



The influence of land cover and conservation areas on priority bird species in British Columbia, Canada

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Abstract

Conservation areas (CAs) are critical tools in biodiversity conservation, yet their relationship to species of highest conservation need (i.e., species that are rare, range-restricted, sensitive to habitat change, or under significant threat) and the habitats they depend on is understudied. We apply a dynamic occupancy modeling framework to point count data from surveys both in and outside of Canadian Intermountain Joint Venture (CIJV) and Pacific Birds Habitat Joint Venture (PBHJV) CAs in British Columbia (BC), Canada and data from the BC Marsh Monitoring Program from 2021 to 2024, asking whether sites within CAs contain greater proportions of priority habitat compared to sites in adjacent unprotected areas, and thus promote the occupancy of conservation priority birds. We uncovered strong relationships between priority bird occupancy and environmental conditions, but little difference in most priority habitat proportions between sites in CAs and unprotected areas. We only detected a relationship between a site's conservation status and priority bird occupancy in two of ten priority bird groups. Aerial insectivores and species at risk act-listed birds in CIJV showed reduced site extinction probability in CA sites, perhaps due to greater foraging opportunities from the more prevalent wetland habitat. Using insights gained from our models, we make recommendations for conservation practitioners looking to ensure CAs can better benefit bird species with the greatest need. Our results contribute to the broader understanding of the role CAs play in biodiversity conservation, and suggest that they require special attention to effectively preserve priority species.

Keywords Protected areas · Conservation areas · Species at risk · Dynamic occupancy modeling · Migratory bird joint ventures

Zusammenfassung

Der Einfluss von Landnutzung und Schutzgebieten auf prioritäre Vogelarten in British Columbia, Kanada

Schutzgebiete sind entscheidende Instrumente für den Erhalt der biologischen Vielfalt, doch ihr Zusammenhang mit Arten, die den höchsten Schutzbedarf haben (d. h. Arten, die selten sind, ein begrenztes Verbreitungsgebiet haben, empfindlich auf Lebensraumveränderungen reagieren oder erheblich bedroht sind), sowie mit den Lebensräumen, von denen sie abhängig sind, ist bislang nur unzureichend erforscht. Wir wenden ein dynamisches Modellierungsrahmenwerk auf Punktzählungen aus Erfassungen sowohl innerhalb als auch außerhalb der Naturschutzgebiete des Canadian Intermountain Joint Venture (CIJV) und des Pacific Birds Habitat Joint Venture (PBHJV) in British Columbia (BC), Kanada an sowie auf Daten aus dem BC Marsh Monitoring Programm aus den Jahren 2021 bis 2024 und untersuchen, ob Standorte innerhalb der Schutzgebiete einen höheren Anteil an prioritären Lebensräumen aufweisen als angrenzende, ungeschützte Gebieten und somit die Besiedlung

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durch Vögel mit hoher Schutzpriorität fördern. Wir konnten starke Zusammenhänge zwischen der Besiedlung durch prioritäre Vogelarten und den Umweltbedingungen feststellen, jedoch kaum Unterschiede bei den Anteilen prioritärer Lebensräume zwischen Standorten in Schutzgebieten und ungeschützten Gebieten. Bei nur zwei von zehn prioritären Vogelgruppen konnten wir einen Zusammenhang zwischen dem Schutzstatus eines Standorts und der Besiedlung durch prioritäre Vogelarten feststellen. Bei Insektenfressern und Arten des „Species at Risk Act“ zeigte sich eine geringere Aussterbewahrscheinlichkeit innerhalb von Schutzgebieten, was möglicherweise auf bessere Nahrungsmöglichkeiten aufgrund der häufiger vorkommenden Feuchtgebiete zurückzuführen ist. Auf der Grundlage unserer Erkenntnisse geben wir Empfehlungen für Naturschutzfachleute, die sicherstellen mögen, dass Schutzgebiete den Vogelarten mit dem größten Schutzbedarf zugutekommen. Unsere Ergebnisse tragen zu einem umfassenderen Verständnis der Rolle bei, die Schutzgebiete beim Erhalt der biologischen Vielfalt spielen, und legen nahe, dass ihnen besondere Aufmerksamkeit gewidmet werden muss, um prioritäre Arten wirksam zu schützen.

Introduction

Conservation areas (CAs) remain a cornerstone in achieving global biodiversity goals (Pringle 2017; Geldmann et al. 2019), a role underscored by recent international commitments to formally conserve 30% of lands and waters by 2030 ('30-by-30'; CBD 2022). Correspondingly, research into the ability of CAs to achieve biological targets has increased dramatically over the last three decades (Santos Silva et al. 2025). Much of this research seeks to better understand the qualities of CAs that influence use of the area by biological communities, often by comparing their characteristics to measures such as species richness or abundance. In these approaches, it is recognized that CA efficacy is first derived from what exactly is protected, and that activities such as habitat stewardship and restoration may create additional benefit.

However, few studies have focused directly on the use of CAs for priority species (e.g., Santangeli et al. 2023) – those that are rare, range-restricted, sensitive to habitat change, or under significant threat – most instead examining more general groups of species (e.g., Geldmann et al. 2019). Thus, the CA features that generate positive outcomes for priority species are poorly understood. Increasing this understanding is critical, as when examined, measures associated with priority species (i.e., rarefaction-based richness, endemism) indicate that priority species do not always benefit from CAs (Gray et al. 2016; Santangeli et al. 2023).

Further, studies of priority species have generally evaluated biological outcomes through inventories of species richness and diversity, offering little insight into the mechanisms by which CAs may benefit priority species. Understanding these outcomes requires linking priority species' occupancy to the habitats they rely on and assessing how an area's conservation status interacts with those drivers. By modeling species-habitat associations and occupancy dynamics across both CAs and adjacent unprotected sites we can examine how site colonization and extinction process (MacKenzie et al. 2003) relate to habitats and to a site's conservation status, identifying the factors that promote priority species occupancy (e.g. Peach et al. 2019). Studies applying this

approach to broader pools of species have suggested that (1) CAs may provide a 'landing pad' for species undergoing range shifts by preserving habitats they depend on unavailable elsewhere (e.g. Thomas et al. 2012), leading to increased colonization probabilities, and (2) by resisting habitat loss (Li et al. 2024), CAs may decrease site extinction probability by providing the stable resources necessary for population persistence (Peach et al. 2019). These ideas are largely untested for priority species and address important elements of CA design and management for the species which need it most in the face of widespread habitat loss and shifting range dynamics.

Migratory Bird Joint Ventures (JVs) are regional partnerships across North America in which governmental and non-governmental organizations work together to protect bird habitat and regionally prioritized bird species through land securement, restoration, conservation planning, and monitoring. JVs identify priority bird species by combining continental (e.g., NAWMP 2004; Panjabi et al. 2021) and regional assessments of conservation priority, data on population size and trends, and jurisdictional responsibility (e.g., CIJV 2021; PBHJV 2021). Critically, JVs typically designate 'priority habitats' derived from the ecological requirements of their listed priority birds and use these to guide CA designation and management. CAs, as defined by Canadian Intermountain Joint Venture (CIJV) and Pacific Birds Habitat Joint Venture (PBHJV), are any terrestrial or aquatic space secured, restored, or stewarded for the long-term maintenance of natural land cover through formal legal tools, ranging from direct ownership (fee simple) and title-registered covenants to long-term conservation management agreements. Thus, CAs managed by JV partners range from government-designated protected areas (e.g., wildlife management areas, parks) to lands held or managed by non-governmental organizations. JVs' prioritization planning processes offer a significant opportunity to assess whether current conserved lands truly capture the specific habitats that priority species depend on, and thus investigate whether CAs currently may promote the occupancy of priority bird species above the surrounding baseline by examining the processes of site colonization and extinction.

Taking advantage of targeted data collection and priority species lists from two JVs, we assess the amount of priority habitat cover within survey sites in CAs compared to survey sites in adjacent unprotected areas, and the relationships between priority habitats, CAs, and the occupancy of groups of priority birds united by ecological traits or conservation status (e.g. waterfowl, aerial insectivores, species listed in conservation legislation). We compare across CAs managed by partners within the CIJV and PBHJV and adjacent unprotected areas in British Columbia (BC), Canada. First, we predict that survey sites in CAs will contain greater proportions of priority habitat cover, as CAs are generally less vulnerable to habitat loss (Li et al. 2024). If this is the case, we predict that sites within CAs will promote priority species occupancy by either having increased site colonization probabilities or decreased site extinction probabilities. JV priority species – being rarer, in decline, or more specialized to priority habitats – are likely to benefit from greater availability of priority habitats in a region experiencing widespread land conversion through urban sprawl, agriculture, and logging (CIJV 2021; PBHJV 2021), and secondary activities taking place (i.e., habitat restoration and stewardship) may translate to higher quality habitats. On the other hand, if survey sites in CAs and unprotected areas contain similar priority habitat cover, we would expect occupancy patterns to be primarily driven by the distribution of these habitat features across the landscape, regardless of formal conservation status.

