was also mapped to enhance understanding. In Kouchibouguac, predicted densities of Rusty Blackbird and Canada Warbler were generally low except one portion close to the seaside, which corresponds on satellite maps to an area of treed bog, whereas areas of high Olive-sided Flycatcher density were more evenly distributed across the park (Figure 5.19). Coefficient of variation did not conform to any obvious pattern. There were some data gaps in prediction in this park due to lack of coverage for some covariate layers.

Fundy showed uniformly low predicted Rusty Blackbird densities (Figure 5.20). The few small areas of high Olive-sided Flycatcher and Canada Warbler density followed river valleys. Coefficient of variation increased on slopes and coastal areas. Cape Breton Highlands showed relatively large swathes of high density areas, particularly in the central highlands portion of the park (Figure 5.21). Coefficients of variation were greater nearing to the coast.

Predicted densities for all species were low across the Seaside Adjunct of Kejimkujik except for a few very small patches in estuarine areas. Coefficients of variation increased with proximity to the coast (Figure 5.22). Kejimkujik (mainland) appears to have higher densities of Olive-sided Flycatcher and Canada Warbler in the western portion of the park, with Rusty Blackbird isolated to a few patches. Kejimkujik is relatively well-sampled for bird species compared to the other parks, and a dataset of locations of these species was visually compared to the density map (Figure 5.23). Known locations of Olive-sided Flycatcher and Canada Warbler recorded from 2005-2015 showed relatively good agreement with predicted densities, though a portion of this dataset was included in BAM training data. The Rusty Blackbird prediction map showed very poor agreement with known locations. Higher coefficients of variation for all species occurred in the eastern side of the park.

The total predicted population of territorial males across all national parks was 11 for Rusty Blackbird, 358 for Olive-sided Flycatcher, and 1092 for Canada Warbler (Table 5.15). Mean predicted Rusty Blackbird population density was ≤ 0.001 territorial males/ha for all parks. Olive-sided Flycatcher predicted means ranged from 0.006 males/ha (Kejimkujik Seaside) to 0.014 males/ha (Cape Breton Highlands). Kejimkujik Seaside also had the lowest mean population density for Canada Warbler, at 0.025 males/ha, whereas Cape Breton Highlands had the highest, at 0.045 males/ha. Predicted population sizes in Kejimkjujik Mainland were more than twice as high as Fundy National Park, which in turn was approximately twice that of Kouchibouguac.

Predicted densities within parks were compared to areas outside of parks in the same ecodistrict, results varied. For Olive-sided Flycatcher, predicted densities inside parks were equal or greater than that of ecoregion comparison areas for all ecoregions (Table 5.16; Figure 5.24). This difference was significant for ecoregions 123 (mean difference = 0.007 males/ha, $n = 7$, $P < 0.001$) and 129 (mean difference = 0.002 males/ha, $n = 38$, $P < 0.001$). Canada Warbler predicted densities were only higher in parks for ecoregion 123, and the differences between parks and randomly selected areas elsewhere in the ecoregion was most pronounced in ecoregions 122 (mean difference = 0.024 males/ha, $n = 19$, $P < 0.001$) and 129 (mean difference = 0.016, $n = 28$, $P < 0.001$). Highest predicted densities of Olive-sided Flycatcher were observed in ecoregions 128, 124, and 122, with highest densities of Canada Warbler observed in ecoregions 122, and 123.

5.4. DISCUSSION

I used the largest available avian point count dataset in New Brunswick and Nova Scotia to generate habitat models to support population size predictions and conservation. The application of species-specific offsets allows for correction of detectability and sample bias, homogenizing surveys across protocols. This allows for predicted densities of these species that are comparable between species and regions.

5.4.1. Habitat associations and model performance

In my models, covariates describing wetness and forest cover were considered to be the most proximate to reflecting biological species needs. Highly-selected covariates do correspond with known ecological associations of these three species. My models did not include measures of climate, which are commonly used at larger spatial extents. Johnson (1980) described a hierarchical model of habitat selection in which climate is viewed as controlling first-order selection (determining geographic ranges), and vegetation influences second-order selection. Typically, climate conditions are thought to be most important at large spatial extents, and vegetation to be an important driver of local variation (Forsman & Mönkkönen 2003). Although on smaller scales climate may not be seen as a factor, it is important not to omit it from consideration. This is particularly true for birds, as this group has been widely documented to have experienced recent distributional shifts due to climate change (e.g. Nogués-Bravo et al. 2012). It is anticipated that these shifts will continue (Cumming et al. 2013)

Variation in vegetation at scales between 0.1 and 10 ha is a known driver of boreal songbird distribution (e.g Bayne & Hobson 1997; Hobson & Bayne 2000; Holmes et al. 2008). The contribution of vegetation cover types observed in my models corresponds with known ecological associations of these species. Olive-sided Flycatcher was associated with coniferous species in which it nests across its range. Higher Olive-sided Flycatcher densities corresponded to greater proportions of wetness across the territory buffer, likely necessary for meeting invertebrate biomass foraging requirements. Lower mean canopy closures and a median standard deviation of canopy height across the territory suggest sites that are patchy, with a mix of treed and open areas. This reflects the species' preference for edges, as they are known to nest in emergent trees alongside wetlands, as well as barrens, burns, and cuts (Altman & Sallabanks 2010).

Canada Warbler male density was higher where forest cover was included tree species common to mixedwood stands. Although in southwest Nova Scotia Canada Warbler are known to nest in ecosystems with a component of *Acer rubrum* (CHAPTER 2; CHAPTER 3), Canada Warbler densities were negatively associated with sites with large proportions of *Acer* spp. This may either be an indicator of a dilution effect by grouping *Acer* at the genus level, or reflecting the effect of forest communities in northern Nova Scotia and New Brunswick, where *A. rubrum* swamps are less common. A further explanation may be the nature of the small patches that Canada Warbler occupy. Individual effects of tree cover variables were stronger at the local scale, corresponding to habitat within the Canada Warbler's small territory. Canada Warbler's relationship with forest structure variables suggest density is higher on patchy landscapes, supported by its association with higher landscape complexity. The importance of variable forest structure is important to Canada Warbler, who require vertical complexity of trees, shrubs, and forest floor microsites for nesting, foraging, and territorial displays (Reitsma et al. 2010). These habitat features may be conserved by forest management activities, as non-protected areas had slightly higher densities of Canada Warbler than protected areas. Low standard deviation of depth to water table indicates a need for a relatively homogenous moisture regime, with wetness being consistent across Canada Warbler-occupied sites.

Rusty Blackbird exhibited more variation in model subset selection than other species, and also showed few patterns within model-selected variables. This is likely due to the small sample size of the training data (77 locations, some of which may have included detections in transit), which may have been insufficient to elucidate density-habitat relationships for this species. The association with *Abies* and *Picea* was consistent with known nesting requirements (Matsuoka et al. 2010a; Powell et al. 2014), however, few conclusions can be drawn about the habitat preferences of this species from these models. Due to the highly-divergent selection of the Rusty Blackbird model and unrealistic population estimates (e.g. predicting only one male in Kejimkujik (mainland) when more birds have been directly observed), predictions and covariate associations for this model should not be considered accurate. Models for Olive-sided Flycatcher and Canada Warbler both exhibit trends consistent with known species biology and deliver realistic population estimates based on the size of the park, and are likely to be reliable.

5.4.2. Depth to water table as a proxy for wetness

Though vegetation cover is often used as the main explanatory covariate for local to regional-scale species distribution modelling (e.g. Bustamante & Seoane 2004; Bellis et al. 2008; Atamian et al. 2010), hydrological variables may predict distribution equally well or even greater for some species (Barker et al. 2014). Vegetation cover layers are also limited by their static nature due to successional and disturbance processes. Forest inventory layers in Nova Scotia have relatively high levels of inaccuracy in areas occupied by Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler (CHAPTER 3). My results suggest depth to water table mapping to be a promising tool for improving model accuracy. This type of feature creates microclimates that determine temperature and moisture regimes on small scales (Anderson et al. 2012), and is less likely to change as quickly as forest cover.

In my analysis, model subsets using depth to water table proved to have the highest explanatory power. Surface wetlands layers were drastically outperformed in predicting bird abundance, likely due to differences in methods of classification between these GIS layers. DTW is able to capture small wetlands that escape delineation from aerial photographs (Murphy et al. 2007), and border accuracy surpasses conventional delineation from aerial photography (White et al. 2012). Kreakie et al. (2012) compared models for waterfowl that DTW as a proxy for wetland features against those that used open wetland cover derived from satellite imagery. Their DTW-based models had slightly higher scores than wetland cover for an index of classification accuracy. Accurately modelling subsurface wetness may be especially important for species like Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler, who use wet forest habitats that are not easily identifiable from aerial photography. The WETLANDS subset was never selected for Canada Warbler, and rarely selected for Olive-sided Flycatcher, reinforcing that wet forest habitat is difficult to detect from traditional aerial delineation of wetlands.

The ability of models to interact forest cover and wetness offers potential to capture wet forest habitats that are difficult to capture by other means. For Olive-sided Flycatcher, which will nest in forest edges immediately adjacent to relatively dry habitats (as well as adjacent to wetlands), the WETxFOR subset was most explanatory. However, Olive-sided Flycatcher population density increased with a greater proportion of the territory buffer with a DTW ≤ 1 m, reinforcing the importance of moisture regime.

Though DTW data appears more useful than photo-derived wetlands or forest layers alone, it should be noted that it does not include information on water extraction and management, a factor which may become more pronounced at finer scales (Kreakie et al. 2012). Furthermore, increasing availability of high-resolution LiDAR will allow for greater identification of features ecologically relevant to these species, such as understory deciduous shrub cover. Techniques for this are developing (e.g. Pouliot et al. 2006) and have shown effectiveness at predicting habitat for songbirds by characterizing vertical canopy structure (Goetz et al. 2010; Vogeler et al. 2013). Such data may be particularly useful for species like Canada Warbler, which require a complex vertical structure.

5.4.3. Using national parks to protect species at risk populations

Habitat suitability for these three species has been declining in New Brunswick and Nova Scotia (Panjabi et al. 2012). Both Canada Warbler and Olive-sided Flycatcher showed negative associations of density with human footprint and roads, as well as the positive association with connectedness and complexity. This suggests these species at risk may not be able to tolerate an as-yet undefined threshold of anthropogenic disturbance. As disturbance was not temporally coupled with point count years in this analysis, further work must be done to determine disturbance thresholds. As such, it becomes important to conserve remaining breeding habitat, and permanent protected areas offer a means to do so. However, existing protected areas do not adequately capture areas of high density of these species, or a large proportion of the extant population.

Partners in Flight completed range-wide population predictions of these species, estimating the combined New Brunswick and Nova Scotia populations of Olive-sided Flycatcher and Canada Warbler at 8 300 and 73 000 individuals, respectively (Partners In Flight Science Committee 2013). However, they use different data sources and methodologies, estimating effective detection radius with a different method than the QPAD method used here. Haché et al. (2014) used the BAM dataset and QPAD correction to recreate national population estimates for Olive-sided Flycatcher and Canada Warbler, constraining them according to both BAM and PIF range limits. They estimated the total number of territorial Olive-sided Flycatcher males in New Brunswick and Nova Scotia at approximately 12 800, and 166 Canada Warbler males. When comparing my predicted population sizes in national parks to these regional estimates (358 Olive-sided Flycatcher territorial males and 1092 Canada Warbler territorial males), national parks encompass 2.8-4.3% of the Olive-sided Flycatcher population and 0.65-1.5% of the Canada Warbler population. Given that national parks cover 1.4% of the study area, the proportion of population protected is representative for Canada Warbler, but is less than half of what is necessary to be representative for Olive-sided Flycatcher. It should be noted that the 4 national parks studied here encompass natural landscapes, whereas outside of parks, significant proportions of the province have been transformed due to agriculture, logging, or other disturbances, all of which were included to varying degrees in the random samples of ecoregions. Future work should compare populations within forested areas of parks against only forested areas in surrounding ecoregions, by eliminating non-forest areas from GIS analysis. This may give some insights into habitat quality, rather than just availability.

Parks did have higher predicted densities of Olive-sided Flycatcher than randomly selected surrounding areas in the same ecoregion, but Canada Warbler had lower predicted densities in protected areas for 5 of 6 ecoregions. These results suggest that national parks in this region may have representative areas of usable habitat for Olive-sided Flycatcher, but do not capture adequate habitat for Canada Warbler. Thus protected areas status appeared to confer no benefit (or in some ecoregions be slightly negative) for Canada Warbler. Existing protected areas may not be adequately capturing high-quality habitat for these species.

As the landscape outside of parks and protected areas continues to change from anthropogenic disturbance (such as urban expansion), more areas will be rendered unusable for these species. Features I have identified as being important for these species are at risk of change or loss. In Nova Scotia, wetlands under 100 m^2, unless designated as being of special significance, do not receive legal protection (Province of Nova Scotia 2011). However, small wetlands may be particularly relevant for these species for foraging (Powell et al. 2010a). The proportion of forest dominated by mixedwood stands in New Brunswick has been decreasing over the past half-century as related to changing disturbance regimes and forest harvesting (Amos-Binks et al. 2010).

In a situation of ongoing population decline and loss and conversion of breeding habitat, it is imperative to protect areas with high population densities. However, in New Brunswick and Nova Scotia, existing national parks alone are not able to fulfill this role for Olive-sided Flycatcher and Canada Warbler. Although it is important to ensure the continued maintenance and protection of high-density areas within national parks, to effectively steward regional populations, national parks managers will need to work in tandem with managers of other protected areas, the forest management sector, and the public.

5.5. TABLES AND FIGURES

Table 5.1: National Parks within the study area of New Brunswick and Nova Scotia.

Province	National Park	Ecoregions	Area (ha)*	Perimeter (km)	Centroid Lat/Long
NB	Kouchibouguac	Maritime Lowlands	24 199	120.5	-64.929104, 46.828302
	Fundy	Southern New Brunswick Uplands/Fundy Coast	21 051	78.2	-65.038689, 45.618185
NS	Cape Breton Highlands	Nova Scotia Highlands/Cape Breton Highlands	96 663	212.1	-60.640798, 46.721488
	Kejimkujik (Mainland)	Southwest NS Uplands	39 698	82.5	-65.300387, 44.371300
	Kejimkujik (Seaside)	Atlantic Coast	2 095	70.3	-64.825776, 43.854574

*Park area size from GIS layers mapping national parks Canada (Geomatics Canada; Natural Resources Canada)

Table 5.2: Number of Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA) observed at point counts in Nova Scotia and New Brunswick in the Boreal Avian Modeling project database.

Species	Birds at point count locations				
	0	1	2	3	≥4
RUBL	46903	50	14	5	8
OSFL	46179	776	25	0	0
CAWA	46322	609	41	7	1

Table 5.3: Model subsets and descriptions of covariates used at each stage in hierarchical Poisson log-linear models of Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA) density. All covariates were measured at either the local (L) buffer size (50 m for Rusty Blackbird and Canada Warbler, 100 m for Olive-sided Flycatcher), or the territory (T) buffer size (250 m for all species).

Model Stage	**Subset A: WETLANDS**	**Subset B: WETNESS**	**Subset C: WETxFOR**
1. Wetness	1.0 Null 1.1 Dominant wetland type (L) 1.2 Perimeter of wetland + stream length (T) 1.3 Proportion wetland (T)	1.0 Null 1.1 Proportion of area with DTW classified "wet" (≤1 m) (L) 1.2 Proportion with DTW classified "wet" (≤1 m) (T) 1.3 Standard deviation of DTW (T)	1-2.0 Null 1-2.1 Tree species coverage (CASFRI) x proportion of area with DTW classified "wet" (≤1 m) (L) 1-2.2 Tree species coverage (CASFRI) x proportion of area with DTW classified "wet" (≤1 m) (T)
2. Forest Cover	2.0 Null 2.1 Tree species coverage (CASFRI) (L) 2.2 -Tree species coverage (CASFRI) (L)	2.0 Null 2.1 Tree species coverage (CASFRI) (L) 2.2 -Tree species coverage (CASFRI) (T)	
3. Forest Structure	3.0 Null 3.1 Mean canopy closure (L) 3.2 Mean canopy closure (T) 3.3 Standard deviation of canopy closure (L) 3.4 Standard deviation of canopy closure (T) 3.5 Mean canopy height (L) 3.6 Standard deviation of canopy height (T)	3.0 Null 3.1 Mean canopy closure (L) 3.2 Mean canopy closure (T) 3.3 Standard deviation of canopy closure (L) 3.4 Standard deviation of canopy closure (T) 3.5 Mean canopy height (L) 3.6 Standard deviation of canopy height (T)	3.0 Null 3.1 Mean canopy closure (L) 3.2 Mean canopy closure (T) 3.3 Standard deviation of canopy closure (L) 3.4 Standard deviation of canopy closure (T) 3.5 Mean canopy height (L) 3.6 Standard deviation of canopy height (T)
4. Landscape Complexity	4.0 Null 4.1 Mean landscape complexity (T)	4.0 Null 4.1 Mean landscape complexity (T)	4.0 Null 4.1 Mean landscape complexity (T)

Model Stage	**Subset A: WETLANDS**	**Subset B: WETNESS**	**Subset C: WETxFOR**
5. Disturbance	5.0 Null 5.1 Leading CASFRI disturbances (T) 5.2 Mean human footprint index (T)	5.0 Null 5.1 Leading CASFRI disturbances (T) 5.2 Mean human footprint index (T)	5.0 Null 5.1 Leading CASFRI disturbances (T) 5.2 Mean human footprint index (T)
6. Road Distance	6.0 Null 6.1 Distance from road	6.0 Null 6.1 Distance from road	6.0 Null 6.1 Distance from road
7. Landscape Connectivity	7.0 Null 7.1 Mean connectivity index (T)	7.0 Null 7.1 Mean connectivity index (T)	7.0 Null 7.1 Mean connectivity index (T)
8. Protection Status	8.0 Null 8.1 Protected/Unprotected	8.0 Null 8.1 Protected/Unprotected	8.0 Null 8.1 Protected/Unprotected

Table 5.4: Description and short names of covariates used at each stage in hierarchical Poisson log-linear models of Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA) abundance.

