

CONTRIBUTED PAPERS

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

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Abstract

Understanding how habitat fragmentation affects individual species is complicated by challenges associated with quantifying species-specific habitat and spatial variability in fragmentation effects within a species' range. We aggregated a 29-year breeding survey data set for the endangered marbled murrelet (*Brachyramphus marmoratus*) from >42,000 forest sites throughout the Pacific Northwest (Oregon, Washington, and northern California) of the United States. We built a species distribution model (SDM) in which occupied sites were linked with Landsat imagery to quantify murrelet-specific habitat and then used occupancy models to test the hypotheses that fragmentation negatively affects murrelet breeding distribution and that these effects are amplified with distance from the marine foraging habitat toward the edge of the species' nesting range. Murrelet habitat declined in the Pacific Northwest by 20% since 1988, whereas 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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KEYWORDS

Brachyramphus marmoratus, center-periphery hypothesis, Northwest Forest Plan, occupancy model, old-growth forest, scale-dependent effects, species-centered approach, species distribution model

Efectos de la fragmentación sobre las especies en peligro a lo largo de un gradiente desde el interior hasta el borde de su distribución

Resumen: Es complicado entender el efecto de la fragmentación del hábitat sobre las especies individuales debido a los retos asociados con la cuantificación de hábitats específicos por especie y la variabilidad espacial de los efectos de la fragmentación dentro de la distribución de la especie. Combinamos los datos de un censo reproductivo realizado durante 29 años para el mérgulo jaspeado (*Brachyramphus marmoratus*) de >42,000 sitios boscosos a lo largo del noroeste del Pacífico (Oregón, Washington, y el norte de California, EE. UU.). Construimos un modelo de distribución de especie (MDE) en el cual los sitios ocupados estuvieron vinculados con imágenes de Landsat para cuantificar el hábitat específico del mérgulo y después usamos los modelos de ocupación para comprobar la hipótesis de que la fragmentación afecta negativamente la distribución reproductiva de la especie y que estos efectos se amplifican con la distancia entre el hábitat de forrajeo marino y el borde de la distribución de anidación de la especie. El hábitat del mérgulo declinó en la zona en un 20% a partir de 1988, mientras que la proporción de hábitat que comprende bordes incrementó en un 17%, lo que indica un aumento en la fragmentación. Además, la fragmentación del hábitat del mérgulo a escala de paisaje (a de 2 km de las estaciones de censo) afectó negativamente a la ocupación de sitios potenciales de reproducción y estos efectos se amplificaron cerca del borde de la distribución. La probabilidad de ocupación disminuyó en un 37% (95% IC -54 a 12) por cada 10% de incremento en el hábitat de borde (es decir, fragmentación) en la costa, pero en el borde de la distribución (88 km tierra adentro), esta probabilidad disminuyó en un 99% (95% IC 98 a 99). De forma contraria, la probabilidad de ocupación incrementó en un 31% (95% IC 14 a 52) por cada 10% de incremento en el hábitat de borde local (a 100 m de las estaciones de censo). La evasión de la fragmentación a gran escala y el uso de hábitats con calidad reducida y fragmentados a nivel local podría explicar la falta de recuperación poblacional del mérgulo. Más allá, nuestros resultados resaltan que los efectos de la fragmentación pueden estar matizados, depender de la escala y tener variación geográfica. Es importante tener conciencia de estos matices para desarrollar estrategias de conservación a nivel paisaje para las especies que experimentan fragmentación y pérdida del hábitat a gran escala.

PALABRAS CLAVE

bosque antiguo, efectos dependientes de la escala, estrategia centrada en la especie, hipótesis del centro-periferia, modelo de distribución de especies, modelo de ocupación Plan Forestal del Noroeste, *Brachyramphus marmoratus*

