1 Fragmentation effects on an endangered species across a gradient from the interior to edge of

2 its range

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ABSTRACT

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Habitat fragmentation is a global phenomenon that negatively impacts many species. Understanding how fragmentation affects individual species, however, is complicated by challenges with quantifying species-specific habitat and spatial variability in fragmentation effects within a species' range. We aggregated a 29-year breeding survey dataset for the endangered Marbled Murrelet (Brachyramphus marmoratus) from >42,000 forest sites throughout the Pacific Northwest (Oregon, Washington, and northern California, USA). We built a species distribution model (SDM) linking occupied sites with Landsat imagery to quantify murrelet-specific habitat, then used occupancy models to test the hypotheses that (1) fragmentation negatively affects murrelet breeding distribution, and (2) these effects are amplified with distance from the marine foraging habitat towards the edge of the species' nesting range. Murrelet habitat declined in the Pacific Northwest by 20% since 1988 while the proportion of habitat comprising edges increased by 17%, indicating increased fragmentation. Furthermore, fragmentation of murrelet habitat at landscape scales (within 2 km of survey stations) negatively affected occupancy of potential breeding sites, and these effects were amplified near the range edge. On the coast, the odds of occupancy decreased by 37% (95% confidence interval [CI]: -54% to 12%) for each 10% increase in edge habitat (i.e., fragmentation), but at the range edge (88 km inland) these odds decreased by 99% (95% CI: 98% to 99%). Conversely, odds of murrelet occupancy increased by 31% (95% CI: 14% to 52%) for each 10% increase in local edge habitat (within 100 m of survey stations). Avoidance of fragmentation at broad scales but use of locally fragmented habitat with reduced quality may help explain the lack of murrelet population recovery. Further, our results emphasize that fragmentation effects can be nuanced, scale-dependent, and geographically variable. Awareness of these nuances is critical for developing landscape-level conservation strategies for species experiencing broad-scale habitat loss and fragmentation.

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64 INTRODUCTION

Habitat loss and degradation from anthropogenic disturbances is the leading cause of biodiversity decline worldwide and is expected to continue in the future (Pimm & Raven, 2000; Newbold et al., 2015). Fragmentation - the breaking apart of habitat into smaller, more isolated patches - often results from habitat loss, but evidence regarding how fragmentation per se (independent of habitat loss; *sensu* Fahrig, 2003) impacts biodiversity is mixed (Fahrig, 2013, 2017; Haddad et al., 2015; Fletcher et al., 2018; Fahrig et al., 2019). Some species benefit from fragmentation due to augmented habitat and resource diversity, reduced competition, and resulting predator refuges (Fahrig, 2017; Fahrig et al., 2022). For other species, fragmentation is detrimental because it creates patches insufficient for meeting space or life history requirements, alters local habitat, and affects landscape connectivity (Lindenmayer & Fischer, 2006; Fahrig et al., 2022). Identifying species negatively impacted by fragmentation is critical given that large, contiguous tracts of undisturbed land are dwindling globally (Haddad et al., 2015).

Uncovering fragmentation effects on target species is complex. First, because habitat loss and fragmentation often occur simultaneously, researchers must control for habitat amount to examine effects of fragmentation per se (Fahrig, 2013; Hadley & Betts, 2016). Secondly, fragmentation assessments often rely on human-defined land cover types (e.g., forest, grassland) that are useful to managers but are often imprecise habitat representations for individual species (Betts et al., 2014). Measuring habitat fragmentation requires understanding the species' perception of the landscape, yet studies rarely take a species-centered approach (Betts et al., 2014; Halstead et al., 2019). Additionally, intra-species fragmentation effects can vary in space. The center-periphery hypothesis posits that populations at the range edge can have reduced genetic variation and demographic performance resulting from exposure to distinct stressors such as reduced bioclimatic suitability (Péron & Altwegg, 2015; Williams & Newbold, 2021), novel predator and competitor assemblages (Orme et al., 2019), and lower immigration rates (Hargreaves et al., 2014). Disturbances like fragmentation could thus exacerbate effects of these stressors at range edges while individuals inhabiting range interiors may select fragmented areas to minimize competition (Orme et al., 2019; Banks-Leite et al., 2022). Thus, for some species, inference regarding fragmentation effects may depend on study location, and effective conservation strategies may vary spatially. However, data are rarely collected across sufficiently large gradients of a species' range to enable testing this hypothesis, particularly in the temperate zone.