By providing a first look at whether CAs capture priority habitats and identifying the mechanisms driving occupancy, we can inform a strategic framework for designing networks that effectively support priority species. Such insights are critical for ensuring that 30-by-30 targets translate into tangible biodiversity recovery.

Methods

Joint venture point counts

The CIJV and PBHJV are broad partnerships aiming to further the conservation of birds in the interior of BC, Canada, and along the Pacific coast of Alaska, Washington, Oregon, and California, USA, and BC, Canada, respectively (CIJV 2021; PBHJV 2021). CIJV, bounded by the Coastal Mountains to the west and the Rocky Mountains to the east, holds a great diversity of habitats due to its significant variation in elevation, including grasslands, shrublands and productive wetlands in valley bottoms and moist coniferous and alpine forests at high elevation (CIJV 2021). Extensive grassland conversion to urban and agricultural land has taken place at lower elevations, particularly in the Okanagan, Thompson, and Columbia Valleys (CIJV 2021). PBHJV's jurisdiction in

BC, Canada, contains highly productive wetland, estuarine, and farmland environments surrounded by humid coastal rainforests at low elevation and cool boreal and alpine forest at high elevations (PBHJV 2021). At low elevations, significant land conversion for urban or agricultural use has taken place, primarily in the Fraser Valley and on the eastern side of Vancouver Island, BC (PBHJV 2021).

From 2021 to 2024, a series of avian point counts (hereafter 'JV point counts') were conducted in the Columbia and Okanagan Valleys (CIJV) and in the Lower Mainland and Vancouver Island (PBHJV), BC, Canada (Rivas 2023). JV point counts were conducted in JV CAs and in adjacent unprotected areas twice annually between mid-May and July, shortly before or after sunrise (Rivas 2023). Detections of all birds by sight, song, or call at an unlimited distance within five minutes were noted, and the first minute of detection and binned distance from the observer (0–50 m, 50–100 m, > 100 m) were recorded. Surveyed CAs were managed by a wide range of partners within the CIJV and PBHJV network, from government bodies to non-profit land trusts, and were impacted by a wide range of historical conservation intervention and human use, from little to no intervention and regular human use (e.g., a publicly accessible provincial park) to active habitat restoration and highly limited access (e.g., a land trust accessible only to the associated land managers). This is representative of the broader CA network in BC, which is influenced by a range of management bodies and operational styles, with varying degrees of human use. As truly random sampling of unprotected areas was not possible in landscapes dominated by private property, three factors guided the selection of survey sites in unprotected areas: 1) surveyor safety, 2) legal accessibility, and 3) geographic proximity to the associated CA. Consistent with these decision factors, surveyed unprotected areas tended to be within 1 km to 3 km, but in rare cases up to 5 km, of the associated CA, and could be ecologically contiguous with that CA or fragmented by interceding disturbed habitat. This resulted in a range of habitats being surveyed in unprotected areas, from areas of greater human disturbance (e.g., dikes, golf courses, peri-urban environments), to areas with fairly intact natural cover, consistent with the heterogeneous landscape of natural and disturbed habitats that exist across BC (CIJV 2021; PBHJV 2021).

British Columbia marsh monitoring program

The BC marsh monitoring program (BCMMP) is a volunteer science program aiming to monitor marsh birds and amphibians at marshes across the province, coordinated jointly by Birds Canada and WildResearch. Each marsh (selected by participants and program staff) is surveyed by a single observer, at times with multiple survey sites within a marsh separated by 250 m (Reurink et al. 2021).

Counts are conducted at each survey site twice annually, in the months of May and June, separated by at least ten days (Bradley et al. 2021). A site may be surveyed either in the morning (from 30 min before to ‘a couple of hours after’ sunrise) or in the evening (from 3 h before sunset until dark). Observers note passive detections of all birds within a 100 m radius from the observation point for five minutes, binning observations into those detected in the first three minutes of listening and those detected in the final two minutes of listening. All birds detected by sight, song, or call are counted, except those which fly over without stopping within the count radius (excluding aerial foragers actively foraging within the survey area). From 2022 onwards, observers additionally note whether they were able to identify at least 90% of detected birds by sight, song, or call to the species level. BCMMP participants select the sites they survey, and tend to select sites in marshes near where they live. As these surveys were not a part of the targeted JV point counts, sites were not selected with position relative to CAs in mind, and thus surveyed marshes could be in publicly accessible CAs or could be on private or public lands without any formal conservation statute.

Bird data

Bird data from JV point counts and the BCMMP were downloaded from NatureCounts (Ducks Unlimited Canada et al. 2025; WildResearch et al. 2025) and collated to make use of all available data and maximize geographic coverage. As these data were collected using similar protocols, they were combined for analysis without transformation or model adjustment. Any counts from the BCMMP where the observer noted they were unable to identify at least 90% of the detected birds were excluded. This generally represented less than 3% of surveys in a given survey year. As these data were not available for surveys in 2021, we assumed a similarly low rate of failed identification in 2021 and retained all 2021 surveys, considering the effect negligible in the outcome of our analyses.

Priority species in CIJV and PBHJV were identified based on continental, national, and provincial assessments of conservation need (e.g. NAWMP 2004; Panjabi et al. 2021) and examinations of the JV’s responsibility for a species global population (i.e., the proportion of the global population that breeds in the respective JV; see Chapters 4–5 of CIJV 2021; PBHJV 2021; see Table S1, S2). Detections of priority species from each monitoring program from 2021 to 2024 were filtered to those within the 5 min survey period and within 100 m of the observer. These detections were then summarized into priority species groups complementing the

operational groupings in CIJV (2021) and PBHJV (2021). In CIJV, observations were grouped into waterfowl, aerial insectivores, birds of prey, forest birds, shorebirds, grassland-open shrubland birds, and wetland birds (Table S1). Birds listed as grassland birds and ‘other birds’ in CIJV (2021) were combined into a group containing detections and non-detections of grassland and open shrubland birds. In PBHJV, observations were combined into groups containing detections and non-detections of waterfowl, aerial insectivores, forest birds, shorebirds, wetland birds, and other birds (Table S2). We opted to not create a group for seabirds listed in PBHJV (2021) as neither the JV point counts nor the BCMMP surveyed nearshore marine habitat. In both JVs, when a species was listed under two groups it was included in both groups’ datasets. Additionally, detections were summarized by endangered status, creating a group containing species listed in the Canadian Species at Risk Act (SARA) for each JV (hereafter SARA birds; Table S1, S2). From these, groups were assessed for data quality and quantity. Groups that were detected in at least two of the four study years and were detected in a minimum of 60 surveys were retained for analysis (see ‘Model fit’ and ‘Model selection’ in electronic supplementary material for reasoning). This led to analysis of five CIJV groups (waterfowl, aerial insectivores, forest birds, grassland-open shrubland birds, SARA birds) ranging in size from six to 21 detected species and five PBHJV groups (waterfowl, aerial insectivores, forest birds, wetland birds, SARA birds) ranging in size from two to 19 detected species. Alongside bird detection data, survey ordinal date and survey time were retained.

Environmental data

Environmental data were summarized around each survey site. Geolocated points representing each survey site were buffered to circular polygons with a radius of 500 m around each point. This radius was selected as it is commonly applied to represent the home range size of most small- to medium-sized birds (Lee et al. 2021). Median elevation at a site was extracted from the GMTED2010 dataset (Danielson and Gesch 2011). Maps of the distribution of each priority habitat derived from a number of satellite data sources were available as polygon datasets from CIJV (2021) and PBHJV (2021). The proportion of area covered by each priority habitat type around each site was calculated by dividing the area of each priority habitat’s polygon contained by the survey site’s buffer by the area of the survey site’s buffer. This proportion was calculated for the following priority habitat types: freshwater wetlands (including small lakes), riparian forest, wetland-associated uplands (CIJV only), grasslands

(CIJV only), estuary (PBHJV only) and agricultural lands (PBHJV only). Additionally, the annual proportion of area covered by built environments was extracted from the ESRI Sentinel-2 Land Cover dataset (Karra et al. 2021). As this data was only available from 2021 to 2023, surveys in 2024 were assigned the proportion of built environment cover from 2023. We opted to include this measure in models as urbanization is a major driver of priority habitat loss in both JVs (CIJV 2021; PBHJV 2021).