破碎化对一种濒危物种从其分布区内部到边缘的梯度影响

【摘要】了解栖息地破碎化对单一物种的影响是十分复杂的,因为量化物种特异的栖息地及物种分布区内破碎化影响的空间变异性仍具有挑战。本研究整理了濒危的斑海雀 (*Brachyramphus marmoratus*) 29 年的繁殖调查数据,这些数据来自整个太平洋西北地区(美国俄勒冈州、华盛顿州和加利福尼亚州北部)超过 42000 个森林位点。我们建立了一个物种分布模型,将该物种分布位点与 Landsat 图像整合,以量化斑海雀特异的栖息地范围,并利用占域模型检验了以下假设:栖息地破碎化会对斑海雀繁殖区的分布产生负面影响,且这些影响会沿海洋觅食栖息地向巢域范围边缘放大。我们发现,自 1988 年以来,太平洋西北地区的斑海雀栖息地减少了 20%,而栖息地边缘的比例却增加了 17%,这表明破碎化程度增加。此外,在景观尺度上(调查站点 2 公里范围内),栖息地破碎化对斑海雀潜在繁殖地利用情况产生了负面影响,且这些影响在分布区边缘被放大了。在海岸附近,边缘栖息地(即破碎化栖息地)每增加 10%,斑海雀占域率会下降 37% (95% 置信区间为 12-54%),但在分布区边缘(内陆 88 公里)占域率下降则高达 99% (95% 置信区间为 98-99%)。相反地,局部边缘栖息地(调查站点 100 米范围内)每增加 10%,斑海雀的

占域率就会增加 31% (95% 置信区间为 14-52%)。斑海雀回避大尺度破碎化的栖息地, 但会利用质量下降的局部破碎化栖息地, 这可能是其种群没有得到恢复的原因。此外, 我们的研究结果强调, 破碎化的影响可能是细微、尺度依赖且存在地理差异的。意识到这些细微差别对于为经历大尺度栖息地丧失和破碎化的物种制定景观尺度的保护策略至关重要。【翻译:胡怡思;审校:聂永刚】

关键词: 斑海雀(*Brachyramphus marmoratus*), 中心-外围假说, 西北森林计划, 占域模型, 原始林, 尺度依赖效应, 以物种为中心的方法, 物种分布模型

INTRODUCTION

Habitat loss and degradation from anthropogenic disturbances is the leading cause of biodiversity decline worldwide and is expected to continue (Newbold et al., 2015; Pimm & Raven, 2000). Fragmentation often results from habitat loss, but evidence regarding how fragmentation per se (independent of habitat loss [Fahrig, 2003]) affects biodiversity is mixed (Fahrig, 2013, 2017; Fahrig et al., 2019; Fletcher et al., 2018; Haddad et al., 2015). 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 (Fahrig et al., 2022; Lindenmayer & Fischer, 2006). Identifying species negatively affected 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 (Fahrig, 2013; Hadley & Betts, 2016). Second, 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, intraspecific 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, such as fragmentation, could thus exacerbate effects of these stressors at range edges, whereas individuals inhabiting range interiors may select fragmented areas to minimize competition (Banks-Leite et al., 2022; Orme et al., 2019). 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) of the United States. 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 fire-based 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 trade-offs between timber production and biodiversity conservation (Spies et al., 2019).

The murrelet is a small seabird in the family Alcidae with a range stretching from the Aleutian Islands, Alaska, south to Monterey Bay, California (Nelson, 2020) (Figure 1). 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 (Becker et al., 2007; Betts et al., 2020;

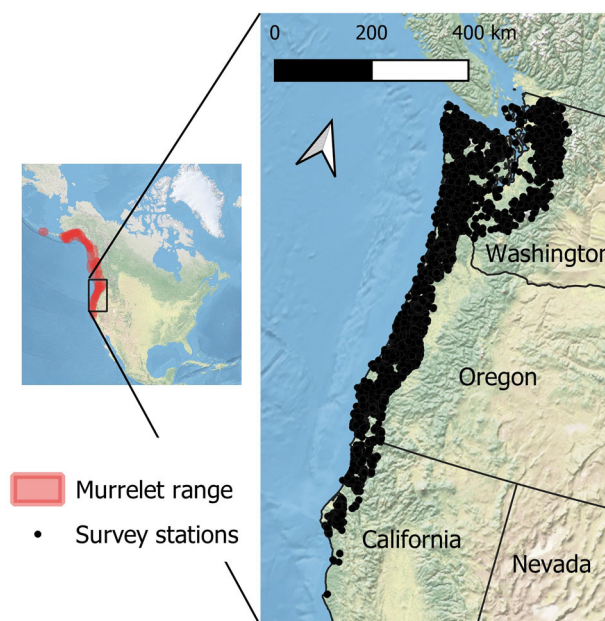


FIGURE 1 Survey stations (40,786 total) where audiovisual surveys of marbled murrelets were conducted from 1988 to 2016 throughout the species' range (Fink et al., 2020) in the Pacific Northwest (USA).