Landscape-level conservation planning has been particularly salient and controversial in the Pacific Northwest (Washington, Oregon, and northern California), USA. Historically, the area between the Cascade Mountains and the Pacific Ocean was dominated by Douglas-fir (*Pseudotsuga menziesii*) forests in a mosaic of successional stages driven by an infrequent firebased disturbance regime. These forests became a timber production hub in the United States (Adams & Latta, 2007), and by the early 1990s old growth and late-successional forests were well below historic levels (Wimberly et al., 2000). The 1994 Northwest Forest Plan (NWFP) has since focused on protecting old-forest habitat for species like the Marbled Murrelet (*Brachyramphus marmoratus*; hereafter, murrelet), resulting in a prolonged, contentious debate regarding tradeoffs between timber production and biodiversity conservation (Spies et al. 2019).

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The murrelet is a small seabird in the family Alcidae with a range stretching from the Aleutian Islands south to Monterey Bay, USA (Figure 1; Nelson, 2020). Long-term climatic shifts and acute marine heating events have reduced diet quality for murrelets which forage in the near-shore marine environment, reducing reproductive success and occupancy of nesting habitat (Peery et al., 2004; Becker et al., 2007; Betts et al., 2020). In the Pacific Northwest, murrelets typically nest on large tree limbs in old forests found <90 km inland (Raphael et al., 2018). Consequently, loss of old coastal forests from logging and wildfires also reduces recruitment (Raphael et al., 2018; Betts et al., 2020; Nelson, 2020). Despite being protected throughout the Pacific Northwest and Canada, murrelet populations have not recovered in the past two decades (McIver et al., 2021).

Although fragmentation of murrelet breeding habitat is hypothesized to hinder population growth, past studies have often failed to account for confounding variables (e.g., habitat amount, species perception, range heterogeneity), and evidence remains ambiguous (Burger & Page, 2007; Zharikov et al., 2006, 2007a). Previous research suggests murrelets nest in old growth areas with less edge (e.g., Rodway & Regehr, 2002; Ripple et al., 2003), likely because nest predation rates can be $2.5 \times$ greater near forest edges than patch interiors (Raphael et al., 2002; Malt & Lank, 2007, 2009). Survey data also indicate inland and at-sea murrelet distributions (Meyer & Miller, 2002; Meyer et al., 2002; Raphael et al., 2015), are positively correlated with contiguity of proximal breeding habitat (although this relationship may deteriorate at broad scales; Lorenz et al., 2021). Conversely, research from British Columbia, Canada, found murrelets select nest sites near forest edges (Zharikov et al., 2006, 2007b; but see Burger & Page, 2007). This may occur because murrelets often travel along natural canopy gaps (e.g., creeks) when approaching nests (Nelson, 2020), and clearcut openings could be used similarly. Regardless of the mechanism, developing effective landscapelevel conservation schemes requires clarity regarding the effects of landscape structure on murrelet distributions.

In this study, we aggregated murrelet surveys conducted over a 29-year period at >40,000 forest locations across the Pacific Northwest (Figure 1). We linked remotely sensed land-cover covariates with murrelet detections to build year-specific murrelet species distribution models (SDMs) and quantify habitat (Betts et al., 2014). We then combined SDMs and survey data to address three objectives. First, we examined how distribution of murrelet habitat has changed over 3 decades. Second, we tested the hypothesis that fragmentation per se (i.e., after controlling for local habitat amount) influences murrelet distributions. If murrelets avoid fragmented habitat due to harsher microclimatic conditions (Raphael et al., 2002) or increased nest predation, we would predict a negative association between fragmentation and murrelet occupancy. However, if murrelets select breeding sites near forest edges to facilitate nest access, we would predict a positive association. Lastly, we tested the hypothesis that fragmentation effects are amplified at the edge of the species' range. Across the Pacific Northwest, abrupt changes in precipitation and vegetation lead to a lack of adequate nesting habitat 40-80 km inland while reliance on the nearshore marine foraging environment constrains the distance murrelets can travel to nest sites. Thus, forest tracts further from the coast are closer to the murrelet's terrestrial range edge (Fig. 1) and ecologically more marginal

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due to increased distance from a food source. We therefore predict that negative edge effectswill increase with distance-from-coast.