For the purposes of this study, we defined CAs as any terrestrial or aquatic space secured, restored, or stewarded for the long-term maintenance of natural land cover through formal legal tools, ranging from direct ownership (fee simple) and title-registered covenants to long-term conservation management agreements following the working definition of CIJV and PBHJV. To ascertain this status, we compared sites to four sources: the Canadian Protected and Conserved Areas Database (Environment and Climate Change Canada 2023), the BC Local and Regional Greenspaces dataset (Government of British Columbia 2024), the BC Non-Governmental Organization Conserved Areas Database (British Columbia NGO Conservation Areas Database Technical Working Group 2025) and communication with the JV Coordinator for CIJV and PBHJV to correct known discrepancies with the true JV CA landbase and these datasets (pers. comm. A. Huang).

To compare environmental conditions between sites in CAs and adjacent unprotected areas, pairwise Wilcoxon ranked sum tests were performed for each environmental variable between sites in CAs and adjacent unprotected areas within each JV. CA sites that could not be linked to CAs in the applied spatial datasets were excluded from this sub-analysis (i.e., those included as CA sites due to discrepancies between the JV CA landbase and the other applied spatial datasets). As the 500 m buffer around CA sites often extended beyond the borders of the associated CA, and the buffer around unprotected sites occasionally extended within the borders of nearby CAs, measures of environmental variables were adjusted only for this sub-analysis to be calculated based on values strictly in the overlap of CA sites' 500 m buffers and the associated CA polygon or the overlap of unprotected sites' 500 m buffers and area not included in any CA polygon. To get a single proportion of built environment cover at a site to use in comparison, the values from 2021 to 2023 were averaged.

Model construction

BCMMP and JV point count data were analysed under a single-species dynamic occupancy modeling framework (MacKenzie et al. 2003). In these models, multiple visits to a site within a period of population closure, where a site's occupancy state is assumed to be fixed, allow for calculation

of a probability of detection for that period, better estimating the unobserved 'true occupancy' (MacKenzie et al. 2003). An initial estimate of site occupancy is made during the first closure period by modeling of initial occupancy probability, and then a site's occupancy state is then allowed to change between closure periods through models of the meta-population processes of site colonization and site extinction (MacKenzie et al. 2009). In our data, we assumed population closure within a breeding season when surveys were conducted and allowed occupancy to change between years at a site. Considering that repeated surveys generally took place within two to four weeks of each other and that birds tend to occupy the same location for long periods of time while breeding, we believe this assumption to be reasonable. Additionally, closure for occupancy modeling only requires that a single individual remains at the site throughout the period of closure, allowing for the absorption of a degree of individual movement or mortality (Mackenzie et al. 2017).

Models were built separately for each species group in each JV and detections of all species in a group were pooled and treated as a 'single-species'. Thus, model results are only produced at the group-level, and not at the species-level. We opted to coerce our multi-species data to a single species model framework as dynamic multi-species occupancy models are still early in their development and limited in the number of species they can incorporate (e.g. Kleiven et al. 2023). Pooling detections in a group to create a 'single species' per group allowed us include data from species with sparse detections and draw broad, group-level insights.

To adjust our occupancy estimates for imperfect detection, we included several covariates in each species group's global detection submodel (Eq. 1). We tested the effect of a linear and quadratic term of survey start time and ordinal date on detection probability. Rather than including observer effect directly in the model (which would lead to failures in convergence due the high numbers of observers), a polynomial spatial term comprised of linear and quadratic terms for latitude and longitude, as well as their interaction, was included in addition to other detection probability covariates to account for spatial autocorrelation in detection probability (Tozer 2016; de Zwaan et al. 2024). Spatial autocorrelation in detection probability is likely a proxy for the effect of the observer as spatially clustered surveys (i.e., multiple points around one marsh or in one CA) were usually conducted by the same observer. All variables were standardized before use in modeling.

$$\begin{aligned}
 \text{detection probability} &\sim \text{intercept} \\
 &+ \text{survey start time} + \text{survey start time}^2 + \text{ordinal date} \\
 &+ \text{ordinal date}^2 + \text{latitude} + \text{longitude} \\
 &+ \text{latitude}^2 + \text{longitude}^2 + \text{latitude} * \text{longitude}
 \end{aligned} \tag{1}$$

We tested the effect of median elevation, all selected land cover types, and conservation status (i.e., the site's position inside or outside of a CA) on initial occupancy, colonization, and extinction probability (Eq. 2). The same spatial term applied to detection probability was also applied to initial occupancy, colonization, and extinction probability models to account for spatial autocorrelation in these parameters. All model parameters were fit with intercepts. As it was core to our research question, we included the conservation status term in all initial occupancy, colonization, and extinction probability models. Multicollinearity was assessed in global models using variance inflation factors, which indicated that variances were highly inflated in our initial occupancy, colonization, and extinction models due to multicollinearity. Pearson correlation coefficients for all environmental covariates are included in electronic supplementary material Table S3. These global models were assessed for goodness-of-fit and then taken through a multi-stage model selection procedure outlined in the electronic supplementary material.

initial occupancy probability OR colonization probability

OR extinction probability ~ *intercept*

+ *conservation status* + *median elevation*

+ *urban environment cover* + *freshwater wetland cover*

+ *riparian forest cover* + *wetland associated upland cover*

(*CIJV only*) + *grassland cover (CIJV only)*

+ *agricultural land cover (PBHJV only)* + *estuary cover*

(*PBHJV only*) + *latitude* + *longitude* + *latitude*²

+ *longitude*² + *latitude* * *longitude*.

(2)

Model inference

The same single-species dynamic occupancy modeling procedure was carried out using Markov-chain Monte Carlo modeling in the STAN environment (STAN Development Team 2025) using the best model from the model selection procedure (see electronic supplementary material) to extract posterior distributions of model parameters. This Bayesian approach was used in addition to the frequentist model selection procedure to improve model fit, as sparse data with correlated predictors led to very imprecise estimates under frequentist models. Bayesian models, being able to borrow information from the prior distribution, improved model estimate precision dramatically. The best model for each species was fit with 4 chains for 5,000 iterations with a burn-in of 2,000 iterations and a thinning-rate of 1. We extracted the 95% credible interval (CI) from 8,000 models draws to gauge support for effect size strength. All MCMC model parameters had Gelman-Rubin statistics equal to

one and effective sample sizes between 5,000 to 12,000 for all parameters, indicating good model convergence and accurate and stable estimates.

Software

All statistical analyses were conducted in *R* version 4.5.2 (R Core Team 2025). Environmental covariates were extracted using *terra* (Hijmans et al. 2024) and land cover statistics were calculated using *landscapemetrics* (Hesselbarth et al. 2023). Land cover comparisons were conducted using *ggpubr* (Kassambara 2023). Occupancy models were fit using *unmarked* (Chandler et al. 2024), goodness-of-fit tests were performed using *AICcmodavg* (Mazerolle 2023) and model selection was carried out using *MuMIn* (Bartoń 2023). Markov chain Monte Carlo iterations were fit with *ubms* (Kellner 2023).

Results

Conservation area characteristics

Surveys took place at 219 sites in CIJV (Fig. 1), with 80 sites in unprotected areas and 139 sites in CAs. Information on CA establishment date was available for 116 CA sites and International Union for Conservation of Nature (IUCN) protected area category (Dudley 2008) was available for 114 CA sites from the Canadian Protected and Conserved Areas Database (Environment and Climate Change Canada 2023). Based on these data, surveyed CAs in CIJV ranged in establishment date from 1923 to 2018. 105 CA sites fell within habitat/species management areas (IUCN category IV protected areas), five fell within national parks (IUCN category III protected areas), and four fell within strict nature reserves (IUCN category Ia protected areas). In PBHJV, surveys took place at 286 sites (Fig. 2), with 116 sites in unprotected areas and 170 sites in CAs. CA establishment date was available for 122 CA sites and IUCN protected area category was available for 109 CA sites (Environment and Climate Change Canada 2023). Surveyed CAs ranged in establishment year from 1978 to 2022. 108 CA sites fell within habitat/species management areas (IUCN category IV protected areas), and one fell within a strict nature reserve (IUCN category Ia protected areas).

