Effects of anthropogenic disturbance on sensitive wildlife and habitats

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Abstract

The cumulative ecological impacts of broad-scale anthropogenic disturbances, such as forestry or energy development, are a challenge to predict and evaluate. Here, I evaluate the potential of future run-of-river (ROR) hydropower development to impact riparian ecosystems in British Columbia, Canada. I found the projected spatial footprint of ROR in the riparian zone to be 40 times smaller than the footprint of existing disturbance from forestry, roads, and powerlines, but concentrated in watersheds that currently have low levels of disturbance. Habitat degradation for small riparian vertebrates from ROR development was cumulative with substantial existing impacts. I also tested whether harvest data in Species Distribution Models can aid in evaluating species responses to logging at different scales and sensitivity levels using a simulation framework. I found that logging becomes a strong predictor of species distributions at landscape scales, or when the spatial heterogeneity of forestry exceeds that of other variables (e.g. climatic or topographical) in the model.

Keywords: Spatial ecology; forestry; run-of-river hydropower; anthropogenic disturbance; species distribution models; riparian zones

To my grandparents, Albika and Leonid, for founding and binding a family across time and space.

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journey and steadied me when I wavered, and shows me every day that love and forests can go hand in hand.

Table of Contents

List of Tables

List of Figures

List of Acronyms

BC	British Columbia
ROR	Run-of-River
SDM	Species distribution model
WCC	Watershed of conservation concern

Chapter 1.

Executive summary

1.1. Thesis introduction

Disturbances play a key role in shaping species distributions by modifying the biophysical environment and thus altering the quantity and quality of habitat and resources available for wildlife. Ecological disturbances are relatively infrequent events which define the range of ecological variation within a given system (Landres et al. 1999), and can be characterized by their areal extent, magnitude, frequency, predictability, and rotation period (Sousa 1984). Currently, most ecosystems experience the effects of anthropogenic disturbances which exceed the range of natural or historical variability in disturbance regimes, and pose pressing questions about the ability of biodiversity to persist in the disturbed ecosystems (Carlisle et al. 2011).

Anthropogenic disturbances that are patchy and widely distributed across a landscape, such as agriculture, resource extraction, and urban development, create a high potential for cumulative environmental impacts (Leu et al. 2008). Cumulative impacts can refer to the aggregate impacts of a monotypic disturbance, e.g. a residential development with many individual building sites, or the compounding effect of several heterotypic disturbances, e.g. siltation from road building plus runoff from agriculture into streams of the same watershed (Canter and Kamath 1995). Evaluating the cumulative impacts of widely distributed anthropogenic disturbances is difficult because their effects on ecosystem components are often non-additive (synergistic or antagonistic) (Paine et al. 1998, Darling and Côté 2008), manifest rapidly when they cross ecological thresholds (Huggett 2005, Taylor and Krawchuk 2006), or are expressed over large spatial or temporal scales that are difficult to measure.

Predicting the impacts of anthropogenic disturbance on species and ecosystems is necessary at the landscape scale at which important land-use planning and management decision-making are made (Turner 1989). Managers could apply information on the scope of potential future impacts of cumulative anthropogenic disturbance(s) on species and ecosystems within their jurisdictions towards making informed and strategic trade-offs between conservation and development. Currently, most empirical assessments of anthropogenic impacts are conducted at scales much smaller than the landscapes and regions that managers are interested in (Bengtsson et al. 2002). While field studies have identified correlative relationships between many anthropogenic disturbances and wildlife responses at local scales, predicting species responses at landscape and larger scales remains challenging (Hamer and Hill 2000).

In this thesis I used British Columbia (BC), Canada, as a case study for evaluating and predicting the potential impacts of anthropogenic disturbance on sensitive species and their habitats. BC encompasses a large geographic area with high ecological importance both in Canada, providing habitat for 70% of Canada's vertebrate species, and globally, with the world's largest coastal temperate rainforest and extensive interior forests providing habitat for large North American mammals like grizzly bears, cougars, wolves and wolverines (Stevens 1995). BC is also rich in natural resources, with a long history of extensive logging and associated infrastructure development that disturbed many of the region's biodiverse landscapes (Marchak 2011). In the future, energy development is emerging as a major source of anthropogenic disturbance, with the widespread adoption of dispersed energy technologies including small hydropower and wind generation. Such developments make future predictions about potential impacts to species difficult given current approaches and the state of our knowledge.

In Chapter 2, I focused on ecologically sensitive riparian ecosystems, and conducted the first province-wide evaluation of the potential cumulative ecological footprint of future Run-of-River hydropower development relative to the footprint of existing logging and linear infrastructure in BC. I analyzed the spatial relationship between the distribution of existing and potential future anthropogenic disturbance, because while their target resources (high value valley bottom trees, and high-gradient, small rivers) are spatially disjunct in many of the watersheds characteristic of BC's mountainous regions, reliance on shared road and powerline infrastructure, and regional differences in resource distribution challenge this initial assumption. I compared their relative total footprints in riparian zones to quantify the additional habitat degradation that might result from ROR development. I also quantified the marginal riparian habitat degradation from future ROR development for 15 sensitive riparian vertebrates and compared that to the existing habitat degradation from existing anthropogenic drivers (roads, powerlines, forest loss). Finally, I identified watersheds of high conservation concern, where relatively dense riparian disturbance from potential ROR development overlaps with high priority conservation areas for riparian vertebrates, and I evaluated how the spatial definition of these conservation hotspots changed under two opposing conservation approaches, one that prioritizes ROR development that avoids relatively currently intact watersheds (called land sparing) and one that prioritizes ROR development that avoids watersheds with relatively high levels of existing disturbance (called land sharing).

In Chapter 3, I focused on methods for detecting the response of species distributions to anthropogenic disturbance at broad spatial extents. I quantified the accuracy of species distribution models constructed with and without logging intensity as a predictor variable for hypothetical species that ranged from being insensitive to logging (model coefficient = 0) to those with strong negative sensitivity to logging (model coefficient = -1). I further evaluated model accuracy across three nested spatial scales (landscape, regional, and sub-continental). I also quantified how the importance of logging, relative to other environmental predictors, changed as a function of spatial scale, testing the prediction that greater spatial heterogeneity will drive the importance of disturbance for modeled species distributions.

1.2. Thesis conclusion

In this thesis, I used two spatial approaches to evaluate the role of anthropogenic disturbance on species and ecosystems. In Chapter 2, my analysis of the footprint of potential ROR development suggests that ROR may cause habitat degradation that will be concentrated in more intact watersheds and ecoregions, while having a smaller spatial extent than the large existing footprint of anthropogenic disturbance in BC. The increase in degraded habitat within a sub-set of small riparian vertebrate species' core habitat will be marginal, but has the potential to affect low-impact watersheds that may play an important role in maintaining species persistence across BC by providing habitat for source populations and maintaining connectivity. This spatial pattern presents an ironic trade-off between the local and global impacts of climate change (Lovich and Ennen 2011). Globally, ROR development is considered a better energy technology alternative than more traditional sources that have higher greenhouse gas emissions (Jaccard et al. 2011a). On the other hand, climate models and projections predict that climate-sensitive species will shift (and are already shifting) into high-elevation locales to escape climate regimes that are rapidly becoming unsuitable within their current distributions (Parmesan and Yohe 2003, Lenoir et al. 2008). This way, at the scale of BC, ROR development is projected to create anthropogenic habitat disturbance in currently intact, higher-elevation areas that may serve as important climate refugia for sensitive species in the near future. Further studies investigating ROR impacts could project climate-driven species (plant and animal) range shifts and refine my estimates of potential overlap between the footprint of ROR development and species distributions in BC.

Another fruitful avenue for future research is investigating the effects of multiple ROR projects on river networks within and across watersheds. Because of the connected and directional structure of river networks, the effects of ROR development on stream temperature, sediment transport and biotic connectivity could propagate downstream and become amplified in higher order reaches beyond the confluence of two smaller, impacted streams. Future studies could identify aquatic reaches and species at high risk from ROR development by predicting where the greatest downstream cumulative effects of ROR development are likely to overlap with habitat for obligate aquatic species.

In the planning exercise of Chapter 2, my criteria for identifying the watersheds of conservation concern were the conservation priority value for sensitive vertebrates and habitat degradation due to existing and potential disturbance. In reality, all planning exercises that attempt to balance resource development and conservation goals will need to consider the socio-economic costs and benefits of the proposed projects and weigh them against the conservation value they may compromise. My study examined only one suite of biodiversity (small terrestrial vertebrates), and weighed all the species equally, and all biodiversity as a whole as being equal weight to disturbance. Depending on the perceived or established values of stakeholders, certain species, groups of species, or even the same species in different regions may get weighed differently relative to each other and development layers, and so change the distribution of both win-win solutions for conservations and development, and the location of the most high-conflict areas. More complex planning exercises in the future can use existing information about the electrical yields and annual costs of potential ROR projects as additional layers in the prioritization scheme, and add nuance to species weighting schemes.

In chapter 3 we explicitly tested the role of disturbance in predicting species distributions relative to other commonly used and widely accepted climatic and topographic predictors using simulated species data and real environmental layers. We found that a spatial comparison between distribution models that included and excluded a disturbance layer can correctly reflect the underlying species sensitivity to disturbance. At landscape extents, disturbance plays a major role in driving species distributions, and omitting it from SDMs for even moderately sensitive species is likely to contribute to inaccurate predictions, leading to problematic planning and management recommendations. The scales at which specific disturbance regimes will play a major role in a given species distribution model will likely vary, as we found the predictive importance of disturbance as a variable to be proportional to its spatial heterogeneity relative to other environmental factors.

To test the role of disturbance in SDMs, I initially surveyed the literature to identify species with a range of positive and negative responses to anthropogenic disturbance, in whose distributions I expected disturbance to play roles proportional to the species sensitivity. I selected six widely distributed bird species from BC, three with different levels of negative association with logging and three with positive associations with logging. In my final analysis, I did not use the occurrence data I collected for these species due to irreconcilable data quality issues (see below), but in the course of my literature review I found that characterising a species response to disturbance is difficult due to the inconsistency of metrics used. For the studies I included, those with direct or indirect references to a species' response to logging, metrics included: relative abundance, changes in abundance, density and presence (Appendix D). As human disturbance continues to grow, a standardized metric of species sensitivity to disturbance that can be used to rank and prioritize species for protection and mitigation from new or existing disturbances would aid conservation planning efforts.

For chapter 3, the positive spatial correlation between logging and species occurrence data made it impossible for us to use existing, provincial-scale occurrence data to test the role of disturbance in distribution models. All species that we tested showed a positive correlation with logging, which made analysis of the spatial response of species to logging, and the strength of the relationship, inconclusive. This observation highlights the importance of using data that is unbiased in relation to any of the predictors used in species distribution models.

As the planet moves into the Anthropocene, the effects of human activity and development on species and ecosystems are reaching geologic proportions (Barnosky et al. 2012). As ecologists, we are faced with evaluating and predicting those effects at scales that stretch the limits of traditional ecology (Moss 2000). Collecting data, conducting and replicating experiments, and testing predictions at the larger scales of human impact (landscape, regional and continental) is often impossible given the available time and resources we have to answer pressing environmental questions. In this thesis, I explored the utility of publicly available species occurrence data, distribution models, development projections, and spatial overlap analysis to provide broad-scale insight into the potential cumulative effects of anthropogenic disturbances. As we move forward, exploratory studies such as these will become increasingly important for framing the needs of more focused and detailed investigations of how our actions are affecting the biosphere.

Chapter 2.

Cumulative disturbance to riparian zones and small terrestrial vertebrates by future run-of-river hydropower

2.1. Abstract

Compounded anthropogenic disturbances are threatening biodiversity across the globe but new developments are still rarely evaluated for their contribution to cumulative impacts. Many renewable energy technologies (e.g. wind, solar, small hydropower) rely on distributed networks of many sites to meet large-scale energy needs, and present a challenge to conventional environmental assessment. In British Columbia, Canada, a renewable energy industry comprised primarily of many small Run-of-River (ROR) diversion dams is poised to expand in the future, with over 600 pending license applications. Development of new ROR projects will overlap with existing anthropogenic disturbances, including forest habitat degradation due to logging, roads, and powerlines, in a spatially non-random but currently unknown manner. Using a government database of 1,641 potential ROR development locations, we projected a ‘potential ROR footprint’ encompassing riparian areas occupied by the construction of all projects and their associated infrastructure (e.g. roads, powerlines), and created an ‘existing anthropogenic disturbance footprint’ of riparian areas currently affected by logging, roads, and powerlines. We found that presence of potential ROR disturbance was positively correlated with existing disturbance in 3,731 assessed watersheds, but the relationship between watersheds with large potential ROR footprints and watersheds with large existing resource footprints (Spearman’s *rho* = -0.21, $p<0.001$) was negative. This suggests that habitat degradation from ROR development will be additive with existing disturbance, but most extensive in areas that are relatively intact. We also calculated the additional riparian habitat disturbance that future ROR development would create across the modeled distributions of 15 disturbance sensitive and riparian-associated small vertebrates. We found that ROR development will create direct riparian habitat degradation on up to 1% of the species total distribution, in addition to existing riparian habitat degradation (5-25%), and increase relative habitat degradation by an area of up to 8%. Watersheds of conservation concern (WCC), where high vertebrate conservation value overlapped with large potential ROR development, were concentrated in six ecoregions (~73% of WCCs by area), but were distributed across 83% of ecoregions with potential ROR development. These results suggest that strategic planning could be useful as a broad regional tool for renewable energy development, but insufficient to avoid a significant portion of development/conservation conflicts, for which a more local perspective will be needed. However, strategic planning can be helpful to meet broad conservation goals such as avoiding cumulative impacts in highly disturbed watersheds or prioritizing the protection of intact watersheds from new disturbance.

2.2. Introduction

The expanding reach of anthropogenic disturbance across natural ecosystems is the major conservation concern of the 21st century (Kitzes et al. 2008). A component of this disturbance is the area converted for human use (e.g. agriculture) or occupied by human structures (e.g. roads, buildings), often termed the ‘human footprint’ (Burger and Gochfeld 2012). Ecological changes associated with the expanding human footprint, driven primarily by agriculture and resource development (Lambin et al. 2001), have resulted in habitat disturbance, degradation, and fragmentation for species that depend on natural habitats and native ecosystems (Wilcove et al. 1998, Ceballos and Ehrlich 2002). As part of this global trend, the footprint of renewable energy development is increasing rapidly due to social and environmental pressures. Understanding the aggregate impact of widespread renewable energy development challenges traditional site-level environmental impact assessment (Grecian et al. 2010, Masden et al. 2010). Many widely implemented renewable energy technologies (e.g. wind, solar, small hydro (Brower et al. 2014)) each have relatively small infrastructure footprints, but commercial scale development requires many distributed individual sites to meet growing energy demands (Abbasi and Abbasi 2000), with the potential to generate new impacts in intact areas and compound impacts with existing disturbances (Fthenakis and Kim 2009).

In British Columbia (BC), Canada, a growing renewable energy industry focused on small Run-of-River (ROR) hydropower provides a unique case study to forecast cumulative habitat degradation caused by the footprint of renewable energy development (Jaccard et al. 2011b). Run-of-river hydropower (ROR) has been advanced as a key part of meeting an estimated electricity deficit in BC of approximately 20,000 GWh by 2030 (BC Hydro 2013), with nearly 80 projects in operation or construction and over 600 pending water license applications (BC Hydro 2013). Though thousands of ROR hydropower projects have been developed globally, we have a very limited mechanistic understanding of specific ecological impacts and how they scale across landscapes and regions (Anderson et al. 2014).

The terrestrial impacts of ROR development are expected to be concentrated in the riparian zone because ROR dams and their infrastructure (roads, penstocks, head ponds, powerhouses, and powerlines) are closely associated with rivers. The riparian zone, the physical area and biological community adjacent to freshwaters (Naiman and Decamps 1997), regulates fluxes of energy, materials, and biota between terrestrial and freshwater ecosystems (Naiman and Decamps 1997, Décamps et al. 2004, Sweeney et al. 2004). Riparian zones also provide habitat for wildlife (Naiman et al. 1998, Tschaplinski and Pike 2008) including foraging opportunities (O’Connell et al. 1993), denning and nesting sites (Thompson 1988, Pearson and Manuwal 2001), microsites with favourable conditions that serve as shelter and refugia (Wilkins and Peterson 2000, Gallant et al. 2009), and corridors for movement and dispersal (Naiman et al. 1993, Chad-McLeod 2003). The removal of vegetation and build-up of infrastructure required for ROR development can cause habitat degradation for species that depend on the various resources and features of the riparian zone, and disrupt the ecological and biophysical processes of the riparian zone. Anthropogenic activity has already disturbed the majority of riparian ecosystems in British Columbia’s forested lands, as well as the American Pacific Northwest (Kauffman 1987). On BC’s Central Coast, 59% of valley bottom forests have been logged (Pearson 2010), while in the interior dry forests, 20% of forest area has been affected by harvesting since 1950 (Klenner et al. 2008). In northwest inland United States forests, 70% of riparian zones are subject to grazing pressure (Hessburg and Agee 2003). These large-scale disturbances with long histories in the region will likely remain the dominant anthropogenic footprint on the landscape for the foreseeable future. However, evaluating the potential cumulative impacts of further development like ROR hydropower with existing disturbances becomes very important given the large temporal and spatial extent of anthropogenic stress riparian forest ecosystems have already experienced in the region.