METHODS

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Marbled Murrelet occupancy surveys

We gathered data on historical murrelet breeding distributions by aggregating audiovisual surveys collected at inland forests between 1988 and 2016 from: the US Forest Service; US Bureau of Land Management; Oregon Departments of Forestry, Parks and Recreation, and Fisheries and Wildlife; California Department of Fish and Wildlife; Washington Department of Fish and Wildlife; Redwood National and State Parks; timber companies (Louisiana-Pacific, Miller-Rellim, Pacific Lumber, and Arcata Redwood); Hoopa Indian Reservation; and university researchers (Figure 1). Most surveys were conducted around proposed timber harvest sites with one survey station per 8-10 ha. Site-level sampling effort varied with number of stations, but station size (200 m radius circle) was standardized (Evans Mack et al. 2003), so we conducted all analyses at the station level. Stations were surveyed iteratively until murrelet breeding activity was recorded at the site or the minimum number of required surveys was conducted (5-9 surveys in each of 2 years, Evans Mack et al., 2003). Each 2-h morning survey was conducted by a trained observer who recorded all murrelet detections and behaviors following standardized protocols for identifying murrelet breeding activity (Evans Mack et al., 2003).

We reduced this dataset to stations in the murrelet's nesting range within the Pacific Northwest (Lorenz et al., 2021; Figure 1). We aggregated data from stations <100 m apart and eliminated surveys not conducted between 15 April and 5 August, the recommended sampling window (Evans Mack et al., 2003). This left 42,008 survey stations. Some stations were sampled in multiple years, but we only used data from the station's first sampling year in all analyses to avoid pseudo-replication. The annual number of stations surveyed for murrelets ranged from 139 in 2016 to 3,043 in 2001. Stations were well-distributed across gradients in habitat amount and fragmentation over the 29-year period (see Figure S1.1 in Appendix S1). Most stations were concentrated between 10-40 km from the coast, but some were up to 100 km inland (Figure S1.2). We reclassified survey results into a detection/non-detection dataset where detections only included "occupied behaviors" indicative of nesting activity (e.g., sub-canopy flights, landing, stationary calling; Evans Mack et al., 2003). We excluded above-canopy circling (typically considered an "occupied behavior") because it cannot be reliably associated with a precise nest location.

185 Species distribution modeling

Using MaxEnt, we built a model that predicts probability of presence at unique points in
 space and time, then used this model to build year-specific murrelet SDMs covering our study
 area. MaxEnt model inputs included the 2,029 stations where murrelet occupancy was

189 recorded, and 10,000 background locations randomly distributed in space and time. We used 190 random locations rather than non-detection stations because the species has low detectability 191 and failing to record occupancy does not guarantee absence (Evans Mack et al., 2003; Valente et 192 al., 2021). We modeled occupied and background locations as a function of three covariate 193 types. First, we used Landsat Collection 1 surface reflectance data (30-m pixel resolution; 194 https://www.usgs.gov/landsat-missions/landsat-surface-reflectance) from 1985 to 2020 to 195 characterize environmental variables. We used raw reflectance data rather than forest structure 196 variables derived from Gradient Nearest Neighbor (GNN) map products (Ohmann & Gregory, 1972002) because (1) we did not want to propagate error from GNN imputations into our SDM, (2) 198 avian SDMs based on raw reflectance data perform well (Shirley et al., 2013; Betts et al., 2022), 199 and (3) future murrelet habitat mapping under the NWFP will also use raw reflectance data (M. 200Raphael, personal communication). After masking clouds and shadows, we used Continuous 201 Change Detection and Classification (CCDC) algorithms (Zhu & Woodcock, 2014) in Google 202 Earth Engine (Gorelick et al., 2017) to break the spectral data time series into different temporal 203 segments, each characterized by a set of harmonic parameters. We used median peak 2-band 204 enhanced vegetation index day of year (day 182) from MODIS Global Vegetation Phenology 205 product (DOI: 10.5067/MODIS/MCD12Q2.006) as the mapped day each year and extracted 206 CCDC harmonic parameters on day 182 for all locations. Secondly, we included categorical 207 covariates representing mapped disturbances from 1972 to 2002 (Healey and Cohen 2004) and 208 from 1985 to 2020 (Landscape Change Monitoring System; Cohen et al., 2018; Healey et al., 2092018). Finally, we incorporated topographic variables, including physiodiversity, topographic 210 diversity, multi-scale topographic position index, and elevation (Theobald et al., 2015). Because 21 sampling occurred over a 29-year period, covariates for each station were measured in the year 212 213 214 215 216 21 220 22 222 223 224 225