Most measured environmental conditions, including the proportion of cover of most priority habitat types, did not differ significantly between survey sites in CAs and survey sites in adjacent unprotected areas. In CIJV, the amount of wetland-associated upland land cover (Wilcoxon $p=0.45$), built environment land cover ($p=0.41$), riparian forest cover ($p=0.27$), and grassland cover ($p=0.51$) and the median elevation ($p=0.27$) did not differ significantly. However,

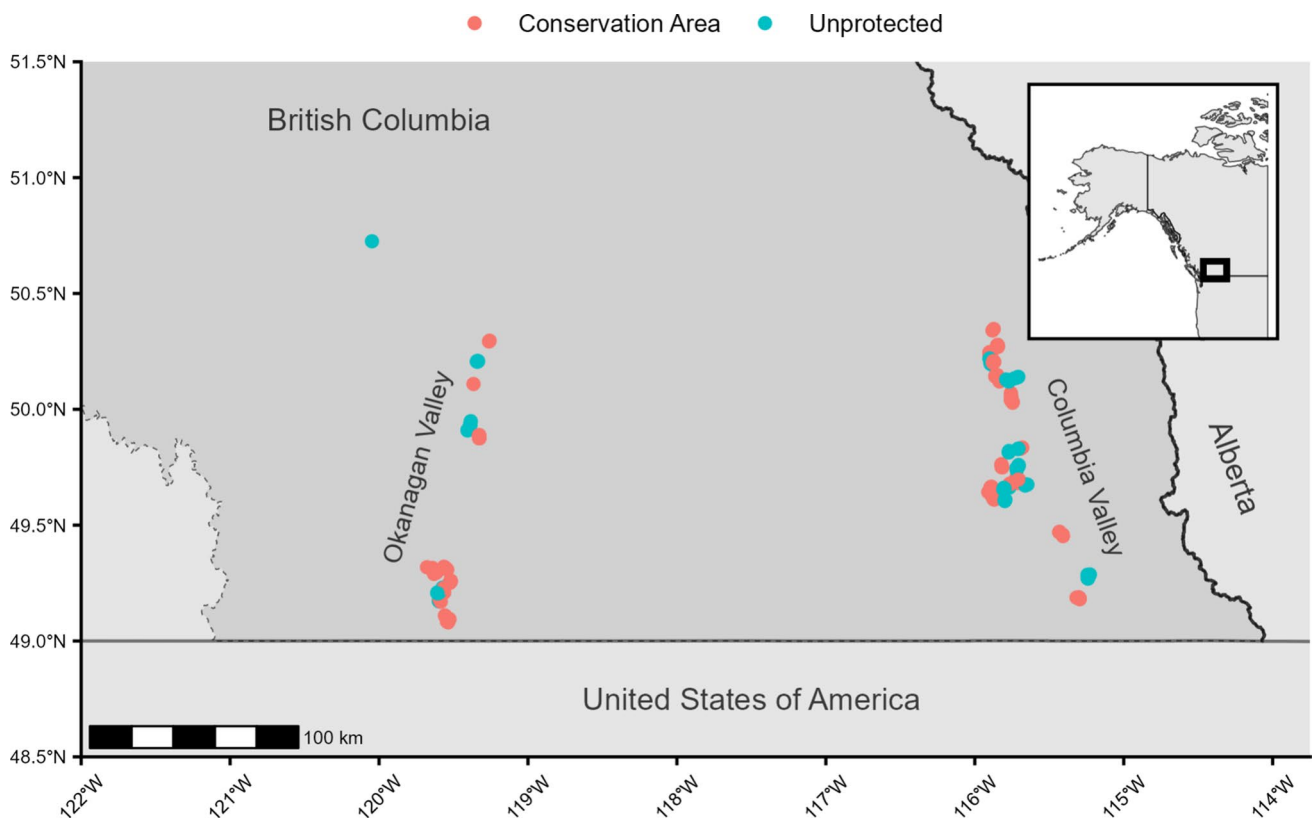


Fig. 1 Bird survey points within the Canadian Intermountain Join Venture (CIJV) in the Columbia and Okanagan Valleys, British Columbia (BC), Canada. The shaded area represents the area of CIJV within BC, Canada

CIJV CA sites had significantly greater freshwater wetland cover than in sites in unprotected areas (p value < 0.01). In PBHJV, the amount of riparian forest ($p = 0.38$), estuary land cover ($p = 0.92$), and agricultural land ($p = 0.43$), and the median elevation ($p = 0.23$) did not differ significantly between sites in CAs and sites in unprotected areas. PBHJV CA sites had freshwater wetland land cover that was significantly greater than in sites in unprotected areas ($p < 0.01$), and had significantly less built land cover than sites in unprotected areas ($p < 0.01$).

Model selection and inference

Several environmental conditions, including the cover of several priority habitat types, had strong effects (i.e., 95% CI of effect size did not include zero) on initial occupancy, colonization, and extinction probabilities among CIJV species groups. Five environmental terms had a strong effects in CIJV species group's initial occupancy probability models: median elevation negatively influenced the initial occupancy probability of aerial insectivores, freshwater wetland cover and built environment cover negatively influenced the initial occupancy probability of grassland-open shrubland birds, wetland associated upland cover positively influenced the

initial occupancy probability of waterfowl, and grassland cover negatively influenced the initial occupancy of waterfowl while positively influencing the initial occupancy probability of grassland-open shrubland birds (Table 1a). The spatial term (Table S4) was never selected among CIJV species groups' initial occupancy models. Two environmental terms had strong effects in CIJV species groups' colonization probability models, with built environment cover decreasing colonization probability for grassland-open shrubland birds, and grassland cover decreasing colonization probability for waterfowl and SARA birds (Table 1b). Two environmental terms had strong effects in CIJV species group's extinction probability models: median elevation decreased extinction probability for grassland-open shrubland birds and wetland associated upland cover had a negative effect on extinction probability for waterfowl (Table 1c). The spatial term was never selected in any CIJV species groups' colonization or extinction probability model (Table S4).

Environmental model terms also had a variety of strong effects in initial occupancy, colonization, and extinction probability models for PBHJV species groups. Five environmental terms had strong effects in PBHJV species groups' initial occupancy probability models (Table 2a). Median elevation had a positive effect on the initial occupancy