Very generally, cumulative impacts can be defined as “effects of an additive, interactive, synergistic or irregular (surprise) nature, caused by individually minor, but collectively significant actions that accumulate over time and space” (Harriman and Noble 2008) in (Duinker et al. 2013), which can affect environmental conditions (Li et al. 1994), population level responses (Gilbert and Chalfoun 2011), and community dynamics (Crain et al. 2008). For the purposes of this study, cumulative impacts were geographically evaluated as the spatial overlap between footprints of different anthropogenic disturbances and valued ecosystem components (Halpern et al. 2008). Due to its broad definition, cumulative impacts can be taken to mean the additive or non-additive effects of all potential anthropogenic activities on a valued ecosystem component, however our study aligns more closely with the above definition, which does not imply comprehensive assessment, but rather additive impacts of some selected set of individually minor disturbances. In BC, the projected increase in development of ROR hydropower presents an opportunity to use spatial accounting as a proxy for more specific ecological impacts, and to predict the cumulative impacts of one growing future and the prevalent existing human disturbance in riparian zones. Given their relatively small size and limited number of physically suitable locations, the aggregate spatial extent of all future ROR projects cannot be larger than or even similar in extent to the large footprint of existing disturbance. However, the spatial distributions of potential ROR project locations relative to existing anthropogenic disturbance poses an interesting question about the potential for compounding impacts of overlapping footprints or dispersed impacts of spatially disparate footprints.

Expectations for the spatial relationship between existing and potential anthropogenic disturbance in the riparian zone are complicated by the interplay of several factors. Fundamentally, the environmental associations of the logging industry and the ROR industry (and thus, their associated linear infrastructure) are spatially disjointed in the context of BC's geography. ROR projects in BC are typically sited in high-gradient streams which are concentrated in mountainous terrain (elevation mean=577m, SD=342), while logging has historically targeted large valuable trees in low elevation forests (e.g. over 90% of valley bottom forests on Vancouver Island have been logged (BC Vegetation Resource Inventory, 2012)). These opposing environmental associations create the expectation that the footprint of future ROR development will potentially generate riparian habitat degradation in currently more intact landscapes. However, several factors qualify this expectation. In many of the intensively logged regions of the province, the high value forests were targeted first and as they were harvested, more recent logging moved to middle and upper slope stands. As well, while the locations for producing electricity through ROR technology most efficiently may be sited in upper slope, high-gradient areas, economic considerations may result in future ROR development clustered near existing roads and powerlines, whose locations are driven by a complex set of historical, engineering, and economic factors. The upwards creep of logging and the economic incentives for building ROR near existing infrastructure may compound habitat degradation in riparian habitats. Knowing whether most ROR impacts will have high spatial overlap with areas of existing disturbance can help guide empirical studies to either focus on ROR impacts in isolation, or in systems with existing impacts.

One way to add focus and detail to studies of cumulative impacts of emerging resource development beyond the strictly spatial overlap of various industries is to predict the simultaneous impacts of habitat degradation on species of particular public or conservation concern (Copeland et al. 2009). While science on the terrestrial impacts of ROR projects has yet to outline specific mechanisms of impact on taxa of concern (Anderson et al. 2014), characterizing the ecological requirements of riparian associated vertebrates across a broad taxonomic range can generate expectations for potential mechanisms through which riparian habitat degradation may impact their persistence. For example, amphibians are known to be sensitive to changes in microclimate due to forest loss (Wahbe et al. 2004), while nesting birds face an increased risk of nesting failure at habitat edges created by fragmentation (Robinson et al. 1995, Lees and Peres

2008), and mammals depend on riparian areas for unique foraging and denning resources (Mccomb et al. 1993, O'Connell et al. 1993). Many small vertebrate species in BC from the three taxa above have relatively small home ranges and are at risk from riparian habitat degradation within their home range, though through different mechanisms. As well, this group of species have very different biogeographic distributions within BC, and because ROR potential is not uniformly distributed across the province, we expect that the overlap between focal riparian species from this group and high ROR potential will be spatially non-random, with a higher potential overlap with species associated with high-gradient, fast-flowing streams. Broader taxonomic expectations, though, are unclear. Quantifying the threat of habitat degradation for species of concern from this emerging industry, in conjunction with existing disturbances in the landscape, can inform strategic planning and encourage proactive mitigation.

Strategic conservation planning, the practice of systematically evaluating priority areas for conservation (Margules 2000, Pressey and Bottrill 2009), is increasingly focused on meeting multi-species conservation goals in the context of the surrounding natural and human landscape (Moilanen et al. 2005). This often requires prioritizing protection of high conservation value areas, such as species rich or ecologically unique hotspots (Myers et al. 2000), and deciding whether to focus protection on hotspots in highly disturbed, versus relatively intact, landscapes (but see Kareiva and Marvier 2003. If ecosystem management and conservation goals aim to avoid impacts in otherwise intact areas, development can be concentrated in areas of existing disturbance, known as the 'land sparing' conservation paradigm (Fischer et al. 2008). Conversely, if the goal is to avoid cumulative or compounding impacts (existing and new), development can be distributed over larger, including intact, areas, known as the 'land sharing' paradigm (Phalan et al. 2011). However, such aims are rarely made explicit in environmental impact assessment or environmental planning, and as the pace of resource extraction and development continues to escalate, there is a need for planning approaches to encompass the potential for aggregate ecological impacts of resource development and consider sparing and sharing alternatives. Comparing potential development scenarios under alternative conservation strategies, such as sparing or sharing, is most effective in the early stages of an industry's growth, when there is still opportunity to identify priority conservation areas, and to make deliberate, strategic decision on criteria for project development.

In this study, we (1) quantified the spatial overlap between the riparian footprint of potential ROR development and that of existing recent anthropogenic disturbance (logging, roads, powerlines) as a proxy for evaluating whether habitat degradation from future ROR development will be compounded or dispersed, (2) estimated the extent of additional riparian habitat degradation expected from the development of potential ROR sites using estimated, mapped distributions of 15 focal riparian species, and (3) used strategic conservation planning tools to predict where watersheds of greatest conflict between biodiversity conservation and ROR development will be located, and whether these areas of conservation concern are concentrated or dispersed across the regions where ROR development potential exists. We compared the distribution of watersheds of high conservation concern (WCC) under two scenarios with contrasting values placed on overlap between new and existing disturbance, one that minimizes (land sharing) and one that maximizes (land sparing) overlap with the footprint of existing anthropogenic disturbance, and compared how avoiding development in the WCCs in each scenario affected the amount of electricity generated across the remaining projects in BC.

2.3. Methods

2.3.1. Riparian zones in BC

British Columbia is a large (950,000 km^2), geographically and ecologically diverse province in Western Canada. Coastal and interior forests cover ~650,000 km^2 of the province, with riparian zones interspersed throughout, where 91% of forested hexagon centroids (see Chapter 3 methods) are within 1km of a stream. BC is home to ~3000 native plant (eFlora BC) and 527 vertebrate species (MOE 2014). The riparian zone is critical habitat for many species across the province (e.g. 29% of vertebrates in the Pacific Coastal Ecoregion are riparian obligates, (Naiman et al. 2000)), and important supplementary habitat for many more (Kauffman 1987, Naiman et al. 1998). To define the terrestrial riparian zone for our analysis, which captures the vegetative community adjacent to the stream (Wagner and Hagan 2000, Lee et al. 2004, Tschaplinski and Pike 2008), we delineated a 100m buffer extending out from the channel centerline. Because streams generally increase in width with order, our buffer captured more aquatic and less terrestrial riparian habitat on higher order streams. We buffered all permanent streams in the BC Watershed Atlas (WSA), which delineates the hydrologic system based on Canada's National Topographic System at the 1/50 000 scale (Appendix A – Table A1). Due to this relatively coarse resolution, some of the smallest first and second order streams may be absent from the WSA, and some minor inaccuracy in the lower order reaches may be present (Moore and Richardson 2003).

2.3.2. Footprint of Potential Run-of-River (ROR) Sites

ROR hydropower is a technology best suited to high-gradient, fast-flowing streams, and can generate electricity from relatively small projects, making it an attractive low-carbon, small-footprint energy option for BC's future. ROR projects divert between 5-90% of available streamflow through a pipe (called a penstock) to turn a power-generating turbine downstream and return the water to the streambed 1-10 km from the diversion point. All ROR projects require access roads, as well as powerlines to connect to the electric grid. To estimate how future ROR development may add to and overlap with the footprint of existing anthropogenic disturbance from logging, roads and powerlines, we used a government (BCHydro) database identifying all suitable locations for ROR project development in BC (N = 7,281), and the electrical and economic attributes associated with the potential project at each location (further detail in Appendix A – Supplementary text). For this study, we used only potential ROR development locations with an estimated per unit energy costs of less than \$500/MWh (N = 1641), a threshold we derived by projecting the official rate increases planned for the next 5 years (BC Hydro 10 year plan, http://www.newsroom.gov.bc.ca/2013/11/10-year-plan.html) 25 years forward, for a rate of ~\$240/MWh in 2040. We then doubled that approximate value to account for the changes in the economics of some of the potential projects, since some projects can become much cheaper and thus more likely to be built if new roads and powerlines are built for nearby projects. We calculated an aggregate potential ROR footprint across BC by combining three components (Figure 2-1 (2)): 1) the combined estimated physical footprint of each project, consisting of the dam (circular buffer around point location using estimated footprint from BCHydro), and the penstock between the dam and the powerhouse (5m buffer), for a total of ~11,000 ha across all 1,641 projects; 2) to capture habitat degradation on the road surface, roadside clearing and immediately adjacent edge, we applied a 100m buffer (Forman et al. 1997) to all road centerlines of the 50,550 km of new roads required to connect new projects to existing roads; 3) we applied a buffer around 7,590 km of new powerlines required to connect new projects to existing transmission corridors to capture the mature forest habitat degradation associated with ongoing vegetation clearing and other effects of the powerline and its right-of-way, with buffers ranging from 10-64m as a function of voltage (Appendix A – Table A1). Both the roads and powerlines necessary for our selected projects were extracted from a partner BC hydro database to the potential ROR locations database, which provided spatially explicit predictions of where future roads and powerlines necessary to support those projects would be located.

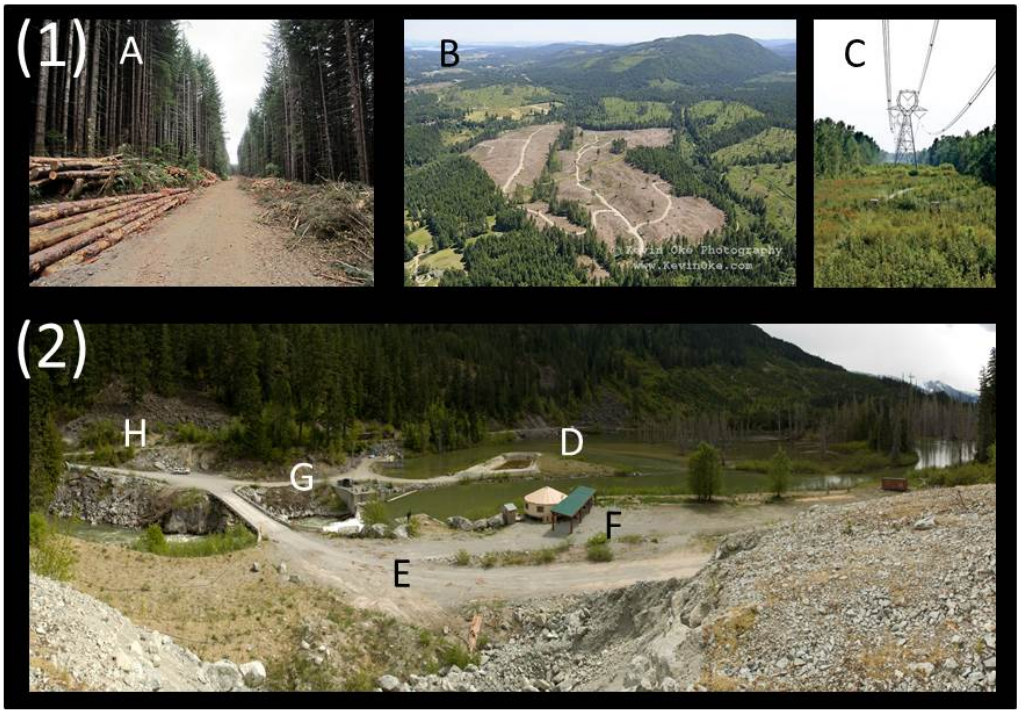


Figure 2-1 The anthropogenic disturbances whose footprints we include in our study. 1) Existing disturbance: (A) logging road, (B) clearcut, and (C) powerline and right of way. 2) Potential ROR disturbance: (D) headpond, (E) access road, (F) construction and maintenance footprint, (G) weir, and (F) an underground penstock. Powerline to ROR project not depicted.

To characterize the spatial relationship between potential future ROR development and the footprint of existing anthropogenic disturbance in BC, we focused on the most spatially extensive types of disturbances associated with resource development in the province: logging and linear infrastructure features (roads and powerlines) (Figure 2-1 (1)). We created an aggregate spatial dataset of anthropogenic forest loss between 1990 and 2012 using two data sources: a spatially explicit dataset of logging in BC, compiled by the BC Forest Practices Board from reports submitted by logging tenure licensees, which had excellent provincial coverage at a 100m resolution, but was missing several areas held by private logging companies. We supplemented this dataset with Hansen *et al*'s (2013) global forest change (from 2000-2012) Landsat-based dataset, at a 30m resolution (Appendix A – Table A1) using ArcGIS (Version 10.1, ESRI, Redlands). We reclassified the combined dataset to a 1km resolution to match the resolution of the climate and topography layers.

Clear-cut logging has affected approximately 30% of BC's forests (Ministry of Forests Mines and Land Operations 2010), and has produced a mosaic of recently clear-cut patches surrounded by a matrix of forest in various stages of seral recovery. Clear-cut patches range in size from one to several km^2, and are connected by an extensive network of paved and unpaved roads which, combined with the transportation and electrical transmission system needed to connect and support BC's human population centres, creates more than 500,000 km of roads (BC Digital Road Atlas (DRA), Appendix A – Table A1) and more than 60,000 km of powerlines in the province. The 22 year time window we used captured logged stands in the initiation and establishment stages of succession (Song 2002), which represent degraded habitat for the disturbance sensitive, late-seral associated species we focus on in this study. The logging dataset included clear-cut logging, bark beetle kill salvage logging, and permanent forest conversion to agricultural or urban uses, and excluded forest loss due to fire unless it burned over harvested areas. The impacts associated with logging roads are in some ways even more extensive than the cutblocks themselves (Forman 1988), so to account for the habitat degradation from the road surface, roadside clearing, and immediate edge effects, we applied a buffer to all existing road centerlines (from the BC Digital Road Atlas), with a 100m buffer for paved roads (Forman et al. 1997), a 50m buffer for unpaved roads, and a 1m buffer for roads classified as 'overgrown', 'decommissioned', or ‘unknown’ (DRA, Appendix A – Table A1). Similarly, we applied the same powerline buffers as outlined above for potential ROR sites and applied them to all existing powerlines in BC. We combined the forest loss, buffered road, and buffered powerline datasets to create a shapefile representing the aggregate footprint of the majority of existing anthropogenic disturbance.

2.3.3. Overlap between existing and potential anthropogenic disturbance and riparian zones

To evaluate whether future ROR project development will be spatially cumulative or disparate from the existing anthropogenic footprint, we calculated their respective footprints in riparian zones across BC. We intersected the aggregate footprint of potential ROR development with all riparian zones to create a provincial overlap dataset, consisting of ~19,900 individual polygons, and did the same for the footprint of all existing anthropogenic disturbance (~400,000 individual overlap polygons). To estimate the relative extent of the habitat degradation caused by existing and potential disturbance, we compared the sum area of their respective riparian zone overlap. In addition, to evaluate our assumption that the disturbance of potential ROR projects will be concentrated in the riparian zone, we quantified what proportion of the aggregate footprint of potential ROR development is encompassed within the 100m riparian zone (as described above). It’s important to note that while we quantified riparian impact based solely on the spatial footprint of infrastructure corridors and recent logging within the riparian zone we defined, the riparian zone is also closely linked with upslope processes, and its suitability as habitat for species can be compromised by disturbance outside the riparian zone proper such as sedimentation from logging and roads, debris flows and mudslides. Riparian logging more than 22 years ago also negatively affects habitat suitability for disturbance-sensitive species, but since some of the stark structural differences characteristic of early seral stands begin to attenuate after the establishment stage (Song 2002), we did not consider older logging in our study.

We used two spatial scales, local and regional (*sensu* Pearson and Dawson 2003), to conduct our analysis. We quantified the spatial extent of the overlap between disturbance and riparian zones within units defined by the standard hydrologic subdivisions (Assessment Watersheds) of BC, which are relevant to field studies and monitoring programs (Carver and Gray 2010), and range in area from 1 km^2 to 1000 km^2 (hereafter ‘watersheds’). We calculated two metrics within each watershed: 1) the presence of any amount of overlap between the riparian zone and one of, or both, disturbance types in the watershed, and 2) the total area of overlap between each disturbance regime (existing and potential) divided by the total area of the riparian zone in the watershed. We also calculated the presence and extent of spatial overlap between riparian zones and disturbances at a regional scale, which is more relevant for management and strategic planning. As units, we used the BC Ecoregion Classification (Banner et al. 1996), defined by major physiographic and minor macroclimatic differences (Demarchi 2011), ranging from 2000 km^2 to 90000 km^2 (depicted in Appendix A – Figure A1). We scored all ecoregions with any existing disturbance overlap within their boundaries as having existing riparian anthropogenic disturbance, and tabulated the number of ecoregions containing any watersheds with potential overlap between riparian zones and ROR development. We also calculated the total area of potential riparian habitat degradation in each ecoregion and noted where the 20% of ecoregions with the greatest proportion of potential riparian habitat degradation are located as a moderately inclusive criteria for focusing on the regions facing the greatest potential cumulative impacts.