Model Stage	Covariate	Short Name	Type	Units
1. Wetness	Dominant wetland vegetation type	WET_VEG	Categorical	Vegetation Class
	Stream length + wetland perimeter	WET_LENGTH	Continuous	m
	Proportion of buffer that is wetland	WET_TOTAL	Continuous	Proportion
	Proportion of bugger with WAM classified as wet (<=1m depth to water table)	DTW_PROP	Continuous	Proportion
	Standard deviation of depth to water table	DTW_STD	Continuous	m
1-2. Wetness x Landcover	Leading species x wet/not wet	Multiple*	Continuous	Species x m^2 x Proportion
2. Landcover	CASFRI cover types and proportion within buffer	Multiple*	Continuous	Species x m^2
3. Structure	Mean canopy closure	CANCL_AV	Continuous	%
	Standard deviation of canopy closure	CANCL_STD	Continuous	%
	Mean of canopy height	HT_AV	Continuous	m
	Standard deviation of canopy height	HT_STD	Continuous	m
4. Landscape Complexity	Category of landscape complexity dominating buffer	COMPLEXITY	Categorical	Class
5. Disturbance	Proportion of buffer disturbed (CASFRI)	Multiple**	Continuous	Proportion
	Mean human footprint index	FOOTPRINT	Continuous	Index

Model Stage	Covariate	Short Name	Type	Units
6. Road	Distance from road	ROAD	Continuous	m
7. Landscape Connectivity	Mean connectedness index	CONNECTED-NESS	Continuous	Index
8. Protected Areas	Protection status	PROTECT	Categorical	Class

*Variables derived from CASFRI forest cover indicate area occupied by a tree species, including: Abie_bals, Abie_pice, Abie_spp, Acer_rubr, Acer_sacc, Acer_spp, Alnu_spp, Betu_alle, Betu_papy, Betu_popu, Betu_spp, Fagu_gran, Frax_spp, Hard_into, Hard_nonc, Hard_tole, Hard_unkn, Lari_deci, Lari_lari, NOSC_HARD, NOSC_SOFT, Pice_abie, Pice_glau, Pice_mari, Pice_rube, Pice_spoo, Pinu_bank, Pinu_resi, Pinu_spp, Pinu_stro, Pinu_sylv, Popu_balb, Popu_spp, Popu_trem, Prun_sero, Quer_rubr, Soft_unkn, Thuj_occi, Tsug_cana, Ulmu, amer, Uncl_spp. Refer to Cosco (2011) for variable descriptions.

**Variables derived from CASFRI disturbance layers indicate area occupied by a given disturbance type, including: Burn (BU), Cut (CO), Other (OT), Partial Cut (PC), Slide (SI), and Windfall (WF).

Table 5.5: Spatial data layers used for covariate extraction.

Layer	Description	Data Year	Resol-ution (m)	Rights	Citations
Avian Point Count Dataset	BAM and BBS project data	2014	vector	Boreal Avian Modelling Project	Cumming et al. 2010
Common Attribute Schema for Forest Resource Inventory (CASFRI)	National extent of provincial forest resource inventories, standardized to a common schema	2008-2014	vector		Cosco 2011; Cumming et al. 2015
National Ecological Framework for Canada	Canada's ecological framework, including ecozones, ecoprovinces, ecoregions, and ecodistricts.	2013	vector	CGDI National Frameworks Data; Agriculture and Agri-Food Canada	Marshall et al. 1999
Human Footprint	Extent and relative intensity of human influence on terrestrial ecosystems via human settlement, access, landscape transformation, and infrastructure	2001-2006	90	Wildlife Conservation Society Canada; Conservation Biology Institute: Data Basin	Sanderson et al. 2002; Woolmer et al. 2008
Landscape Complexity	The variety of microclimates on the landscape as function of topography, elevation range, and moisture gradients	2001-2006	90	The Nature Conservancy - Eastern Conservation Region; Conservation Biology Institute: Data Basin	Anderson et al. 2012; Anderson & Clark 2012

Layer	Description	Data Year	Resol-ution (m)	Rights	Citations
Local Connectedness	Strength of structural connections between natural ecosystems on a local landscape, measured as outward permeability of ecological flows from one cell to its neighbours	2005	90	The Nature Conservancy - Eastern Conservation Region; Conservation Biology Institute: Data Basin	Anderson et al. 2012; Anderson & Clark 2012
National Parks	Boundaries of National Parks	2012	vector	Geomatics Canada; Natural Resources Canada	
Protected Areas – NB	Boundaries of Protected Natural Areas and Provincial Parks In New Brunswick.	2011-2014	vector	Department of Natural Resources/GeoNB	
Protected Areas – NS	Boundaries for National Parks, Provincial Parks, Provincial Wildlife Areas, and other protected areas in NS	2013	vector	Nova Scotia Parks and Protected Areas New Brunswick	
Roads	Normalized Canadian road network	2014		Government of Canada; Natural Resources Canada; Earth Sciences Sector; Canada Centre for Mapping and Earth Observation	
Streams and Waterways - NB	New Brunswick Hydrographic Network, delineating surface drainage features for New Brunswick	2012-2014	vector	New Brunswick Department of Natural Resources/GeoNB	

Layer	Description	Data Year	Resol-ution (m)	Rights	Citations
Streams and Waterways – NS	Provincial hydrographic features at 1:10 000 scale	unk	vector	Nova Scotia Department of Natural Resources	
Wet Areas Mapping – NB	Map of depth to water table derived from digital elevation models, indicating likelihood of water saturation	2004-2005	10m	Forest Watershed Research Center, University of New Brunswick	Murphy et al. 2009
Wet Areas Mapping – NS	Map of depth to water table derived from digital elevation models, indicating likelihood of water saturation	unk	10m	Nova Scotia Department of Natural Resources	Murphy et al. 2009
Wetlands – NB	Wetlands identified from 1:10 000 aerial photography, including wetland type, vegetation, and photograph year	2003-2012	vector	NB Department of Environment and Local Government	Department of Natural Resources Fish and Wildlife Branch 2006
Wetlands – NS	Wetlands identified from 1:10 000 aerial photography, including wetland type, vegetation, and photograph year, adapted to the Canadian Wetland Classification system	2000-2002	30m (sharp-ened 15m)	Nova Scotia Department of Natural Resources	

Table 5.6: Wetland vegetation type equivalencies between NB and NS, as determined from the Canadian Wetlands Classification Guide.

NB Veg Type	**NS Veg Type Equivalent**	**Reclassification**
Forested Hardwood Vegetation	Treed	Treed
Forested Softwood Vegetation	Treed	Treed
Alders	Low shrub/tall shrub	Shrub
Shrub Vegetation, except alders	Low shrub/tall shrub	Shrub
Emergent Vegetation	Graminoid	Graminoid
Open Water	Aquatic Vegetation	Aquatic
Open Water Un-vegetated	Water	Water/Exposed
Coastal/Shoreline Feature Vegetated	Salt Marsh	(excluded)
Coastal/Shoreline Feature	none	(excluded)
None	Exposed	Water/Exposed

Table 5.7: Replicates (grid squares) within Maritimes National parks for comparison with replicates randomly sampled elsewhere in the corresponding ecoregion.

		Replicates		Ecoregion Area (ha)		Percent Ecoregion in Park
National Park	**Ecoregion**	**Total in Park**	**Number Compared**	**In Park**	**Total**	
Cape Breton	128	36	27	27,915	1,551,054	1.8%
	129	45	38	68,748	234,077	29.4%
Fundy	121	12	10	11,430	1,317,982	0.9%
	123	9	7	9,621	481,733	2.0%
Kejimkujik Mainland	124	25	22	39,698	1,636,318	2.4%
Kejimkujik Seaside	125	4	0	2,095	728,169	0.3%
Kouchibouguac	122	22	19	24,199	3,019,141	0.8%

Table 5.8: The two most frequently selected variables at each model stage for three subsets of 240 bootstrapped log-linear Poisson model runs for Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA). Results labelled by subset (A – WETLANDS, B – WETNESS, C – WETxFOR) and buffer size (L = local, T = Territory). Column title abbreviations: S = Subset, F = Frequency, % = Percent selected.

Stage	**CAWA**				**OSFL**				**RUBL**			
	S	**Stage & Covariate**	**F**	**%**	**S**	**Stage & Covariate**	**F**	**%**	**S**	**Stage & Covariate**	**F**	**%**
1-2. Wetness & Forest Cover	B	1.3 DTW_STD (T) 2.2 CASFRI (T)	185	77.1	C	1-2.2 CASFRIxWET_PROP (T)	218	90.8	B	1.3 DTW_STD (T) 2.2 CASFRI (T)	118	49.2
	B	1.3 DTW_STD (T) 2.1 CASFRI (L)	52	21.7	A	1.2 WET_LENGTH (T), 2.2 CASFRI (T)	16	6.7	A	1.1 WET_TYPE (L) 2.1 CASFRI (L)	73	30.4
3. Forest Structure	B	3.1 CANCL_STD (L)	144	60	C	3.6 HT_STD (T)	116	48.3	B	3.2 CANCL_STD (T)	66	27.5
	B	3.6 HT_STD (T)	68	28.3	C	3.1 CANCL_AV (L)	56	23.3	A	3.1 CANCL_STD (L)	29	12.1
4. Landscape Complexity	B	4.1 COMPLEX (T)	230	95.8	C	4.1 COMPLEX (T)	171	71.2	B	4.0 Null	104	43.3
	B	4.0 Null	8	3.3	C	4.0 Null	47	19.6	A	4.0 Null	70	29.2
5. Disturbance	B	5.2 FOOTPRINT (T)	226	94.2	C	5.2 FOOTPRINT (T)	218	90.8	B	5.2 FOOTPRINT (T)	129	53.8
	B	5.1 CASFRI_DIST (T)	12	5	A	5.2 FOOTPRINT (T)	16	6.7	A	5.2 FOOTPRINT (T)	87	36.2
6. Road Distance	B	6.0 Null	203	84.6	C	6.0 Null	211	87.9	B	6.1 ROAD_DIST	95	39.6
	B	6.1 ROAD_DIST	35	14.6	A	6.0 Null	11	4.6	A	6.0 Null	71	29.6
7. Landscape Connectivity	B	7.1 CONNECT (T)	238	99.2	C	7.1 CONNECT (T)	119	49.6	B	7.0 Null	89	37.1
	C	7.1 CONNECT (T)	2	0.8	C	7.0 Null	99	41.2	A	7.0 Null	75	31.2
8. Protection Status	B	8.0 Null	128	53.3	C	8.0 Null	149	62.1	B	8.1 PROTECT (L)	134	55.8
	B	8.1 PROTECT (L)	110	45.8	C	8.1 PROTECT (L)	69	28.8	A	8.1 PROTECT (L)	93	38.8

Table 5.9: Selection frequencies of covariates at model stages 3-8 within three subsets of 240 bootstrapped log-linear Poisson model runs for Canada Warbler. Covariates are labelled by buffer size, local (L) and territory (T). Column title abbreviations: F = Frequency, % = Percent selected.

		WETLANDS		**WETNESS**		**WETxFOR**	
Stage	**Stage and Covariate**	**%**	**F**	**%**	**F**	**%**	**F**
Struct	3.0 Null	0.0	0	0.0	0	0.0	0
	3.1 CANCL_AV (L)	5.4	13	3.3	8	3.3	8
	3.2 CANCL_AV (T)	12.1	29	5.0	12	1.7	4
	3.3 CANCL_STD (L)	58.3	140	60.8	146	67.1	161
	3.4 CANCL_AV (T)	0.0	0	0.0	0	0.0	0
	3.5 HT_AV (L)	3.3	8	2.5	6	0.4	1
	3.6 HT_STD (T)	20.8	50	28.3	68	27.5	66
Complex	4.0 Null	24.6	59	3.3	8	17.5	42
	4.1 COMPLEXITY (T)	75.4	181	96.7	232	82.5	198
Disturb	5.0 Null	0.0	0	0.0	0	0.0	0
	5.1 CASFRI_DIST (T)	19.2	46	5.0	12	9.2	22
	5.2 FOOTPRINT (T)	80.8	194	95.0	228	90.8	218
Road	6.0 Null	87.5	210	85.4	205	90.8	218
	6.1 ROAD (L)	12.5	30	14.6	35	9.2	22
Connect	7.0 Null	0.0	0.0	0.0	0	0.0	0
	7.1 CONNECT	100.0	240	100.0	240	100.0	240
Protect	8.0 Null	40.4	97	53.8	129	47.1	113
	8.1 PROTECT (L)	59.6	143	46.3	111	52.9	127

Table 5.10: Selection frequencies of covariates at each model stage across three subsets of 240 bootstrapped log-linear Poisson model runs for Rusty Blackbird.

Stage	Subset	Covariate*	F	%
1-2. Wetness & Forest Cover	WETNESS	DTW_STD (T), CASFRI (T)	118	49.2
	WETLANDS	WET_TYPE (L), CASFRI (L)	73	30.4
	WETLANDS	WET_TYPE (L), CASFRI (T)	15	6.2
	WETxFOR	Null	10	4.2
	WETNESS	DTW_STD (T), Null	7	2.9
	WETNESS	DTW_STD (T), CASFRI (L)	5	2.1
	WETLANDS	WET_TYPE (L), Null	3	1.2
	WETNESS	WET_PROP (T), CASFRI (T)	2	0.8
	WETNESS	WET_PROP (T), CASFRI (L)	2	0.8
	WETNESS	WET_PROP (T), Null	1	0.4
	WETNESS	WET_PROP (L), CASFRI (T)	1	0.4
	WETLANDS	WET_LENGTH (T), Null	1	0.4
	WETLANDS	Null, CASFRI (L)	1	0.4
	WETLANDS	Null, Null	1	0.4
3. Forest Structure	WETNESS	CANCL_STD (T)	66	27.5
	WETLANDS	CANCL_STD (L)	29	12.1
	WETLANDS	CANCL_AV (L)	28	11.7
	WETNESS	CANCL_AV (L)	26	10.8
	WETNESS	Null	20	8.3
	WETLANDS	HT_STD (T)	19	7.9
	WETNESS	CANCL_STD (L)	11	4.6
	WETNESS	HT_STD (T)	10	4.2
	WETLANDS	CANCL_STD (T)	8	3.3
	WETxFOR	CANCL_STD (T)	6	2.5
	WETLANDS	Null	5	2.1
	WETxFOR	CANCL_AV (T)	4	1.7
	WETLANDS	CANCL_AV (T)	4	1.7
	WETNESS	HT_AV (L)	2	0.8
	WETNESS	CANCL_AV (T)	1	0.4
	WETLANDS	HT_AV (L)	1	0.4
4. Landscape Complexity	WETNESS	Null	104	43.3
	WETLANDS	Null	70	29.2
	WETNESS	COMPLEXITY (T)	32	13.3
	WETLANDS	COMPLEXITY (T)	24	10
	WETxFOR	Null	7	2.9
	WETxFOR	COMPLEXITY (T)	3	1.2
5. Disturbance	WETNESS	HUMAN_FOOTPRINT (T)	129	53.8
	WETLANDS	HUMAN_FOOTPRINT (T)	87	36.2
	WETxFOR	HUMAN_FOOTPRINT (T)	7	2.9
	WETNESS	CASFRI_DISTURB (T)	6	2.5

Stage	Subset	Covariate*	F	%
	WETLANDS	CASFRI_DISTURB (T)	6	2.5
	WETxFOR	CASFRI_DISTURB (T)	2	0.8
	WETxFOR	Null	1	0.4
	WETNESS	Null	1	0.4
	WETLANDS	Null	1	0.4
6. Road Distance	WETNESS	ROAD_DIST (L)	95	39.6
	WETLANDS	Null	71	29.6
	WETNESS	Null	41	17.1
	WETLANDS	ROAD_DIST (L)	23	9.6
	WETxFOR	ROAD_DIST l(L)	8	3.3
	WETxFOR	Null	2	0.8
7. Landscape Connectivity	WETNESS	Null	89	37.1
	WETLANDS	Null	75	31.2
	WETNESS	CONNECT (T)	47	19.6
	WETLANDS	CONNECT (T)	19	7.9
	WETxFOR	Null	10	4.2
8. Protection Status	WETNESS	PROTECT (L)	134	55.8
	WETLANDS	PROTECT (L)	93	38.8
	WETxFOR	PROTECT (L)	10	4.2
	WETNESS	Null	2	0.8
	WETLANDS	Null	1	0.4

*Covariates are labelled by buffer size, local (L) and territory (T). Column title abbreviations: F = Frequency, % = Percent selected.

Table 5.11: Selection frequencies of covariates at each model stage across three subsets of 240 bootstrapped log-linear Poisson model runs for Olive-sided Flycatcher. Covariates are labelled by buffer size, local (L) and territory (T).