Peery et al., 2004). 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 (Betts et al., 2020; Nelson, 2020; Raphael et al., 2018). Despite being protected throughout the Pacific Northwest and Canada, murrelet populations have not recovered in the past 2 decades (McIver et al., 2021).

Although fragmentation of murrelet breeding habitat is hypothesized to hinder population growth, past studies have often not accounted for confounding variables (e.g., habitat amount, species perception, range heterogeneity), and evidence remains ambiguous (Burger & Page, 2007; Zharikov et al., 2006; Zharikov, Lank, Huettmann, et al., 2007). Murrelets may nest in old-growth areas with less edge (e.g., Ripple et al., 2003; Rodway & Regehr, 2002), likely because nest predation rates can be 2.5 times greater near forest edges than patch interiors (Malt & Lank, 2007, 2009; Raphael et al., 2002). 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, several studies show murrelets select nest sites near forest edges (Zharikov et al., 2006; Zharikov, Lank, & Cooke, 2007) (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 landscape-level conservation schemes requires clarity regarding the effects of landscape structure on murrelet distributions.

We aggregated murrelet surveys conducted over 29 years 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 3 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 predicted a negative association between fragmentation and murrelet occupancy. However, if murrelets select breeding sites near forest edges to facilitate nest access, we predicted a positive association. Finally, 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, and reliance on the nearshore marine foraging environment constrains the distance murrelets can travel to nest sites. Thus, forest tracts farther from the coast are closer to the murrelet's terrestrial range edge (Figure 1) and ecologically more marginal due to increased distance from a food source. We therefore predicted that negative edge effects will increase as distance from the coast increases.

METHODS

Marbled murrelet occupancy surveys

We gathered data on historical murrelet breeding distributions by aggregating audiovisual survey data collected at inland forests from 1988 to 2016. Data were from the U.S. Forest Service; U.S. 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); the Hoopa Indian Reservation; and university researchers (Figure 1). Most surveys were conducted around proposed timber harvest sites with 1 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 data set 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 used data only from the station's first sampling year in all analyses to avoid pseudoreplication. The annual number of stations surveyed for murrelets ranged from 139 in 2016 to 3043 in 2001. Stations were well-distributed across gradients in habitat amount and fragmentation over the 29-year period (Appendix S1). Most stations were concentrated between 10 and 40 km from the coast, but some were up to 100 km inland (Appendix S2). We reclassified survey results into a detection and nondetection data set where detections included only "occupied behaviors" indicative of nesting activity (e.g., subcanopy flights, landing, stationary calling [Evans Mack et al., 2003]). We excluded above-canopy circling (typically considered occupied behavior) because it cannot be reliably associated with a precise nest location.

Species distribution modeling

Using MaxEnt, we built a model to predict probability of presence at unique points in space and time and then used this model to build year-specific murrelet SDMs covering our study area. MaxEnt model inputs included the 2029 stations where murrelet occupancy was recorded and 10,000 background locations randomly distributed in space and time. We used random locations rather than nondetection stations because