To test whether potential ROR development is correlated with areas of existing logging and linear infrastructure we used two complementary approaches: 1) we calculated what percentage of watersheds with potential ROR development sites have any existing disturbance present, and tested this value against a null expectation generated from the percentage of already disturbed watersheds province-wide (80%), and 2) within watersheds with potential ROR development sites, we used the Spearman rank correlation to test whether the proportion of potential riparian habitat degradation from the footprint of ROR development is related (positively or negatively) to the proportion of existing riparian habitat degradation. As an additional measure, we also calculated the percentage of watersheds where the riparian footprint of potential ROR development exceeds that from existing disturbance.

2.3.4. Overlap between potential ROR footprint and riparian species distributions

We evaluated how much the riparian footprint of potential ROR development adds to existing riparian habitat degradation within the modeled distributions of 15 focal riparian species in BC that are sensitive to forest disturbance. We limited our analysis to small terrestrial vertebrate species (under 20 kg) that either occur exclusively in, or are closely associated with, the riparian zone (Appendix B – Table B1). We selected the species for our study from an initial list of >230 Pacific Northwest terrestrial vertebrates identified as riparian associates by O'Connell et al (1993). We excluded fish because terrestrial riparian habitat degradation does not impose a direct footprint on aquatic habitat, though it often degrades fish habitat suitability by affecting trophic pathways (Wallace et al. 1997, Kawaguchi and Nakano 2001) and instream conditions (Carlisle et al. 2011), predicting which was beyond the scope of this study. From O'Connell's list, we eliminated all species not present in BC, all species larger than 20kg because they tend to be far-ranging mammals that are better able to mitigate the effects of riparian habitat degradation caused by potential ROR development through movement; all bats and reptiles; and all species associated strictly with the lentic environment which do not use terrestrial riparian habitat because the mechanism of impact from riparian forest habitat degradation will be very different from terrestrial species, and so incomparable. We also restricted our analysis to animals, though riparian plants are potentially even more vulnerable to anthropogenic disturbance due to their lack of mobility and more restricted habitat requirements.

We used data from the primary literature documenting changes in abundance, density, occurrence, or frequency as a result of logging or other forest-related anthropogenic disturbance (such road and powerline construction or agricultural land conversion) to assess sensitivity to forest loss and degradation (Appendix B – Table B2). We made the assumption that species that respond negatively to anthropogenic forest loss or degradation will also respond negatively to degradation caused by the infrastructure associated with ROR hydropower construction. We binned species into coarse sensitivity categories since the metrics of response to forest disturbance varied across the studies we reviewed. For species where all studies identified a response in the same direction, we assigned 'strong' disturbance sensitivity, either positive or negative; where the majority of studies identified a response in a given direction we assigned a ‘moderate’ sensitivity; we classified a lack of a measurable response, or mixed and contradictory responses across studies, as ‘neutral’ (Appendix B – Table B2). Four of the 23 species we evaluated had neutral or mixed responses to forest loss or degradation, and four had a positive association with forest disturbance. We quantified the area of overlap between the footprint of existing anthropogenic disturbance and the 100m riparian zone within the distributions of the remaining 15 species that had negative responses to forest disturbance, and then repeated the same calculations for overlap between the footprint of potential ROR development and the riparian zone. Across species, we compared both the absolute differences in the expected area of riparian habitat degraded by ROR disturbance, and the relative increase in degraded habitat, which we calculated as the area of additional degraded habitat as a percentage of existing degraded habitat.

Species distributions were modeled at the scale of BC using an ensemble of species distribution modeling (SDM) methods (‘Biomod2’ in R, (Georges and Thuiller 2012)). SDMs are correlative models that use the relationships between environmental characteristics and species localities to predict species relative occurrence probabilities spatially (Elith and Leathwick 2009, Franklin 2013). We used 12 climatic and topographic variables (Appendix A – Table A1) standardized to a BC wide extent at a 1km grid resolution, and species locality data (1990 onwards) from published sources, including the Breeding Bird Atlas, Breeding Bird Survey, Global Biodiversity Information Facility, and the BC Conservation Data Center (Appendix A – Table A1). We generated pseudo-absences (PAs) for the model in a spatially random manner across cells that did not have species presence points, creating a number of PAs equal to the number of species presence localities for that species (Liu et al. 2005).

Our ensemble predictions incorporated the outputs of up to 10 different models (GLM, Maximum Entropy, and others, see Appendix A – Table A2), representing a range of spatial predictive methods, to balance the strengths and weakness of individual models. We weighted the outputs for all models for every species by the True Skill Statistic (TSS), a metric that evaluates model accuracy by testing whether outputs created from 80% of the data points predict the location of the remaining 20%, on a scale of -1 to 1 (Allouche et al. 2006). We found that TSS values for models used in ensemble SDMs in this study ranged from 0 to 1 with a mean of 0.7, a value well above the TSS>0.3 rule of thumb for model accuracy (Araújo et al. 2011). The weighted outputs of all the modeling methods for a single species were combined in a committee averaging approach to create both a continuous (range 0-1000) and a binary (presence, absence) ensemble distribution output (Thuiller et al. 2009). To quantify the area of overlap between species distributions and existing and future disturbance we used the binary outputs, derived by classifying the continuous output into presence cells (habitat suitability score ≥500) and absence cells (habitat suitability score < 500) based on the recommended prevalence threshold (Allouche et al. 2006) More conservative thresholds would have provided a more restricted distribution and thus, greater proportional overlap with low-elevation disturbance patterns; conversely, a more inclusive threshold would generate a larger presence distribution and include more overlap between species and upslope disturbances.

2.3.5. Watersheds of conservation concern under sparing and sharing planning scenarios

As an exercise in strategic conservation planning we identified, within all watersheds where ROR disturbance is possible, watersheds of conservation concern (WCC), which have simultaneously high conservation value for the 15 disturbance-sensitive riparian vertebrates used above and the potential for a relatively large proportion of riparian habitat to be degraded by future ROR development. While these species represent a very small fraction of BC’s floral and faunal diversity, they encompass a range of life history types, ecologies, and biogeographic distributions that make them a useful proxy for biodiversity values in the province. Multi-species approaches such as these are more data intensive and create more complex outputs than widely used singles-species approaches like flagship or umbrella species, but are more likely to represent a broader suite of organisms across complex landscapes (Simberloff 1998, Roberge and Angelstam 2004). We characterized the distribution of WCCs across ecoregions to highlight areas of high potential conflict between ROR development and biodiversity, and to quantify tradeoffs between scenarios that prioritize land sharing vs land sparing. We identified WCCs under two watershed ranking scenarios: (1) where WCCs were identified as watersheds with relatively high potential ROR development and relatively high levels of existing anthropogenic disturbance (sparing), and (2) where WCCs were identified as watersheds with relatively high potential ROR development and relatively low levels of existing anthropogenic disturbance (sharing).

To identify WCCs, we used the systematic conservation planning software Zonation version 4 (Lehtomäki and Moilanen 2013, Moilanen et al. 2014). Zonation can handle continuous probabilistic or binary presence/absence species distribution inputs, large raster datasets, and can balance species distributions, connectivity, costs, and needs of alternative land uses in the same ranking scenario (Moilanen et al., 2009, 2011). A distinguishing benefit of Zonation is that it provides a ranked cell output, instead of a fixed set of solutions for a given suite of conservation planning parameters like the commonly used Marxan (Possingham et al. 2002). Zonation's output allows for identifying a range of conservation priority areas, depending on the available resources (such as land for protected areas or funding) from the same ranking scenario (Moilanen et al. 2012). For the purpose of this study, we used the additive-benefit function of Zonation with an exponent $z = 0.25$. Under this function, conservation value is additive across biodiversity features (species distributions), and cells are ranked in relation to their sum species richness, though in a non-linear way, whereby as the area of a species range that is ranked increases, its weight in the biodiversity score of subsequent cells decreases (Arponen et al. 2005). The Zonation algorithm can be characterized as the maximal retention of weighted, range size-normalized species richness, while accounting for complementarity in species spatial representation. The Zonation output is a ranking of all raster cells ranging from highest conservation priority (1) to least conservation priority (0).

We used modeled species presence distributions and level of riparian habitat degradation (existing and potential) aggregated to watersheds as criteria for the Zonation ranking algorithm, and designated the top 10% of ranked watersheds in the deterministic Zonation solution as WCCs. We ran two ranking scenarios (sparing vs. sharing) using both the existing and potential disturbance layers and species distributions layers created in the previous analysis. Two of the layers remained the same in both scenarios: the layer quantifying the level of potential riparian habitat degradation per watershed from ROR development (weight =1), and a layer of species richness calculated by summing the binary SDM outputs of 15 species (generated in the previous section, weight = 1). We used either the layer quantifying riparian habitat degradation from existing anthropogenic disturbance (weight = 1) or its inverse to create the alternative scenarios, and ranked all watersheds based on these 3 criteria under the assumption that all 1641 ROR projects are developed.

Because we simultaneously maximized biodiversity value for our focal species and level of potential ROR disturbance, the highest ranked watersheds should be interpreted as having the highest potential for conflict between (a subset) of biodiversity and future ROR development, rather than best conservation solutions. Under the sharing scenario, the WCCs were watersheds with relatively high levels of existing anthropogenic disturbance, watersheds that are not meeting land sharing goals, but rather compounding impact in already disturbed watersheds. Under the sparing scenario, we used the inverse of the proportion of riparian habitat degradation due to existing anthropogenic disturbance to identify watersheds of concern which currently have relatively low levels of existing anthropogenic disturbance i.e. these watersheds were not meeting land sparing goals, and instead are locations where ROR development is introducing disturbance in currently intact watersheds. We ran both ranking analyses using only watersheds with potential ROR development footprint (n = 3,731 watersheds). We identified regions with highest potential for conservation concern development by calculating the percentage WCCs (by area) within each ecoregion in each scenario and identifying ecoregions with high proportion of WCCs (Appendix A – Table A3). We then asked how the distributions of WCCs across ecoregions shift depending on the conservation approach (sparing or sharing) by subtracting the sparing model WCCs from the sharing model WCCs and quantifying the differences. We also quantified the potential decreases in energy production that might be expected if projects in WCCs were excluded in future development, and whether those decreases differed between sparing and sharing scenarios.

2.4. Results

2.4.1. Overlap between existing and potential anthropogenic disturbance and riparian zones

In British Columbia, the potential habitat degradation from the ROR hydropower industry is concentrated in the ecotone between terrestrial and aquatic environments, such that 40% of the entire footprint of potential ROR development intersects with riparian zones. Our regional aggregations showed that watersheds with potential ROR riparian disturbance were present in 30 of the 42 terrestrial ecoregions in BC, but the sum area of direct riparian habitat degradation from the aggregate footprint of potential ROR development was 40 times smaller than the footprint of existing anthropogenic disturbance in riparian zones in the last 22 years (39,000 ha and 1.6M ha, respectively). In the ecoregions where the proportion of riparian habitat degradation from potential ROR development is highest (n=6, 20%), overlap with the ROR footprint occupies 2.0% to 4.3% of total riparian zone (Table 1); these ecoregions were located on Vancouver Island, the southern and northern Coast Mountains, and the southern Rockies. Except for the Vancouver Island ecoregions, which have relatively high existing riparian habitat degradation from logging and linear infrastructure, the mountainous mainland regions with high ROR footprint potential have relatively low current riparian habitat degradation (Figure 2-2). At the watershed scale, we found that twenty percent of all watersheds in BC (3,731 of 19,469) have potential for some overlap between riparian zones and the footprint of potential ROR development. Within these watersheds, the presence of ROR potential was positively correlated with the presence of existing anthropogenic disturbance: ninety percent (363 out of 3,731) of watersheds already have existing anthropogenic disturbance in the riparian zone (logging, roads, powerlines), so most of the footprint of potential ROR development would affect riparian zones in already disturbed watersheds. This positive correlation is significantly higher than would be expected if the potential ROR footprint was distributed randomly across BC, where only 80% of watersheds have existing disturbance from the sources we considered (Chi-square = 155.4, $p<0.001$). In contrast, the proportion of riparian habitat degraded due to the footprint of potential ROR development per watershed was negatively correlated with the proportion of existing riparian habitat degradation across watersheds (Spearman's rho= -0.21, p<0.001). We also found that in 24% of the watersheds with potential for ROR development, there was greater habitat degradation from potential ROR development than that from existing disturbance. Watersheds where potential ROR development footprint exceeded that of existing anthropogenic disturbance were distributed throughout BC, but had higher average elevations than the watersheds where the proportion of habitat currently degraded exceeded the potential degradation from ROR. Specifically, the mean elevation in the watersheds was 1310m and 1104m, respectively, with 75% of former watersheds having a mean elevation > 100m, and only 58% of latter watersheds having a mean elevation>1000m.

Table 2-1 Focal sensitive riparian-associated species.

Common name	Scientific name	Sensitivity to mature forest disturbance	Class	n
Western Redback Salamander	*Plethodon vehiculum*	Moderately negative	Amphibia	86
Coastal Tailed Frog	*Ascaphus truei*	Strongly negative	Amphibia	1873
Red-Legged Frog	*Rana aurora*	Strongly negative	Amphibia	390
American Dipper	*Cinclus mexicanus*	Moderately negative	Aves	8
Pacific-slope Flycatcher	*Empidonax difficilis*	Moderately negative	Aves	848
Harlequin Duck	*Histrionicus histrionicus*	Moderately negative	Aves	210
Common Merganser	*Mergus merganser*	Moderately negative	Aves	683
Marbled Murrelet	*Brachyramphus marmoratus*	Strongly negative	Aves	289
Mink	*Neovison vison*	Moderately negative	Mammalia	77
Shrew Mole	*Neurotrichus gibbsii*	Moderately negative	Mammalia	20
Pacific Water Shrew	*Sorex bendirii*	Moderately negative	Mammalia	26
Water Shrew	*Sorex palustris*	Moderately negative	Mammalia	18
Canadian River Otter	*Lontra canadensis*	Moderately negative	Mammalia	60
American Marten	*Martes americana*	Strongly negative	Mammalia	921
Fisher	*Martes pennanti*	Strongly negative	Mammalia	247

2.4.2. Overlap between potential ROR footprint and riparian species' distributions

Based on our literature review, we identified 15 small vertebrate species that were closely associated with riparian zones and had empirically documented negative responses to anthropogenic forest degradation (Table 3-1). We calculated that absolute riparian habitat degradation from existing anthropogenic disturbance was between 5% and 26% across their modelled range in BC. In contrast, only 0.06% to 0.9% of these species' modeled riparian habitat will be degraded from overlap with the potential ROR footprint (Figure 2-3). The footprint of potential ROR development will add the greatest relative amount of riparian habitat degradation relative to the existing anthropogenic footprint for Tailed Frogs (*Ascapus truei*, an 8% increase), Harlequin Ducks (*Histrionicus histrionicus*, 5% increase), and Marbled Murrelets (*Brachyramphus marmoratus*, 4% increase), and create the smallest relative amount of additional riparian habitat disturbance for Fishers (*Martes pennanti*, a 0.4% increase), Mink (*Neovison vison*, 1.8% increase), and Marten (*Martes americanus*, 1.9% increase).

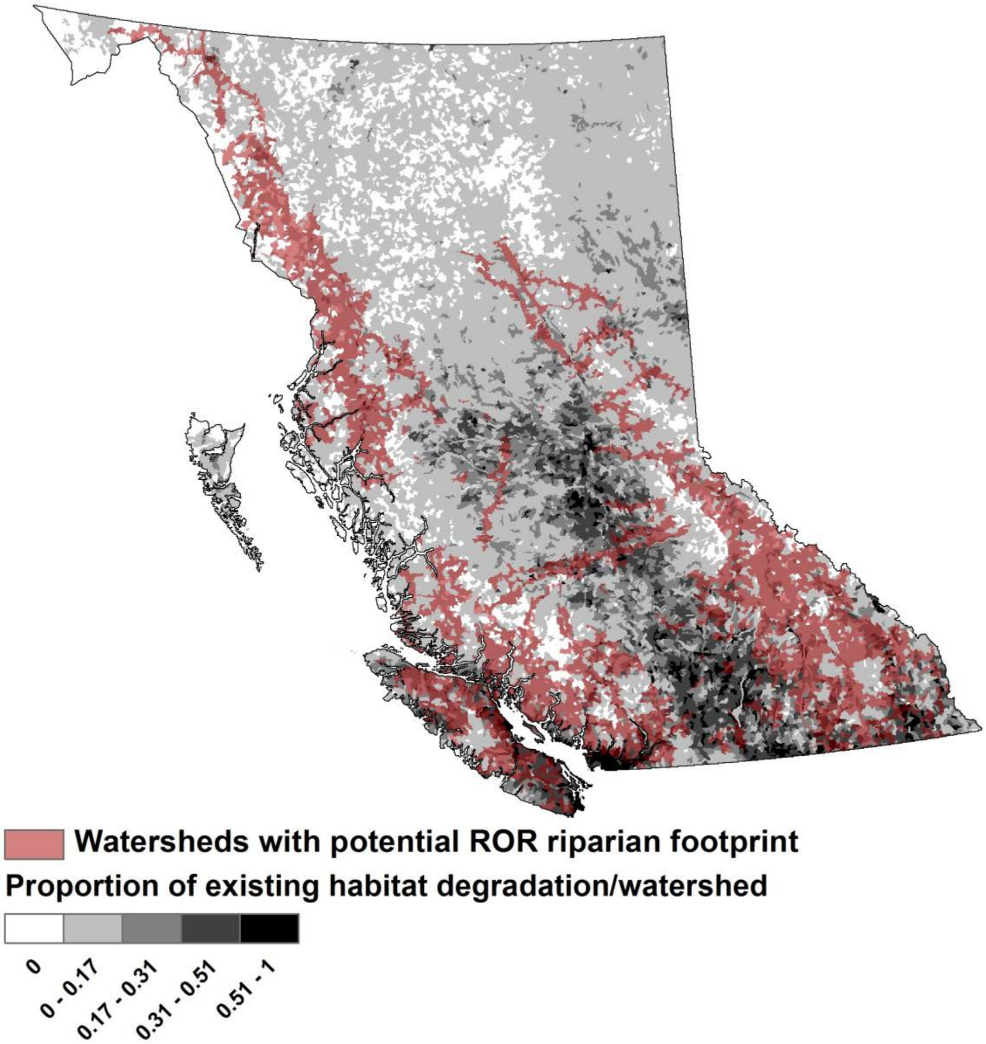
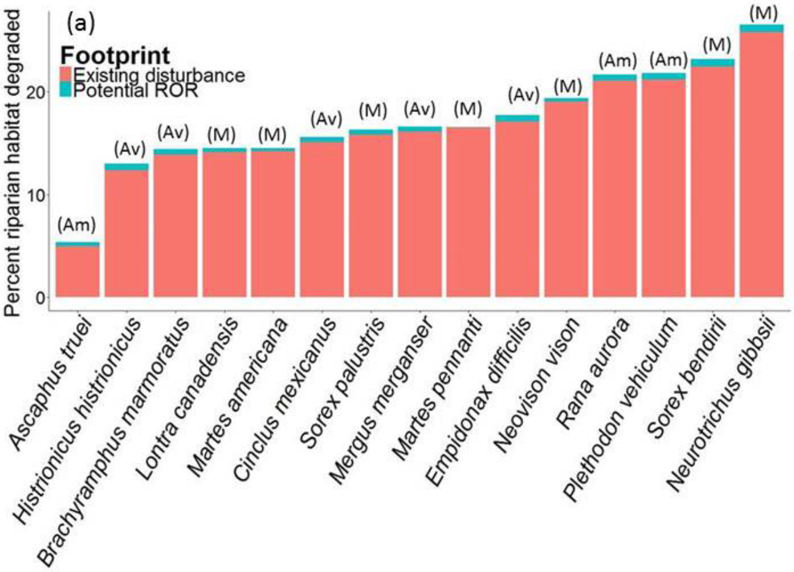


Figure 2-2 Potential Run-of-River (ROR) development relative to existing resource footprint. The underlying grayscale represents the proportion of overlap between the riparian zone and the footprint of existing anthropogenic disturbance (per watershed). The red overlay represents all watersheds which have a potential ROR footprint > 0 in the riparian zone. The outlines and names of the 40 terrestrial ecoregions from our study are available in Appendix A – Figure A1.