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the station was sampled. We excluded distance-from-coast in the SDM because including it created correlation between this and the habitat estimates extracted from the SDM, making it impossible to discern covariate effects in occupancy models (see below). We built the MaxEnt model using a complementary log-log data transformation where 50% of presence data were used for training, and 50% for validation. To account for heterogeneity in random sampling of training sites, we built 20 MaxEnt models and estimated model predictive performance by calculating the mean area under the Receiver Operator Characteristic Curve (AUC). Finally, we used fitted MaxEnt models to create year-specific SDMs from 1985-2020 by generating pixel-level predictions of murrelet occupancy probability. We used mean annual predicted values from the 20 replicates as the final maps. **Temporal changes in habitat** We reclassified annual SDM pixels into habitat/non-habitat using an objective cutpoint (habitat = presence probability >0.45) that maximized the sum of the model's sensitivity and 226 specificity on the Receiver Operator Characteristic Curve (Halstead et al., 2019). Thus, our 227 habitat designation is murrelet-specific and based on biophysical conditions enabling species

occupancy (see Appendix S2 for a complimentary analysis using a higher SDM threshold value). We then used annual GNN map products (Ohmann & Gregory, 2002;

https://lemmadownload.forestry.oregonstate.edu/) to identify pixels with open canopies, including urban areas and forests with conifer cover ≤40%. Murrelet habitat pixels adjacent to an open canopy cell were further classified as a "hard edge" and we used the distribution of hard edges to represent regional fragmentation (Figure 2). We did not distinguish between natural (e.g., creek corridors or windthrow gaps) and anthropogenic (e.g., clearcuts) hard edges. We quantified temporal changes in murrelet habitat by summing the amount of habitat and hard-edge pixels annually for the entire study area, then separately based on 5 land ownership categories (Phalan et al. 2019): federal (e.g., national parks and forests), state (e.g., state parks and forests), private industrial (predominantly forest industry lands), private non-industrial (e.g., small family-owned land holdings), and other (e.g., lands owned by local governments, native American tribes, or under private conservation easements). We calculated habitat amount from 1988-2020 but only calculated edge area through 2017 due to lack of contemporary GNN layers.

Model covariates

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To quantify effects of habitat amount and fragmentation on murrelet breeding distributions, we measured the proportion of the area around each survey station consisting of habitat (hereafter, habitat amount) and hard edges (hereafter, edge habitat), respectively (Figure 2). This represents a focal-plot study design, and we recognize there is disagreement whether fragmentation effects should be measured using focal-plots or replicate landscapes (Fletcher et al., 2018; in press; Fahrig et al., 2019). We chose the focal-plot design because we expected murrelet habitat selection to be driven by characteristics proximal to possible nest sites rather than characteristics of arbitrarily defined landscapes in which these sites fell (Mayor et al., 2009). Because habitat selection is a multi-scale process (Meyer et al., 2007; Mayor et al., 2009), we measured habitat and edge proportions in 7 buffers around each station with radii measuring 0.1, 0.5, 1, 2, 3, 4, and 5 km. We chose the 2 km buffer (hereafter, *landscape* scale) to represent the scale at which landscape-level processes occur (e.g., dispersal and predator density effects) because (1) previous work has shown this scale is relevant to murrelets (Meyer et al., 2002), and (2) variables measured within 2 km were highly correlated $(r \ge 0.7)$ and therefore redundant with corresponding variables in 0.5 to 5 km buffers. We chose the 0.1 km buffer as the scale relevant to local processes (hereafter, *local scale*) such as nest visibility to predators and nest site accessibility.

Finally, we quantified proximity of survey stations to the murrelet's breeding range edge by measuring distance-from-coast. Points further from the coast are closer to the range edge given that murrelets rely on the marine foraging environment and nesting structure is typically unavailable >40-80 km inland. Calculations and variable extractions were conducted using Google Earth Engine (Gorelick et al., 2017) or R v 4.1.1 operating on the Smithsonian Institution High Performance Computing Cluster (https://doi.org/10.25572/SIHPC).

269 Statistical analyses

We tested for effects of habitat amount, edge habitat, and distance-from-coast on murrelet breeding activity using static occupancy models (MacKenzie et al., 2002). These models assume sampling stations are closed to changes in occupancy - defined here as presence of "occupied behaviors" (Evans Mack et al., 2003) - over repeated surveys within a breeding season and use repeated surveys to account for the probability of detecting occupancy. Importantly, these models provide unbiased occupancy estimates even when sampling effort varies across survey stations because missing observations contribute no information to the model likelihood (MacKenzie et al. 2002). We fit occupancy models in R (v. 3.6.3) using the unmarked (v. 1.1.0) package (Fiske & Chandler, 2011). To facilitate model convergence, we standardized all covariates by subtracting the mean and dividing by the standard deviation.