the species has low detectability and failing to record occupancy does not guarantee absence (Evans Mack et al., 2003; Valente et al., 2021). We modeled occupied and background locations as a function of 3 covariate types. First, we used Landsat Collection 1 surface reflectance data (30-m pixel resolution [<https://www.usgs.gov/landsat-missions/landsat-surface-reflectance>]) from 1985 to 2020 to characterize environmental variables. We used raw reflectance data rather than forest structure variables derived from gradient nearest neighbor (GNN) map products (Ohmann & Gregory, 2002) because we did not want to propagate error from GNN imputations into our SDM, avian SDMs based on raw reflectance data perform well (Betts et al., 2022; Shirley et al., 2013), and future murrelet habitat mapping under the NWFP will also use raw reflectance data (M. Raphael, personal communication). After masking clouds and shadows, we used continuous change detection and classification (CCDC) algorithms (Zhu & Woodcock, 2014) in Google Earth Engine (Gorelick et al., 2017) to break the spectral data time series into different temporal segments, each characterized by a set of harmonic parameters. We used median peak 2-band enhanced vegetation index day of year (day 182) from MODIS Global Vegetation Phenology product (<https://doi.org/10.5067/MODIS/MCD12Q2.006>) as the mapped day each year and extracted CCDC harmonic parameters on day 182 for all locations. Second, we included categorical covariates representing mapped disturbances from 1972 to 2002 (Healey & Cohen, 2004) and from 1985 to 2020 (Landscape Change Monitoring System; Cohen et al., 2018; Healey et al., 2018). Finally, we incorporated topographic variables, including physioidiversity, topographic diversity, multiscale topographic position index, and elevation (Theobald et al., 2015). Because sampling occurred over 29 years, covariates for each station were measured in the year 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 with a complementary log–log data transformation in which 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 to 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 or nonhabitat with an objective cut point (habitat = presence probability >0.45) that maximized the sum of the model's sensitivity and specificity on the receiver operator characteristic curve (Halstead et al., 2019). Thus, our habitat designation was murrelet

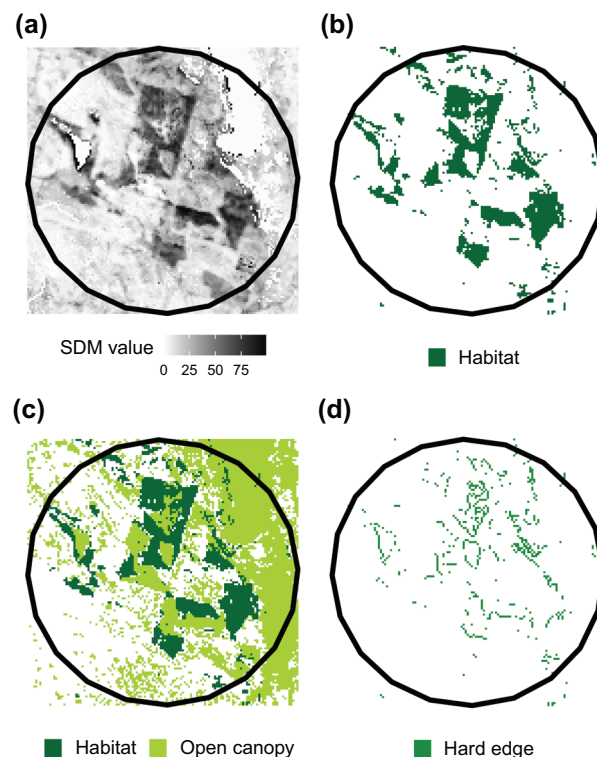


FIGURE 2 Amount and fragmentation of marbled murrelet habitat within 2 km (black circles) of 40,786 sampling stations surveyed from 1988 to 2016: (a) murrelet occupancy probability in 30-m cells from a species distribution model (SDM), (b) murrelet habitat and nonhabitat based on an objective cut point in the SDM, (c) murrelet habitat overlaid with open canopy cells (i.e., open-canopy forest or nonforest), and (d) hard edges, defined as boundaries between open areas and murrelet habitat. Habitat amount and fragmentation are the proportion of the landscape with habitat or hard edges, respectively.

specific and based on biophysical conditions enabling species occupancy (see Appendices S3 & S4 for a complimentary analysis with a higher SDM threshold value). We then used annual GNN map products (Ohmann & Gregory, 2002 [<https://lemmdownload.forestry.oregonstate.edu/>]) to identify pixels with open canopies, including urban areas and forests with conifer cover $\leq 40\%$. 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 and then for 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, Indigenous peoples, or under private conservation easements). We calculated habitat amount from 1988 to 2020, but we only calculated edge area through 2017 due to lack of contemporary GNN layers.