2.4.3. Watersheds of conservation concern under sparing and sharing planning scenarios

We identified WCCs under two ranking scenarios, and found that these areas of highest potential conflict between future ROR development and a subset of vertebrate diversity were widely but unevenly distributed across the geography of potential ROR development in BC. WCCs identified under the sharing and sparing scenario occurred in 24 and 25 of the 30 ecoregions in BC that have potential ROR development, respectively. The majority of WCCs were concentrated within six primary ecoregions in both the sharing (Pacific Ranges, Eastern Vancouver Island, Northern Columbia Mountains, Western Vancouver Island, Fraser Plateau and the Lower Mainland) and sparing (Pacific Ranges, Eastern Vancouver Island, Northern Columbia Mountains, Boundary Ranges, Omineca Mountains and the Lower Mainland) planning scenarios (73% and 74%, respectively), four of which were the same between scenarios (Figure 2-4 (a) and (b)), (Appendix A – Table A3). Over a third (38%) of WCCs were spatially identical between the sharing and sparing scenarios (Figure 2-4 (c)), (Appendix A – Table A3) and occurred in 22 different ecoregions. Of the WCCs identified only in the sharing scenario, where overlap was minimized between ROR development and areas of high existing anthropogenic disturbance, 58% were located in four lowland ecoregions on Vancouver Island, in the southern Coast Mountains, and in the central interior (Appendix A – Table A3, column '*Sharing unique WCCs (km2)*'). In the sparing scenario, 64% of the unique WCCs were located in four mountainous ecoregions on the mainland coast (Appendix A – Table A3, column '*Sparing unique WCCs (km2)*') (Figure 2-4 (c)). Despite these overall regional differences, the distribution of individual WCCs unique to either scenario was checkered in some regions, such that some sharing and sparing WCCs were close or adjacent to each other, especially in the highly disturbed and biodiverse lower mainland and Vancouver Island (Figure 2-4 (c), inset). We also evaluated differences in ROR-related energy metrics between the sparing and sharing scenarios. We found that under the sharing scenario, 182 projects which are projected to produce a total of 4239GWh/yr in annual firm energy were located within the WCCs identified in that scenario. In comparison, 198 projects with a projected sum annual firm energy of 6012 GWh/yr would be located in the WCCs identified under the sparing scenario.



(b)

Scientific name	**Relative increase in habitat loss**
Ascaphus truei	8.21
Histrionicus histrionicus	5.00
Brachyramphus marmoratus	4.00
Empidonax difficilis	3.66
Cinclus mexicana	3.43
Sorex bendirii	3.29
Sorex palustris	3.20
Plethodon vehiculum	3.16
Lontra canadensis	2.92
Neurotrichus gibbsii	2.92
Mergus merganser	2.92
Rana aurora	2.81
Martes americanus	1.92
Neovison vison	1.74
Martes pennanti	0.38

Figure 2-3 (a) Riparian habitat degraded due to overlap with the existing anthropogenic footprint from logging and linear infrastructure (pink), and the footprint of potential ROR development (blue), across the BC distribution of disturbance-sensitive riparian species. Letters represent taxa: Am = amphibians, Av = birds, M = mammals. (b) The amount of riparian habitat the footprint of ROR development will affect, relative to existing riparian habitat degradation from anthropogenic disturbance. Total riparian distribution areas for every species can be found in Appendix A – Table A4.

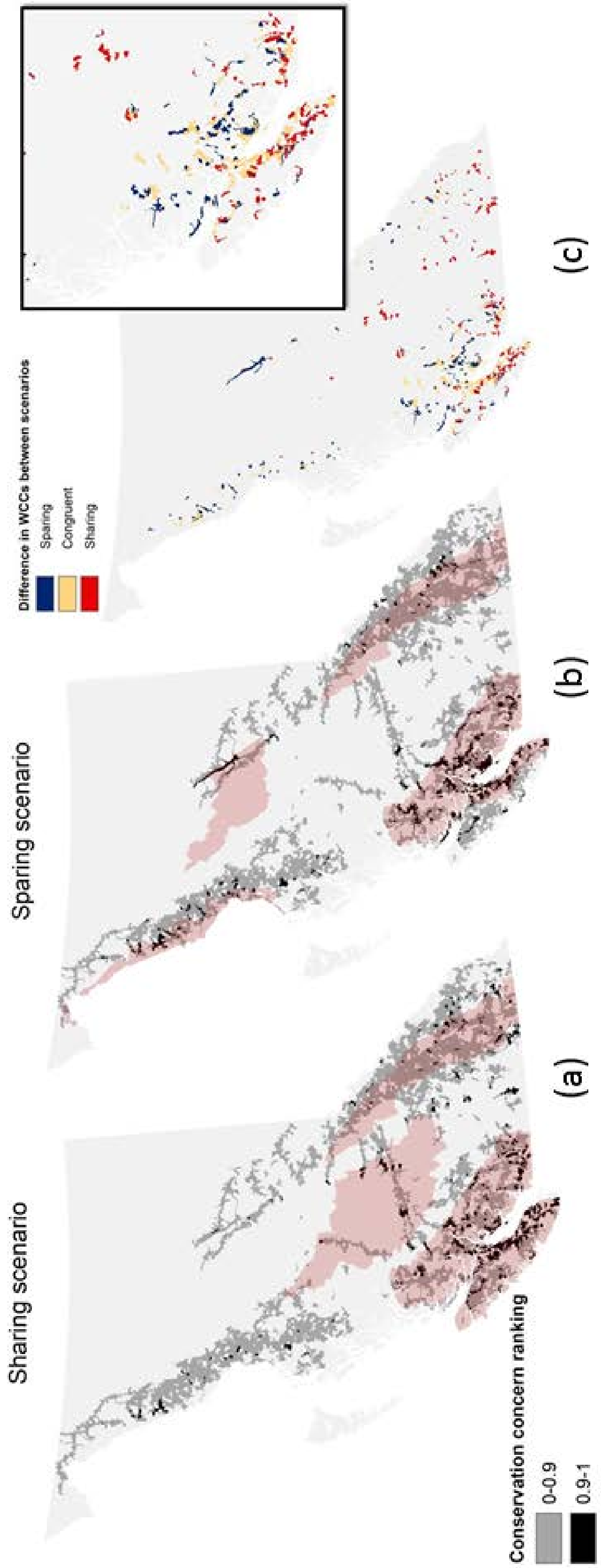


Figure 2-4 (a, b) Conservation concern ranking results from both planning scenarios. Red transperancies are the 6 ecoregions containing the majority of WCCs. Under the sharing scenario (a), the identified WCCs are highly disturbed by logging and linear features, while in the sparing scenario (b) the identified WCCs have relatively low existing disturbance. Similarities (yellow) in the spatial location of watersheds of conservation concern (WCCs) between the two scenarios (c) are shown in comparision to WCCs unique to sparing (blue) and sharing (red) scenarios, with the inset highlighting Vancouver Island and southwestern BC. Ecorgion names and boundaries are available in Appendix A – Figure A1.

2.5. Discussion

2.5.1. Spatial overlap with existing anthropogenic disturbances

Using relatively liberal estimates of ROR development potential ($500/MWh), we found that the potential footprint of ROR development in riparian zones in BC was 40 times smaller than the existing riparian footprint of logging in the last 22 years and linear infrastructure. Based on the footprint of potential ROR development, we found that 90% of the watersheds with potential ROR disturbance were already impacted, supporting the expectation that ROR disturbance will have spatial overlap with existing disturbance at the watershed scale. However, the level of potential ROR disturbance per watershed, measured as the proportion of riparian habitat degraded, was negatively correlated with the level of existing habitat degradation from logging and linear infrastructure, suggesting that the majority of the ROR footprint will be located in areas away from areas heavily impacted by existing disturbance. Taken together, these seemingly contradictory results provide a more nuanced prediction that while habitat degradation caused by potential ROR development will mostly add to existing habitat degradation, it will disproportionately increase degradation in riparian zones of relatively intact watershed ecosystems. The degradation of intact habitat in disturbed landscapes has been shown to decrease the probability of long-term species persistence by fragmenting and removing potential refuge habitat for sensitive species already facing high anthropogenic pressures (Sedell et al. 1990). Beyond the immediate impacts of habitat disturbance, resource extraction and development activities can also adversely affect sensitive species by greatly increasing the likelihood of further human activity and subsequent habitat degradation (Boakes et al. 2010). Such cumulative habitat degradation can lead to local species extinctions (Brooks et al. 2002, Parks and Harcourt 2002), affect animal behavior (Madsen 1995), facilitate species invasions (Trombulak and Frissell 2000), and induce ecosystem state-shifts (Scheffer et al. 2001). Considering the large and far-reaching footprint of existing anthropogenic disturbance in BC, new and compounding habitat degradation from future development has the potential to create or intensify these negative effects in landscapes across the province.

Our estimate of the habitat degradation and disturbance caused by existing and potential anthropogenic activities across BC is likely to be a conservative starting point for evaluating potential impacts on sensitive species. This is because while the habitat degradation associated with the physical footprint of anthropogenic activity, which is the leading reason of animal and vascular plant species listing in the US, evidently has strong impacts on habitat suitability for species (Wilcove et al. 1998), the effects of habitat disturbance and degradation extend out far beyond the immediate footprint through mechanisms such as fragmentation, edge effects (Miller and Hobbs 2000, Flashpohler et al. 2001), behavioral cascades (Hebblewhite et al. 2005), and facilitating species invasions (Stapanian et al. 1998). The riparian community is often affected by upslope habitat disturbances that we did not account for such as mass wasting events, even if the actual riparian zone is not physically impacted (Nakamura et al. 2000). Also in the riparian zone, effects of existing logging and infrastructure, as well as potential ROR development, may extend far beyond the physical footprint that we measured due to the connected and directional nature of riverine networks. Effects of riparian forest degradation in upstream riparian zones, such as stream warming and increased sedimentation (Davies and Nelson 1994, Gomi et al. 2006) can propagate downstream and affect stream and riparian ecosystem integrity (Li et al. 1994, Richardson and Neill 1998, Freeman et al. 2007, Ncea et al. 2015) even in watersheds where the footprint may not cause direct habitat degradation. Finally, our analysis likely captured the riparian terrestrial habitat degradation of low order, higher elevation streams more comprehensively than habitat degradation in higher order streams due to the fact we imposed a consistent buffer of 100m around the stream centerlines, which would have captured more aquatic and less terrestrial riparian habitat in higher-order streams with more developed riparian zones.

To quantify the spatial footprint of anthropogenic disturbance in BC, we had to decide on simple criteria for defining the extent of each type of disturbance. Because of the uncertainty about the road surface and roadside clearing of individual roads, we created inclusive, wide buffers that were certain to capture the physical road infrastructure as well as some of the edge effects that may extend into the surrounding ecosystem. For the logging component of the existing anthropogenic footprint, we only included the logged polygons themselves, discounting edge effects and likely underestimating the true extent of the footprint. However, adding a buffer would not change the spatial distribution of the existing anthropogenic footprint but only expand it slightly, and thus the conclusions about the relative extent and overlap between ROR development and existing disturbance would remain largely the same.

Though we treated the footprints in our study as spatially and temporally homogenous, the ecological effects of logging and other temporary forest clearing (e.g. for ROR construction) are not static or of equal severity, and forest regeneration provides habitat for early-successional species in ways that the footprints of infrastructure such as roads, powerlines, and penstocks, do not (Marzluff and Ewing 2001, Slonecker et al. 2013). Thus, a portion of what we considered habitat degradation for the species in this study, which are associated with late seral forest types, is likely temporary and such areas may become suitable for some species in the future. Another simplification we made for this analysis was restricting the components of existing disturbance to recent logging (past 22 years), roads and powerlines, when other types of human disturbance exist including urbanization, land conversion for agriculture, and mining and energy development. However, these additional forms of anthropogenic disturbance have a much smaller footprint than logging in BC, which has affected 30% of all forests have been logged since 1840, compared to just 3% of forests converted to all other human uses combined (Ministry of Forests Mines and Land Operations 2010), while roads are a good proxy for intensity human industrial activity (Mcgurk and Fong 1995). Similarly, our analysis focuses exclusively on one form of renewable energy development (ROR), while future resource development in BC will also include natural gas, wind power, and others. While we focused on ROR development due to its high overlap with riparian ecosystems, future studies aimed specifically at managing cumulative impacts by avoiding overshooting thresholds such as linear road density, degree of fragmentation or proportion of old growth forest loss, need to consider all major and likely anthropogenic developments in a region or landscape (Schneider et al. 2003).

2.5.2. Additional habitat degradation caused by ROR development on sensitive species

We found that the riparian footprint of potential ROR development had overlap with less than one percent of any species total riparian distribution, and was two or three orders of magnitude smaller than the aggregate footprint of existing forestry, road and powerline corridors already within the species ranges. The level of existing riparian habitat disturbance within species distributions was high, ranging from 5% to 26%. While the ROR-related increase is absolutely and relatively small, habitat degradation of any magnitude has the potential to reduce the available suitable habitat in a landscape (Lande 1987) past the extinction threshold, which typically creates extinction debt within a meta-population and eventually leads to regional extinction (Hanski and Ovaskainen 2002). Therefore, in watersheds where existing levels of riparian habitat degradation are close to the extinction thresholds for some of the resident species, a moderate increase in habitat degradation from ROR development could lead to rapid and unexpected species declines or extirpations (Kareiva and Wennergren 1995, Fahrig 1997). As well, ROR development has potential to affect the few remaining watersheds within the focal species distributions that have not experienced recent logging and are currently free of transportation and transmission infrastructure. Introducing any anthropogenic disturbance in otherwise intact areas greatly increases the probability of subsequent human access, development, and habitat degradation (Rosa et al. 2013), with adjacency to a road or a converted cell increasing probability of focal cell conversion many fold in a global time series study between 1700 and 1990 (Boakes et al. 2010). Maintaining intact, roadless areas is an effective conservation strategy that can protect multiple valued biodiversity components in forested regions (Strittholt and Dellasala 2001), and can play an important role in maintaining the resilience of ecosystems in the face of ongoing anthropogenic disturbance (Sedell et al. 1990) by providing connectivity between high-quality habitat for animals (Gillies and St Clair 2008), source populations that maintain regional species pools (Mosquera et al. 2000), seed banks for vegetative regrowth (Chazdon 2003), and as potential climate refugia (Keppel et al. 2012).

We found that the three classes of terrestrial vertebrates we examined differed moderately in the level of potential habitat degradation from ROR expected in riparian zones across their modelled range. Birds face the largest potential range-wide increases in ROR-related habitat degradation relative to the existing footprint of anthropogenic disturbance across their range. While relatively small additional habitat degradation can affect habitat suitability for bird species if it reduces the availability of key resources such as nesting sites (Cockle et al. 2010), effects on species persistence may be mediated by birds' vagility and ability to secure critical resources elsewhere through movement. On the other hand, many bird species, particularly in logged landscapes (Machtans et al. 1996), rely on riparian corridors for dispersal, and will avoid movement over even relatively minor forest interruptions in continuous forests (Laurance et al. 2004). We also found that mammals as a group had the lowest potential increases in degraded riparian habitat across their distributions, while the amount of habitat degradation for the amphibians we examined (n=3) varied and its effects are likely to depend on whether the loss disrupts movement or connectivity corridors (Becker et al. 2007). While we found differences between the average relative increases across the three classes of vertebrates, there was greater inter-species than inter-class variation in our results, suggesting that applying measures such as mitigating edge effects (e.g. softer edges) or maintaining vegetated movement corridors may be better implemented on a species-specific basis.