Stage	Subset	Covariate	F	%
1-2. Wetness & Forest Cover	WETxFOR	CASFRIxWET PROP	218	90.8
	WETLANDS	WET_LENGTH (T), CASFRI (T)	16	6.7
	WETNESS	WET_LENGTH (T), CASFRI (T)	4	1.7
	WETNESS	DTW_STD (T), CASFRI (T)	2	0.8
3. Forest Structure	WETxFOR	CANCL_AV (L)	56	23.3
	WETxFOR	CANCL_STD (L)	39	16.2
	WETLANDS	CANCL_AV (L)	11	4.6
	WETxFOR	HT_AV local	7	2.9
	WETNESS	CANCL_AV (L)	4	1.7
	WETLANDS	HT_STD (T)	2	0.8
	WETLANDS	CANCL_STD (L)	2	0.8
	WETNESS	HT_STD (T)	1	0.4
	WETNESS	CANCL_AV (T)	1	0.4
	WETLANDS	HT_AV local	1	0.4
	WETxFOR	COMPLEXITY (T)	171	71.2
4. Landscape Complexity	WETLANDS	COMPLEXITY (T)	12	5
	WETNESS	COMPLEXITY (T)	4	1.7
	WETLANDS	Null	4	1.7
	WETNESS	Null	2	0.8
	WETxFOR	FOOTPRINT (T)	218	90.8
5. Disturbance	WETNESS	FOOTPRINT (T)	6	2.5
	WETxFOR	Null	211	87.9
6. Road Distance	WETxFOR	ROAD (L)	7	2.9
	WETNESS	Null	5	2.1
	WETLANDS	ROAD (L)	5	2.1
	WETNESS	ROAD (L)	1	0.4
	WETxFOR	CONNECT (T)	119	49.6
7. Landscape Connectivity	WETLANDS	CONNECT (T)	14	5.8
	WETNESS	CONNECT (T)	6	2.5
	WETLANDS	Null	2	0.8
	WETxFOR	Null	149	62.1
8. Protection Status	WETLANDS	Null	9	3.8
	WETLANDS	PROTECT (L)	7	2.9
	WETNESS	PROTECT (L)	3	1.2
	WETNESS	Null	3	1.2
	WETNESS	Null	8	3.3

Table 5.12: Selection frequencies of covariates at model stages 1-2 within three subsets of 240 bootstrapped log-linear Poisson model runs for Rusty Blackbird. Covariates are labelled by buffer size, local (L) and territory (T). Column title abbreviations: F = Frequency, % = Percent selected.

	WETLANDS			**WETNESS**			**WETxFOR**		
Stage	**Stage and Covariate**	**%**	**F**	**Stage and Covariate**	**%**	**F**	**Stage and Covariate**	**%**	**F**
Wet	1.0 Null	23.3	56	1.0 Null	0.4	1	1-2.0 Null	94.6	227
	1.1 WET_VEG (L)	64.6	155	1.1 DTW_PROP (L)	0.4	1	1-2.1 CASFRIxDTW_PROP (L)	5.4	13
	1.2 WET_LENGTH (T)	12.1	29	1.2 DTW_PROP (T)	5.8	14	1-2.2 CASFRIxDTW_PROP (T)	0.0	0
	1.3 WETPROP (T)	0.0	0	1.3 DTW_STD (T)	93.3	224			
Cover	2.0 Null	5.8	14	2.0 Null	4.6	11			
	2.1 CASFRI (L)	43.3	104	2.1 CASFRI (L)	22.9	55			
	2.2 CASFRI (T)	50.8	122	2.2 CASFRI (T)	72.5	174			

Table 5.13: Selection frequencies of covariates at model stages 3-8 within three subsets of 240 bootstrapped log-linear Poisson model runs for Rusty Blackbird. Covariates are labelled by buffer size, local (L) and territory (T). Column title abbreviations: F = Frequency, % = Percent selected.

		WETLANDS		**WETNESS**		**WETxFOR**	
Stage	**Stage and Covariate**	**%**	**F**	**%**	**F**	**%**	**F**
Struct	3.0 Null	8.8	21	14.2	34	2.1	5
	3.1 CANCL_AV (L)	26.7	64	20.0	48	30.4	73
	3.2 CANCL_AV (T)	2.5	6	1.7	4	10.8	26
	3.3 CANCL_STD (L)	20.8	50	19.2	46	1.7	4
	3.4 CANCL_AV (T)	30.0	72	30.8	74	43.8	105
	3.5 HT_AV (L)	0.8	2	1.3	3	7.9	19
	3.6 HT_STD (T)	10.4	25	12.9	31	3.3	8
Complex	4.0 Null	56.3	135	79.2	190	58.8	141
	4.1 COMPLEXITY (T)	43.8	105	20.8	50	41.3	99
Disturb	5.0 Null	1.3	3	0.8	2	1.7	4
	5.1 CASFRI_DIST (T)	7.9	19	4.6	11	4.2	10
	5.2 FOOTPRINT (T)	90.8	218	94.6	227	94.2	226
Road	6.0 Null	70.0	168	44.2	106	70.8	170
	6.1 ROAD (L)	30.0	72	55.8	134	29.2	70
Connect	7.0 Null	84.2	202	64.6	155	82.1	197
	7.1 CONNECT	15.8	38	35.4	85	17.9	43
Protect	8.0 Null	1.3	3	1.3	3	0.8	2
	8.1 PROTECT (L)	98.8	237	98.8	237	99.2	238

Table 5.14: Top ranked covariates explaining variation in density estimates for Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA) for each model subset. Models represent the most-selected variable from each stage of the model-building process. Scale of variable is indicated as local (L) or territory (T).

Species	Subset	Top ranked model
RUBL	WETLANDS	Count ~ WET_VEG (L) + CASFRI (T) + CANCL_AV (T) + FOOTPRINT (T) + PROTECT (L)
	WETNESS	Count ~ DTW_STD (T) + CASFRI (T) + CANCL_AV (T) + FOOTPRINT (T) + ROAD (L) + PROTECT (L)
	WETxFOR	Count ~ CANCL_AV (T)+ FOOTPRINT (T) + PROTECT (L)
OSFL	WETLANDS	Count ~ WET_LENGTH (T) + CASFRI (T) + HT_STD (T) + COMPLEX (T) + FOOTPRINT (T) + CONNECT (T)
	WETNESS	Count ~ DTW_STD (T) + CASFRI (T) + HT_STD (T) + COMPLEX (T) + FOOTPRINT (T) + CONNECT (T)
	WETxFOR	Count ~ CASFRIxDTW_PROP (T) + HT_STD (T)+ COMPLEX (T) + FOOTPRINT (T) + CONNECT (T)
CAWA	WETLANDS	Count ~ WET_LENGTH (T) + CASFRI (T) + CANCL_STD (L) + COMPLEX (T) + FOOTPRINT (T) + CONNECT (T) + PROTECT (L)
	WETNESS	Count ~ DTW_STD (T) + CASFRI (T) + CANCL_STD (L) + COMPLEX (T) + FOOTPRINT (T) + CONNECT (T) + PROTECT (L)
	WETxFOR	Count ~ CASFRIxDTWPROP (T) + CANCL_STD (L) + COMPLEX (T) + FOOTPRINT (T) + CONNECT ter + PROTECT (L)

Table 5.15: Predicted population density and numbers of territorial males of Rusty Blackbird (RUBL), Olive-sided Flycatcher (OSFL), and Canada Warbler (CAWA) in 5 Maritime national parks.

Park	**Park area (ha)**	**Mean population density (territorial males/ha)**			**Predicted Number of Territorial Males**		
		RUBL	**OSFL**	**CAWA**	**RUBL**	**OSFL**	**CAWA**
Kouchibouguac	24,199	<0.001	0.011	0.016	1	29	43
Fundy	21,051	<0.001	0.013	0.031	0	43	105
Cape Breton Highlands	96,663	0.001	0.014	0.045	9	217	695
Kejimkujik (Mainland)	39,698	<0.001	0.011	0.038	1	67	242
Kejimkujik (Seaside)	2,095	<0.001	0.006	0.025	0	2	7
Total	401, 506	<0.001	0.011	0.031	11	358	1092

Table 5.16: Results of *t*-tests for predicted mean density (territorial males/ha) of Olive-sided Flyatcher (OSFL) and Canada Warbler (CAWA) in national parks and surrounding randomly-selected areas of the same size in six ecoregions in New Brunswick and Nova Scotia.

			Park		**Ecoregion**		
Ecoregion	**Species**	**n**	**Mean**	**SD**	**Mean**	**SD**	***P***
121	OSFL	10	0.011	0.001	0.011	0.009	0.812
	CAWA	10	0.032	0.008	0.036	0.014	0.321
122	OSFL	19	0.011	0.002	0.008	0.005	0.051
	CAWA	19	0.018	0.006	0.042	0.012	**<0.001**
123	OSFL	7	0.014	0.003	0.007	0.003	**<0.001**
	CAWA	7	0.028	0.005	0.025	0.021	0.382
124	OSFL	22	0.010	0.003	0.010	0.005	0.941
	CAWA	22	0.037	0.012	0.039	0.016	0.640
128	OSFL	27	0.010	0.003	0.010	0.004	0.599
	CAWA	27	0.036	0.015	0.038	0.014	0.558
129	OSFL	38	0.015	0.003	0.013	0.003	**0.001**
	CAWA	38	0.046	0.018	0.062	0.014	**<0.001**

Table 5.17: Selection frequencies of covariates at model stages 1-2 within three subsets of 240 bootstrapped log-linear Poisson model runs for Olive-sided Flycatcher. Covariates are labelled by buffer size, local (L) and territory (T). Column title abbreviations: F = Frequency, % = Percent selected.

	WETLANDS			**WETNESS**			**WETxFOR**		
Stage	**Stage and Covariate**	**%**	**F**	**Stage and Covariate**	**%**	**F**	**Stage and Covariate**	**%**	**F**
Wet	1.0 Null	0.0	0	1.0 Null	0.0	0	1-2.0 Null	0.0	0
	1.1 WET_VEG (L)	0.4	1	1.1 DTW_PROP (L)	1.7	4	1-2.1 CASFRIxDTW_PROP (L)	0.0	0
	1.2 WET_LENGTH (T)	99.6	239	1.2 DTW_PROP (T)	65.0	156	1-2.2 CASFRIxDTW_PROP (T)	100	240
	1.3 WETPROP (T)	0.0	0	1.3 DTW_STD (T)	33.3	80			
Cover	2.0 Null	0.0	0	2.0 Null	0.0	0			
	2.1 CASFRI (L)	0.0	0	2.1 CASFRI (L)	0.0	0			
	2.2 CASFRI (T)	100	240.0	2.2 CASFRI (T)	100.0	240			

Table 5.18: Selection frequencies of covariates at model stages 3-8 within three subsets of 240 bootstrapped log-linear Poisson model runs for Olive-sided Flycatcher. Covariates are labelled by buffer size, local (L) and territory (T). Column title abbreviations: F = Frequency, % = Percent selected.

		WETLANDS		**WETNESS**		**WETxFOR**	
Stage	**Stage and Covariate**	**%**	**F**	**%**	**F**	**%**	**F**
Struct	3.0 Null	0.4	1	0.0	0	0.0	0
	3.1 CANCL_AV (L)	30.8	74	43.3	104	26.3	63
	3.2 CANCL_AV (T)	0.0	0	0.4	1	0.0	0
	3.3 CANCL_STD (L)	30.8	74	9.2	22	19.2	46
	3.4 CANCL_AV (T)	0.0	0	0.4	1	0.0	0
	3.5 HT_AV (L)	10.4	25	1.3	3	3.3	8
	3.6 HT_STD (T)	27.5	66	45.4	109	51.3	123
Complex	4.0 Null	20.0	48	22.5	54	20.8	50
	4.1 COMPLEXITY (T)	80.0	192	77.5	186	79.2	190
Disturb	5.0 Null	0.0	0	0.0	0	0.0	0
	5.1 CASFRI_DIST (T)	0.0	0	0.0	0	0.0	0
	5.2 FOOTPRINT (T)	100.0	240	100.0	240	100.0	240
Road	6.0 Null	91.7	220	85.8	206	96.3	231
	6.1 ROAD (L)	8.3	20	14.2	34	3.8	9
Connect	7.0 Null	10.8	26	11.3	27	45.4	109
	7.1 CONNECT	89.2	214	88.8	213	54.6	131
Protect	8.0 Null	55.0	132	53.8	129	67.9	163
	8.1 PROTECT (L)	45.0	108	46.3	111	32.1	77

Table 5.19 Selection frequencies of covariates at model stages 1-2 within three subsets of 240 bootstrapped log-linear Poisson model runs for Canada Warbler. Covariates are labelled by buffer size, local (L) and territory (T). Column title abbreviations: F = Frequency, % = Percent selected.

	WETLANDS			**WETNESS**			**WETxFOR**		
Stage	**Stage and Covariate**	**%**	**F**	**Stage and Covariate**	**%**	**F**	**Stage and Covariate**	**%**	**F**
Wet	1.0 Null	2.1	5	1.0 Null	0.0	0	1-2.0 Null	2.9	7
	1.1 WET_VEG (L)	26.7	64	1.1 DTW_PROP (L)	0.0	0	1-2.1 CASFRIxDTW_PROP (L)	11.3	27
	1.2 WET_LENGTH ter	71.3	171	1.2 DTW_PROP (T)	0.0	0	1-2.2 CASFRIxDTW_PROP t(T)	85.8	206
	1.3 WETPROP (T)	0.0	0	1.3 DTW_STD (T)	100.0	240			
Cover	2.0 Null	0.4	1	2.0 Null	0.4	1			
	2.1 CASFRI (L)	31.3	75	2.1 CASFRI (L)	21.7	52			
	2.2 CASFRI (T)	68.3	164	2.2 CASFRI (T)	77.9	187			

Table 5.20: Selection frequencies of covariates at each model stage across three subsets of 240 bootstrapped log-linear Poisson model runs for CAWA. Covariates are labelled by buffer size, local (L) and territory (T). Column title abbreviations: F = Frequency, % = Percent selected.

Stage	**Subset**	**Covariate**	**F**	**%**
1-2. Wetness & Forest Cover	WETNESS	DTW_STD (T), CASFRI (T)	185	77.1
	WETNESS	DTW_STD (T), CASFRI (L)	52	21.7
	WETxFOR	CASFRIxDTW_PROP (T)	2	0.8
	WETNESS	DTW_STD (T), Null	1	0.4
3. Forest Structure	WETNESS	CANCL_STD (L)	144	60
	WETNESS	HT_STD (T)	68	28.3
	WETNESS	CANCL_AV (T)	12	5
	WETNESS	CANCL_AV (L)	8	3.3
	WETNESS	HT_AV (L)	6	2.5
	WETxFOR	CANCL_STD (L)	2	0.8
4. Landscape Complexity	WETNESS	COMPLEXITY (T)	230	95.8
	WETNESS	Null	8	3.3
	WETxFOR	Null	1	0.4
	WETxFOR	COMPLEXITY (T)	1	0.4
5. Disturbance	WETNESS	FOOTPRINT (T)	226	94.2
	WETNESS	CASFRI_DIST (T)	12	5
	WETxFOR	FOOTPRINT (T)	2	0.8
6. Road Distance	WETNESS	Null	203	84.6
	WETNESS	ROAD (L)	35	14.6
	WETxFOR	Null	2	0.8
7. Landscape Connectivity	WETNESS	CONNECT (T)	238	99.2
	WETxFOR	CONNECT (T)	2	0.8
8. Protection Status	WETNESS	Null	128	53.3
	WETNESS	PROTECT (L)	110	45.8
	WETxFOR	Null	1	0.4
	WETxFOR	PROTECT (L)	1	0.4

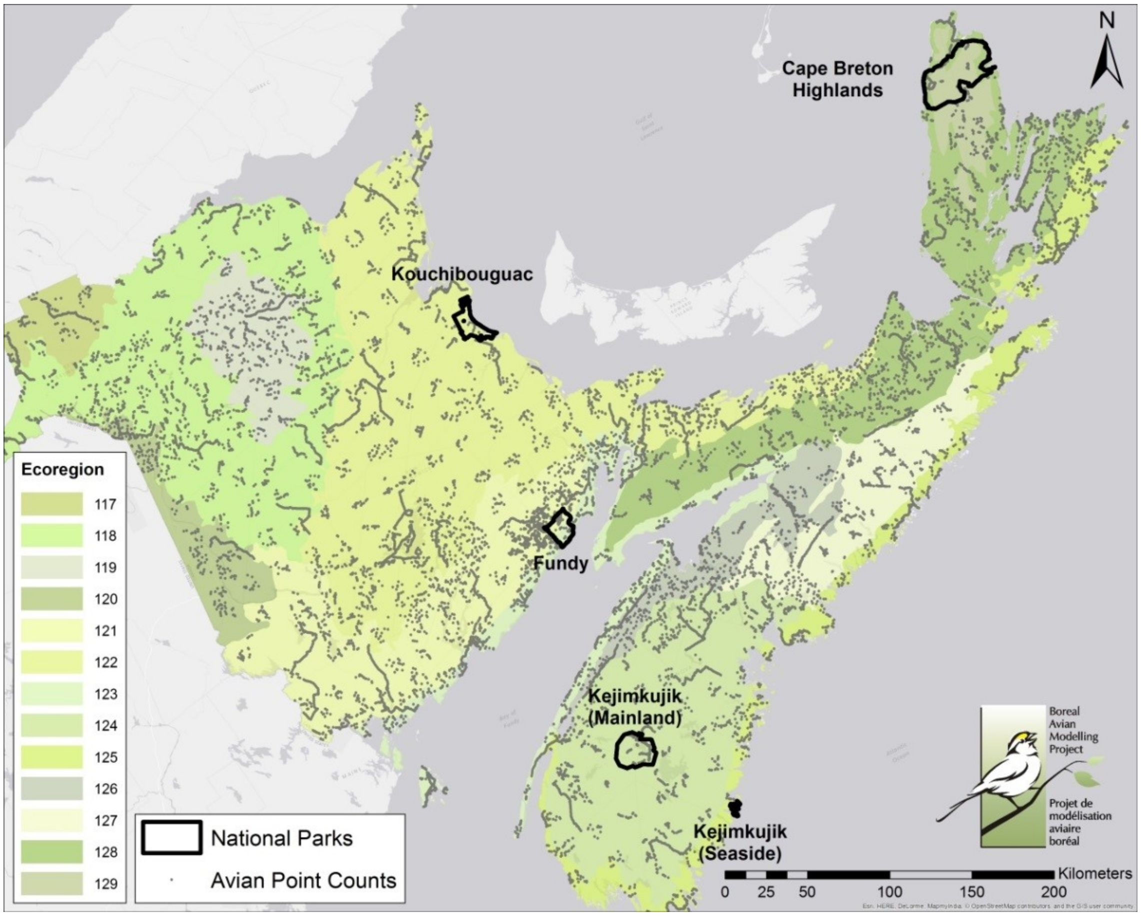

Figure 5.1: Location of all Nova Scotia and New Brunswick point counts in the Boreal Avian Modelling Project database. Abundance data from these locations were used to generate bird habitat models for the national parks shown on the map.