Model covariates

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 (Fahrig et al., 2019; Fletcher et al., 2018, 2023). 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 multiscale process (Mayor et al., 2009; Meyer et al., 2007), we measured habitat and edge proportions within 7 radii around each station: 0.1, 0.5, 1, 2, 3, 4, and 5 km. We chose the 2-km radius area (hereafter, landscape scale) to represent the scale at which landscape-level processes occur (e.g., dispersal and predator density effects) because this scale is relevant to murrelets (Meyer et al., 2002) and variables measured within 2 km were highly correlated ($r \geq 0.7$) and therefore redundant with corresponding variables in 0.5- to 5-km radius areas. We chose the 0.1-km radius area 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 its distance from the coast (distance from coast). Points farther from the coast were 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 4.1.1 operating on the Smithsonian Institution High Performance Computing Cluster (<https://doi.org/10.25572/SIHPC>).

Statistical analyses

We tested for effects of habitat amount, edge habitat, and distance from coast on murrelet breeding activity with static occupancy models (MacKenzie et al., 2002). These models rely on the assumption that 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 repeated surveys are used to account for the probability of detecting occupancy. 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 fitted occupancy models in R 3.6.3 with the unmarked 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 1222 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 [SD] = 1.49 surveys/station [1.00]) (ownership information in Appendix S5). Data from ~5% of survey stations used in occupancy models ($n = 1990$ 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 were emergent properties from the SDMs. These characteristics were therefore not directly related to the cell-specific properties used to distinguish them as murrelet habitat for SDM development.

We modeled detection probability with covariates known to affect 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; <https://lemmdownload.forestry.oregonstate.edu/>), a quadratic day-of-the-year effect, and a data source covariate to account for potential detection heterogeneity introduced by local land management practices. Finally, 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 manifest only below a threshold in habitat amount (Andr  n, 1994; Betts et al., 2006). Thus, we 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 not significant at both the local ($\beta = -0.02$, 95% confidence interval [CI] -0.11 to 0.07 , $Z = -0.50$, $p = 0.62$) and landscape scales ($\beta = 0.05$, 95% CI -0.02 to 0.12 , $Z = 1.27$, $p = 0.20$), suggesting fragmentation effects varied 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. 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 other covariates included in our models ($|r| < 0.61$) (Appendix S6). We evaluated the final model's fit (model structure in Appendix S7) by comparing the Pearson's chi-square statistic from the original data set with a distribution of 1000 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).