Our estimates of proportional riparian habitat degradation from potential ROR development may be underestimated because the species distributions we generated are likely to be conservative in the areas where ROR development potential is high. In BC, 90% of species occurrence data points that we collected in an exhaustive search of public, open-access, government, or research NGO databases were located within 200m of roads, many of which are logging roads. This creates a bias for most distributions modeled on these data, where they are likely skewed towards logged areas and human population centers (Prendergast et al. 1993, Freitag et al. 1998), and distributions in higher elevations and the lightly populated north are underrepresented. If the modeled distribution is skewed towards logged areas and away from the elevations where most ROR potential is concentrated (mean levation = 577m, sd=342), overlaps between those parts of species distributions and the ROR footprint may be underrepresented in this analysis. As well, a range of other species whose overlap with existing and potential disturbance we did not examine, including facultative riparian vertebrates (e.g. bears, wolves, ungulates, and bats), fish which are often negatively impacted by the temperature and turbidity changes in streams after riparian forest disturbance (Davies and Nelson 1994, Li et al. 1994, Hartman et al. 1996), stream invertebrates which play an important role in the riparian food web (Baxter et al. 2005), and riparian plants which are restricted to the riparian zone and provide important and unique habitat to many other species (Woinarski et al. 2000, Pusey and Arthington 2003, Ober and Hayes 2008), may be equally or more affected by their cumulative effects.

2.5.3. Strategic conservation planning

Balancing development pressures with conservation priorities such as protecting sensitive species and productive habitats requires strategic planning at regional scales (Duinker and Greig 2006, Therivel and Ross 2007). In this study, we found that conservation approaches can be explicitly included in spatial conservation planning, and tradeoffs in development outcomes under contrasting conservation approaches (i.e. land sparing vs land sharing) can be quantified and compared. In our study, most watersheds of conservation concern (WCCs) were concentrated in a few ecoregions in both sparing and sharing scenarios, representing regions that merit attention as the areas of highest potential conflict between ROR development and a subset of vertebrate biodiversity. The location of ~60% of WCCs was different under the sparing and sharing scenarios, demonstrating that the spatial distribution of conflict areas will differ depending on conservation goals, and highlighting the importance of making decisions about conservation approaches early in the planning phases of industrial expansion while freedom to making strategic decisions still exists. Choosing a certain conservation approach can involve making decisions about acceptable costs and tradeoffs. In our scenarios, the projects in the identified WCCs from the sparing scenario produced almost 2000 GWh/yr more energy than the projects in the sharing scenario WCCs, suggesting that avoiding development incompatible with land sparing goals (i.e. avoiding building ROR projects in relatively intact watersheds) can be more costly than following a land sharing approach and avoiding additional ROR development in heavily disturbed watersheds. Choosing between these two approaches will most likely also lead to unequal benefits to vertebrate biodiversity conservation, which could be quantified, but was beyond the scope of this study. In contrast, not all WCCs were contained within the top six ecoregions, with one quarter distributed across the remaining 18 and 19 (depending on scenario) of the 30 ecoregions where ROR potential is present, and WCCs from the sparing and sharing scenarios were located close or adjacent to each other in some ecoregions. Therefore, avoiding or mitigating ROR development only in regions with the greatest number of WCCs would miss a quarter (or more, depending on the cutoff used to define ‘top’ ecoregions) of potential high-conflict watersheds, which emphasizes the importance of considering multiple scales when analyzing the costs and benefits of avoiding or mitigating development in biologically important areas.

Conclusions about the biodiversity benefits of adopting either approach, sparing or sharing, will also vary based on the ecological values that are deemed most important (Lertzman and MacKinnon 2013). We examined species richness as a proxy for ecological value, which is a ‘fine-grained’ approach often amenable to protection of relatively small parcels within watersheds, often representing core habitat for the species. This kind of approach can be compatible with land sharing, which results in a more dispersed footprint that affects a larger number of watersheds but which can avoid species core habitat across most of its range. If we had chosen to focus on more coarse-scale ecological values, such as maintaining disturbance and succession processes across an area whose biota can sustainably regenerate from the disturbance (Pickett and Thompson 1978), choosing a land sparing approach may be more suitable because large areas of undisturbed habitat are necessary to allow for these larger processes to manifest (Lertzman and MacKinnon 2013).

Strategic planning for distributed, renewable energy development such as ROR (or wind or solar), can benefit from using spatial accounting tools to predict and estimate the potential cumulative habitat degradation caused by multiple projects of the same type as well as account for potentially compounding impacts among different anthropogenic disturbances. Mounting evidence supports the importance of evaluating separate sources of disturbance in the same landscape simultaneously because their effects on habitat can combine to affect native species and in non-additive (synergistic or antagonistic) ways (Canter and Kamath 1995, Paine et al. 1998), leading to unexpected ecological responses (Travis 2003, Christensen et al. 2006, Crain et al. 2008) such as the rapid decline in habitat specialists on landscapes experiencing incremental habitat loss, climate change, or both (Travis 2003). The degradation of aquatic and riparian habitat for riparian specialists, coupled with the extensive existing upslope forest degradation, may pose a similar risk to some of the species in our study system. Despite the potential for non-additive and interactive effects (Darling and Côté 2008), many environmental impact assessments remain single-project focused, and fail to account for cumulative impacts (Fidler and Noble 2012).

2.5.4. Conclusion

This study is the first quantitative evaluation of the potential aggregate environmental impacts of ROR development at large spatial scales. We found that while the incremental increases in habitat degradation from potential ROR development in BC are relatively small compared to existing disturbance, ROR contributes to a very large cumulative riparian disturbance that may have effects beyond the physical footprint, and represents just one of several anthropogenic disturbances projected to grow in the province. Our results were based on a deterministic development scenario involving the construction of a set of hypothetical ROR projects at spatially explicit locations. We expect the overall spatial patterns identified in this study to be representative of potential future overlap between ROR disturbance, existing disturbance, and riparian habitats and species because ROR development is restricted to the areas where high-gradient stream and road and powerline access create favourable conditions for projects. However, variation in the economics of ROR development, electrical supply and demand, or provincial energy policy will all modify the exact number and location of projects to be built. As well, ROR development may pose a greater species-specific risk of habitat degradation to taxa that we did not consider, such as riparian plants and fishes.

Habitat degradation by future ROR development has the potential to affect riparian ecosystems both in highly disturbed watersheds, where the additional ROR footprint may reduce habitat availability for species below a critical landscape threshold, as well as in watersheds with low levels of existing disturbance, where ROR development will open the ‘disturbance front’ and greatly increase probability of subsequent human activities. Habitat degradation from ROR development may also have disproportionate effects on species persistence if located in areas where it will reduce the availability of key resources or disrupt habitat connectivity for sensitive species. Identifying these possibilities will require a finer spatial scale of analysis than what we used in this study. We identified a subset of ecoregions that contained the largest total area identified as watersheds of conservation concern under two different conservation approaches, land sharing, which identified WCCs with high existing disturbance, and land sparing, which identified WCCs as watersheds that are currently relatively intact. These are the areas of greatest potential for conflict between conservation and development, and can provide focus for regional strategic planning.

We used a scenario-based approach, similar to other studies that projected the footprints of future development, in order to evaluate the potential cumulative impacts on wildlife prior to major but spatially distributed industrial development (Theobald et al. 1997, Copeland et al. 2009, Evans and Kiesecker 2014). In our study, we expanded the scope of the analysis by evaluating the potential spatial extent and distribution of ROR development in BC relative to existing anthropogenic disturbance. Including BC's most extensive existing anthropogenic disturbance (logging and roads) brings the results of this analysis closer to the kind of cumulative impact evaluations necessary to comprehensively consider the tradeoffs and synergies of new development in landscapes with a history of human disturbance. Spatially explicit accounting of habitat degradation for sensitive species is one of the most accessible tools available to quantify cumulative impacts and inform strategic planning for anthropogenic disturbances whose ecological impacts in specific systems have been understudied. To refine coarse estimates of potential impacts by new development such as those we provide in this analysis, we need to identify the ecological mechanisms by which sensitive species could be impacted by such development. Due to the distributed nature of ROR hydropower, we need to consider not only the impacts caused directly by the footprint of ROR infrastructure (within the river channel as well as in the surrounding terrestrial environment), but also the potential indirect and downstream ecological impacts. In the coming decades, as many countries and jurisdictions prioritize climate change mitigation through the development of decentralized networks of renewable energy technologies, conducting evaluations of potential cumulative impacts in advance of such development will become increasingly important tool to quantify the tradeoffs between local ecological costs and global environmental integrity.

Chapter 3.

Using species distribution models (SDMs) to detect species responses to logging intensity at multiple spatial extents

3.1. Abstract

Anthropogenic disturbances that are spatially extensive, such as forestry or road building, can affect species habitat suitability. However, information gained from empirical studies about species responses to altered habitat conditions does not directly translate to predictions about responses of the species' distributions at large spatial scales. In addition, disturbance variables have been found to be poor predictors of species distributions in species distribution models (SDM). In this study, we evaluate the performance of SDMs in predicting species occurrence in the presence of logging pressure across a range of spatial extents of analysis and species sensitivities to logging. To explicitly test the issues of extent and species sensitivity we simulated species with a range of negative sensitivities to logging at three nested spatial extents in British Columbia (sub-continental: 944,735 km^2, regional: 167,822 km^2, and landscape: 31,596 km^2). We compared two types of SDMs, both using presence data extracted from simulated distributions, with one (LOG) model based on climatic, topographic, land-cover, and logging predictors, and a NOLOG model based on climatic, topographic, land-cover predictors only. The NOLOG models overpredicted species presence relative to the LOG models, and the degree of overprediction increased with the strength of species sensitivity to logging. At the landscape extent, up to 51% of the area the NOLOG models identified as presence was overpredicted, and at the sub-continental extent, up to 21% was over-predicted. Over-predicted cells also had higher mean logging intensity

(up to 31% higher) than cells that were correctly predicted by both models, and the magnitude of this difference decreased with increasing spatial extent. We also found that at smaller spatial extents, greater heterogeneity of logging relative to other variables led to an increase in predictive power of logging. These results demonstrate the explanatory power of disturbances in the SDMs of species that are sensitive to the resulting habitat changes, and the importance of including landscape disturbance in the bioclimatic models of those species. This study also highlights the potential utility of SDMs for predicting the direction and magnitude of species spatial responses to disturbances at broad spatial scales, particularly where the spatial heterogeneity of disturbance exceeds the heterogeneity of climatic and topographical drivers.

3.2. Introduction

Many terrestrial anthropogenic disturbances alter the distribution of species (Hannah et al. 1994, Devictor et al. 2008), yet the direction and magnitude of impacts are often difficult to detect at broad spatial extents. Ecosystem disturbances from resource extraction activities such as logging cut blocks, oil and gas well pads, or distributed energy development, result in a mosaic of patches of modified habitat distributed across large areas (landscape to continent, 10-10000 km^2). These patchy and spatially extensive disturbances can affect species through direct habitat degradation or modification at the disturbance site (Soutiere 1979, Grindal and Brigham 1998, Lain et al. 2008), and across the broader landscape through habitat fragmentation (Dyer et al. 2002, Wahbe et al. 2004), edge effects (Donovan et al. 1997), and altered animal behavior (Doherty et al. 2008), creating a complex ‘signal’ of change in species distributions. Furthermore, for activities such as logging, vegetation regrowth and ecological succession post disturbance add to the complexity of detecting impacts, and the potential synergistic effects with other human activities. In light of widespread wildlife population declines, many attributed to land-cover change (Dirzo et al. 2014), being able to link specific anthropogenic disturbances with quantitative changes to species distributions is of key interest to conservation planners and land managers (Cushman 2006).

The spatial distributions of plants and animals are shaped by a hierarchal set of environmental variables that are suggested to act as filters for species occurrence at different spatial and temporal extents (Levin 1992, Willis and Whittaker 2002, Vicente et al. 2011). Pearson and Dawson (2003) proposed a ‘scale domain’ framework that relates the variables that typically affect species distributions with the spatial extents where they have their greatest influence. For example, climate and geologic history are considered to influence species distributions at regional to global extents (200 km to >10000 km), topography acts at local to regional extents (1 km to 2000 km), and land use characteristics determine species occurrence at site to landscape extents (0.01 km to 200 km) (Pearson and Dawson 2003). The importance of different variables across the scale domain framework is likely proportional to the spatial extent at which these variables exhibit greatest heterogeneity (Vicente et al. 2014). For example, climatic factors show the greatest heterogeneity across broad spatial extents and define the physiological limits of species ranges (Thuiller et al. 2004). In contrast, factors such as vegetation type show substantial heterogeneity over smaller spatial extents, and affect species distributions at landscape extents (Kie et al. 2002). For example, as the spatial extent decreases in size, responses of populations, meta-populations or communities to habitat disturbance can be quantified using resource selection functions in a well-established framework of hierarchical habitat selection (Johnson 1980), and using static and dynamic occupancy modeling approaches that account for imperfect detection (Russell et al. 2009, Zipkin et al. 2010), ideally in a Before-After Control-Impact design (Popescu et al. 2012).

Currently, the most common approach for predicting both current and future species distributions is through presence-only species distribution modeling (SDM) (Franklin 2013). SDMs are correlative models that use the relationships between species localities and environmental characteristics to predict species occurrence probabilities spatially (Elith and Leathwick 2009, Franklin 2013). SDMs are often built using climatic and topographic predictors, and because of the availability of such data for most parts of the world, models have been used extensively to predict species occurrence across many spatial extents (Guisan et al. 2013), and to forecast potential range shifts in the face of changing climate (Amen et al. 2011, Araújo et al. 2011). However, using only climatic variables, and excluding other factors that are important in shaping species distributions, such as biotic interactions (Ober and Hayes 2008, Hof et al. 2012), geographic dispersal barriers, local adaptation (Hampe 2004), evolutionary history (Hoffmann and Kellermann 2006), and human impacts and habitat alterations (Jiménez-Valverde et al. 2008), could produce misleading distribution predictions and alter the interpretation of variable importance (Austin 2002). Studies that incorporated land-cover, land-use and vegetation variables into correlative SDMs found that these variables often play an important role at intermediate (landscape to region, 10-2,000 km) extents (Thuiller et al. 2003, Tingley and Herman 2009). Consequently, we expect that logging or natural disturbance, which act to modify certain land-cover types, would shape species distribution patterns at landscape and smaller extents. For example, studies incorporating disturbance in species distribution models have found that certain parameters of the fire regime (wildfire occurrence, frequency, variability, or departure from historical return intervals) play a lesser role in predicting distribution of fire-sensitive plant species at regional extents (e.g. California: 423,970 km^2 (Crimmins et al. 2014), or the Cape Floristic Region: 78,555 km^2 (Tucker et al. 2012)) than climatic and topographic factors.

Logging, which affects ~2% of global land area annually (Hooke et al. 2012), is one of the most spatially extensive forms of ongoing anthropogenic habitat disturbance. Unlike deforestation for agriculture or suburban uses, which may have a permanent character, forest disturbance from logging is transient or temporary. Vegetation regrowth and succession can mitigate the effects of forest disturbance for some species across relatively short time extents (e.g., stand initiation and establishment stage, 0-25 years) (Hannon and Drapeau 2005), while other species, such as old-growth specialists, may require decades post-disturbance to recover (Bart and Forslnan 1992). Logging can also increase species diversity by attracting early successional and generalist species (Hunter and Schmiegelow 2010). However, industrial logging normally results in forest landscapes with different characteristics and species assemblages than would expected in forests under natural disturbance regimes, such as wildfire in the boreal forest (Lertzman and Fall 1998). Many empirical studies have documented site level changes in species abundance (Lance and Phinney 2001), movements (Wahbe et al. 2004), and utilization of habitat (Parker and Morton 1977) in response to logging disturbance, but the magnitude and direction of the response can vary greatly within and among taxa (e.g., mammals (Fisher and Wilkinson 2005), birds (Imbeau et al. 2001), and amphibians (deMaynadier and Hunter Jr. 1995, Cushman 2006)). Differences in the strength of species site-level response to logging are often attributed to the degree of habitat specialization (Devictor et al. 2008), the degree to which critical habitat features are affected (Berg et al. 1994), and the ability of species to avoid or capitalize on the new habitat through movement (Campbell Grant et al. 2010). The uncertainties in species responses to logging, and the temporary habitat shifts associated with this disturbance, pose unique challenges to evaluating species distributions in landscapes influenced by large-extent logging regimes.

In this study we use an SDM framework using simulated presence-only data to evaluate the relationships between species occurrence and logging disturbance across spatial extents. Given that previous modeling studies provide conflicting evidence on the importance of including non-climatic variables as predictors in presence-only species distribution models, a critical question arises: is the lack of predictive ability of disturbance variables due to (1) the spatial mismatch between the scale of the study and the available data and the scale domain at which disturbance acts to shape distributions, or (2) the lack of sensitivity of the species to landscape disturbance relative to other variables. In this study, we critically evaluate the interplay between species sensitivity to disturbance and spatial extents using a simulation approach.

We created species distributions using climate, topography, land cover, and forestry data for a suite of simulated species with different imposed sensitivities to logging relative to the other variables (10 pseudo-species negatively impacted by logging with a relative sensitivity range = -0.01 to -1). We then tested the ability of presence-only distribution models to detect species range shifts in response to variation in the intensity of logging across landscape and regional extents by comparing spatial outputs of models built with and without logging. We quantified logging intensity as the proportion of forest cut between 1975 and 1999 per 14km^2 landscape unit. Given that we imposed negative logging sensitivities, we expected that models without logging (i.e. relying on climate and topography only) to overpredict distributions in logged areas. Adopting a simulation approach allowed us to evaluate the performance of species distribution models for detecting these shifts across spatial extents and a range of sensitivities without the biases common in large-extent species locality data typically collected by citizens and volunteers near population centers and roads (Prendergast et al. 1993, Reddy and Davalos 2003). We simulated our pseudo-species using climate, topography and logging data from British Columbia (BC), Canada.