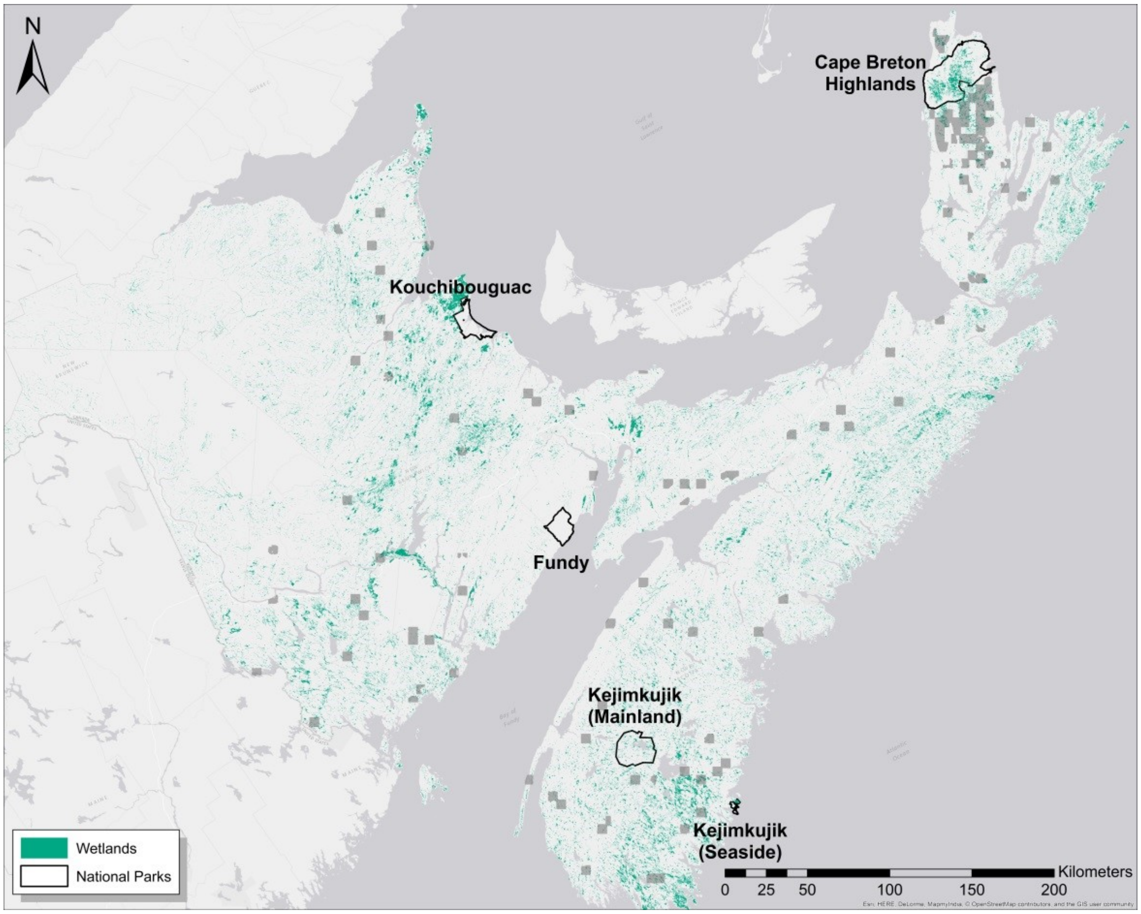

Figure 5.2: Areas with a depth to water table less than or equal to 1 metre are labelled as wetlands. For comparison of predicted avian population density between parks and their surrounding ecoregions, grid cells (gray squares) were randomly selected from the study area. Data source: Forest Watershed Research Center, University of New Brunswick; NS Department of Natural Resources.

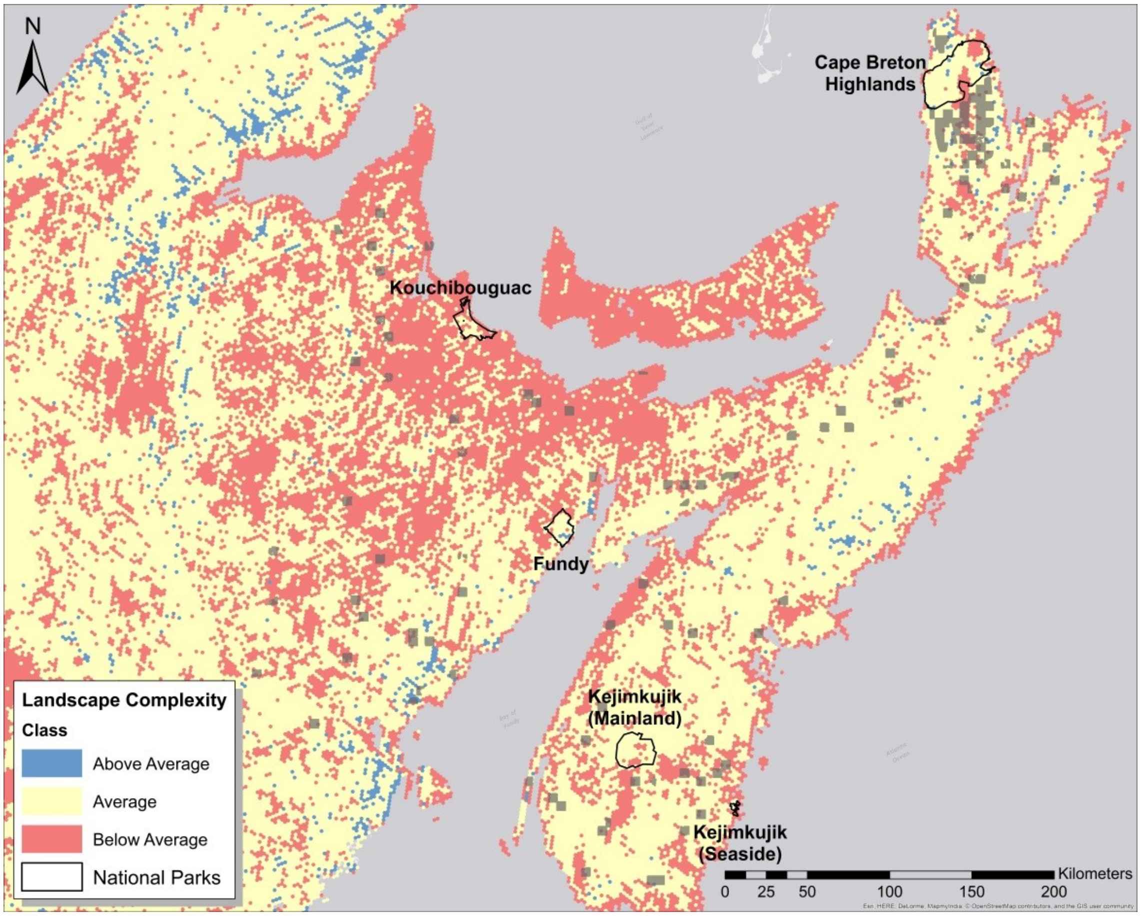

Figure 5.3: Map of study areas in relation to classification of landscape complexity for the Northern Appalachian/Acadian ecoregions. For comparison of population density between parks and their surrounding ecoregions, grid cells (gray squares) were randomly selected from the study area. Data source: The Nature Conservancy; Conservation Biology Institute: Data Basin.

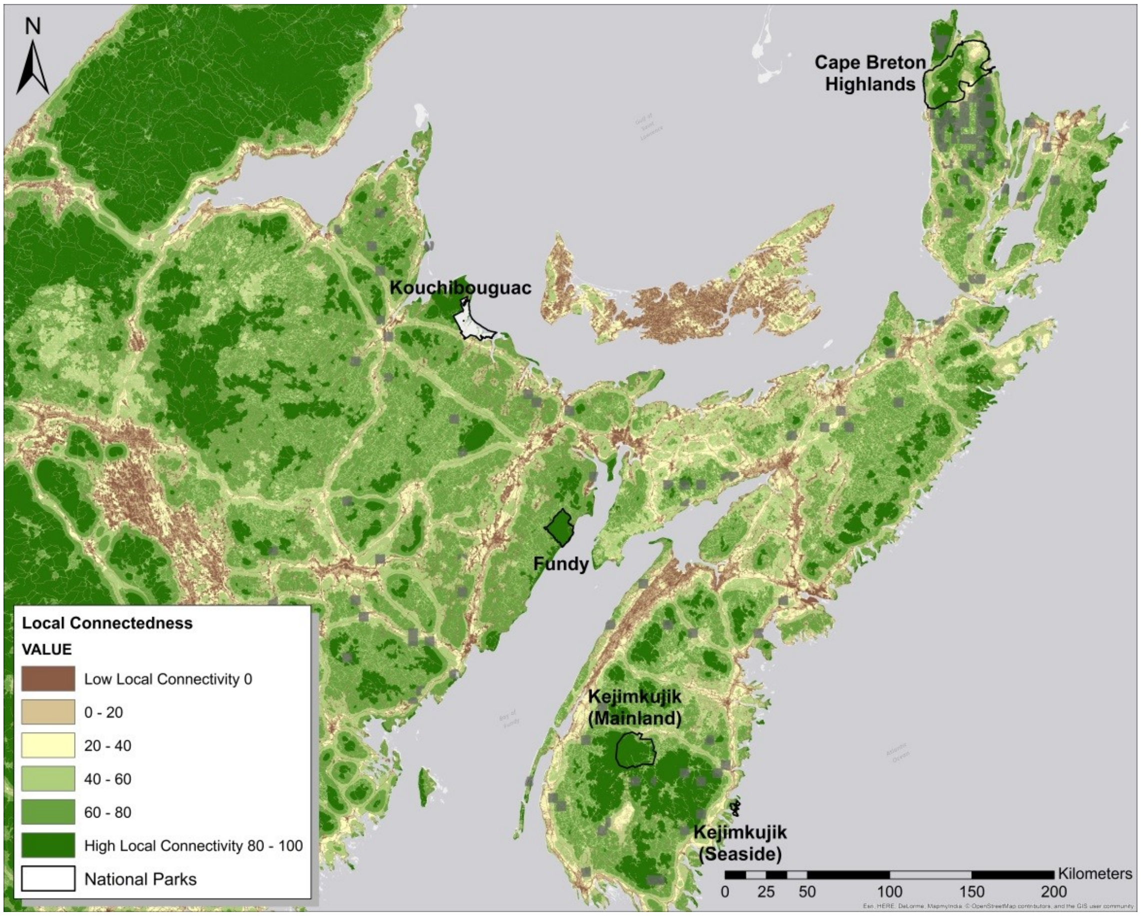

Figure 5.4: Map of study areas in relation to local connectedness within New Brunswick and Nova Scotia. Grid cells (gray squares) were randomly selected from outside of protected areas. Data source: Government of Canada; Natural Resources Canada; Earth Sciences Sector; Canada Centre for Mapping and Earth Observation.

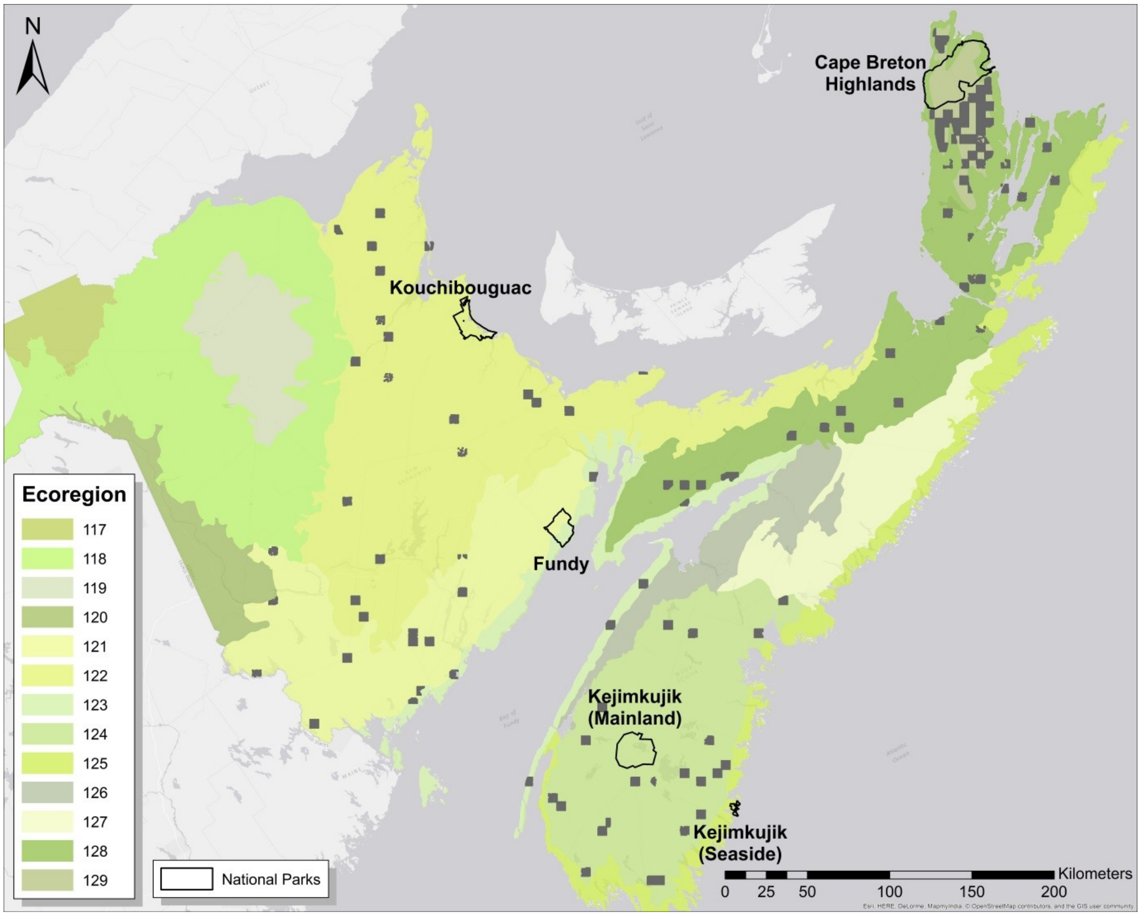

Figure 5.5: Ecoregions of New Brunswick and Nova Scotia. Gray squares show randomly selected non-park replicates used for comparison with the corresponding national park within the same ecoregion. Ecoregions data source: CGDI National Frameworks Data.