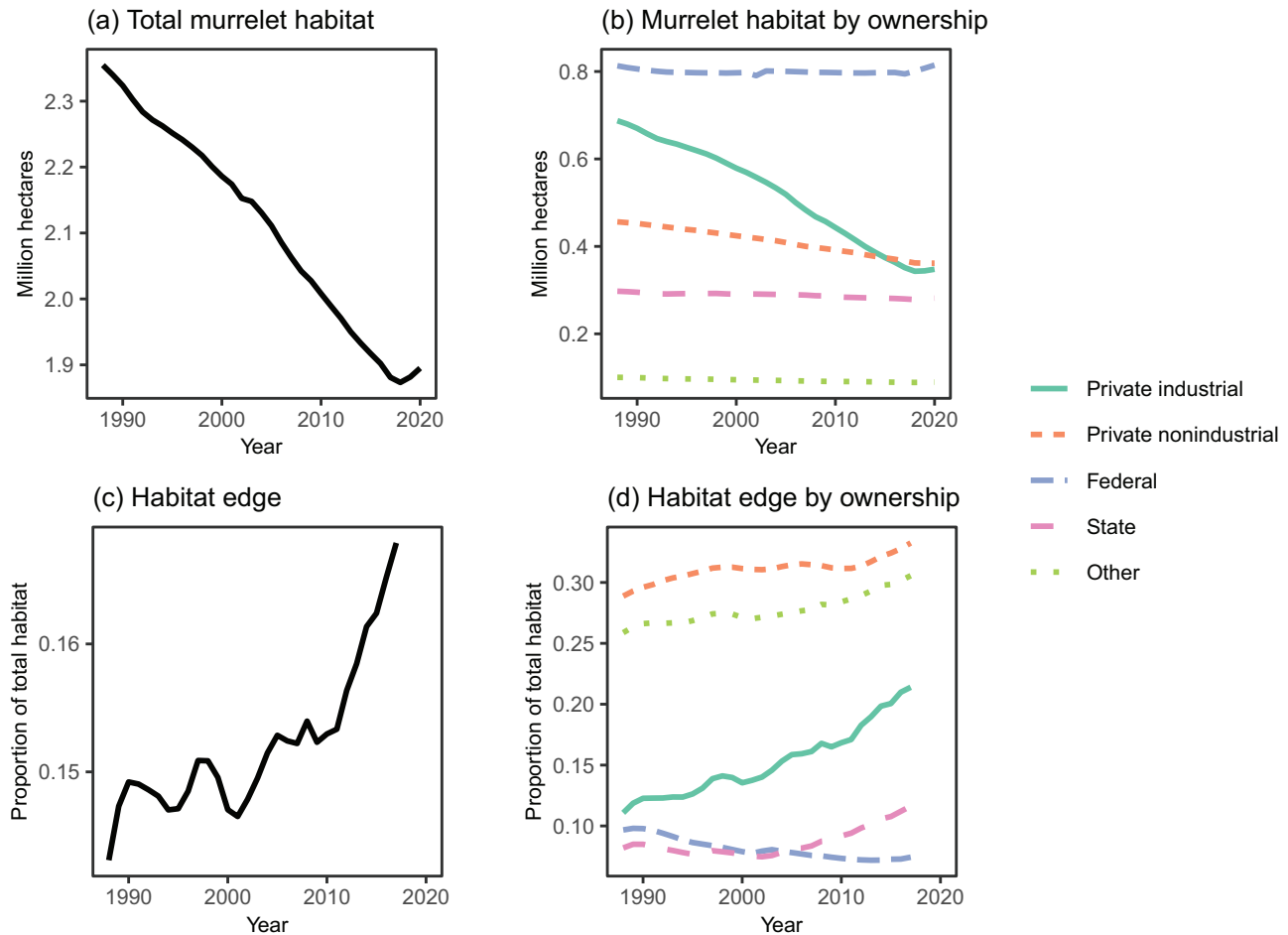


FIGURE 3 Long-term trends in marbled murrelet habitat in the Pacific Northwest (USA) based on annual species distribution models: (a) total murrelet habitat from 1988 to 2020, (b) distribution of murrelet habitat by ownership, (c) proportion of total murrelet habitat that is edge (i.e., bordering open-canopy forest or nonforest), and (d) distribution of murrelet edge habitat by ownership.

RESULTS

Temporal changes in habitat

Our SDM effectively distinguished areas of likely murrelet breeding habitat. The AUCs for model building and validation were 0.840 and 0.826, respectively; thus, a randomly selected occupied site had a greater SDM value than a randomly selected background point >80% of the time.

Annual SDMs indicated murrelet habitat declined by nearly 20% in the Pacific Northwest from 1988 to 2020, a loss of almost 500,000 ha (Figure 3a). Private industrial lands accounted for 74% of those losses, and private nonindustrial lands accounted for another 20% (Figure 3b). The only long-term increases occurred on federal lands, although this gain was only 2000 ha over the 32-year period. As the total amount of murrelet habitat declined in this region, the remaining habitat became more fragmented. The percentage of murrelet habitat comprising hard edges (i.e., adjacent to young, open-canopy forest or nonforest) increased by 17% from 1988 to 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 complementary examination of higher value murrelet habitat yielded remarkably similar results (Appendices S3 & S4). State-specific results are in Appendices S8–S12.

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. After accounting for imperfect detection, our occupancy estimates ranged from 4.8% (95% 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 Appendix S13.

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% CI 1.13 to 1.18) for each 10% increase in murrelet habitat within 100 m (Figure 5a). We found similarly strong

