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RESEARCH ARTICLE

Spatially concentrating logging could mitigate climate-magnified fragmentation risks to a globally endangered bird

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Abstract

1. Rising timber demand is transforming forest structure globally, profoundly affecting biodiversity and climate resilience. Logging-driven fragmentation is potentially a major driver of biodiversity loss in production landscapes, yet its interactions with escalating climate stressors remain poorly understood.
2. We combine two decades of Landsat-derived habitat metrics with 29,000 surveys of the marbled murrelet (*Brachyramphus marmoratus*)—an iconic Pacific Northwest old-forest specialist seabird affecting management of >10 million hectares. Controlling for habitat amount and detection probability, increasing landscape-scale forest edge amount sharply reduces murrelet occupancy, with impacts worsening under unfavourable climate-driven ocean conditions.
3. Comparing alternative landscape-scale timber harvest strategies, spatially concentrated logging consistently supports higher murrelet populations than fragmented approaches producing equivalent wood volumes, with benefits amplified under adverse ocean conditions. However, historical harvesting policies in the Pacific Northwest have instead driven severe habitat fragmentation, which we show is eroding the value of core set-aside forests on federal and conservation lands and ultimately rendering murrelets more vulnerable to climate change.
4. *Synthesis and applications:* We map key opportunities to boost populations by reducing edginess around remaining nesting habitat and investigate these opportunities' spatial distribution across land ownership and timber productivity gradients. Concentrating logging could be critical for mitigating fragmentation and climate threats for murrelets and potentially other forest-dependent species amid rising timber demand.

KEYWORDS
climate change, forest management, fragmentation, logging, old-growth biodiversity

1 | INTRODUCTION

Biodiversity within forest landscapes is under growing pressures globally from climate-driven threats, including wildfires, pest outbreaks and shifting temperature regimes (Anderegg et al., 2022; Bousfield et al., 2023). Designing resilient wood production landscapes that sustain biodiversity while meeting rising timber demands is a major challenge (Betts et al., 2021), particularly as climate change exacerbates and global wood demand increases >50% by 2050 (Peng et al., 2023). Besides driving direct potential losses in forest habitat, one of the most pervasive consequences of logging is forest fragmentation (Ma et al., 2023), whereby logging roads and harvesting operations divide contiguous forests into isolated patches, reducing habitat connectivity and interior forest quality (Brodie et al., 2025). Globally, 70% of forests occur within 1 km of an edge (Haddad et al., 2015), with logging a principal driver of new forest edge creation in both temperate and tropical biomes (Betts et al., 2019; Bourgoin et al., 2024; Sims et al., 2025).

Theory predicts that climate change may amplify the impacts of forest fragmentation, especially for forest-dependent biodiversity (Opdam & Wascher, 2004; Travis, 2003). Hypothesised mechanisms for this process include: (i) altered precipitation and temperature regimes magnifying the spatial extent or severity of edge effects or preventing species dispersal (Koelemeijer et al., 2023; Parra-Sanchez & Banks-Leite, 2020; Weeks et al., 2023), (ii) diminished or asynchronous food availability following climate shocks heightening species' vulnerability to degraded interior forest quality (Bush et al., 2020) and (iii) increasing populations of climate-resilient, edge-tolerant 'super-generalist' species outcompeting or preying upon forest-dependent wildlife (Bastille-Rousseau et al., 2018; de Gabriel Hernando et al., 2022). However, the synergistic effects of climate change and fragmentation on biodiversity have been challenging to assess (Oliver et al., 2015). Species' responses to fragmentation can be highly variable, are often confounded by habitat amount (Fahrig, 2003) and can result in both positive and negative outcomes depending on the spatial scale and on species life histories (Valente, Gannon, et al., 2023; Valente, Rivers, et al., 2023). Moreover, long-term data are crucial for detecting biodiversity responses to fragmentation and climate change, yet are rare, especially for cryptic or habitat-specialist species that are expected to be most sensitive to land-use and climate stressors.

Understanding the magnitude and extent to which climate change exacerbates fragmentation is critical for designing wood production strategies that sustain forest-dependent biodiversity into the future (Betts et al., 2021). For example, if climate stressors magnify fragmentation effects, management approaches that concentrate timber production spatially while preserving larger tracts of contiguous habitat may be critical for mitigating future biodiversity losses (Cerullo, França, et al., 2023; Runting et al., 2019). By contrast, more spatially extensive harvesting approaches—regularly applied in boreal, temperate and tropical regions, in part to ostensibly reduce environmental impacts (Bicknell et al., 2015; Nagel et al., 2025)—risk exacerbating fragmentation effects, with the magnitude of impacts likely shaped by both landscape configuration and species' spatial exposure to climate stressors. Yet to date, no empirical study has assessed how much the synergistic effects of climate change and fragmentation shape forest-dependent species' populations, or how alternative timber production strategies might mitigate or compound these risks into the future.