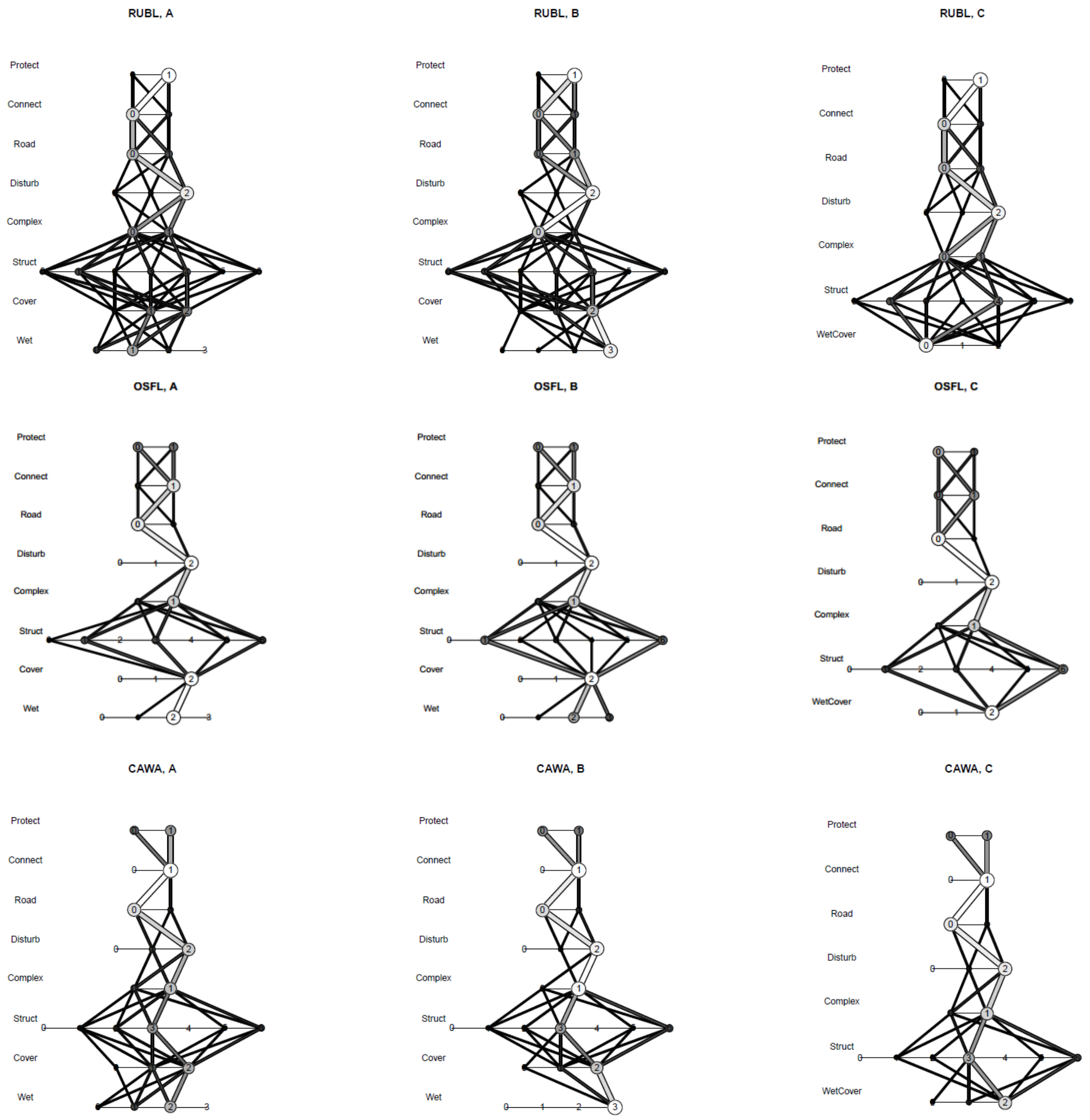

Figure 5.6: Selection paths of variables best explaining variation in density estimation of RUBL, OSFL, and CAWA in New Brunswick and Nova Scotia based on the branching hierarchy model building process. Results for three model subsets (A – WETLANDS, B – WETNESS, C – WETxFOR) represent selection frequencies from 240 bootstrap iterations. Horizontal lines show each model stage, and numbers indicate individual covariates. Shade and thickness of line are proportional to selection frequency, with larger and lighter lines indicating higher selection frequencies.

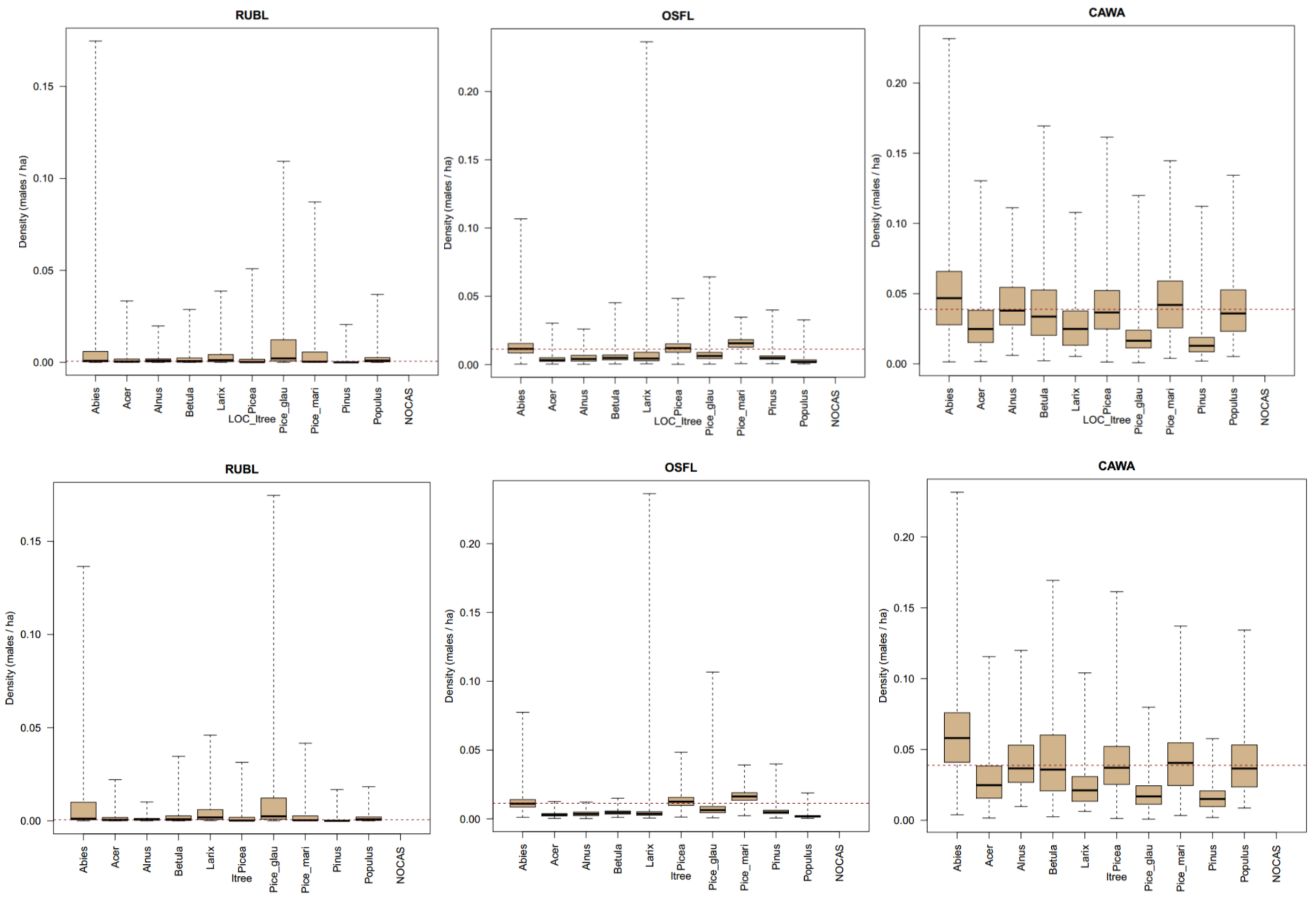

Figure 5.7: Relationship of predicted density of males per hectare to forest cover at two scales for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset). Upper panels show the local scale (50m buffer for RUBL and CAWA, 100m for OSFL) and lower panels show territory scale (250 m buffer).

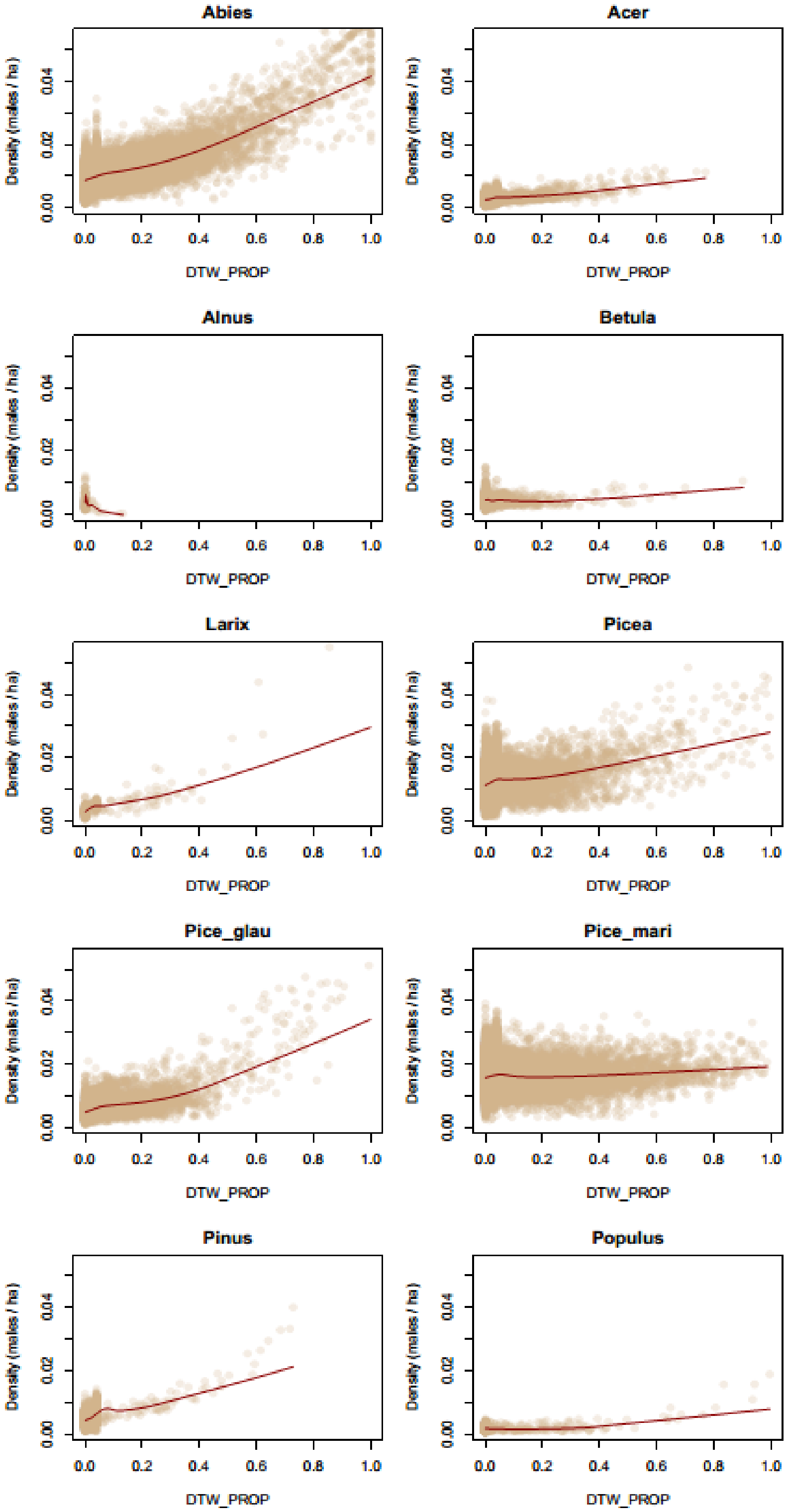

Figure 5.8: Relationship of density of males per hectare to forest cover and proportion of buffer classified as wet (depth to water table ≤1 m) at the territory scale (250 m) for OSFL. Values on the X axis are standardized.

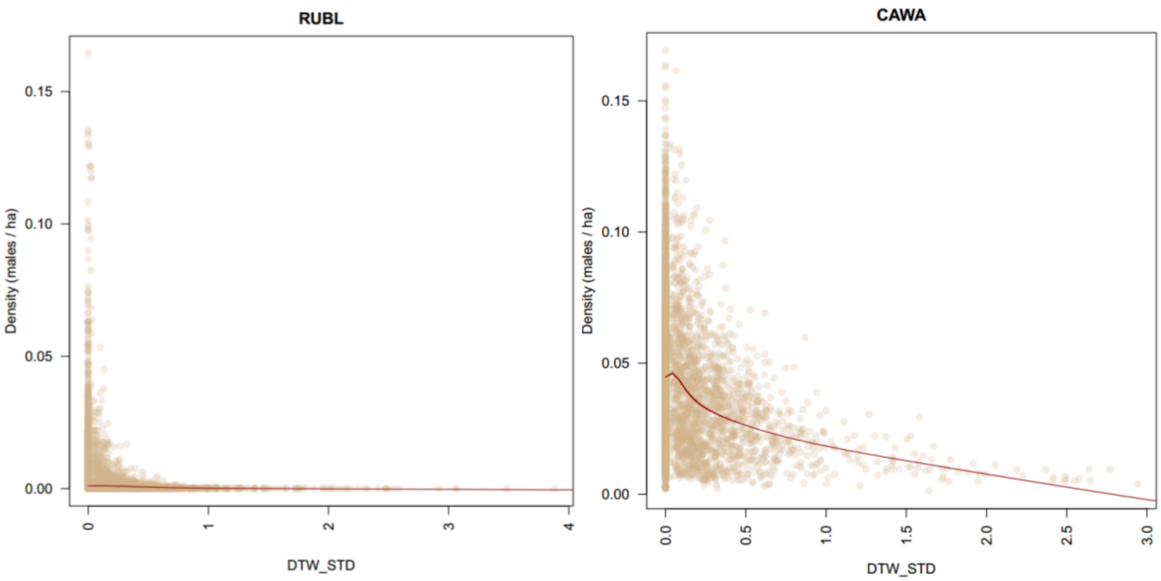

Figure 5.9: Relationship of predicted density of males per hectare to standard deviation of depth to water table at the territory scale (250 m) for RUBL (WETNESS model subset) and CAWA (WETNESS model subset). Values on the X axis are standardized.

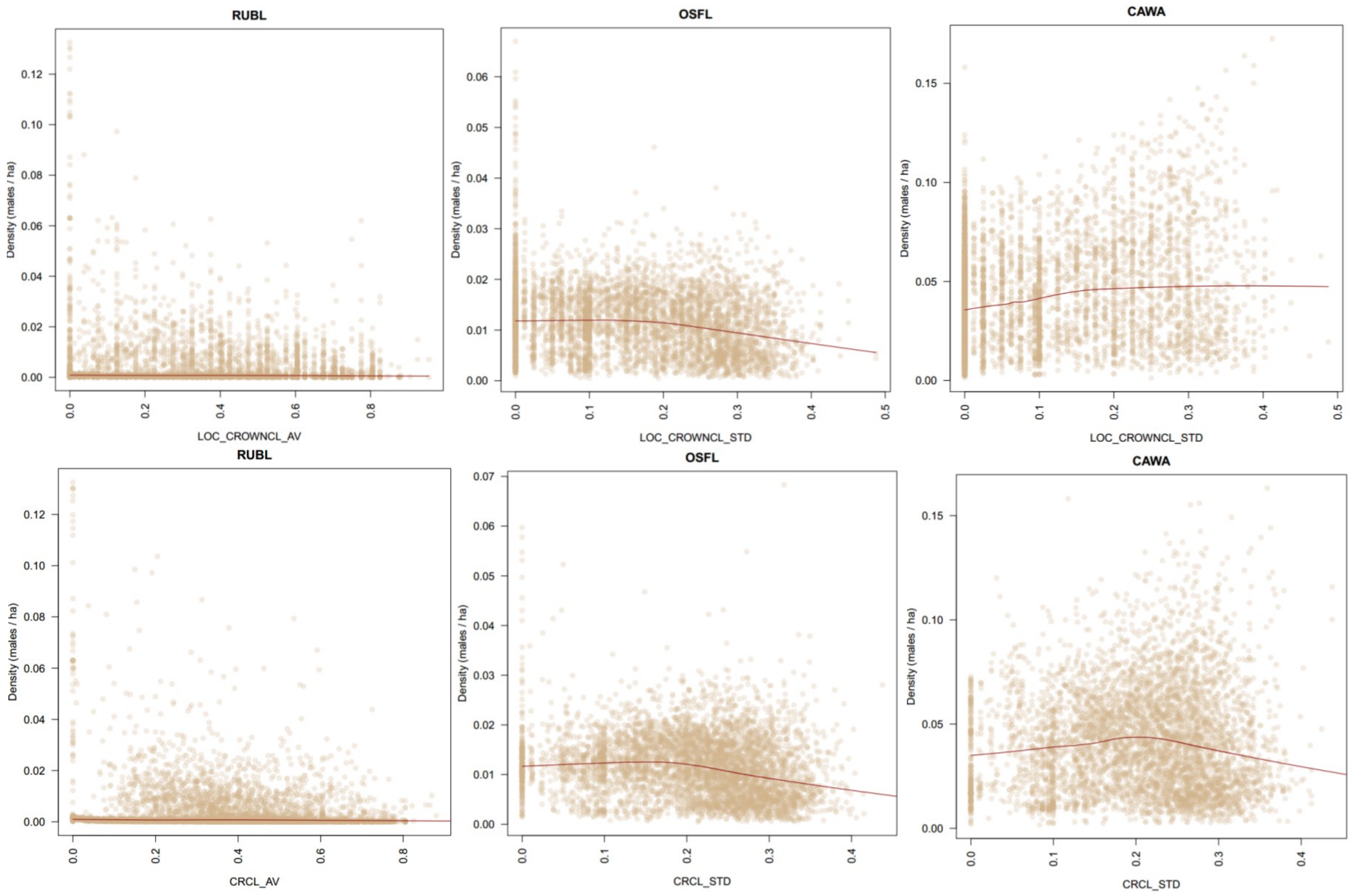

Figure 5.10: Relationship of predicted density of males per hectare to mean and standard deviation of canopy height at two scales for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset). Upper panels show mean canopy height at the local scale (50m buffer for RUBL and CAWA, 100m for OSFL) and lower panels show standard deviation of canopy height at the territory scale (250m buffer). Values on the X axis are standardized.