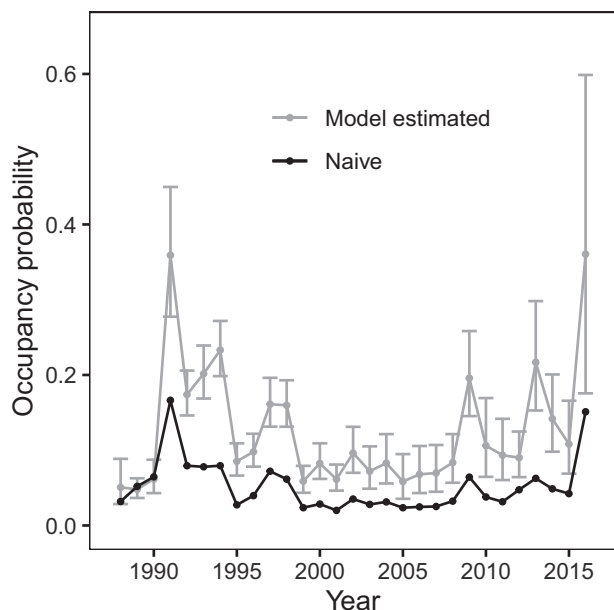


FIGURE 4 Annual naive and model-estimated occupancy probabilities for marbled murrelets based on samples of 40,786 stations surveyed across the Pacific Northwest (USA) from 1988 to 2016.

evidence ($Z = 8.23$, $p < 0.001$) at the landscape scale where the odds of occupancy increased 1.16 times (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% CI 1.14 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 ($Z = -14.78$, $p < 0.001$) because 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 because the interaction effect was weak and not significant ($\beta = -0.03$, 95% CI -0.10 to 0.05 , $Z = -0.74$, $p = 0.46$).

Conversely, murrelet occupancy decreased as fragmentation at the landscape scale increased. Moreover, these effects were amplified farther inland as indicated by a strong negative interaction between distance from coast and landscape-level edge habitat ($\beta = -0.25$, 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 farthest distance from coast at which murrelet occupancy was detected (Figure 5d).

DISCUSSION

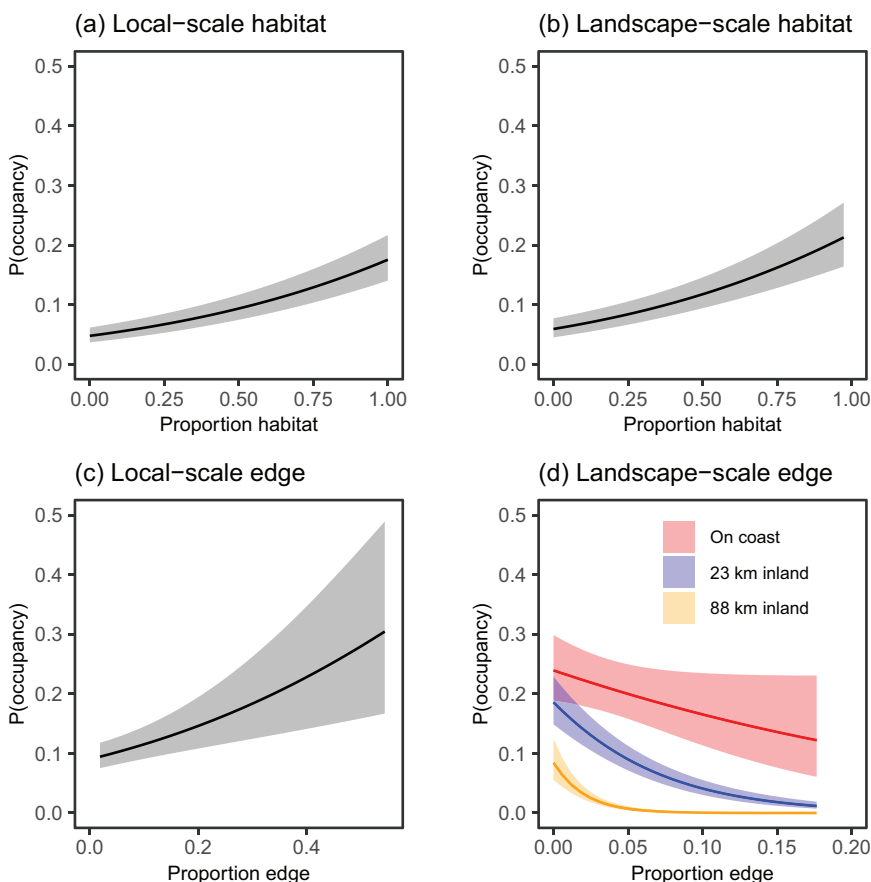
Using 29 years of sampling data and a species-specific habitat model, we found strong evidence that fragmentation (measured

by the proportion of hard edges around sample stations) affects murrelet distributions and that those effects differ across scales. 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; Zharikov, Lank, & Cooke, 2007). 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).