We eliminated 1,222 stations from this analysis because they were within 2 km of our SDM boundary, preventing quantification of landscape-scale covariates. Data for these models thus included 60,633 surveys at 40,786 unique stations over 29 years (mean = 1.49 surveys/station, sd = 1.00; see Table S1.1 for ownership information). Data from ~5% of survey stations used in occupancy models (n = 1,990 occupied stations) were previously used to develop the SDM; although subsequently modeling detections as a function of SDM characteristics may appear circular, all occupancy model covariates measured the spatial distribution of habitat around stations which are emergent properties from the SDMs. These characteristics are therefore not directly related to the cell-specific properties used to distinguish them as murrelet habitat for SDM development.

We modeled detection probability using covariates known to impact murrelet detectability (Betts et al., 2020). These included linear effects of canopy cover and conifer density within 100 m measured from GNN layers (Ohmann & Gregory, 2002; <u>https://lemmadownload.forestry.oregonstate.edu/</u>), a quadratic day-of-the-year effect and a data source covariate to account for potential detection heterogeneity introduced by local land management practices. Lastly, we included a linear effect of local (within 100 m) edge habitat because murrelets are generally more detectable near canopy openings (Evans Mack et al., 2003).

Sometimes fragmentation effects only manifest below a threshold in habitat amount (Andrén, 1994; Betts et al., 2006). Thus, we first tested a model in which occupancy was a linear function of habitat amount, edge habitat, and their interaction at both scales. We also included a linear distance-from-coast effect and a categorical year covariate to account for heterogeneity in annual ocean conditions known to affect inland occupancy (Betts et al., 2020 – similar ocean condition covariates covering our study extent were unavailable). We excluded interactions between year and other model covariates because we did not expect habitat selection to vary annually. The interaction terms between habitat amount and edge habitat were weak and non-significant at both the local ($\beta = -0.02$, 95% CI = [-0.11, 0.07], Z = -0.50, p = 0.62) and landscape scales ($\beta = 0.05$, 95% CI = [-0.02, 0.12], Z = 1.27, p = 0.20), suggesting fragmentation effects vary little with habitat amount. Therefore, in our final model we dropped these interaction terms and replaced them with interactions between edge habitat and distance-from-coast at both scales. Importantly, we could distinguish the independent contributions of habitat amount and edge habitat to murrelet occupancy because there was no strong correlation among these, or any

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other covariates included in our models (|r| < 0.61; Table S1.2). We evaluated the final model's fit (model structure in Appendix S3) by comparing the Pearson's chi-square statistic from the original dataset to a distribution of 1,000 parametrically bootstrapped chi-square statistics, and estimated overdispersion (\hat{C}) by dividing the model's chi-square value by the mean of the bootstrapped values (MacKenzie & Bailey, 2004).

RESULTS

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Temporal changes in habitat

Our SDM effectively distinguished areas of likely murrelet breeding habitat. The AUC for model building and validation were 0.840 and 0.826, respectively. This indicates that a randomly selected occupied site will have a greater SDM value than a randomly selected background point > 80% of the time which is considered excellent discriminatory power (Hosmer et al., 2013).

Annual SDMs indicated murrelet habitat declined by nearly 20% in the Pacific Northwest between 1988 and 2020, a loss of almost half a million hectares (Figure 3a). Private industrial lands accounted for 74% of those losses while private non-industrial lands accounted for another 20% (Figure 3b). The only long-term increases occurred on federal lands, although this gain was only 2,000 ha over the 32-year period. As the total amount of murrelet habitat declined in this region, the remaining habitat became more fragmented; the proportion of murrelet habitat comprising hard edges (i.e., adjacent to young, open-canopy forest or nonforest) increased by 17% between 1988 and 2017 (Figure 3c). This edge increase occurred in all land ownership categories except Federal lands (Figure 3d). The largest increase occurred on private industrial lands where the proportion of murrelet habitat comprising edge nearly doubled. A complimentary examination of higher-value murrelet habitat yielded remarkably similar results to those reported here (Appendix S2). State-specific results are reported in Appendix S4.

Murrelet occupancy patterns

Bootstrapping results indicated our model was a reasonable fit for the empirical data. Although there was some evidence for overdispersion (p = 0.06), it was small (\hat{C} = 1.03) and thus had little impact on our error estimates (Burnham & Anderson, 2002). After accounting for imperfect detection, our occupancy estimates ranged from 4.8% (95% confidence interval [CI]: 3.7% to 6.3%) in 1989 to 36% (95% CI: 17.6% to 59.9%) in 2016 (Figure 4). All model parameter estimates are reported in Table S1.3.