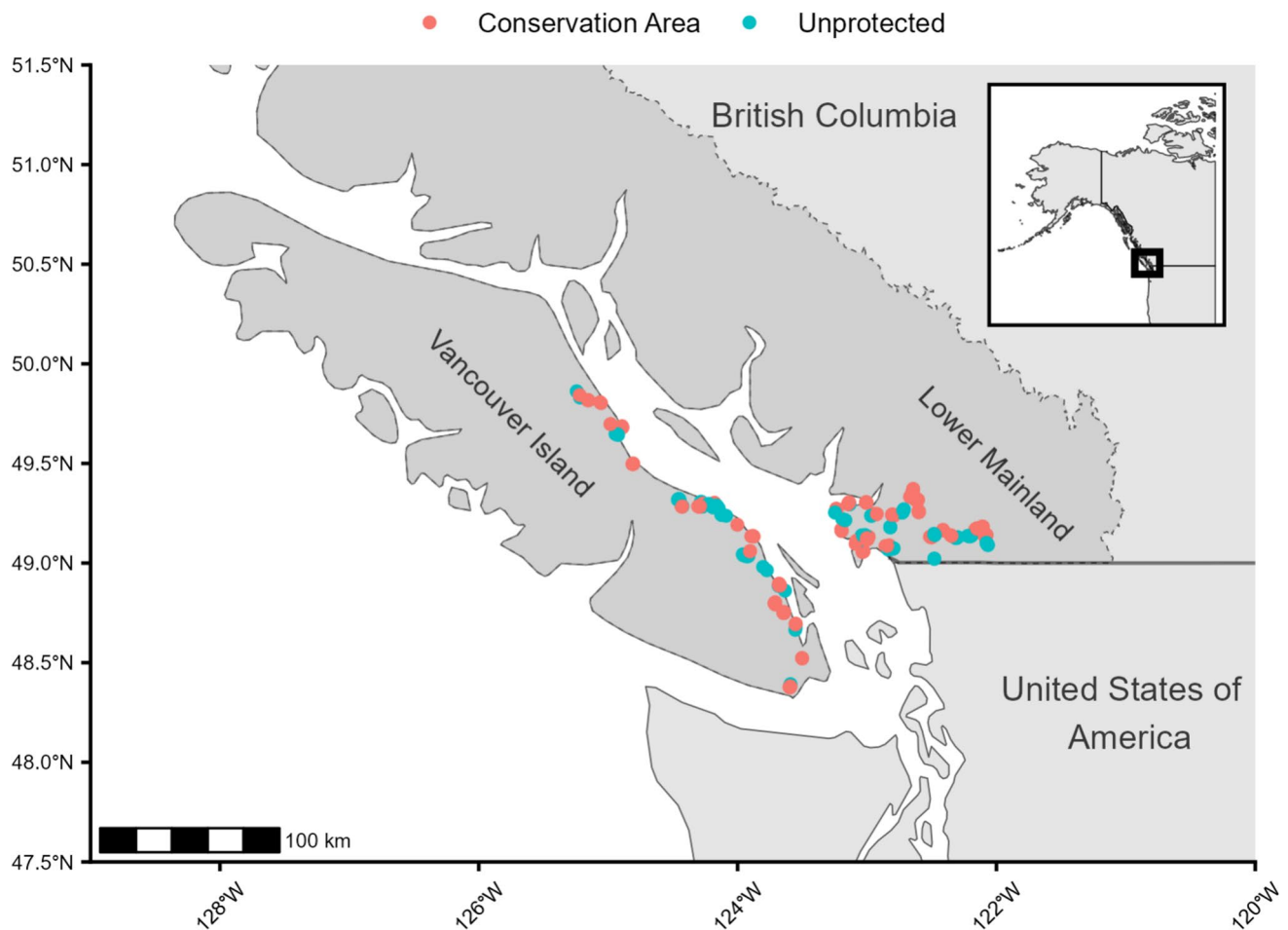


Fig. 2 Bird survey points within the Pacific Birds Habitat Joint Venture (PBHJV) on Vancouver Island and the Lower Mainland, British Columbia (BC), Canada. The shaded area represents the area of PBHJV within BC, Canada, and includes all of Vancouver Island and the Gulf Islands, BC, Canada

probability of forest birds and a negative effect on the initial occupancy probability of aerial insectivores and wetland birds. Freshwater wetland cover had a positive effect on the initial occupancy probability of SARA birds, and riparian forest cover negatively influenced initial occupancy probability for waterfowl while having a positive influence for forest birds. Built environment cover had a negative effect on initial occupancy probability of forest birds and a positive effect on initial occupancy probability for waterfowl, and estuary cover had a positive effect on initial occupancy probability for SARA birds. The spatial term was never selected in the initial occupancy probability models of PBHJV species groups (Table S5). No environmental terms had strong effects in PBHJV species groups' colonization models (Table 2b). Two environmental terms had strong effects in PBHJV species groups' extinction probability models: median elevation had a positive effect on extinction probability for waterfowl while having a negative effect for forest birds, and built environment cover increased the extinction

probability of forest birds (Table 2c). The spatial term had strong effects in the colonization and extinction probability models for aerial insectivores (Table S5).

A site's conservation status rarely had strong effects across priority species groups' initial occupancy, colonization, and extinction probability models. In CIJV, the only significant effects detected were significant negative effects to the extinction probability of aerial insectivores and SARA birds in CA sites compared to unprotected sites (Table 1). In PBHJV, no significant effects of sites' conservation status were detected (Table 2).

Discussion

Our results suggest that local habitat composition and environmental context were stronger predictors of bird occupancy dynamics than conservation status itself at survey

Table 1 Effect sizes (median $\pm$ 95% credible interval) of covariates on initial occupancy (a), colonization (b), extinction probability (c), and detection probability (d) models for Canadian Intermountain Joint Venture priority bird species groups in the Columbia and Okanagan valleys, British Columbia, Canada

Species group	Conservation status	Freshwater wetlands	Riparian forest	Wetland associated upland	Grassland	Built environment	Median elevation
a) Initial occupancy probability							
Waterfowl	-0.21 (-1.04, 0.62)	1.79 (-0.57, 4.48)	0.82 (-2.38, 4.60)	2.15 (0.57, 3.80)*	-5.32 (-9.11, -2.30)*	2.38 (-0.18, 5.47)	-
Aerial insectivores	0.34 (-0.49, 1.21)	-	-	-	-	-	-0.83 (-1.80, -0.29)*
Forest birds	0.00 (-1.07, 1.08)	-	-	-	-	-	-
Grassland-open shrub-land birds	-0.01 (-0.80, 0.77)	-5.73 (-9.98, -2.10)*	-	-	4.77 (1.87, 8.90)*	-4.30 (-7.94, -1.41)*	-
SARA	-0.11 (-1.06, 0.85)	-	-	-	-	-	-
b) Colonization probability							
Waterfowl	0.51 (-0.77, 1.95)	3.01 (-0.48, 7.43)	1.31 (-2.06, 5.33)	-	-4.22 (-8.42, -1.19)*	1.20 (-1.55, 4.33)	-
Aerial insectivores	-0.56 (-1.59, 0.38)	3.43 (-0.10, 7.95)	-	-	-	2.57 (-0.51, 6.56)	-
Forest birds	1.4 (-0.44, 3.90)	-	-	-	-	-	-
Grassland-open shrub-land birds	-0.36 (-1.37, 0.60)	-1.43 (-4.49, 1.19)	-	-	-	-4.46 (-7.85, -1.68)*	-
SARA	-0.76 (-2.08, 0.45)	-	-	-	-2.51 (-5.31, -0.35)*	-	-
c) Extinction probability							
Waterfowl	-0.50 (-2.58, 1.27)	-	-	-4.82 (-10.05, -0.98)*	-	-	-
Aerial insectivores	-1.93 (-3.9, -0.29)*	-	-	0.17 (-2.32, 2.59)	2.62 (-0.23, 5.62)	-0.94 (-4.21, 1.89)	-
Forest birds	-0.88 (-3.07, 0.84)	-	-	-	1.54 (-1.03, 3.80)	-	-
Grassland-open shrub-land birds	-1.51 (-3.67, 0.44)	-	-	-	-	-	-1.72 (-3.04, -0.69)*
SARA	-3.20 (-6.53, -0.66)*	-	-	-	-	-	-
d) Detection Probability							
Waterfowl	-	-	-	-	-0.52 (-0.81, -0.24)*	-	-
Aerial insectivores	-	-	-	-	-	-	-

Table 1 (continued)

Species group	Survey start time	Survey start time ²	Survey ordinal date	Survey ordinal date ²
Forest birds	-0.45 (-0.59, -0.29)*	-	-	-
Grassland-open shrubland birds	1.03 (0.06, 2.02)*	-1.30 (-2.31, -0.31)*	-	-
SARA	-	-	-	-

An asterisk indicates that a term was not only selected, but was a significant effect (i.e., 95% credible interval did not contain zero). A ‘-’ indicates that a term was not selected in that species group best model. SARA refers to priority species which are listed under Canada's Species at Risk Act. Effect sizes for the elements of the spatial term can be found in the electronic supplementary material Table S4

sites across both the CIJV and PBHJV. This finding holds significant strategic insight for those looking to manage and design CAs with priority species in mind.

Environmental features influencing priority bird groups

We found that the priority habitats designated by CIJV and PBHJV (CIJV 2021; PBHJV 2021) often strongly influenced the occupancy of priority species groups. Model outcomes largely aligned with expected bird–habitat relationships used by CIJV and PBHJV to select priority habitats (CIJV 2021; PBHJV 2021). For example, based on literature review and grassland-open shrubland species' natural histories, CIJV (2021) expected grassland land cover to support grassland-open shrubland birds and thus selected grasslands as a priority habitat. In our models, grassland land cover promoted occupancy among grassland-open shrubland birds in CIJV, adding empirical support to this expected relationship. Our results reiterate that these habitats are influential determinants of priority bird occupancy, and remain a useful guiding tool for CA designation in these JVs (Table 1–2, Figs. 3, 4).

Additionally, we document cases in which trade-offs appear to occur, where a habitat that promotes the occupancy of one species group may be negatively associated with that of another group. For example, in CIJV, grassland land cover positively influenced the occupancy of grassland-open shrubland birds but decreased the occupancy of waterfowl and SARA birds (Table 1, Fig. 3). In PBHJV riparian forest cover positively influenced the occupancy of forest birds, but also negatively influenced the occupancy of waterfowl (Table 2, Fig. 4). When conserving a diversity of birds, it is intuitive that conserving a variety of habitats will be necessary, but legacies of historical conservation decisions can bias existing CA networks towards particular types of habitat (e.g. Muise 2025). In CIJV, for example, it appears that most of the land base of the CA network is composed of grasslands (CIJV 2021), and thus new acquisitions may look to conserve habitats that benefit groups which do not benefit from grasslands (i.e., waterfowl, SARA birds). New CA designations must prioritize conserving a suite of habitats so that the benefits are felt by the diversity of priority birds. Conservation organizations should consider these findings when selecting land parcels for acquisition, ensuring multiple priority habitat types are present to support diverse species and minimize trade-offs.