Our findings are consistent with evidence that murrelet inland detections (Meyer & Miller, 2002; Meyer et al., 2002), nest sites (Ripple et al., 2003), and at-sea distributions (Raphael et al., 2015) are negatively associated with broad-scale fragmentation. This may suggest murrelets avoid fragmented areas due to greater predation risk (Malt & Lank, 2007, 2009; Raphael et al., 2002) or abandon historically occupied areas once they become too fragmented (Meyer et al., 2002) or reflect a lack of conspecific information about nesting habitat in fragmented regions (Valente et al., 2021). Conversely, the positive, local-scale fragmentation effect we observed supports previous findings that murrelets nest closer to forest edges than expected by chance (Zharikov et al., 2006; Zharikov, Lank, & Cooke, 2007). 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, and it is unclear whether gaps generated by anthropogenic disturbances (e.g., forest harvest) were used similarly by murrelets. If they were, this could create an ecological trap given that habitat near clearcut edges is presumed to be of lower quality for murrelets (Lorenz et al., 2021) due to higher rates of nest failure (Malt & Lank, 2007, 2009; Raphael et al., 2002).

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 (Banks-Leite et al., 2022; Orme et al., 2019). Defining the range center and edge for a split-habitat species like the murrelet presents unique challenges. One might consider there are 2 range centers for the murrelet, 1 on land and 1 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 toward the coast to feed, and birds venturing out to sea must return to the coast to breed. Further, although 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

FIGURE 5 Predicted values generated from an occupancy model that tested the effects of (a, b) habitat amount, (c, d) edge habitat (representing fragmentation), and distance from coast on marbled murrelet occupancy probability at potential breeding sites. The x-axis scales differ. Landscape-scale edge effects (d) varied with distance from coast and are plotted at the minimum, mean, and maximum distance at which murrelets were detected.



stressors (Banks-Leite et al., 2022). Birds breeding farther inland will experience greater physiological stress from increased travel costs, which could be exacerbated by greater rates of nest predation resulting from habitat fragmentation (Malt & Lank, 2007, 2009; Raphael et al., 2002). The influence of these 2 factors could drive behavioral shifts where inland-nesting birds are more averse, whereas coastal-nesting 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 data set only covered the southern portion that 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 because we used emergent properties from an SDM 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; Zharikov, Lank, & Cooke, 2007), we examined habitat and habitat fragmentation from the perspective of our target species. Because we did not explicitly model forest structure, we lacked information on some of the specific forest characteristics comprising murrelet habitat in the region. We presume that increased murrelet occupancy probability within our SDM was associated with an increase in old-growth forest components (e.g., legacy trees, large nesting platforms, multilayered canopies) preferred

by breeding murrelets (Hamer & Nelson, 1995; Nelson, 2020). However, 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 model that accurately distinguishes likely breeding habitat from random locations, as indicated by our validation tests.

Although our SDM demonstrated 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). We found that the greatest loss and fragmentation of likely murrelet habitat (and high-value murrelet habitat [Appendices S3 & S4]) occurred on private industrial lands, which we initially 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 (Appendix S5). Others have 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 was observational, we could not 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 (Appendix S14), 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 indicated that murrelets exhibiting breeding behaviors tend to occupy landscapes with more contiguous habitat. Murrelet populations have failed to increase over the past 2 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 (Malt & Lank, 2007, 2009; Raphael et al., 2002). 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 (Lorenz et al., 2021; Raphael et al., 2015), future research should examine whether there are additional benefits to protecting contiguous nesting habitat near quality foraging areas.

Although identifying fragmentation effects can be challenging, it is critical for developing effective management strategies and conserving biodiversity. Our study provides an example of how to test for effects of fragmentation while accounting for habitat amount and species-specific habitat requirements. We 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; Fahrig et al., 2019; Fletcher et al., 2018; Haddad et al., 2015). 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 supporting information can be found online in the Supporting Information section at the end of this article.

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