BC has a history of intensive timber harvesting across large areas, as well as strong climatic and topographic gradients, which creates environmental heterogeneity at many spatial extents. Logging has been practiced in BC since the mid 1800’s, but has intensified considerably since the 1950’s. This disturbance typically occurs as a network of clear cut or selectively harvested patches ranging in size from 1 ha to >1000 ha. Logging affects a larger area of BC forests than any other form of human activity in the province (~25% of BC forests have been logged at least once; BC Vegetation Resources Inventory, *geobc.gov.bc.ca*), and creates a shifting mosaic of forest patches of various seral stages. Our goal overall was to test the utility of using SDMs as a tool for detecting the direction and magnitude of changes in species distributions in response to logging. Specifically, our study objectives were to (1) evaluate the effects of failing to account for logging disturbance when predicting species distributions across a range of species’ sensitivities to logging and spatial extents, and (2) to examine the relationship between the heterogeneity of environmental variables and their predictive ability at different spatial extents.

3.3. Methods

To identify how spatially extensive habitat disturbances affect species distributions at broad spatial extents, we explored how simulated species distributions predicted by models with and without a logging variable change in response to species sensitivities to the disturbance, and how the change varies at different spatial extents at which the analysis was conducted (Figure 3-1). Using presence localities extracted from simulated distributions, we fit species distribution models, with (LOG) and without (NOLOG) logging intensity and compared the paired outputs to quantify how much the NOLOG model overpredicted distributions, and assessed the magnitude and spatial pattern of overprediction. A response (overprediction) corresponding to the direction and strength of a species association with logging would indicate that the comparative method correctly reflects underlying species sensitivity to the disturbance. To evaluate if spatial heterogeneity of logging intensity relative to competing predictive variables drives the differences between the paired models, we examined the relationship between the predictive ability of the logging variable and its heterogeneity relative to the climate and topographic variables at the three spatial extents.

3.3.1. Environmental data

To generate the pseudo-species habitat suitability, we chose six general climatic and topographic variables important in driving species occurrence (Gaston 2000), a land-cover variable (proportion forest) to account for the variability in the extent of forested lands across BC (Nogues-Bravo and Martınez-Rice 2004), and a logging intensity variable, which is our variable of interest (see below). We collated data from various spatial repositories (Appendix C – Table C1) and standardized all layers to a 1 km^2 resolution. Each layer was overlain with a grid of 13.7 km^2 hexagons, representing the ‘sites’ or local-extent landscape units whose characteristics determine species habitat suitability. We calculated the mean value of all 1 km^2 cells occurring within each hexagon for the climatic and topographic layers, and the proportion of forest cover in each hexagon. All layers were rescaled between 0 and 100 at the sub-continental extent and clipped to each of three spatial extents: sub-continental (BC-wide, 944,735 km^2), regional (Central and Southern Interior Ecoprovinces, 167,822 km^2), and landscape (Thompson Okanagan Plateau, 31, 596 km^2). All spatial data manipulations were performed in ArcGIS Version 10.2 (ESRI, Redlands, CA) and program R (R Core Team 2014).

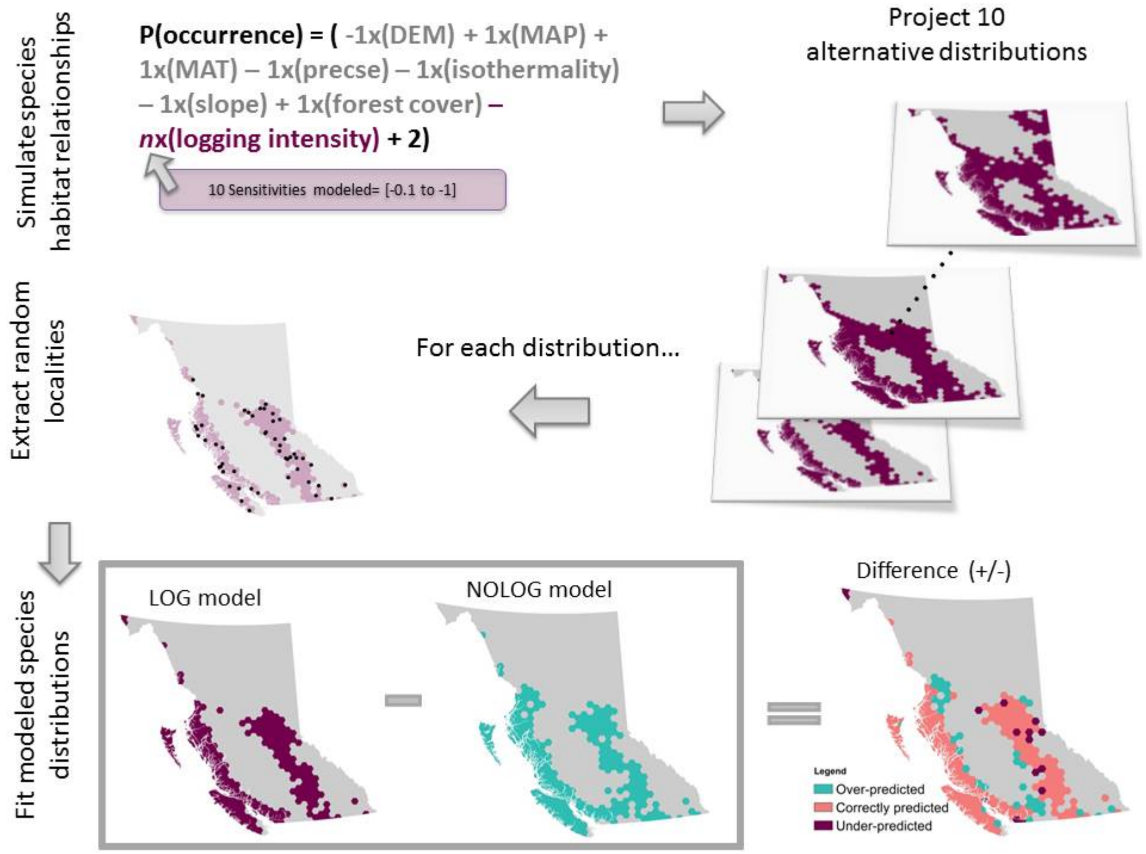


Figure 3-1 The workflow for creating paired SDM models for pseudo-species of varying sensitivity to logging. We created 10 habitat suitability maps based on a GLM model of 7 environmental variables with fixed coefficients of ±1 and a logging intensity variable with a coefficient that varied from -0.01 to -1. DEM = degital elevation model, MAP = mean annual temperature, MAT = mean annual temperature, precse = seasonality of percipitationWe extracted 500 random points from the high-probability areas of the habitat suitability maps and fit two modeled ensemble distribution models based on them – LOG models using all 8 original variables and NOLOG models excluding the logging variable. We subtracted the NOLOG model from the LOG model output to get the difference maps, which we used for subsequent analysis. We present an example for the sub-continental extent, but we repeated these steps at all 3 extents for the analysis.

3.3.2. Logging data

We calculated logging intensity as the percentage of logged forest pixels in each 14km^2 hexagon. We only included pixels logged between 1975 and 1999 to represent the altered (post-harvest) stand characteristics of the initiation and establishment stages of succession (Song 2002). We used the same BC Forest

Practices Board logging dataset as Chapter 2, which had a resolution of 100m and province-wide coverage, except for some gaps where private tree farm licensees did not submit logging records, mostly on Vancouver Island. We reclassified the logging data to a 1km resolution to match the climatic and topographic data. While differentiating between different harvesting methods (clearcut versus various kinds of partial retention) can be important for analyzing real species responses, our simulated pseudo-species did not differentiate between logging methods and we treated all logged pixels as clearcut.

3.3.3. Simulating species occurrence localities

To explicitly test the relationship between species sensitivity to logging and the magnitude and pattern of those species distribution change in response to logging intensity, we simulated a set of hypothetical species with known sensitivities to logging (Hirzel et al. 2001). We used Generalized Linear Models (GLM) in R to create pseudo-species whose habitat suitability is equally influenced by climate, topographic and land-cover variables (coefficients fixed at ±1), but differently influenced by logging intensity, following the general formula:

$$\boldsymbol{Habitat\ suitability} = -\mathbf{1} \times (\boldsymbol{elevation}) + \mathbf{1} \times (\boldsymbol{mean\ annual\ temperature}) + \mathbf{1} \times (\boldsymbol{mean\ annual\ precipitation}) - \mathbf{1} \times (\boldsymbol{precipitation\ seasonality}) - \mathbf{1} \times (\boldsymbol{isothermality}) - \mathbf{1} \times (\boldsymbol{slope}) + \mathbf{1} \times (\boldsymbol{forest\ cover}) - \boldsymbol{n} \times (\boldsymbol{logging\ intensity}) + \boldsymbol{b})$$

where *n* represents the sensitivity of a species to logging intensity, generated at ten levels: -0.01, -0.05, -0.1, -0.15, -0.25, -0.3, -0.4, -0.5, -0.75, and -1, and *b* is a constant whose value sets the minimum habitat suitability to zero.

We modeled these relationships to approximate hypothetical forest-associated vertebrates with home ranges defined by the resolution of the data ($14km^2$ hexagons) and relatively high mobility (since only the proportion of logging per hexagon was considered, not its configuration), such as Bald Eagles (*Haliaeetus leucocephalus*) or American Marten (*Martes americana*) (Buskirk and Mcdonald

1989, Garrett et al. 1993) The GLMs combined the values of each environmental variable at every cell to generate a spatially explicit continuous projection of habitat suitability for each pseudo-species. These were projected at the three spatial extents (sub-continental, regional, landscape), defined by Pearson and Dawson's (2003) ‘scale domain’ framework. We classified the outputs into binary maps, where the top 20% of cells were deemed to be suitable habitat and thus inhabited by the species, representing its true distribution following Hirzel et al. (2001), and the remaining 80% of cells were classified as absence. From these distributions we randomly selected 500 species locality points used as presence data in creating species distribution models.

3.3.4. Modeling species distributions with and without logging intensity

We fit SDMs with and without logging intensity (LOG and NOLOG models, respectively) using the pseudo-species occurrence localities and the topographic, climatic, and land-cover variables in ‘Biomod2’ (Lyet et al. 2013), an ensemble SDM package in R that incorporates the outputs of 10 different modelling methods (Appendix B – Table C2) (Thuiller et al. 2009). We excluded two methods, FDA and MaxEnt, because trial tests showed that they had low predictive ability. We used a weighed committee averaging approach, where the different models are weighted by their True Skill Statistic (TSS) which reflects predictive accuracy (Allouche et al. 2006), and combined to generate 2 outputs: a continuous probabilistic distribution model, and a binary presence/absence distribution model (Thuiller et al. 2009). For each model, we selected pseudo-absences randomly within the same spatial extent as the presence data, whether it was landscape, regional, or sub-continental. We set the number of random pseudo-absences equal to the number of presences for each species (i.e. prevalence = 0.5) in order to avoid spurious measures of accuracy often encountered when prevalence is extremely high or low (McPhersonn et al. 2004, Allouche et al. 2006). We applied an 80/20 locality data split, using 80% of the locality points to create the distribution model, and 20% for testing its accuracy and thus generating the TSS, re-selected pseudo-absences 4 times and ran 8 model replicates for each selection. We obtained a total of 60 ensemble species distribution models: a LOG and a NOLOG model for each of the 10 pseudo-species sensitivities at three spatial extents. We evaluated the predictive accuracy of the LOG models relative to the original GLM-generated distribution using phi correlation coefficients between the presence and absence cells in both distributions.

3.3.5. Spatial overprediction by NOLOG relative to LOG distribution models

To quantify the effect of ignoring logging intensity as a predictor in distribution models for a species whose distribution was simulated with logging sensitivity, we subtracted the binary NOLOG model output from the binary LOG model output. In the resulting ‘difference map’, a value of 0 is given to cells where both LOG and NOLOG models predicted presence (‘correct’), a value of -1 is given to cells where the NOLOG model predicted presence and the LOG model predicted absence (‘overpredicted’), while a value of 1 denotes cells where the LOG model predicted presence and the NOLOG model predicted absence (‘underpredicted’). Cells where both SDMs predicted absence were ignored. Underpredicted cells were produced only when occurrence probability in the LOG model greatly exceeded that of the NOLOG, typically in cells with zero or very low logging intensity values. Because these cells were very infrequent in the distributions, we focused our analysis on comparing correctly predicted and overpredicted cells in each difference map. We calculated the percentage of over-predicted and correctly predicted cells in each difference map, and examined the relationships between percent overpredicted cells, sensitivity level, and spatial extent.

3.3.6. Spatial Bias towards logged areas in NOLOG models

We evaluated the sensitivity levels at which the distributions predicted by LOG and NOLOG models differed most by quantifying logging intensity in the overpredicted areas. We extracted the logging intensity values of all the cells in each difference map, calculated the difference in the means between the correctly predicted and overpredicted cells. For each sensitivity level and spatial extent, we repeatedly selected random pairs of correctly predicted and overpredicted cells using bootstrap resampling (n=30,000 resamples in the ‘bootES’ package in R (Gerlanc and Kirby 2013)), and subtracted their logging intensity values. The difference in forest logging intensity between these two groups of cells represents the effect size of logging intensity relative to species sensitivity: higher logging values in the over-predicted cells indicate that the species is avoiding these cells and the LOG model is predicting absence. Positive values indicate higher logging intensity in overpredicted cells, and greater differences correspond to a stronger bias towards logged areas in the NOLOG models (thus less accurate predictions when logging is ignored). To quantify the differences in the rate of effect size increase between extents, we fitted non-linear regressions to the observed effect sizes as a function of logging sensitivity. We applied a weighted (1/95% CI) non-linear, asymptotic regression forced through the origin (‘SSasympOrig’ function in the ‘stats’ package in R),

$$\theta_1 1\,\{1-\exp[-\exp(\theta_2)\mathrm{x}]\,\}$$

where θ_1 represents the horizontal asymptote and θ_2 is the natural logarithm of the rate constant. We compared the rate constant ($e^{\theta 2}$) to quantify differences in the magnitude of bias between the landscape, regional and sub-continental extents.

3.3.7. Predictive power and relative heterogeneity of logging intensity at different extents

To test whether logging intensity becomes more heterogeneous at smaller extents relative to the other variables, we compared the interquartile range (IQR) across all variables in the models at the three spatial extents. We examined the relationship between the IQR and importance value (IVs) of all variables in the correct (LOG) models to evaluate whether greater heterogeneity corresponds to higher predictive performance. The importance of a variable is calculated as 1 minus the spatial correlation between the original distribution prediction and a prediction made without the focal variable, such that low correlations between the two predictions (i.e. high importance values) are indicative of highly influential variables. We weighed the importance values by model fit (TSS) and averaged across all runs within a single SDM (8 modeling methods, 4 pseudo-absence selections and 8 replicates) to produce a single value for each variable in each LOG model. To compare the IV/IQR relationship across variables, we evaluated IVs in a LOG model where relative logging sensitivity is equivalent to all other variables (-1) to control for the effect of logging sensitivity and focus solely on the relationship between heterogeneity and importance value. Lastly, we compared the importance values of logging intensity across all 10 sensitivity levels for the three study extents.

3.4. Results

3.4.1. SDM modeling performance

We analyzed spatial distribution models of simulated species to quantify the effect of logging intensity as a predictor variable under different conditions. In the historical BC logging dataset we used, 24% of all (100m^2) cells, and 28% of all forested cells, in the province were affected by logging, and we found that 10% of BC's entire land area has been logged at least once since 1800. The greatest concentration of logged cells was in the interior plateau and in the south, though finer regional; patterns have shifted through time. We aggregated the raw dataset into hexagons with 2km radii (from center to vertex): the percentage of forest logged in each hexagon (which was our logging intensity metric) ranged from 0-100%, though the median across all cells was zero, and the median in the subset of cells with logging intensity >0% was 17%.

The species distribution models which included logging intensity (LOG models) were congruent with the original GLM-generated distributions, confirming that the ensemble SDM LOG models were accurate models of the simulated species' true distributions. Phi-correlation coefficients between the original distributions and the LOG models were above 0.9 for all pseudo-species modelled at the landscape extent, and above 0.8 for sub-continental models (Table 1). While all pseudo-species distributions had some part of their range in unlogged cells due to the relatively high abundance of unlogged cells in the province, the modeled distributions shifted increasingly into those cells for species with higher sensitivity to logging intensity (Figure 3-2). The logging intensity in the predicted range varied from 0-79% in the least sensitive species to 0-21% in the most sensitive species at the landscape extent, from 0%-92% in the least sensitive species to 0%-27% for the most sensitive species at the regional extent, and 0%-100% to 0%-33% at the sub-continental extent.

Table 3-1 A phi correlation comparison between the suitable/unsuitable cells of the simulated GLM habitat suitability maps and the presence/absence cells of the LOG models. The results presented are for landscape and sub-continental extents, and show very high congruence. Regional results are intermediate (data not shown).