Among our habitat descriptors, median elevation was most frequently significant in our species groups' models, especially in PBHJV. This is unlikely to represent a direct response to elevation itself, but instead to unmodeled correlated biotic and abiotic gradients that vary with elevation (Hof et al. 2012). These shifts are most obviously

climatic (Austin and van Niel 2011; Santillán et al. 2020) but can also include changes to food availability (Remonti et al. 2009) and other biotic interactions (Santillán et al. 2020). The nature of these correlates is likely different in PBHJV and CIJV, where the ranges of median elevations at surveyed sites were from 0 to 242 m and 278.5 m to 1,149.5 m respectively. In PBHJV, it is unlikely that large differences in climatic condition exist across such a small elevational range. Instead, this may better proxy distance to coastal areas of the Salish Sea and the shores of the Fraser River. This is reflected in weak negative correlations between elevation and riparian forest (Pearson's correlation coefficient = -0.25) and elevation and estuarine habitat (-0.30 ; Table S3). Under this assumption, the negative influence of elevation on the occupancy of waterfowl, aerial insectivores, and wetland birds may be associated with the loss of proximal foraging and breeding habitat in productive riparian, estuarine and intertidal zones. The positive influence of elevation on forest bird occupancy may be attributed to a greater predominance of coniferous forest (an important breeding habitat for priority forest birds such as the Chestnut-backed Chickadee [*Poecile rufescens*]) at higher elevations or other associated habitat changes. In CIJV, the much larger range of surveyed elevations likely encompasses substantial climatic variation. Elevation is also moderately negatively correlated with built environment cover (-0.48 ; Table S3), which, together with local factors, may contribute to the inconsistent effects of elevation on aerial insectivores, and grassland-open shrubland birds. While we speculate on the correlates of elevation driving the patterns we observe, we do not test these explicitly and suggest that future research should investigate these important drivers of priority bird occupancy in the region to improve our understand of species distributions' and better guide future CA designation.

Distributions of priority habitats and birds across conservation and unprotected areas

While not representing a complete inventory of priority habitats in CAs and adjacent unprotected areas, our findings provide a first look at patterns in the distribution of priority habitats across sites in CAs and adjacent unprotected areas in CIJV and PBHJV. Our first prediction that the proportion of land cover of priority habitats would be greater in survey sites in CAs than in survey sites in adjacent unprotected areas was not supported, with most priority habitats showing no significant difference between the two site types. We suggest that this lack of differentiation begets the lack of detectable difference in priority bird groups' initial occupancy, extinction, and colonization probabilities between survey sites in CAs and adjacent unprotected areas.

As we have demonstrated, priority bird occupancy responds strongly to the availability of priority habitats. Given this, it appears that sites in CAs and adjacent unprotected areas surveyed in this study are currently offering a mostly homogenous landscape at the scale of the variables we measured, giving priority birds little variability in priority habitat availability to respond to. The only consistently differentiated habitat type between sites in conserved and unprotected areas was freshwater wetlands, with surveyed CAs in CIJV and PBHJV containing significantly higher amounts. This is likely due to the unique interest in waterfowl conservation, largely operationalized through freshwater lake and wetland conservation, of hunters and naturalists alike (Anderson and Padding 2015). Beyond this habitat type, the lack of differentiation suggests that broad land cover changes have not yet taken place in sites in adjacent unprotected areas. This is likely because the divergent effects of conservation intervention versus the mounting development pressures elsewhere have not yet fully manifested.

Conservation planners may take several insights from the few differentiations we did find in occupancy patterns between survey sites in CAs and adjacent unprotected areas. In the few instances where we did detect effects, a site being within a CA promoted occupancy of priority bird groups by increasing the year-to-year persistence of priority birds at CA sites (i.e., by lowering site extinction between years). We documented two priority species groups – aerial insectivores and SARA birds in CIJV – for which sites within CAs showed strongly decreased extinction probability (Table 1c), pointing to a more consistent use of CA sites year-to-year and higher rates of local extinction in unprotected sites for these species groups. The SARA birds in CIJV are largely composed of aerial insectivores, though we note that the effect for the SARA birds group was stronger than that of the aerial insectivore group, indicating that the SARA-listed aerial insectivores and perhaps the other SARA-listed forest and grassland-open shrubland birds appear to derive particular benefit from sites designated as CAs. The fact that the benefits appear to be related in particular to aerial insectivores suggests that CA sites may hold some benefit to the insect prey they depend on, perhaps by containing higher proportions of freshwater wetland habitat, expanding the breeding habitat of highly-nutritious aquatic insect prey (Génier et al. 2021; Berzins et al. 2022). This habitat-retention benefit would mirror that found in other studies, such as Peach et al. (2019), who found that CAs decreased local extinction probabilities for avian communities in eastern North America, with their ability to preserve important habitat touted as the main driver of this. We see this pattern mirrored here, and echo the conclusions of Peach et al. (2019) that CAs' greatest potential to influence priority bird occupancy is in their ability to preserve the habitats they contain at greater rates than surrounding unprotected landscapes. This also suggests

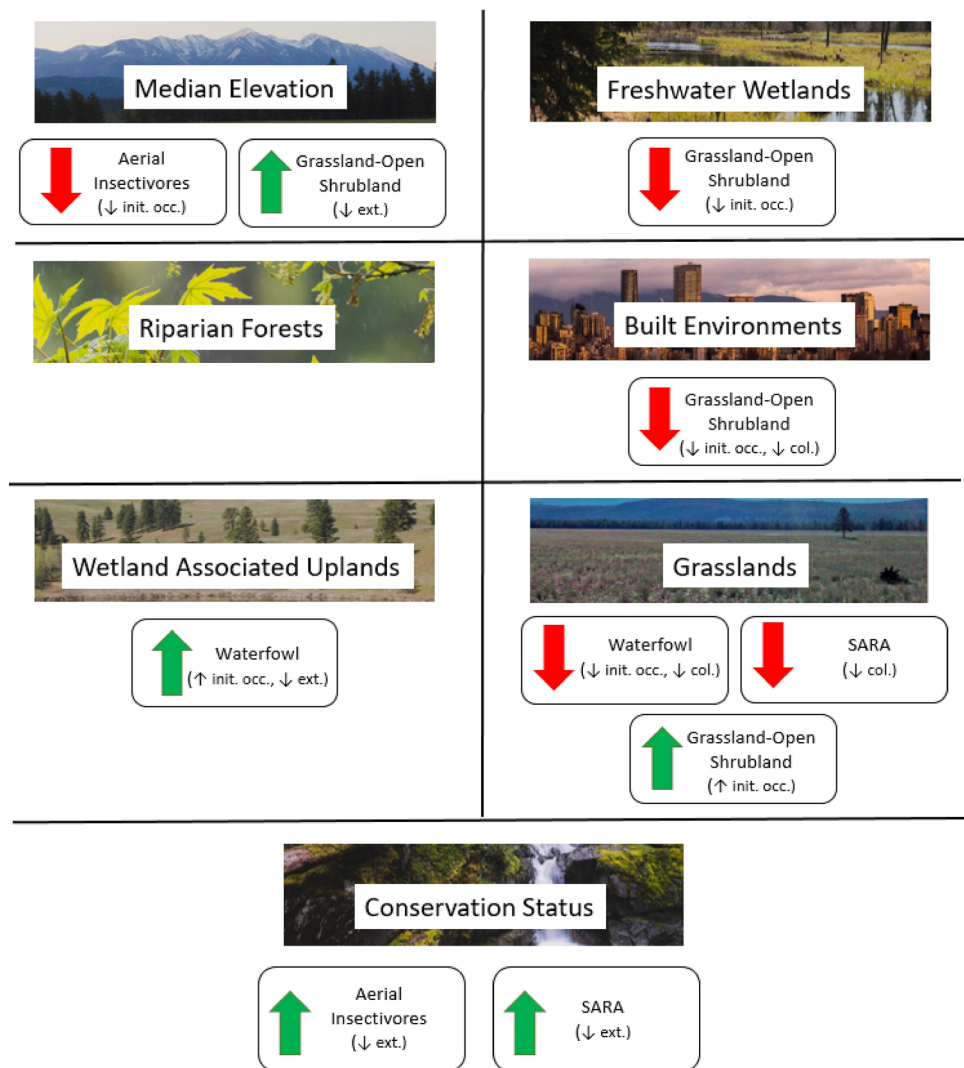
Table 2 Effect sizes (median $\pm$ 95% credible interval) of covariates on initial occupancy (a), colonization (b), extinction (c), and detection probability (d) models for Pacific Bird Habitat Joint Venture prior-

ity bird species groups in the Lower Mainland and Vancouver Island, British Columbia, Canada