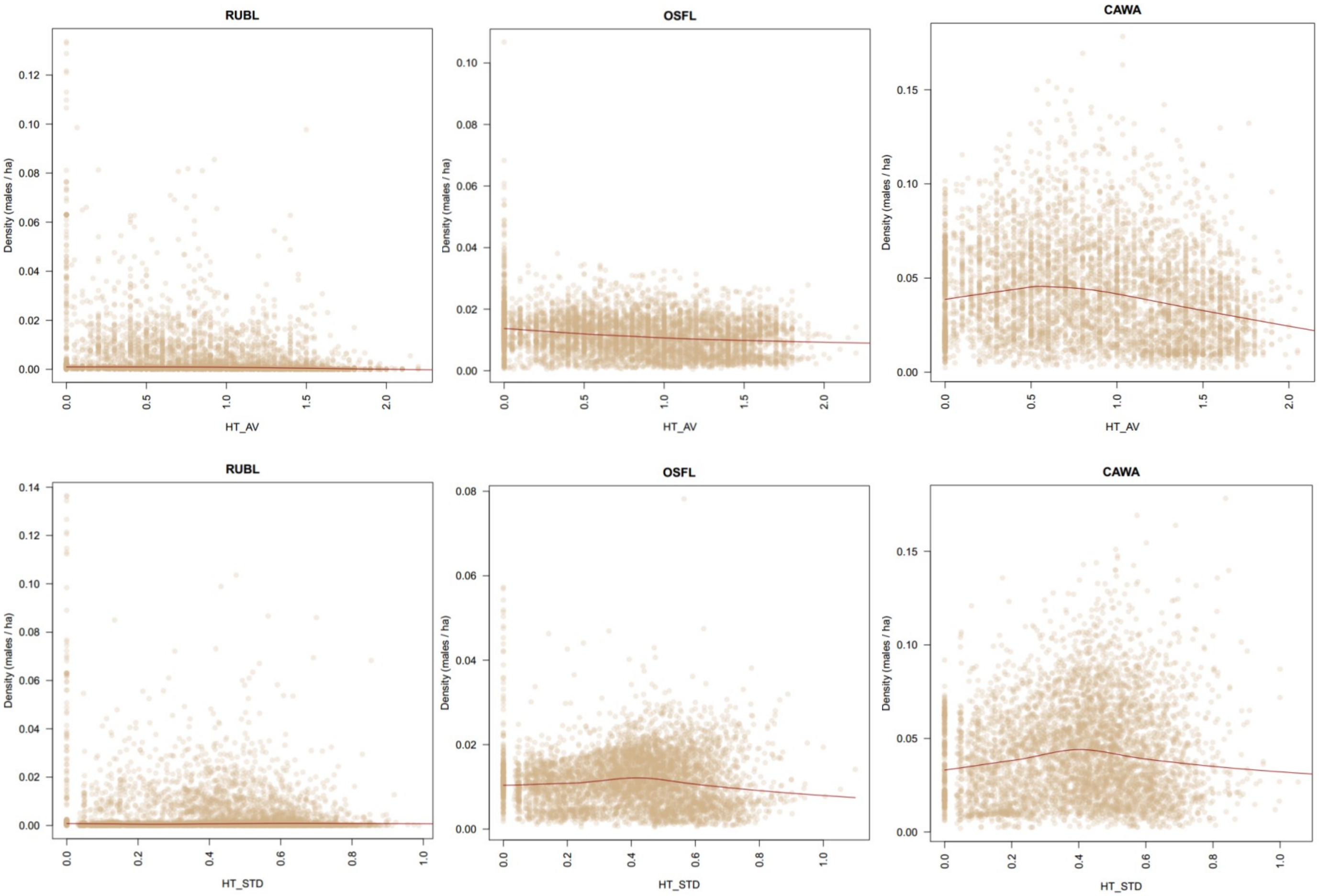

Figure 5.11: Relationship of predicted density of males per hectare to mean and standard deviation of canopy height at two scales for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset). Upper panels show mean canopy height at the local scale (50m buffer for RUBL and CAWA, 100m for OSFL) and lower panels show standard deviation of canopy height at the territory scale (250m buffer). Values on the X axis are standardized.

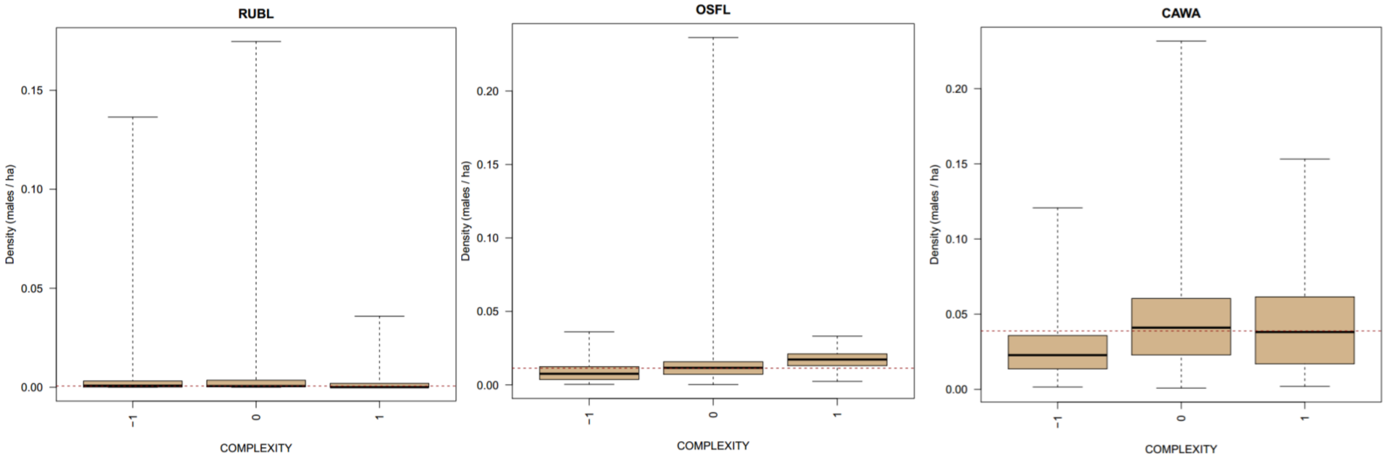

Figure 5.12: Relationship of density of males per hectare to landscape complexity (-1 = below mean, 0 = mean, 1 = above mean) at the territory scale (250 m buffer) for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset).

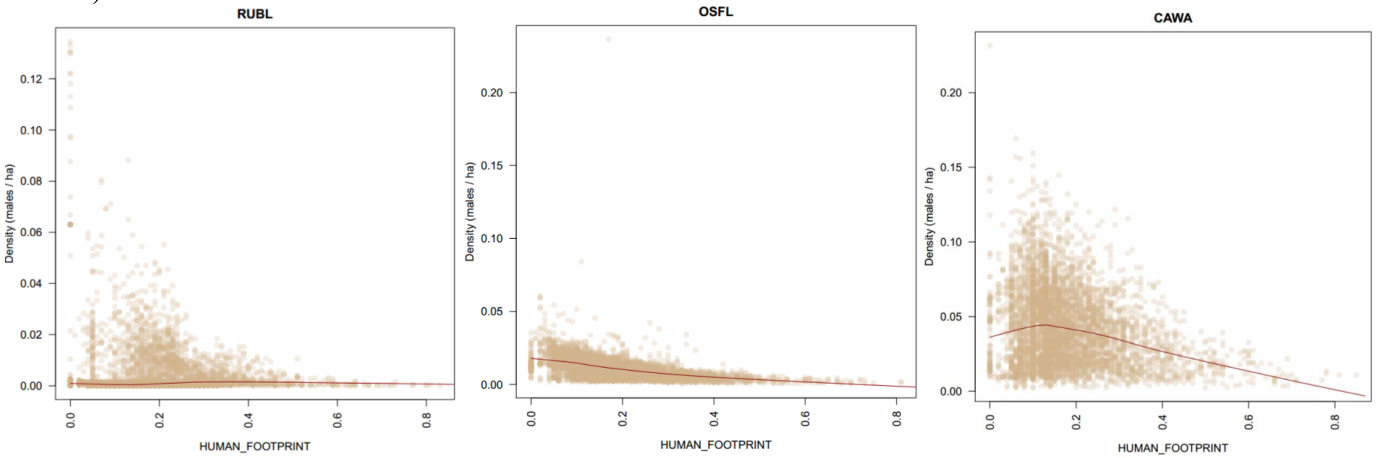

Figure 5.13: Relationship of density of males per hectare to human footprint index at the territory scale (250 m) for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset). Values on the X axis are standardized.

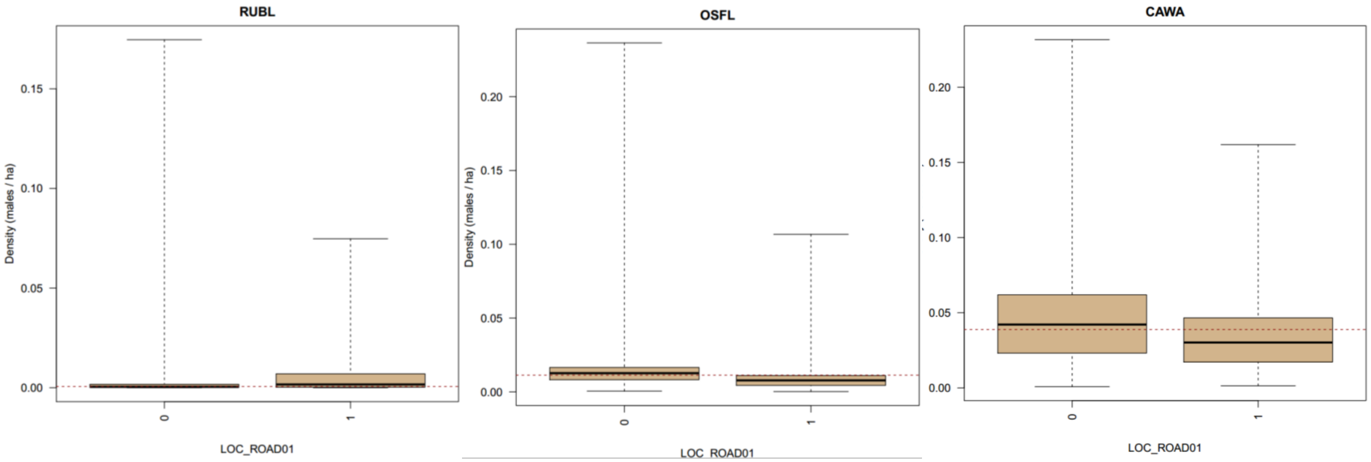

Figure 5.14: Relationship of density of males per hectare to road condition (0 = point count off road, 1 = point count adjacent to road) for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset).

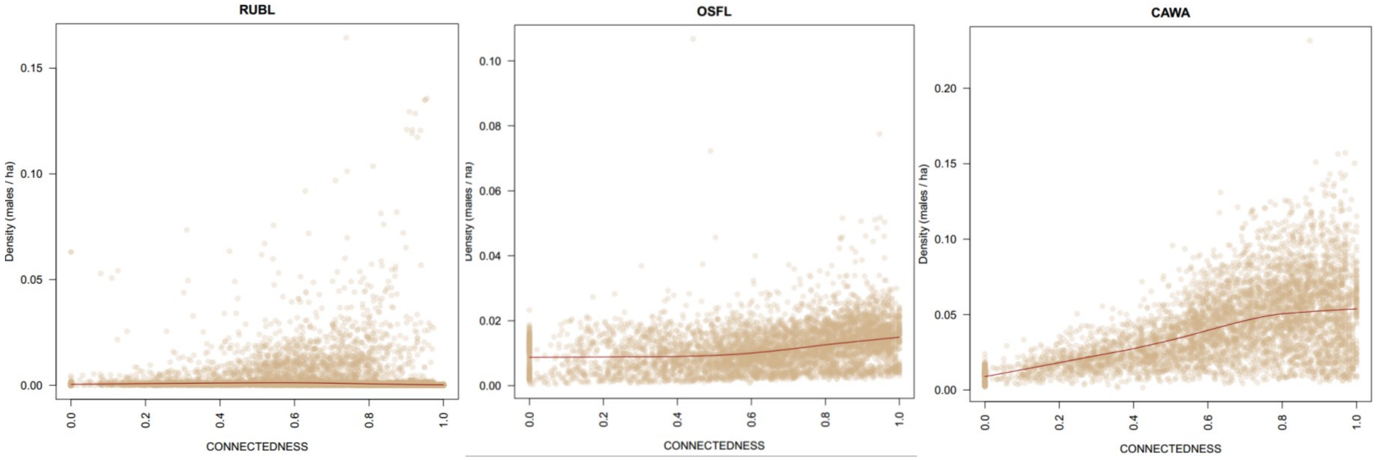

Figure 5.15: Relationship of density of males per hectare to local connectedness index at the territory scale (250 m) for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset). Values on the X axis are standardized.

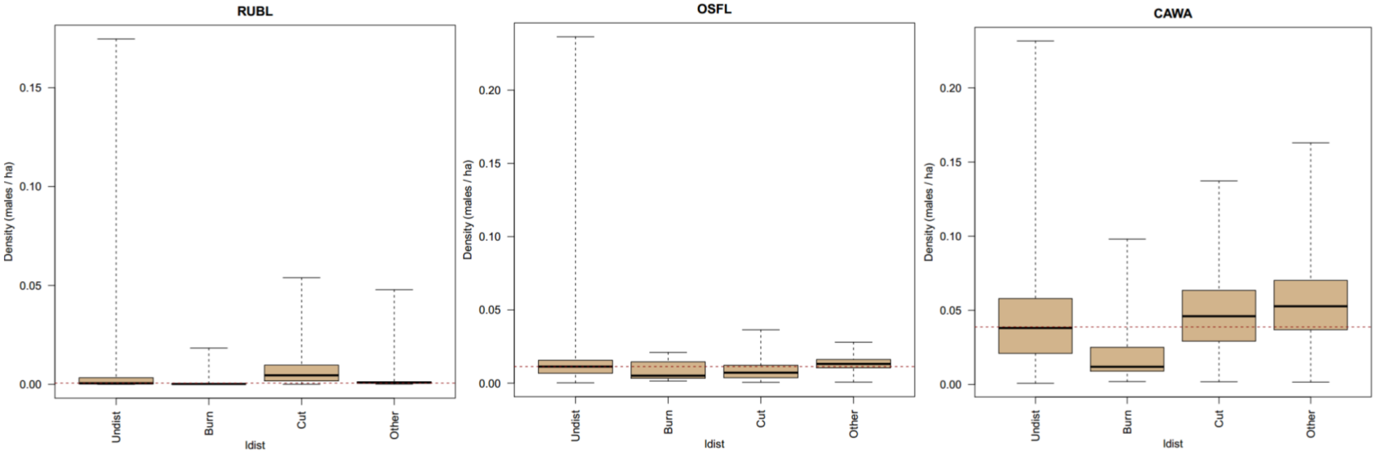

Figure 5.16: Relationship of density of males per hectare to disturbed area within the territory buffer (250 m) for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset).

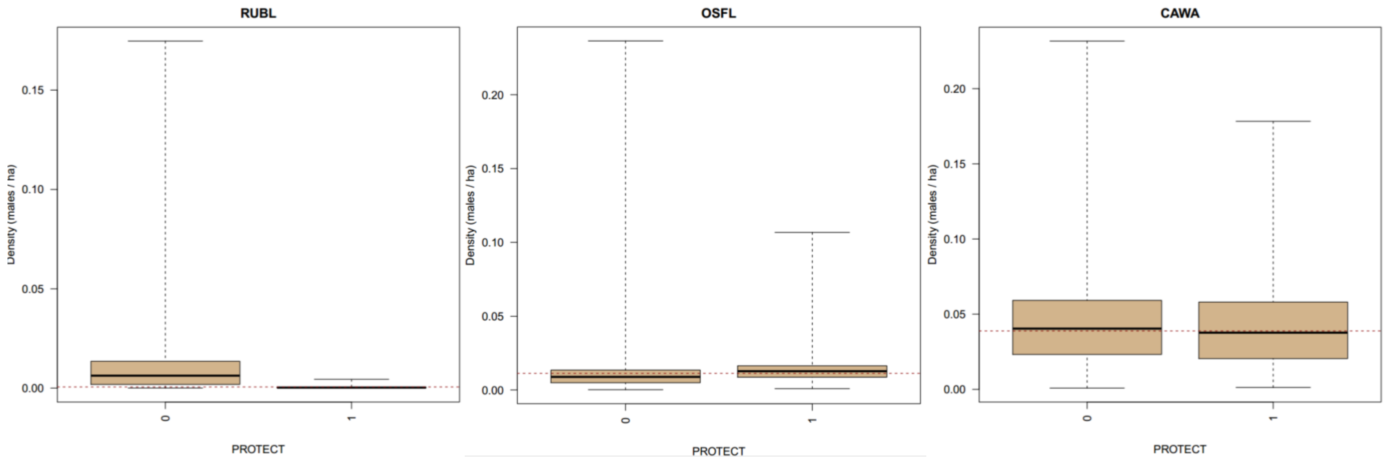

Figure 5.17: Relationship of density of males per hectare to site protection status at the point count location (0 = unprotected, 1 = protected) for RUBL (WETNESS model subset), OSFL (WETxFOR model subset), and CAWA (WETNESS model subset). Values on the X axis are standardized.