Extent	Relative logging sensitivity	Chi-squared	Phi correlation
Landscape	0.01	1905.56	0.92
	0.25	1918.55	0.92
	0.5	2018.41	0.92
	0.75	1953.71	0.93
	1	1956.48	0.93
Sub-continental	0.01	55277.74	0.84
	0.25	54572.80	0.83
	0.5	56511.33	0.85
	0.75	52748.82	0.81
	1	50920.18	0.80

3.4.2. Spatial overprediction by NOLOG models

Models based only on climatic, topographic and land-cover variables (NOLOG) overpredicted the presence of logging-sensitive species (Table 2). For a species with high relative logging sensitivity (-1), NOLOG models over-predicted 51% of cells at the landscape extent. For species with lowest sensitivity to logging (-

0.01), the NOLOG models overpredicted presence in only 2% of the cells at the landscape extent. NOLOG models moderately overpredicted the range of species with intermediate sensitivity levels. This pattern was consistent across all extents (Table 3-2), but became more pronounced with decreasing extent. While the ranges of species with low logging sensitivity (-0.01) were similarly over-predicted at all spatial extents, overprediction for a logging sensitive species (-1) was lowest at sub-continental extent (21% of cells) (Table 3-2).

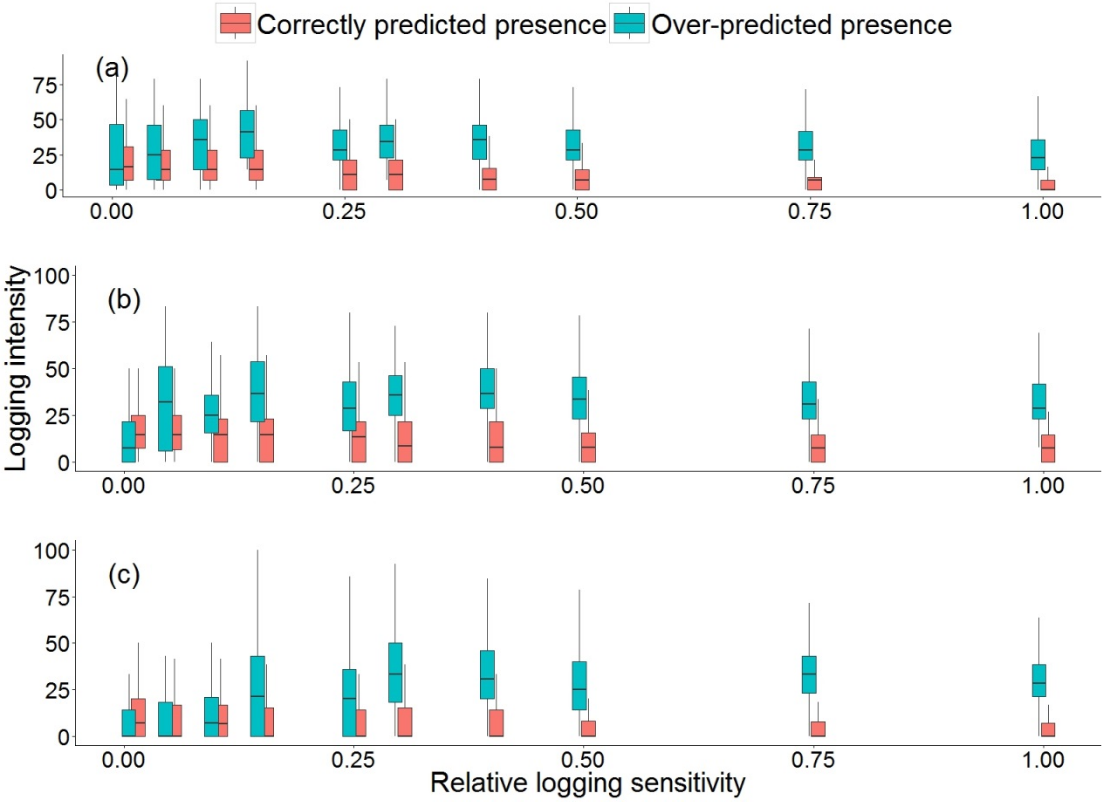


Figure 3-2 The logging intensity in the cells of the difference maps between the LOG and NOLOG models, separated into cells that were correctly predicted (salmon bars) and over-predicted (cyan bars) by the NOLOG models. As relative sensitivity to logging increases, the percent of correctly predicted cells decreases, while the percent of over-predicted cells increases (Table 3-2).

3.4.3. Spatial bias towards logged areas in NOLOG models

As species sensitivity to logging increased, the NOLOG models overpredicted presence in cells with increasingly higher logging intensity compared to the correct distributions (Figure 3-2, a-c). For species with low sensitivity to logging (-0.01), the mean logging intensity in the cells over-predicted by the NOLOG model was very similar to logging intensity in the correctly predicted cells (5-8 % difference, depending on extent), and the 95% confidence intervals closely overlapped. As species became more sensitive, the overpredicted areas became increasingly concentrated in logged cells, and the bootstrapped confidence intervals around the mean logging intensity in the correctly and overpredicted cells started to be consistently different at similar relative sensitivity levels across spatial extents, (0.25-0.3) (Figure 3-2). The differences between mean logging intensity in correctly predicted and overpredicted cells increased, but at different rates across extents. The rate constant of the non-linear regression fitted to the difference was largest at the landscape extent (11), intermediate at the regional extent (7.4), and lowest at the sub-continental extent (4.1): correctly and overpredicted cells started to differ in their logging intensity fastest at lower sensitivity levels at the landscape extent, and slowest at the sub-continental extent. Logging intensity in overpredicted and correctly predicted cells reached maximum difference at 0.25 relative sensitivity at the landscape extent, 0.36 at the regional extent, and 0.48 at sub-continental extent (Figure 3-3).

Table 3-2 The percentage of cells over-predicted by the NOLOG model (relative to the LOG model) in the difference maps. The over-prediction is greatest for species very sensitive to logging, and at the landscape spatial extent. For brevity, wwe present overprediction calculations for five out of the ten pseudo-species which span the range of sensitivity levels and the range of overprediction.

Scale	Relative logging sensitivity	Number of cells in difference map	Number of overpredicted cells	% overprediction
Landscape	0.01	471	11	2.4
	0.25	613	165	26.9
	0.5	749	298	39.8
	0.75	765	296	38.7
	1	853	432	50.6
Region	0.01	2488	157	6.3
	0.25	2644	325	12.3
	0.5	3134	722	23.0
	0.75	3416	1035	30.3
	1	3333	1056	31.7
Sub-continental	0.01	13397	620	4.6
	0.25	15627	1453	9.3
	0.5	16033	2903	18.1
	0.75	16204	2387	14.7
	1	16602	3457	20.8

3.4.4. Relation between variable heterogeneity and predictive performance

The range of climatic heterogeneity became narrower with decreasing spatial extent, while the range of logging intensity increased (Figure 3-4), confirming our assumption that relative logging heterogeneity in BC is highest at the smallest (landscape) extent. The importance values (IVs) of all predictor variables were positively correlated to their heterogeneity (measured as IQR). The importance values (IVs) of logging intensity in LOG models increased with the species sensitivity to logging, but the increase was steepest at the landscape extent (Figure 3-5, Appendix C – Table C3).

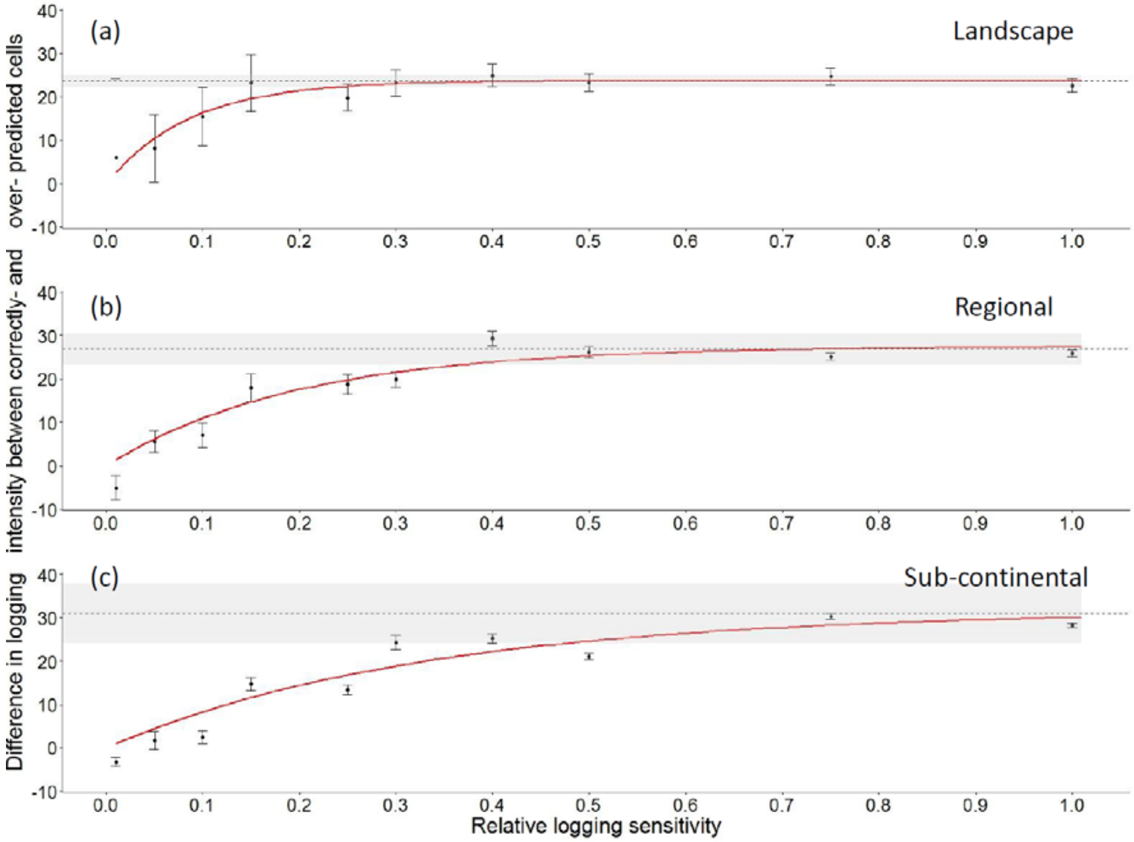


Figure 3-3 The bootstrapped effect size of logging sensitivity on bias in NOLOG models, measured as the difference between the average logging intensity in the correctly predicted and overpredicted cells. Dots represent mean values and whiskers are bootsrapped 95% confidence intervals. The red lines are the best-fit lines from an asymptotic non-linear least squares regression, forced through the origin. The model parameters are the asymptote value (Asym), and the natural log of the rate of change (of the curve before the asymptote = lrc). Landscape (Asym=23.6, lrc=2.4), regional (Asym=26.8, lrc=1.7), sub-continental (Asym=31.0, lrc=1.1). The shaded grey bars are the 95% confidence intervals around the fitted asymptote values.

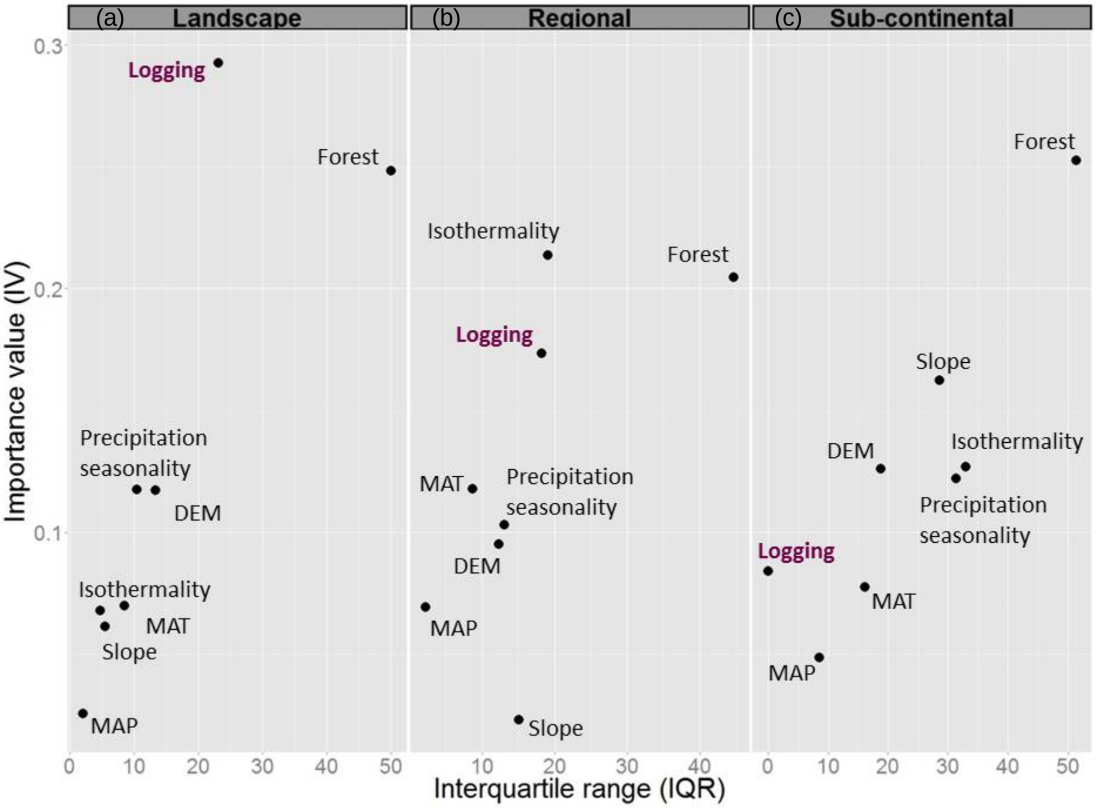


Figure 3-4 The correlation between the heterogeneity (measured as interquartile range) of all variables used for distribution modeling, and their weighted importance value in the LOG models (at logging sensitivity = -1). Relationships are presented for all 3 extents to illustrate how the heterogeneity of logging relative to other factors decreases at larger extents, and how that changes its importance value.

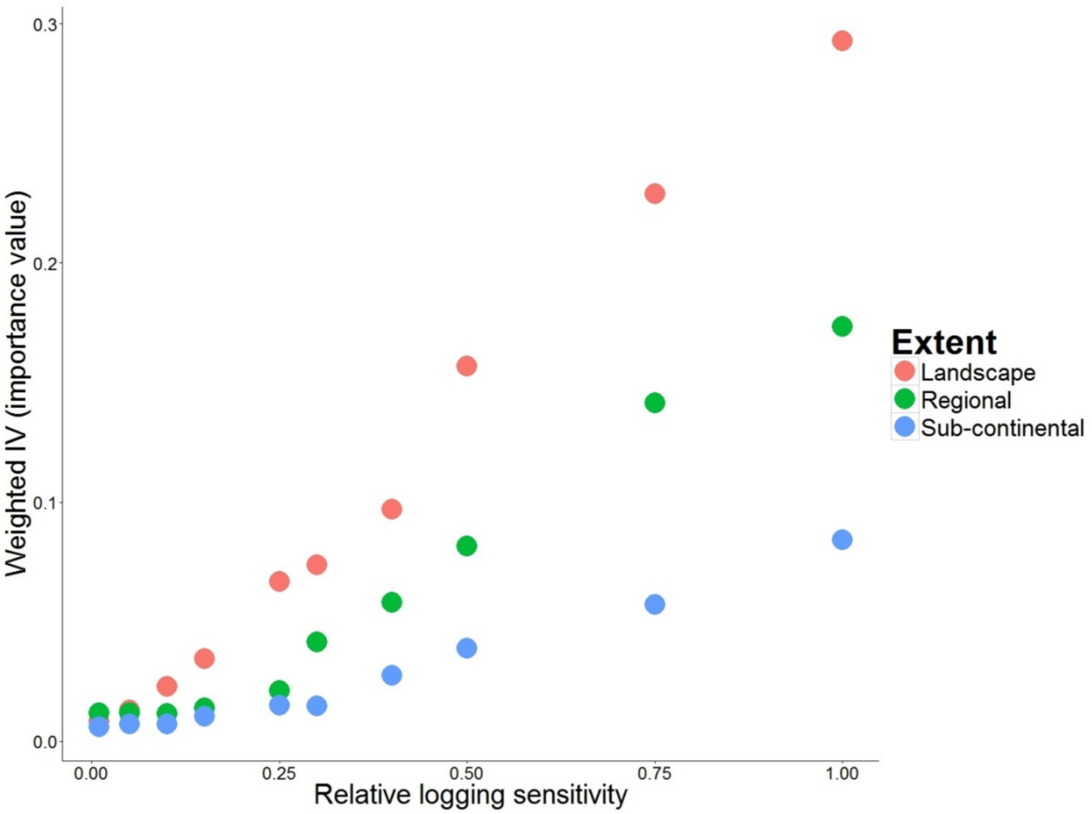


Figure 3-5 The relationship between the pseudo-species sensitivities to logging and the predictive power of logging (measured by importance value) in those species distributions, as predicted by the LOG models. Relationships are shown at the three spatial extents (landscape, regional, sub-continental). Values can be found in Appendix C – Table C3.

3.5. Discussion

Our study highlights the importance of including patchy, spatially extensive disturbances when modeling species distributions, and addresses the call for incorporating habitat characteristics in species distribution models (Pearson et al. 2004, Franklin 2010). We found that logging intensity has a measurable effect on distributions of species with moderate and high sensitivities to logging, and shouldn't be assumed to be too noisy and transient to be of use, especially when modeling distributions at landscape extents (10-200km) (Pearson and Dawson 2003). By using simulated species distributions based on real biophysical data from the province of British Columbia (BC), Canada, our results showed that failing to incorporate the intensity of logging (NOLOG model) resulted in overpredicted species presence, and biased the predictions of occurrence towards heavily logged areas. Conversely, by comparing distributions predicted with and without a logging variable, we obtain a proxy of the direction and strength of a species response to the disturbance. For example, for a species with a logging sensitivity level equal to all other predictors (i.e., most sensitive species simulated), between 20% and 50% of the predicted distribution (Table 2) was overpredicted by the NOLOG model. When comparing logging intensity between correctly predicted and overpredicted cells, average logging intensity in the overpredicted area was 23-31% higher than in the correctly predicted part of the distribution, depending on the spatial extent (Table 3).