Species group	Conservation status	Freshwater wetlands	Riparian forest	Agricultural land	Estuary	Built environment	Median elevation
<i>a) Initial occupancy probability</i>							
Waterfowl	0.31 (-0.60, 1.25)	1.40 (-0.50, 4.13)	-2.48 (-5.17, -0.20)*	1.14 (-0.92, 3.65)	-0.26 (-2.29, 1.90)	2.21 (0.15, 4.85)*	-0.12 (-0.65, 0.43)
Aerial insectivores	0.44 (-0.45, 1.43)	0.29 (-1.71, 3.62)	-0.48 (-2.98, 2.33)	-	-	-	-0.61 (-1.18, -0.09)*
Forest birds	0.29 (-0.57, 1.16)	-1.42 (-2.89, 0.02)	3.67 (0.79, 7.49)*	-	-	-2.56 (-4.34, -0.90)*	1.81 (0.87, 3.26)*
Wetland birds	0.61 (-0.33, 1.62)	-0.09 (-1.73, 1.69)	-	-1.51 (-3.93, 0.60)	-	-	-1.13 (-1.93, -0.49)*
SARA	-0.01 (-0.84, 0.83)	2.86 (0.72, 6.11)*	-	-	2.55 (0.45, 5.38)*	-	-
<i>b) Colonization probability</i>							
Waterfowl	-0.22 (-2.20, 1.37)	-	-0.99 (-4.00, 1.61)	0.99 (-2.19, 3.94)	0.89 (-2.13, 3.86)	0.05 (-2.57, 2.69)	-
Aerial insectivores	-0.88 (-3.51, 1.31)	-0.56 (-4.02, 2.95)	-	-	-	-	-0.97 (-3.53, 0.85)
Forest birds	-0.15 (-1.20, 0.90)	-	1.84 (-1.17, 5.52)	-	-	-	-
Wetland birds	-0.05 (-3.37, 2.35)	-	0.38 (-3.22, 3.96)	-1.65 (-5.84, 1.67)	-	-	-0.63 (-2.31, 0.58)
SARA	-0.26 (-2.26, 1.49)	-	-0.90 (-3.93, 1.91)	0.24 (-2.43, 2.85)	-	0.01 (-2.90, 2.88)	-0.94 (-3.13, 0.21)
<i>c) Extinction Probability</i>							
Waterfowl	-0.49 (-1.97, 0.95)	0.57 (-2.03, 3.18)	-	-0.84 (-3.65, 1.72)	2.01 (-1.60, 6.04)	-0.85 (-3.53, 1.34)	0.75 (0.05, 1.56)*
Aerial Insectivores	-1.76 (-4.74, 0.68)	0.86 (-2.95, 4.32)	-0.75 (-4.89, 2.70)	-0.46 (-4.03, 2.63)	-2.65 (-7.52, 1.04)	0.72 (-2.16, 3.65)	-0.39 (-2.16, 1.24)
Forest Birds	-0.11 (-1.02, 0.83)	-	-	-	-	2.92 (0.86, 5.09)*	-1.38 (-2.48, -0.62)*
Wetland Birds	-0.25 (-2.74, 1.91)	-0.61 (-4.15, 2.31)	-0.35 (-3.66, 2.79)	-	1.30 (-1.67, 4.51)	-0.29 (-3.51, 2.62)	-
SARA	-0.57 (-3.19, 1.58)	-0.68 (-4.44, 2.36)	0.64 (-3.00, 4.28)	-	-	-0.68 (-4.17, 2.37)	-
<i>d) Detection probability</i>							
Waterfowl	-1.06 (-2.41, 0.22)		1.17 (-0.09, 2.50)		-2.08 (-4.41, -0.1)*		1.62 (-0.35, 3.93)
Aerial insectivores	-		-		0.30 (0.11, 0.49)*		-
Forest birds	-0.93 (-1.11, -0.74)*		-		1.90 (-0.07, 4.21)		-1.50 (-3.83, 0.49)
Wetland birds	-		-		-		-
SARA	1.38 (0.23, 2.57)*		-1.28 (-2.50, -0.13)*		-		-
Species group	Survey start time		Survey start time ²		Survey ordinal date		Survey ordinal date ²

An asterisk indicates that a term was not only selected, but was a significant effect (i.e., 95% credible interval did not contain zero). A ‘-’ indicates that a term was not selected in that species group best model. SARA refers to priority species which are listed under Canada’s Species at Risk Act. Effect sizes for the elements of the spatial term can be found in Table S5

Fig. 3 Effect of each environmental variable on occupancy of Canadian Intermountain Joint Venture priority species groups in the Columbia and Okanagan valleys, British Columbia, Canada. Significant effects (i.e. 95% confidence interval does not overlap zero) are noted using directional arrows. Upward-pointing arrows indicate priority bird groups for which occupancy is promoted (i.e. initial occupancy probability [init. occ.] and/or colonization probability [col.] is increased, or extinction probability [ext.] is decreased) and downward-pointing arrows indicate groups for which occupancy is reduced (i.e. init. occ. and/or col. is decreased, or ext. is increased) by increasing values of each environmental variable. SARA refers to priority bird species which are listed under Canada's Species at Risk Act. Photo credit: Kris Cu, Rory Macklin

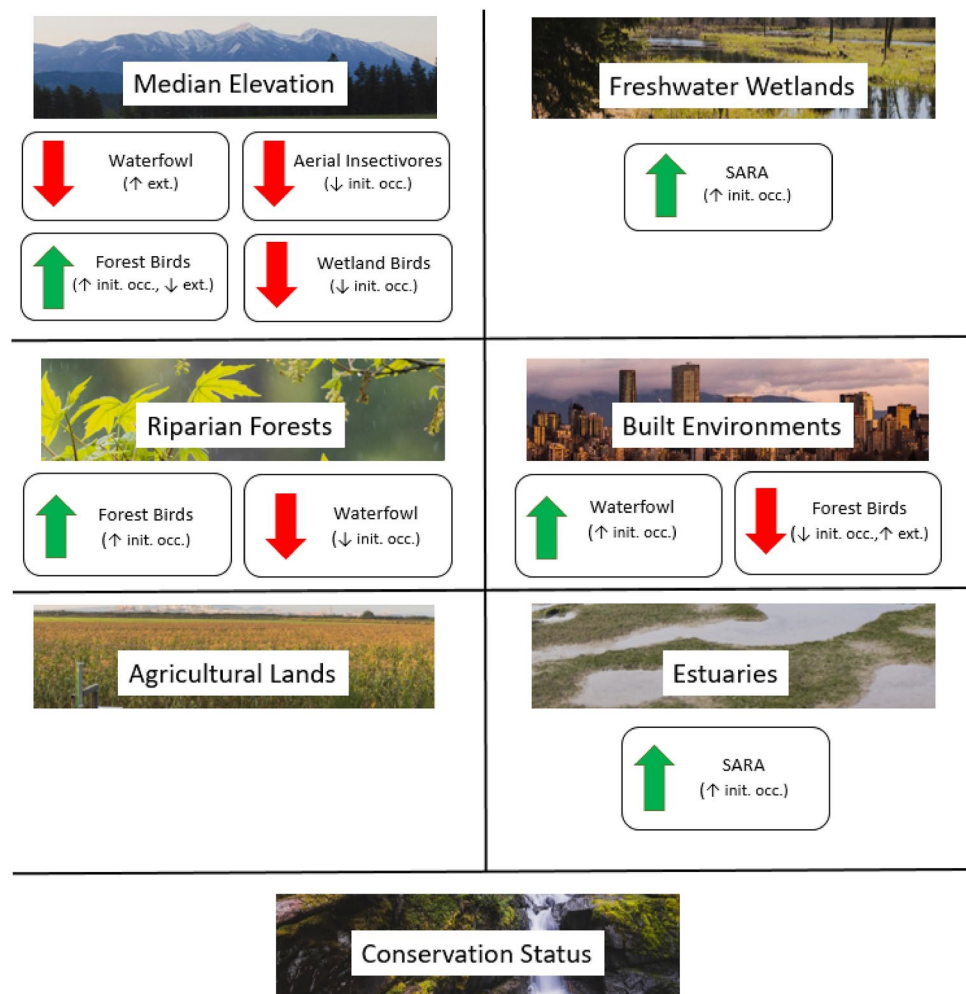


that when CAs contain greater proportions of priority habitats, they can confer significant benefits to priority birds that depend on those habitats.