Murrelets tended to occupy stations surrounded by murrelet habitat at multiple spatial scales. We found strong effects of habitat amount on murrelet occupancy at the local scale (Z = 13.66, p < 0.001) as the odds of occupancy increased by $1.16 \times (95\% \text{ CI: } 1.13 \text{ to } 1.18)$ for each 10% increase in murrelet habitat within 100 m (Figure 5a). We found similarly strong evidence

(Z = 8.23, p < 0.001) at the landscape scale where the odds of occupancy increased by 1.16 ×
(95% CI: 1.12 to 1.20) for each 10% habitat increase within 2 km (Figure 5b).

Murrelet occupancy increased with fragmentation at the local scale. There was a strong positive (Z = 3.67, p < 0.001) effect of local edge habitat on occupancy such that the odds of station occupancy increased by $1.31 \times (95\% \text{ Cl}: 1.14 \text{ to } 1.52)$ for each 10% increase in edge habitat within 100 m (Figure 5c). There was also a strong, negative effect of distance-from-coast on murrelet occupancy (Z = -14.78, p < 0.001), as the odds of station occupancy decreased by 3.1% (95% CI: 2.7 to 3.4%) for each 1 km increase in distance-from-coast (i.e., each 1 km closer to the range edge). However, there was little evidence that local edge effects changed with distance-from coast, as the interaction effect was weak and non-significant (β = -0.03, 95% CI = [-0.10 to 0.05], Z = -0.74, p = 0.46).

Conversely, murrelet occupancy decreased with fragmentation at the landscape scale. Moreover, these effects were amplified further inland as indicated by a strong negative interaction between distance-from-coast and landscape-level edge habitat (β = -0.25, 95% CI = [-0.33 to -0.17], Z = -5.96, p < 0.001). At stations on the coast, the odds of occupancy decreased by only 37% (95% CI: -54% to -12%) for each 10% increase in edge habitat but decreased by 99% (95% CI: -98% to -99%) at stations 88 km inland, the furthest distance-from-coast at which we detected murrelet occupancy (Fig. 5D).

DISCUSSION

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Using 29 years of sampling data and a species-specific habitat model, we found strong evidence that fragmentation (measured by the proportion of hard edges around sample stations) impacts murrelet distributions, and that those effects differ across scales. Importantly, these results cannot be explained by habitat loss alone because we controlled for habitat amount. Murrelets were less likely to occupy stations surrounded by fragmented habitat within 2 km, but more likely to use stations with locally fragmented habitat; this scale-dependent response could partially explain disparate conclusions among previous studies regarding fragmentation impacts on murrelets (Meyer & Miller, 2002; Meyer et al., 2002; Ripple et al., 2003; Zharikov et al., 2006, 2007b). Moreover, when combined with evidence for substantial loss and fragmentation of murrelet habitat in the Pacific Northwest, our findings highlight several plausible explanations for the lack of recovery of murrelet populations despite targeted protection (McIver et al. 2021).

382 Our findings are consistent with evidence that murrelet inland detections (Meyer & 383 Miller, 2002; Meyer et al., 2002), nest sites (Ripple et al., 2003), and at-sea distributions 384 (Raphael et al., 2015) are negatively associated with broad-scale fragmentation. This may 385 suggest murrelets avoid fragmented areas due to greater predation risk (Raphael et al., 2002; 386 Malt & Lank, 2007, 2009), abandon historically occupied areas once they become too 387 fragmented (Meyer et al., 2002), or reflect a lack of conspecific information about nesting 388 habitat in fragmented regions (Valente et al., 2021). Conversely, the positive, local-scale 389 fragmentation effect we observed supports previous findings that murrelets nest closer to

forest edges than expected by chance (Zharikov et al., 2006, 2007b). This could indicate trees near edges can develop larger limbs that provide more murrelet nesting opportunities. Alternatively, this could be driven by murrelet tendencies to travel and nest along open areas such as natural gaps and riparian corridors that facilitate nest access (Nelson, 2020). We did not distinguish natural and anthropogenic canopy gaps in our study, and it is unclear whether gaps generated by anthropogenic disturbances (e.g., forest harvest) are used similarly by murrelets. If they are, this could create an ecological trap given that habitat near clearcut edges is presumed to be lower quality for murrelets (Lorenz et al., 2021) due to higher rates of nest failure (Raphael et al., 2002; Malt & Lank, 2007, 2009).