Our results support the assumption that anthropogenic land-cover disturbance or change plays an important role in species distributions at landscape or intermediate spatial extents (Bolliger et al. 2000, Thuiller et al. 2003). We found that the effects of logging intensity on species distributions were larger at smaller geographic extents. The spatial overpredictions from the NOLOG model were smallest at the sub-continental extent (21% across ~900,000km^2), 1.5 greater at the regional extent (32% across ~168,000 km^2), and 2.5 times more over-predicted at the landscape extent (51% across ~30,000 km^2)). NOLOG models also biased distributions towards heavily logged areas; these biases were most pronounced at higher sensitivities and smallest spatial extents, and decreased with increasing extent size (Figure 3-3).

The extent-dependent results reflected the fact that logging intensity was more heterogeneous relative to the other predictive variables at smaller geographic extents in our study. We found that the predictive ability of variables in the model was positively correlated to their heterogeneity. The explanatory power shifted from being dominated by climatic variables at larger spatial extents to being dominated by logging intensity at the smallest extent. In our study, forest cover had the highest variance among all variables at every extent, resulting in higher explanatory power compared to logging intensity across all models, except for pseudo-species with logging sensitivity -0.75 and -1 at the landscape extent. Because logging is spatially nested within forest land cover, and likely varies across finer extents, the importance of logging intensity likely peaks at landscape extents, but it would decline at increasingly smaller extents as other habitat characteristics, which vary over even smaller extents (such as soil type, edge effects, or biotic interactions (Pearson and Dawson 2003)), gain dominance in driving the patterns of species occurrence and habitat selection (Johnson 1980, Wiens 1989).

Our results corroborate other species distribution modeling studies that have included land-cover and vegetation as predictor variables, and found that these variables often play a secondary role to climate in shaping species distributions at extents ranging from 30,000 km^2 (Provence-Alpes - C'ote d'Azur region) (Lyet et al., 2013) to 5,812,500km^2 (Canadian Boreal forest) (Cumming et al. 2013), and that their explanatory power increased when the extent or grain of the models is reduced (Luoto et al. 2007, Tingley and Herman 2009). However, evidence on the importance of landscape disturbance on shaping species distributions is not equivocal. For example, studies that have explicitly incorporated disturbance metrics into SDMs found that disturbance (i.e., wildfire occurrence, frequency, variability, or departure from historical return intervals) in fire-adapted plant communities in Mediterranean climates had low explanatory power relative to climate, soils and topography for predicting bird and plant species occurrence and abundance (Tucker et al. 2012, Crimmins et al. 2014). The authors attribute this finding to the high spatial correlation between fire regimes and climatic gradients as the likely reason for the unexpectedly low importance of fire variables. This is a reasonable hypothesis given that many forest disturbance regimes are correlated with climatic gradients (Dale et al. 2001). Another potential explanation may be that those models were applied at spatial extents that were too large to detect how the habitat heterogeneity created by fire regimes was influencing species distributions. Our results suggest that at landscape spatial extents, which generally, though not always, have a relatively homogenous climate, the finer-extent heterogeneity of disturbance and its effects on species distributions is more likely to be detected in SDMs. This finding could be applicable to even larger extents if the climatic and topographic gradients are not strong (for example, in lowland tropical regions). In addition, we expect that the predictive power of variables describing human-induced disturbance to be higher than that of natural disturbance variables at landscape and regional extents because they are less likely to be correlated with climatic and topographic gradients (Jordan et al. 2008).

To evaluate the benefits of accounting for logging disturbance in distribution models and examine the levels of species sensitivities and spatial extents at which such analyses are informative, we generated species with imposed logging sensitivity values that were relative to the sensitivity to climate, topographic and land-cover variables. Generating these simple relationships allowed us to isolate the effects of species sensitivity to logging on their spatial distribution patterns. For real species, these relative sensitivity values are unknown *a priori*. Instead, they are usually estimated *a posteriori* by examining standardized coefficients or other statistical measures (e.g., importance values from ensemble SDMs). For some species, there is information about the absolute sensitivity to logging or other disturbances (e.g., species does not occur when forest cover is <50% in a particular landscape). Researchers can use this *a priori* knowledge to make informed decisions about species which are expected to be affected by landscape disturbance (and the direction of the response), the disturbance layers which might be important to include in the SDMs, as well as the extents at which disturbance data can be aggregated. For example, in the context of BC, the Brown Creeper (Dellasala et al. 1996) and Tailed Frog (Wahbe et al. 2004), avoid recently logged areas and are considered highly sensitive to disturbance, while Orange-Crowned Warblers (Dellasala et al. 1996) and stoats (Samson and Raymond 1995) are more abundant in logged sites than old growth forest and are associated with logging. Drawing on these known relationships, and if the presence data does not show extreme spatial bias that would confound the direction of the response (e.g., a species may show a negative response to logging, but location data is biased to records collected along logging roads), species distribution models that include logging variables would be considerably more informative and accurate compared to models that ignore logging. While species distribution models based on mechanistic understanding of species habitat relationships are desirable (Graham et al. 2004), in the absence of empirical data on the species sensitivity to logging, this method can produce preliminary estimates of the effect of disturbance on species distributions.

In this study we demonstrated the utility of SDMs in detecting broad-scale species responses to disturbance, and used simulated data to provide a proof-of-concept for this comparative spatial approach. We recommend future studies apply disturbance/no disturbance model comparisons to locality data that is spatially unbiased for real species with well-described disturbance sensitivity based on field studies, or where clear mechanistic hypotheses exist for how disturbance affects specific habitat requirements. These comparisons also require that the spatial scale of species data being used to create the models are spatially comparable to the logging, or other disturbance, data being tested for predictive power and direction. Considering the temporal aspect of habitat recovery is critical when selecting disturbance-related variables to parameterize distribution models. The ‘time window’ of disturbance should be informed by empirical studies of species life histories and habitat requirements (e.g., old-growth specialist, early successional species). For example, if the timeframe is too narrow relative to the expected response, processes such as extinction debt (Tilman et al. 1994, Brooks et al. 1999) could lead to overestimating occurrence. While preliminary, our approach contributes to our understanding of the performance of species distribution models in complementing empirical studies which aim to predict distribution changes of species in response to anthropogenic disturbance (Bengtsson et al. 2002).

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Appendix A

Supporting material for Chapter 2

Table A1 Sources for the data used in this study

Data	Source	Date
MAP, MAT, Isothermality, precipitation seasonality	WorldClim online database (http://www.worldclim.org/bioclim)	1950-2000
Digital elevation model (DEM)	GeoBC (http://geobc.gov.bc.ca/base-mapping/imagery/products/gridded.html)	NA
Slope	calculated from DEM using the ‘Slope’ tool in ArcMap (Spatial Analyst > Surface > Slope)	NA
Forest cover	Synthesized from recent maps produced by the forest Practices Board (http://www.fpb.gov.bc.ca/)	2012
Logging intensity	A rasterized dataset produced by BC’s Forest Practices Board (http://www.fpb.gov.bc.ca/) , and supplemented by the global Forest Change study by Hansen et al 2013 (http://earthenginepartners.appspot.com/science-2013-global-forest)	1990-2012
BC Watershed atlas (WSA)	Publicly available on GeoBC. We used the stream centreline dataset (https://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?recordUID=4434&recordSet=ISO19115)	NA
Digital road atlas (BC)	Publicly available on GeoBC (http://geobc.gov.bc.ca/base-mapping/atlas/dra/)	NA
Powerlines	BC Hydro (shared under confidentiality agreement)	Current for 2013
BC ecoregion Classification	Provincial, publicly available data (http://www.env.gov.bc.ca/ecology/ecoregions/)	NA
BC Assessment Watersheds	Publicly available on GeoBC (https://apps.gov.bc.ca/pub/dwds/viewOrder.do?orderId=1510790)	NA

Breeding Bird Atlas	http://www.birdatlas.bc.ca/	2004-2012
BC Conservation Data Center	http://www.env.gov.bc.ca/cdc/access.html	2000-2012
Global Biological Information Facility	www.gbif.org	2000-2012
Breeding Bird Survey	http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e	2000-2012

Eceregion name	Code
BOREAL MOUNTAINS AND PLATEAUS	BMP
BOUNDARY RANGES	BOU
CENTRAL ALBERTA UPLAND	CAU
CENTRAL CANADIAN ROCKY MOUNTAINS	CRM
CHILCOTIN RANGES	CHR
CHUGACH MOUNTAINS AND ICEFIELDS	CMI
COASTAL GAP	COG
COLUMBIA HIGHLANDS	COH
EASTERN CONTINENTAL RANGES	ECR
EASTERN HAZELTON MOUNTAINS	EHM
EASTERN VANCOUVER ISLAND	EVI
FRASER BASIN	FAB
FRASER PLATEAU	FAP
GWAII HAANAS	GWH
HAY-SLAVE LOWLAND	HSL
HYLAND HIGHLAND	HHI
INTERIOR TRANSITION RANGES	ITR
LIARD BASIN	LIB
LOWER MAINLAND	LOM
MUSKWA PLATEAU	MPL
NASS RANGES	NRA
NORTHERN ALBERTA UPLAND	NUP
NORTHERN CANADIAN ROCKY MOUNTAINS	NRM
NORTHERN CASCADE RANGES	NCR
NORTHERN COLUMBIA MOUNTAINS	NCM
NORTHERN CONTINENTAL DIVIDE	NCD
OKANOGAN HIGHLAND	OKH
OMINECA MOUNTAINS	OMM
PACIFIC RANGES	PAC
PEACE RIVER BASIN	PRB
PELLY MOUNTAINS	PEM
PURCELL TRANSITIONAL RANGES	PTR
SELKIRK-BITTERROOT FOOTHILLS	SBF
SKEENA MOUNTAINS	SKM
SOUTHERN ALBERTA UPLAND	SAU
SOUTHERN ROCKY MOUNTAIN TRENCH	SRT
ST ELIAS MOUNTAINS	STE
THOMPSON-OKANAGAN PLATEAU	TOP
WESTERN CONTINENTAL RANGES	WRA
WESTERN VANCOUVER ISLAND	WVI
YUKON SOUTHERN LAKES	YSL
YUKON-STIKINE HIGHLANDS	YSH

Figure A1 Terrestrial Ecoregions of British Columbia, n=42

Additional background on dataset underpinning ROR development projections

Though some ROR projects in BC could potentially generate up to 300 GWh of electricity a year, over 90% of the potential projects would generate between 1 and 50 GWh/year, with the mean project generating 20 GWh/yr [data from an engineering dataset compiled by Kerr-Wood-Lydell, and protected by a data sharing agreement]. Given projections for BC's energy shortage by 2030 range from ~13,000 to ~ 24,000 GWh/yr (BC Hydro 2013), around 1000 projects would need to be built if ROR were the sole energy technology satisfying the shortage. Costs per unit energy produced vary widely across the potential sites, from 66 to >200,000 dollars/MWh. For comparison, BC's current residential electricity rates, which are subsidised by the provincial government, range from $75/MWh to $113/MWh. This renders many of the technically possible ROR locations economically unfeasible in the near-term, but high uncertainty remains around the exact economic threshold at which projects are likely to be developed.

Table A2. **The full names of the 10 methods available in Biomod2 for ensemble modeling. For primary references to the individual modeling methods, see** (Thuiller et al. 2009)

Model abbreviation	Full model name
GLM	Generalized Linear Model
GBM	Generalized Boosting Models
GAM	Generalized Additive Models
CTA	Classification Tree Analysis
ANN	Artificial Neural Networks
SRE	Surface Range Envelopes
MARS	Multivariate Adaptive Regression Splines
RF	Random Forests
FDA	Flexible Discriminant Analysis
MaxEnt	Maximum Entropy

Table A3. Regional distribution of watersheds of conservation concern (WCC)

Ecoregion	Sharing WCCs (km2)	Sparing WCCs (km2)	Congruent WCCs (km2)	Sharing unique WCCs (km2)	Sparing unique WCCs (km2)
PACIFIC RANGES	5086	7543	3784	1302	3759
EASTERN VANCOUVER ISLAND	4531	2986	2685	1846	301
NORTHERN COLUMBIA MOUNTAINS	1250	1239	801	449	0
BOUNDARY RANGES	664	1227	664	0	563
OMINECA MOUNTAINS	113	906	9	104	897
LOWER MAINLAND	1086	890	695	391	195
NASS RANGES	426	812	371	55	441
WESTERN VANCOUVER ISLAND	1303	701	349	954	352
YUKON-STIKINE HIGHLANDS	187	500	187	0	313
SKEENA MOUNTAINS	173	476	173	0	303
COASTAL GAP	84	459	84	0	375
CHILCOTIN RANGES	247	389	247	0	142
FRASER PLATEAU	1263	346	213	1050	133
WESTERN CONTINENTAL RANGES	175	319	157	18	162
PURCELL TRANSITIONAL RANGES	612	267	154	458	113
BOREAL MOUNTAINS AND PLATEAUS	0	226	0	0	226
FRASER BASIN	151	176	80	71	96
SELKIRK-BITTERROOT FOOTHILLS	621	104	104	517	0
COLUMBIA HIGHLANDS	372	96	96	276	0
SOUTHERN ROCKY MOUNTAIN TRENCH	345	75	75	270	0
INTERIOR TRANSITION RANGES	117	55	18	99	37
NORTHERN CASCADE RANGES	167	54	54	113	0
CENTRAL CANADIAN ROCKY MOUNTAINS	9	30	0	9	30
THOMPSON-OKANAGAN PLATEAU	649	4	4	645	0
OKANOGAN HIGHLAND	218	0	0	218	0

Table A4. The total, modeled area of the riparian distribution of our study species in BC

Scientific name	Total riparian distribution (ha)
Ascaphus truei	3641284
Brachyramphus marmoratus	1162082
Cinclus mexicanus	3885200
Empidonax difficilis	2136511
Histrionicus histrionicus	3306070
Lontra canadensis	2707081
Martes americana	541180
Martes pennanti	1523223
Mergus merganser	4910370
Neovison vison	4032035
Neurotrichus gibbsii	589802
Plethodon vehiculum	850084
Rana aurora	868662
Sorex bendirii	673443
Sorex palustris	3646977

Appendix B

Supplementary spreadsheet 1

Description:

Table B1 (first sheet): a spreadsheet summarizing the literature we used to identify riparian obligates or closely associated species. Only name of author(s) and year of reference are listed, along with the key information extracted from the paper and used in our classification of species as ‘riparian’; full citations can be found in corresponding cells in ‘Citations for table B1’ (second sheet). Table B2 (third sheet) is a spreadsheet summarizing the literature we used to identify species sensitivity to mature forest disturbance. More detail on defining species sensitivity can be found in Methods section 2.3.5. Full citations for Table B2 can be found in corresponding cells in the fourth sheet, ‘Citations for Table B2’.

File name:

Riparian species literature review and citations.xlsx

Appendix C

Supplementary materials for Chapter 3

Table C1 The environmental layers used for simulating and modeling species distributions in our study

Variable	Source	Date
MAP, MAT, Isothermality, precipitation seasonality	WorldClim online database (http://www.worldclim.org/bioclim)	1950-2000
Digital elevation model (DEM)	GeoBC (http://geobc.gov.bc.ca/base-mapping/imagery/products/gridded.html)	NA
Slope	calculated from DEM using the ‘Slope’ tool in ArcMap (Spatial Analyst > Surface > Slope)	NA
Forest cover	Synthesized from recent maps produced by the BC Forest Practices Board (http://www.fpb.gov.bc.ca/)	2012
Logging intensity	A rasterized dataset produced by BC’s Forest Practices Board (http://www.fpb.gov.bc.ca/) , and supplemented by the global Forest Change study by Hansen et al 2013 (http://earthenginepartners.appspot.com/science-2013-global-forest)	1900-2012

Table C2 **The full names of the 10 models available in Biomod2 for ensemble modeling**

Model abbreviation	Full model name
GLM	Generalized Linear Model
GBM	Generalized Boosting Models
GAM	Generalized Additive Models
CTA	Classification Tree Analysis
ANN	Artificial Neural Networks
SRE	Surface Range Envelopes
MARS	Multivariate Adaptive Regression Splines
RF	Random Forests
FDA	Flexible Discriminant Analysis
MaxEnt	Maximum Entropy

**Table C3	The logging variables IVs for all simulations (at all extents)**

Relative logging sensitivity	Extent	Weighted importance value (IV)
0.01	Landscape	0.009
0.01	Regional	0.012
0.01	Sub-continental	0.006
0.05	Landscape	0.013
0.05	Regional	0.012
0.05	Sub-continental	0.007
0.1	Landscape	0.023
0.1	Regional	0.012
0.1	Sub-continental	0.007
0.15	Landscape	0.034
0.15	Regional	0.014
0.15	Sub-continental	0.011
0.25	Landscape	0.067
0.25	Regional	0.021
0.25	Sub-continental	0.015
0.3	Landscape	0.074
0.3	Regional	0.041
0.3	Sub-continental	0.015
0.4	Landscape	0.097
0.4	Regional	0.058
0.4	Sub-continental	0.027
0.5	Landscape	0.157
0.5	Regional	0.081
0.5	Sub-continental	0.039
0.75	Landscape	0.229
0.75	Regional	0.142
0.75	Sub-continental	0.057
1	Landscape	0.293
1	Regional	0.173
1	Sub-continental	0.084

Appendix D

Supplementary spreadsheet 2

Description:

> Literature review of selected, widespread British Columbia bird species responses to forest habitat disturbance through logging and fire. Authors, publication year, and key result from paper are noted within spreadsheet. Please contact author (Evgenia Dubman) for complete bibliography.

File name:

> Bird responses logging fire disturbance.csv