Thus, conservation planners in the region should look at the existing CA network, future additions to it, and lands outside of the CA network with this in mind. For the existing CA network, its ability to act as bulwarks against habitat loss must be a central consideration in their operation and management. If this is prioritized, these CAs will likely be able to preserve priority habitat at a level above the surrounding landscape which may be more vulnerable to conversion from threats such as urbanization or logging (Li et al. 2024). If so, we may see existing CAs increasing in their value for priority birds as important habitat in unprotected areas become converted to other incompatible land cover types. Secondary activities taking place in CAs, such as restoration

and stewardship, can act to amplify this effect by ensuring retained habitat is of high quality. We additionally note that our results suggest that unprotected areas adjacent to CAs may hold similar levels of priority habitat cover to existing CAs. While this requires further, more systematic evaluation, there is significant opportunity to expand the existing conservation network into these areas, likely facing fewer obstacles to establishing entirely new CAs (Pringle 2017). Critically, these upgraded CAs can act to protect the existing priority habitats adjacent to their current borders against degradation in the future. In areas where the designation of CAs is difficult (e.g., lands legally designated for agriculture), our work suggests that alternative conservation approaches, such as working directly with land owners to promote and conserve biodiversity on their lands (e.g. the Bird-Friendliness Index; Cook 2024), may be important

Fig. 4 Effect of each environmental variable on occupancy of Pacific Bird Habitat Joint Venture priority species groups in the Lower Mainland and Vancouver Island, British Columbia, Canada. Significant effects (i.e. 95% confidence interval does not overlap zero) are noted using directional arrows. Upward-pointing arrows indicate priority bird groups for which occupancy is promoted (i.e. initial occupancy probability [init. occ] and/or colonization probability [col.] is increased, or extinction probability [ext.] is decreased) and downward-pointing arrows indicate groups for which occupancy is reduced (i.e. init. occ. and/or col. is decreased, or ext. is increased) by increasing values of each environmental variable. SARA refers to priority bird species which are listed under Canada's Species at Risk Act. Photo credit: Kris Cu, Rory Macklin, David Bradley



tools to protect the priority habitats and birds those habitats and species that CAs have limited ability to support. Other creative and cost-effective tools like these, jointly with CA designation and management efforts, can bring significant benefit to priority birds across the landscape.

Model assumptions and assessment

In coercing detections of all species in a priority species group to a 'single species', we assume that the drivers of occupancy of the most commonly detected birds in each group are good proxies for the drivers of occupancy of the rarest birds in the groups. Most groups were comprised of a few commonly detected species, and sometimes many other species which were rarely detected (Table S6, S7). In these cases, estimated model parameters are much more strongly informed by the commonly detected birds, and inferences drawn for the entire group are likely biased towards the drivers of occupancy for those more common birds. As groups are designated based on broad ecosystem preference, we believe that the results we draw from the more

common species in the group have at least some applicability to each groups' rarer members. However, the specific habitat requirements of less common species – especially those that are highly specialized for a particular habitat type and quality – should be independently assessed and prioritized in conservation efforts. This could be done by targeted by-species monitoring efforts to increase sample size for rare species to allow modeling, or further development of multi-species dynamic occupancy models (e.g. Kleiven et al. 2023).

We suspect that SARA species groups represent cases where the inferences taken from the common species in those groups may not be representative of the less commonly detected group members. These species are not grouped based on some similarity in ecosystem preference, but instead on endangered status, removing any necessity of overlap in ecological function that would drive similarity in habitat preferences. As a result, the SARA model results, which are driven by the more common aerial insectivores in the groups in both CIJV and PBHJV, are likely not representative of all birds in the group. It is likely these

dominant species drive the surprising result that grasslands appear to negatively impact the occupancy of SARA birds in CIJV (Fig. 3). We wish to be clear that conserving grasslands will not decrease the occupancy the SARA birds that depend on grasslands, such as the poorly detected Bobolink (*Dolichonyx oryzivorus*) and Yellow-breasted Chat (*Icteria virens*). This instance demonstrates that care should be taken in applying the group-level results to all SARA birds, and an examination of the species comprising the majority of detections in these groups should inform further applications.

By the nature of this analysis, we built our models from predictors with some degree of correlation (see Table S3). These correlations led to high variance inflation factors present throughout our models, indicating that coefficient estimates have greater uncertainty due to the inclusion of these correlated predictors than they would in a model without them, occasionally by factors of over 100. This increases our probability of failing to detect relationships between elements of dynamic occupancy and the habitat and conservation status variables we test when they truly exist (type II error; James et al. 2021). These variance inflation factors were computed based on the global model containing all predictors, so it is likely that the final reduced models we make inference on contain smaller sets of predictors which may not hold such strong correlations. We report strong relationships only where 95% credible intervals exclude zero, maintaining a stringent approach to inference to avoid drawing spurious conclusions. This conservative approach may increase the risk of type II errors but ensures that only the most robust and biologically meaningful relationships are emphasized.

Finally, we acknowledge that this study provides an important but spatiotemporally-limited snapshot of priority habitat distributions, bird-habitat associations and occupancy across CAs and adjacent unprotected areas. A more systematic, broader-scale review of the distribution of priority habitats relative to CAs may find patterns at larger scales that differ to those found by our site-level study, and these are critical to investigate in future efforts to designate CAs. At broad spatial scales of habitat selection, it is possible that the priority habitats within CAs aid in pushing unprotected landscapes over thresholds of habitat amount that help maintain populations of priority bird species. This potential benefit is worth further investigation, but is outside of the scope of our study design. Given that our data only captures occupancy dynamics over four breeding seasons, we may fail to detect different or stronger patterns in occupancy, colonization, or extinction probability that may be identified by data covering longer time scales. Additionally, by examining only occupancy we do not test whether CAs may increase the abundance of priority species groups beyond that of adjacent unprotected areas, or whether bird occupancy-habitat associations extend to bird abundance. The decision

to measure occupancy was only made after testing revealed poor performance of abundance models with our data, and in consideration of the difficulties of pooling abundance data for many species with varying degrees of numerical rarity (i.e., highly territorial, individualistic species versus flocking, gregarious species) into species groups. This unmodeled element is an extremely important dimension of conservation management and bird-habitat dynamics and should be investigated further.

Conclusions

Given the international commitment to conserve 30% of lands and water by 2030, rigorously assessing the ability of CAs to support species of highest need is essential to ensure that meeting these numerical targets translates into meaningful biodiversity recovery. Our results demonstrate that the influence of CAs on priority bird occupancy are fundamentally tied to the land cover features they protect. Where CAs align with specific ecological requirements of priority bird groups, they successfully promote occupancy and, crucially, increase their persistence.

While the current conservation network shows a limited ability to increase occupancy for all priority groups simultaneously compared to unprotected areas of similar habitat composition, this underscores the importance of habitat-driven trade-offs in conservation planning. Our findings indicate that a ‘one-size-fits-all’ approach to land conservation may inadvertently overlook certain groups. Furthermore, the comparable occupancy rates observed in surrounding non-conservation habitats suggest that these areas provide vital ecological value, and therefore represent critical opportunities for future long-term securement or management via other conservation mechanisms. Ultimately, investment in CAs that act as bulwarks against habitat loss remains a primary strategy for protecting biodiversity, provided that expansion prioritizes the specific habitat quality and diversity required to support the recovery of the species that need it most.

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Data availability Data from the British Columbia Marsh Monitoring Program and Joint Venture Point Counts are freely available to download from NatureCounts via the digital object identifiers provided in the reference list. Priority habitat shapefiles are available from Pacific Birds Habitat Joint Venture and Canadian Intermountain Joint Venture upon request. Other environmental covariates are accessible from repositories accessible via digital object identifiers provided in the reference list.

Declarations

Conflict of interest The authors declare no competing interests.

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