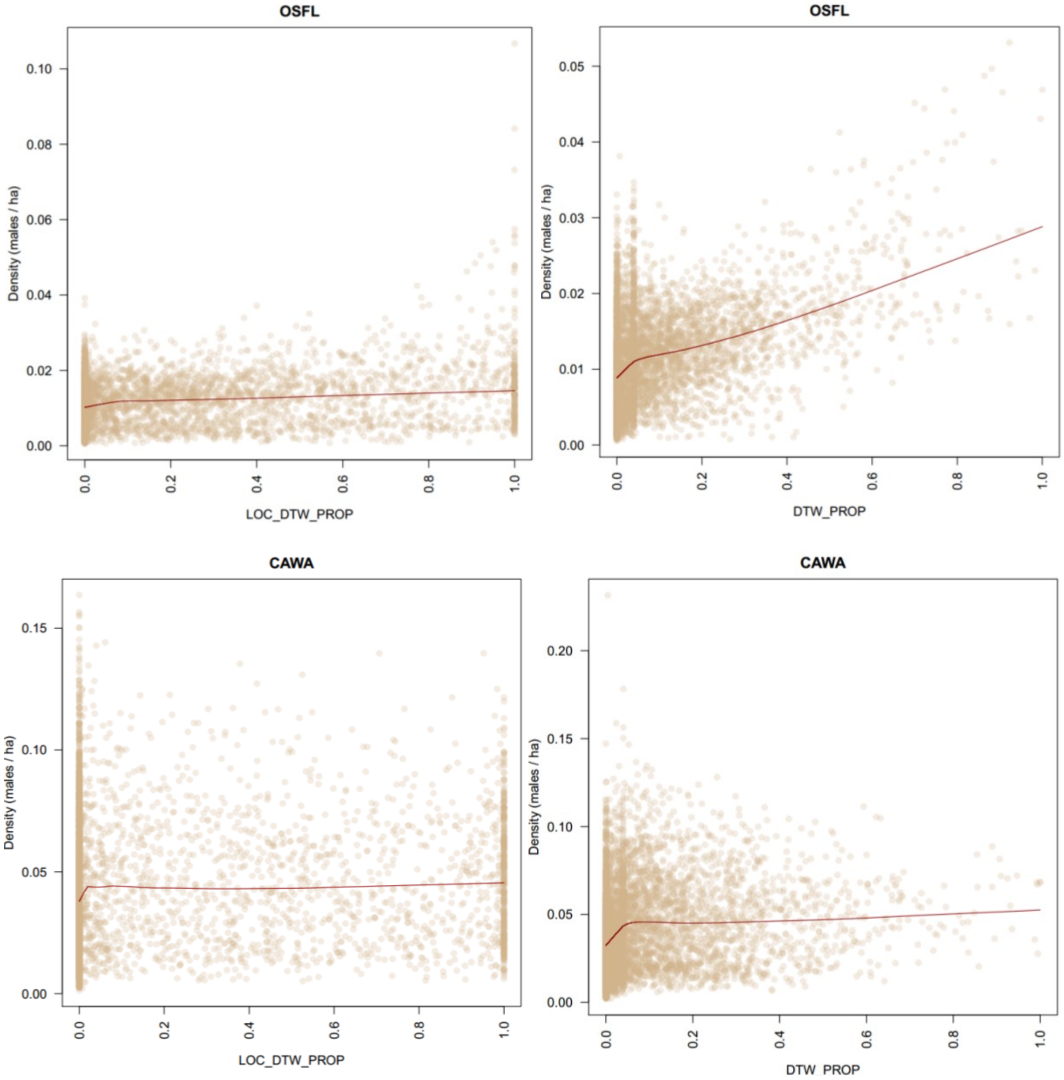

Figure 5.18: Relationship of density of males per hectare to proportion of depth to water table classified as <= 1 in buffers for OSFL and CAWA at the local (50 m for CAWA, 100 m for OSFL, left panels) and territory scale (250 m, right panels). Values on the X axis are standardized.

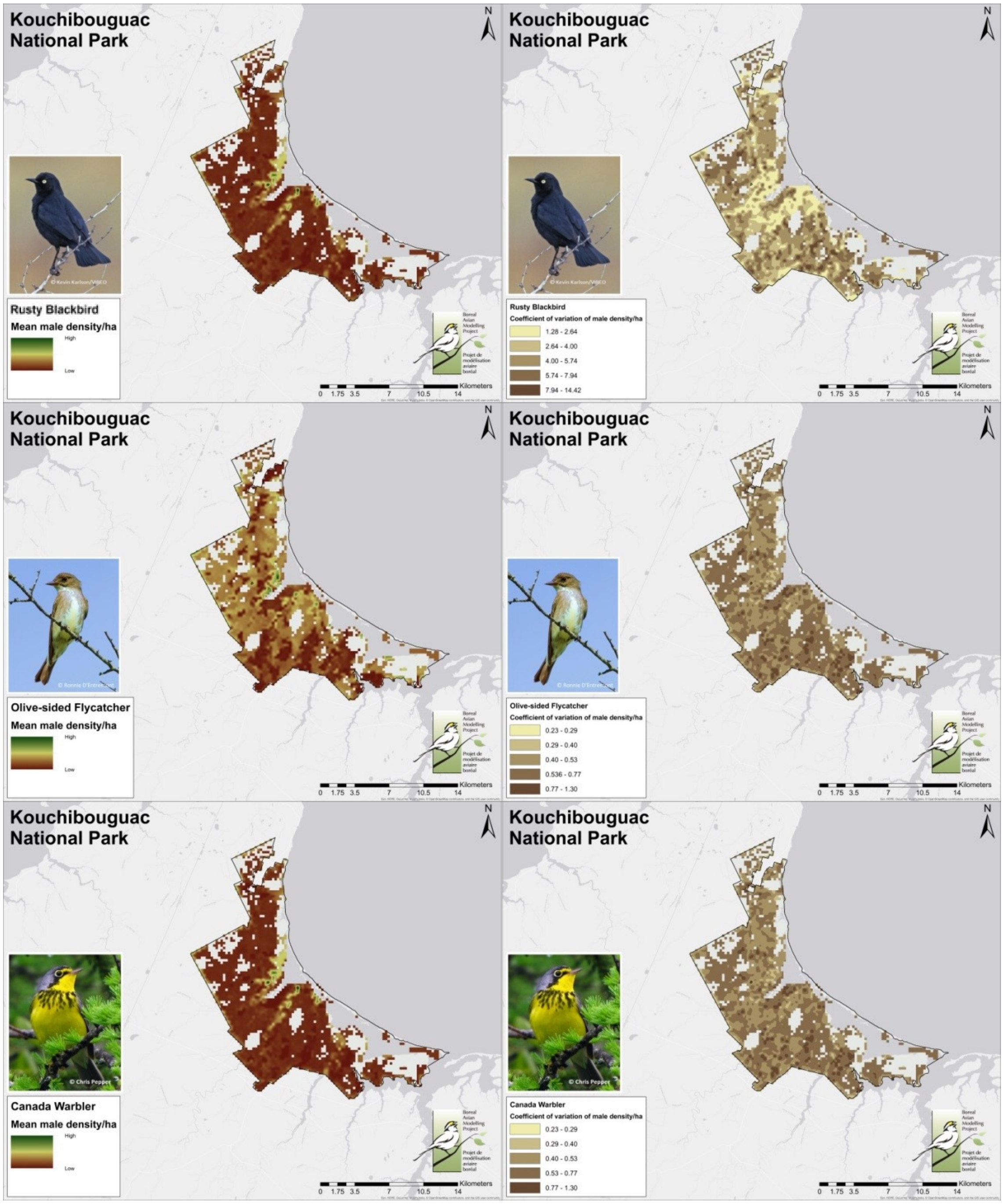

Figure 5.19: Predicted mean density of territorial males/ha (left panels) and coefficient of variation (right panels) for RUBL, OSFL, and CAWA in Kouchibouguac National Park.

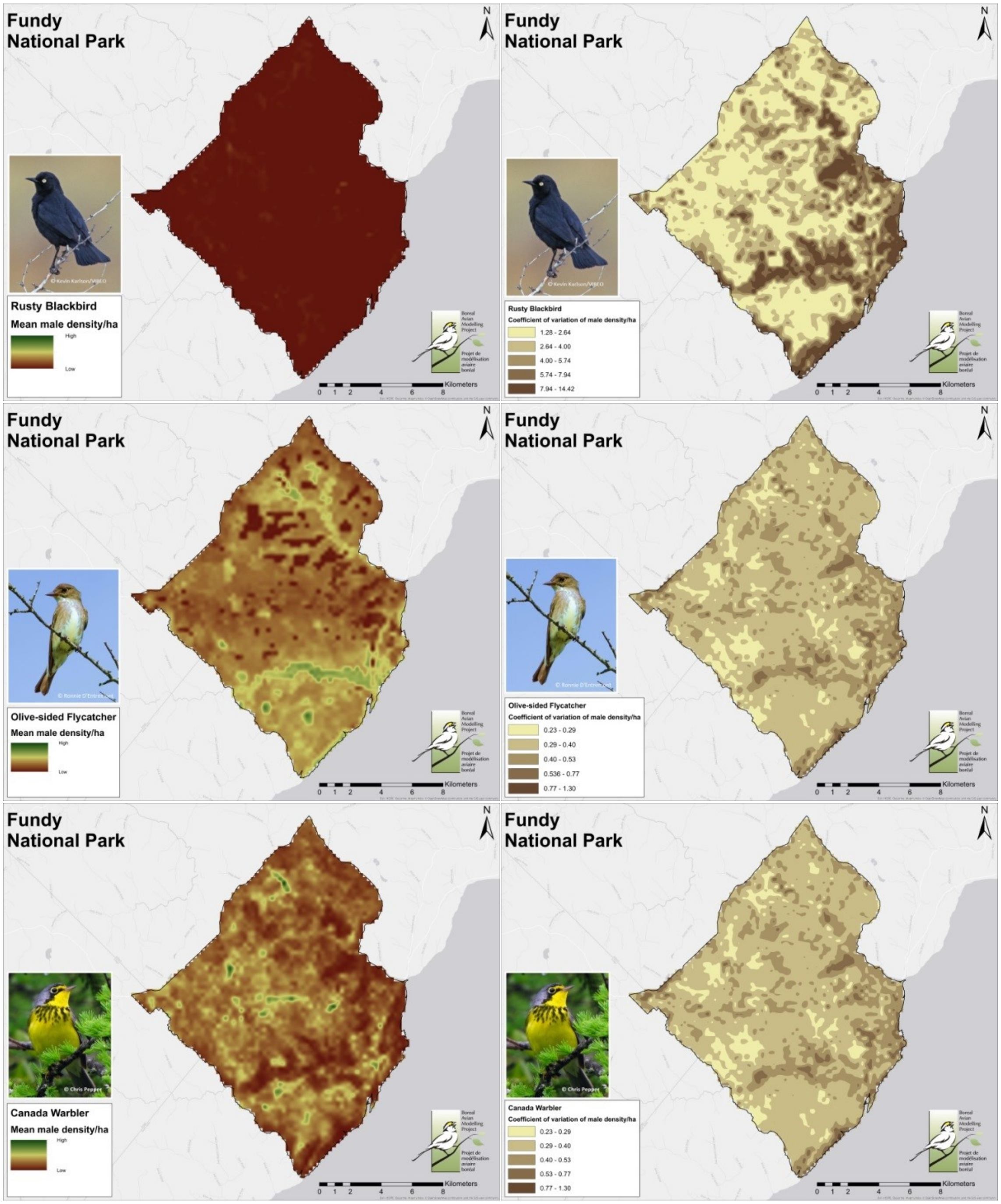

Figure 5.20: Predicted mean density of territorial males/ha (left panels) and coefficient of variation (right panels) for RUBL, OSFL, and CAWA in Fundy National Park.

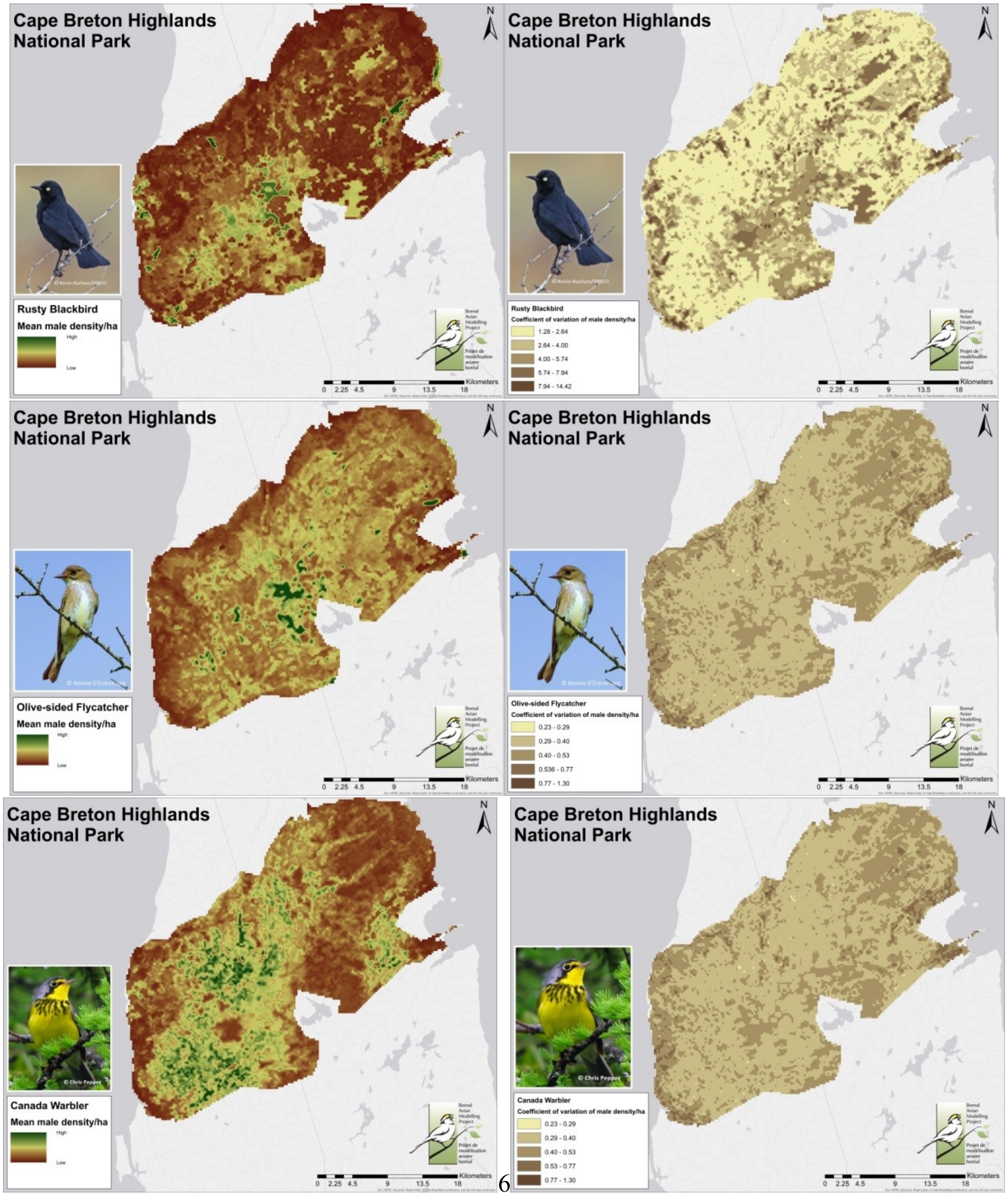

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Figure 5.21: Predicted mean density of territorial males/ha (left panels) and coefficient of variation (right panels) for RUBL, OSFL, and CAWA in Cape Breton Highlands National Park.