After controlling for habitat amount, we also found strong support for the hypothesis that negative effects of landscape fragmentation can be amplified at the range edge (Orme et al., 2019; Banks-Leite et al., 2022). We recognize defining the range center and edge for a splithabitat species like the murrelet presents unique challenges. One might consider there are two range centers for the murrelet, one on land and one at sea. We identified the coast as the center of the species' range across the marine-interior gradient because fitness requires that birds traveling inland must return towards the coast to feed, and birds venturing out to sea must return towards the coast to breed. Further, while range boundaries are typically envisioned as being affected by local habitat characteristics, the murrelet's inland boundary is largely affected by distance from foraging resources. Nonetheless, this unique system created a robust test of the hypotheses that fragmentation effects vary across a species' range, and that disturbance effects are intensified at the range edge due to synergistic stressors (Banks-Leite et al., 2022). Birds breeding further inland will experience greater physiological stress from increased travel costs which could be exacerbated by greater rates of nest predation resulting from habitat fragmentation (Raphael et al., 2002; Malt & Lank, 2007, 2009). The influence of these two factors could drive behavioral shifts where inland-nesting birds are more averse, while coastalnesting birds are more tolerant to nesting in fragmented habitat. We did not test for similar patterns along the latitudinal axis of the species' range because our dataset only covered the southern portion which contains a large gap in inland distribution in California (Nelson, 2020), making it difficult to define the range periphery in this direction. Thus, whether similar patterns exist along a latitudinal gradient is left to future research.

Our study also improved on previous research by using emergent properties from an SDM (see methods) to quantify distribution of likely murrelet habitat. Rather than assuming old forests reliably represent murrelet breeding habitat (e.g., Meyer & Miller, 2002; Meyer et al., 2002; Zharikov et al., 2006, 2007b), our approach examines habitat and habitat fragmentation from the perspective of our target species. Because we did not explicitly model forest structure, we lack information on some of the specific forest characteristics comprising murrelet habitat in the region. However, we presume that increased murrelet occupancy probability within our SDM is associated with an increase in old growth forest components (e.g., legacy trees, large nesting platforms, multi-layered canopies) preferred by breeding murrelets (Hamer & Nelson, 1995; Nelson, 2020). We note, however, that previous work examining murrelet habitat trends has used forest structure variables that are themselves modeled as a function of Landsat reflectance data (Lorenz et al., 2021). By modeling murrelet occupancy as a direct function of reflectance data, we avoided propagating error from this interim step, and produced a habitat

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433 model that accurately distinguishes likely breeding habitat from random locations, as indicated434 by our validation tests.

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While our SDM demonstrates a much steeper murrelet habitat decline than has been previously reported (Lorenz et al., 2021), future modeling efforts under the NWFP will use a modeling approach analogous to ours that is likely to yield similar results (M. Raphael, personal communication). Interestingly, we found that the greatest loss and fragmentation of likely murrelet habitat (and high-value murrelet habitat; Appendix S2) occurred on private industrial lands which we presumed to be dominated by younger, heavily managed stands lacking habitat elements required by murrelets. Nevertheless, private industrial lands have clearly provided murrelet habitat through time as indicated by recorded occupancies in such landholdings (Table S1.1). Previous work has found similar evidence for steep declines in older forest on private industrial lands since the mid-1980s (Phalan et al., 2019). Therefore, the declines in murrelet habitat we observed may reflect a shift in timber production from federal to private lands following implementation of the NWFP (Wear & Murray, 2004).

Because our study is observational, we cannot say with certainty that the relationship between fragmentation and murrelet occupancy implies habitat selection. Murrelets are thought to be philopatric (Nelson, 2020), so it is possible that historically occupied landscapes have tended to be more disturbed over time which could occur if murrelet nesting sites or adjacent stands have been targeted for harvest due to the presence of mature trees. We found no evidence that occupied murrelet stations were more likely to experience fragmentation in recent years than unoccupied stations (Figure S1.3), so this explanation seems unlikely, but cannot be completely ruled out given we could not quantify the history of these sampled points prior to 1986 due to data limitations.