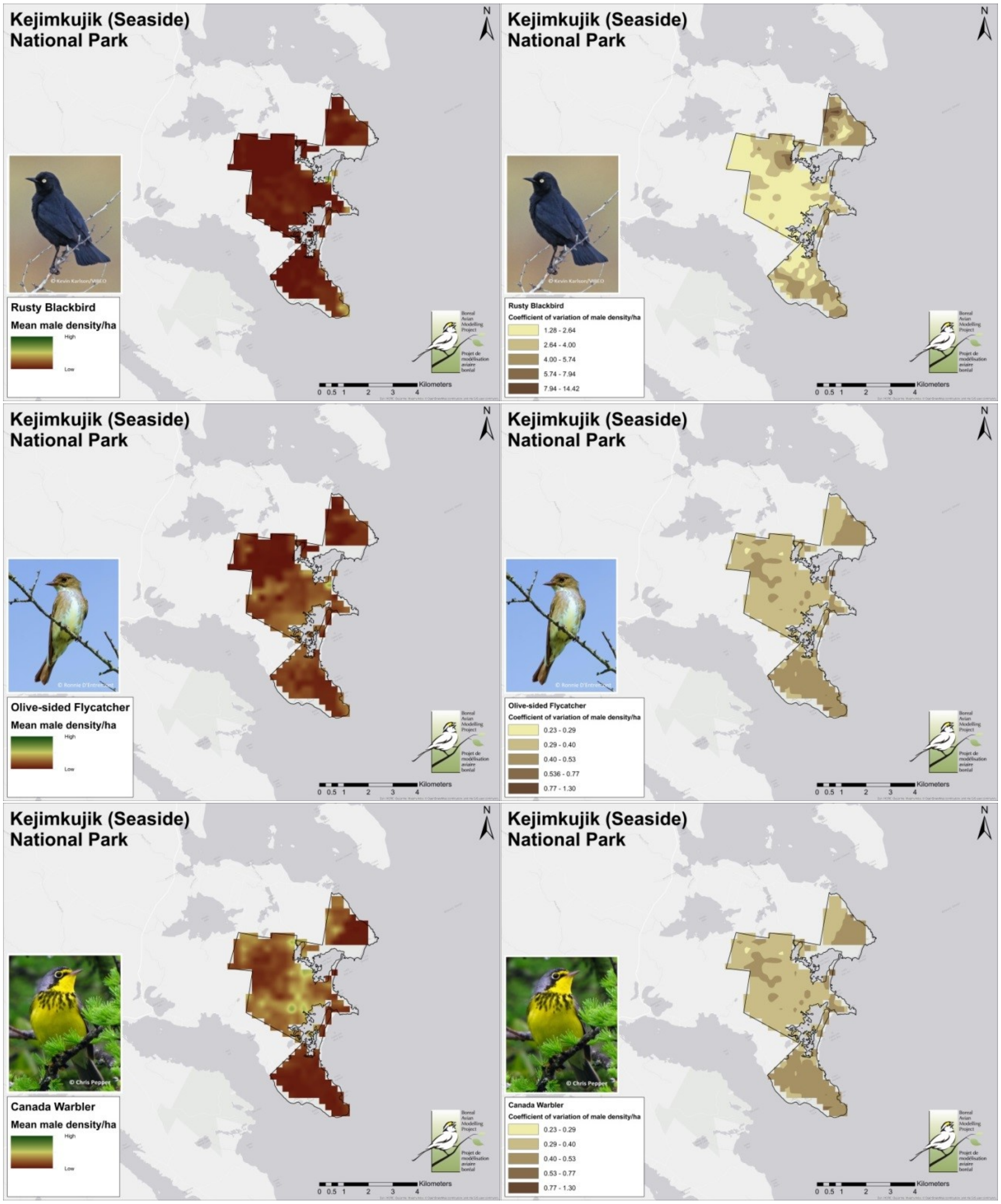

Figure 5.22: Predicted mean density of territorial males/ha (left panels) and coefficient of variation (right panels) for RUBL, OSFL, and CAWA in Kejimkujik Seaside National Park.

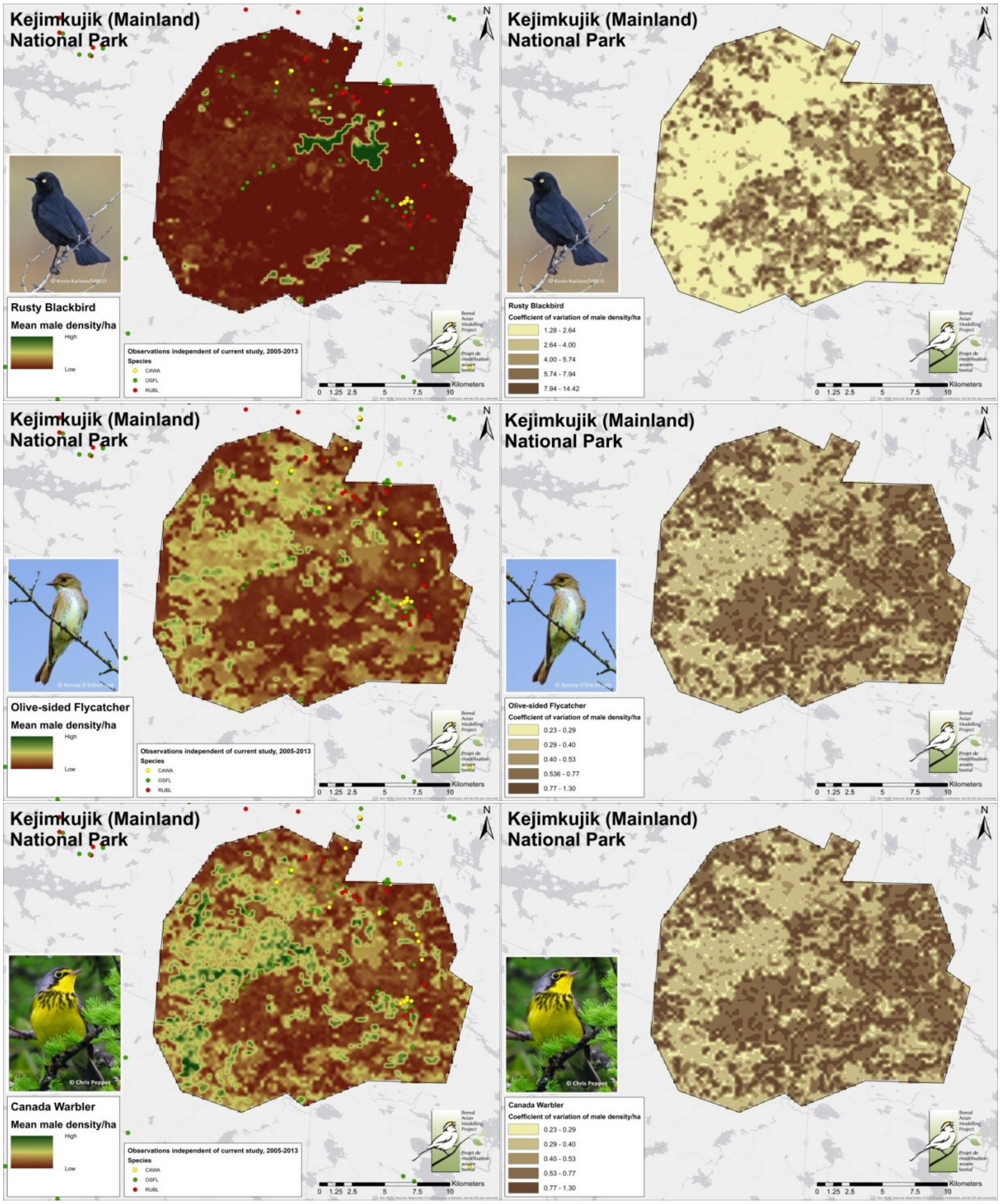

Figure 5.23: Predicted mean density of territorial males/ha (left panels) and coefficient of variation (right panels) for RUBL, OSFL, and CAWA in Kejimkujik Mainland National Park.

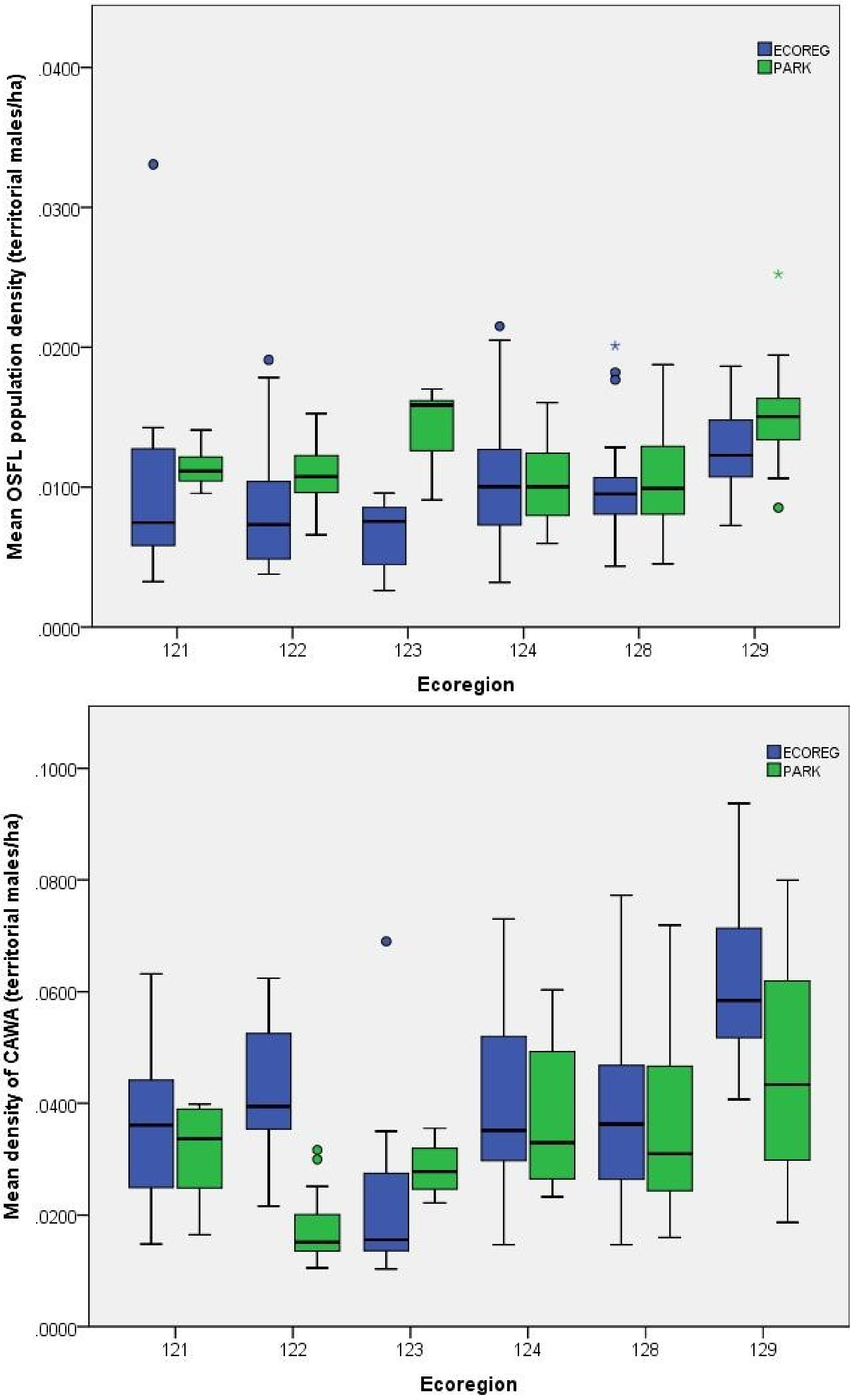

Figure 5.24: Predicted mean density of OSFL and CAWA in national parks and surrounding randomly-selected areas of the same size in six ecoregions in New Brunswick and Nova Scotia.

CHAPTER 6 CONCLUSION

6.1. SPEAKING THE FORESTERS' LANGUAGE

As a discipline, conservation ecology is forced to walk a fine line, straddling the realms of the ideal and the practical. It is almost certainly true that existing protected areas alone will be insufficient to conserve populations of the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in the Maritimes. Although Nova Scotia recently increased its protected areas holdings to 13% of the total landmass (Province of Nova Scotia 2013), it unrealistic to expect that protected areas will undergo significant expansions in the near future. In this context, it is imperative that habitat be protected in managed landscapes, and this thesis endeavoured to provide tools to facilitate that end.

The tools and methods of measurement I used for my fine-scale analyses—FEC, prism plots, canopy cover from densiometer readings, among others—were deliberately chosen as they are tools of the trade in commercial forestry settings (Mitchell et al. n.d.; Korhonen et al. 2006). Vegetation measurements for these landbird species in other jurisdictions have used different methods, such as fixed radius plots (Hunt et al. 2015), and trees were quantified in forestry terms rather than through an understanding of bird biology (e.g. perch trees, Hallworth et al. 2008). These differences in vegetation sampling may limit direct comparability of Nova Scotia habitat results with others across the range. However, when making methods decisions, I had to consider a trade-off: maximizing the generalizability of captured ecological data, or, providing vegetation information that is immediately transferable to a forester's existing skill set. Faced with this difficult choice, and given the imperiled state of these species, I chose the latter.

The habitat associations I measured, containing species-specific vegetation structure and cover knowledge for three landbird SAR, are already being used on the ground by landowners trained during a concurrent public education campaign (Mersey-Tobeatic Research Insitute & Parks Canada 2012). Although woodlot owners and timber cruisers may not have the experience to identify these birds to species, they have the skills to identify key features of their habitat (such as FEC classification, sphagnum mosses, tree species and height, and common fern species).

As discussed in CHAPTER 2, present cutting regulations are likely inadequate to retain wet forest habitat features for these species. These features, including mud puddles, open water, nesting trees, shrubs for nesting and cover, depth to water table across the site, forest composition and height structure, canopy closure, complex ground structure, and particular ecosites, could be removed by harvesting or compromised by the impact of machinery on soils. As anthropogenic effects have a negative impact on population density (CHAPTER 5), where possible, areas large enough to include one or more complete bird territories should be excluded from cutting. Specifically for conservation of the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in managed lands, I propose three management prescriptions in Nova Scotia:

1. During timber cruises and woodlot surveys, managers should be aware of the specific habitat features associated with and ecosites occupied by each species (CHAPTER 2, CHAPTER 3). When encountering these conditions, managers should have the stand surveyed for presence of these species by a wildlife expert before cutting. This is legally required, as harming the nest of species listed in the Species at Risk Act is considered an offence (Government of Canada 2011).

2. Cutting should be limited, or restricted entirely, in ecosites 4, 8, and 12.

3. Buffers around wet forest should be extended to 100 m, at minimum, to avoid destruction of foraging and perching sites within territories.

At the landscape scale, conservation of these species will require the construction of SDMs outside of national parks to direct regional forest management and protected areas planning. This work is already ongoing, as I am collaborating with Shannon Bale (MES candidate, Dalhousie University), BAM, and other scientific contractors to develop landscape-scale SDMs for these species, based on methods developed in this thesis (CHAPTER 4; CHAPTER 5).

As I faced trade-offs between using scientific methods that best reflected the bird's understanding of habitat with practical techniques based on human management tools when measuring fine-scale habitat variables, so did I face similar choices when choosing a spatial dataset for modeling population density. After realizing that SDMs chosen for management scenarios were often misreported or outdated (CHAPTER 4), I developed an easily-interpretable guide for SDM selection targeted specifically at non-academics. Although analyses in Chapter 3 revealed that FRI data can suffer from low accuracy, I used a similar dataset (CASFRI) as a fundamental part of SDMs for these species (CHAPTER 5). Representing tree cover in another way, such as from satellite data or LiDAR, may have increased accuracy of reference data and better captured habitat features relevant to these species (Goetz et al. 2007, 2010; Vogeler et al. 2013). However, FRIs are the standard spatial layers used by governments and foresters when engaging in management planning. Thus, using FRI as a foundational part of my model made it easily portable to other jurisdictions or institutions who may wish to use it for management planning.

Although landscape-level planning and stand-level management prescriptions are important, these alone will not be enough to effectively conserve these SAR. It has been hypothesized for two of these three species that harvested landscapes pose an ecological trap (Powell et al. 2010b; Robertson & Hutto 2013), and this hypothesis needs to be tested in Atlantic Canada. This will require intensive field study of breeding pairs to measure nest success. Furthermore, the present study can make no inferences about the effects of habitat configuration on the occurrence of three focal species. Some of these species may benefit from specific configurations, e.g. large wet areas patches that can sustain clusters of territories, but these hypotheses require testing. This could be studied by monitoring nest success or conceptual modelling (see Villard & Metzger 2014), and should also be tested for varying management intensities. In conjunction with experimental forestry operations to conserve habitat, long-term population monitoring studies or growth models (e.g. Haché et al. 2016) will be essential to facilitate adaptive management for species recovery.

6.2. THE PROBLEM OF HABITAT SATURATION

Although habitat loss is the leading cause of species decline (Kerr & Deguise 2004), this is not true for all species in all locations. Many of the most severe factors implicated in the decline of these SAR cannot be solved by forest management. These include habitat conversion on the wintering grounds (Dahl 1990; Hamel et al. 2008; Greenberg et al. 2011; DeLeon 2012), climate change (Klein et al. 2005; McClure et al. 2012), parasite infections (Barnard et al. 2010), mercury contamination (Edmonds et al. 2010), and predation (Savard et al. 2011). Massive changes in beaver populations since pre-European settlement have affected distribution and availability of wetlands, streams, and wet forests (Naiman et al. 1988), although the impacts for on habitat for these species is unknown.

At least for the Rusty Blackbird, it is thought that habitat is unsaturated in the eastern portion of the breeding range (Harper 2011; Scarl 2013). Given the rapid decline in population, this is likely true for the Olive-sided Flycatcher and Canada Warbler as well. In this case, it is essential to understand habitat quality as well as availability, which can only be done through studies measuring fecundity, nest success, and potentially migratory connectivity (Hobson et al. 2010; Matsuoka et al. 2010a). Such knowledge is urgently needed in particular for these Atlantic populations, which may be vulnerable to rapid range contraction (Greenberg et al. 2011). Large swaths of available but unoccupied habitat may be due to the allee effect, whereby low-density populations are unable to sustain themselves. This has been hypothesized for the Rusty Blackbird, where wintering habitat along the Atlantic Coastal Plain is restricted, and corresponding declines in breeding grounds for this flyway, the Maritime provinces and New England, have been substantial (Greenberg et al. 2011). Furthermore, the effects of habitat fragmentation are not known on these species.

Robust scientific studies can tell us much about the ecology of these species, and the threats facing them, and certainly more research is direly needed. However, as emphasized through this thesis, scientific research ought to be measured with practicality when addressing species at risk. I have endeavoured to bring together the discipline of conservation ecology with traditional forestry practices to develop ecologically-grounded management tools meant for immediate transfer to conservation practitioners. Conserving the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in Atlantic Canada will take dedicated collaboration between scientists, forest managers, government bodies, and the private land-owners. With luck and will, the tools developed in this thesis will be of use to facilitate the recovery of these landbird SAR from the Maritimes.

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