Regardless, our findings clearly indicate that murrelets exhibiting breeding behaviors tend to occupy landscapes with more contiguous habitat. Importantly, murrelet populations have failed to increase over the past two decades (McIver et al., 2021), a period in which we documented a striking reduction and fragmentation of the remaining murrelet habitat in the Pacific Northwest (Figure 3). Thus, our work adds to a growing body of evidence that, in conjunction with changing ocean conditions (Betts et al., 2020), murrelet population growth has been hindered by the distribution and availability of contiguous inland breeding habitat. These findings emphasize that disturbances near murrelet habitat (e.g., road development, timber harvest) likely have a negative effect on breeding activity, particularly if the affinity for locally fragmented sites we observed leads to use of lower quality habitat (Raphael et al., 2002; Malt & Lank, 2007, 2009). Alternatively, efforts to protect or restore sites near existing habitat may create more breeding opportunities and attract more individuals (Valente et al., 2021). Because the relationship between at-sea murrelet abundance and inland habitat remains ambiguous (Raphael et al., 2015; Lorenz et al., 2021), future research should examine if there are additional benefits to protecting contiguous nesting habitat near quality foraging areas.

471 Although identifying fragmentation effects can be challenging, it is critical for developing
472 effective management strategies and conserving biodiversity. Our study provides an example of
473 how to test for effects of fragmentation while accounting for habitat amount and species-

specific habitat requirements. We have also demonstrated that even within an individual species, the effects of habitat fragmentation may not be easily summarized as positive or negative, but instead can be nuanced and affected by locations and scales. Developing a better understanding of these nuances could help bring clarity to general disagreement over the effects of fragmentation on terrestrial biodiversity (Fahrig, 2013, 2017; Haddad et al., 2015; Fletcher et al., 2018; Fahrig et al., 2019). It is also necessary for understanding how to support imperiled species like the Marbled Murrelet that may not recover without implementation of landscape-level conservation plans.

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SUPPORTING INFORMATION

Additional information is available online in the Supporting Information section at the end of the online article.

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Figure 1. To examine the impacts of habitat loss and fragmentation on murrelet breeding distributions, we collated audiovisual survey data collected between 1988 and 2016 at 40,786 survey stations throughout the species' range (Fink et al. 2020) in the Pacific Northwest, U.S.A.

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Figure 2. Quantification of the amount and fragmentation of murrelet habitat within 2 km (black circles) of 40,786 sampling stations surveyed between 1988 and 2016. We first (A) built a species distribution model (SDM) that predicted murrelet occupancy probability in 30-m cells, then (B) dichotomized cells into habitat/non-habitat based on an objective cutpoint in the SDM. We then (C) overlaid open canopy cells (i.e., open-canopy forest or non-forest) and identified hard edges (D) as boundaries between these open areas and murrelet habitat. We calculated habitat amount and fragmentation as the proportion of the landscape comprising habitat or hard edges, respectively.



Figure 3. Long-term trends in murrelet habitat in the Pacific Northwest, U.S.A. based on annual species distribution models. Total murrelet habitat has declined by 0.46 million ha between 1988 and 2020 (A), with the greatest losses occurring on private industrial and non-industrial lands (B). During the same time period, the proportion of the remaining habitat comprising edge (i.e., bordering open-canopy forest or non-forest) increased by 17% (C), with the strongest changes occurring on private industrial lands (D).

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Figure 4. Annual naive and model-estimated occupancy probabilities for Marbled Murrelets based on samples of 40,786 stations surveyed across the Pacific Northwest, U.S.A. during 1988-2016. Estimates were generated from a fitted occupancy model that explored the effects of habitat amount, fragmentation, and distance-from-coast on murrelet distribution patterns. Mean values for all covariates besides year were used for predictions.



0.05

0.00

0.10

Proportion edge

0.15

0.20

Figure 5. Predicted values generated from an occupancy model that tested the effects of habitat amount (A, B), edge habitat (representing fragmentation; C, D), and distance-from-coast on murrelet occupancy probability at potential breeding sites. Note the different x-axis scales across figures. Murrelet occupancy was positively associated with habitat amount at local (100 m) and landscape (2 km) scales, as well as local scale edge habitat. Increased edge habitat at the landscape scale negatively impacted occupancy rates, and the effect increased with distancefrom-coast (effects are plotted at the minimum, mean, and maximum distance-from-coast where we detected murrelets). We generated predicted values using means for other covariates in the model and plotted them between the minimum and maximum values recorded at sampled sites.

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(A) Local-scale habitat

0.50

Proportion habitat

0.75

0.4

1.00

0.25

(C) Local-scale edge

0.2

Proportion edge

0.5

0.4

0.2

0.1

0.0

0.5

0.4

0.1

0.0

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0.0

0.00

P(occupancy) 0.3