The marbled murrelet (*Brachyramphus marmoratus*) is a globally endangered (240-280 K mature individuals) and cryptic sea bird reliant on late-successional and old-growth forests for nesting (The IUCN Red List of Threatened Species, 2026; Divoky & Horton, 1995). Its terrestrial range includes coastal forests of the Pacific Northwest, where intensive historical logging and timber plantation expansion have left a legacy of severe fragmentation (Phalan et al., 2019). Previous research suggests that marbled murrelet populations could potentially be vulnerable to the isolated impacts of habitat fragmentation and warm ocean conditions (Betts et al., 2020; Malt & Lank, 2007; Valente, Rivers, et al., 2023), a dual sensitivity that reflects the species' life history: marbled murrelets forage in nearshore Pacific waters and nest on moss-covered canopy platforms within tall trees up to 100 km from the coastline. To date, marbled murrelet conservation and recovery efforts have driven profound economic and ecological impacts, underpinning a multi-million-dollar consultancy industry, directing hundreds of millions in conservation and monitoring spending, and shaping forest management across >10 Mha of federal, state and private lands in a globally critical wood-basket region (Phalan et al., 2019). Meanwhile, fragmentation in the marbled murrelet's nesting habitat has intensified (increasing 17% between 1988 and 2023; Valente, Rivers, et al., 2023), with marine heatwaves in the Northeast Pacific also becoming more frequent (Ren et al., 2023), potentially reducing murrelet prey availability and quality (Cheung & Frölicher, 2020). The marbled murrelet is thus an iconic example of the challenges faced by many forest-dependent species worldwide: balancing growing timber demands with conservation of forest-dependent species potentially vulnerable to climate change will be a major challenge for the 21st century.

To investigate how climate change and forest fragmentation have jointly influenced population dynamics, we analysed 29,323 marbled murrelet surveys conducted across 20,149 sites over 20 years, integrating data on climate-driven ocean conditions and year-specific Landsat-derived measures of habitat and edge dynamics. It is expected that hard edges between murrelet habitat and open areas (e.g. logging clear cuts) boost nest predation

risk (Malt & Lank, 2007; Nelson & Hamer, 1995) and decrease the availability of suitable nesting areas (Nelson & Hamer, 1995; Valente, Rivers, et al., 2023). We therefore hypothesised that landscape-scale fragmentation would negatively impact murrelet occupancy. However, we also expected that edge effects would intensify following unfavourable ocean conditions, due to reduced parental nest attendance from longer foraging trips at sea and shifts in nest-site occupancy, with higher-condition birds selecting high-quality habitats and lower-condition birds abstaining from or reducing nesting attempts (Martin, 1995).

Building on these insights, we then evaluated which contrasting landscape-level forest management strategies could mitigate climate- and fragmentation-driven threats. Using simulated landscape scenarios, we compared spatially concentrated timber production, which preserves larger intact habitats, with more spatially extensive harvesting approaches that produce equivalent wood volumes yet result in increased overall habitat fragmentation. We hypothesised that concentrated logging would most benefit murrelet populations after poor ocean years, when contiguous habitats have enhanced importance, and under high wood demand, which requires greater land area for production. Finally, we mapped future population changes under varying climate and forest management scenarios and assessed the effectiveness of alternative strategies to mitigating threats across land ownerships. Our findings can help to highlight the historical interplay of climate and fragmentation in shaping populations of an old-forest species and suggest mechanisms for supporting forest-dependent species exposed to the trifecta of land-use, climate change and growing timber demands.

2 | MATERIALS AND METHODS

2.1 | Overview

Our analysis included three components: (1) modelling marbled murrelet occupancy as a function of habitat, fragmentation and climate variables, while accounting for detection probability (Section 2.1.1) (2) simulating murrelet outcomes for alternative forest management scenarios spanning gradients from concentrated to increasingly fragmented production strategies (Section 2.1.2) and (3) projecting future population outcomes under current management and future climate and fragmentation policies across the Pacific Northwest (Section 2.1.3).

2.1.1 | Murrelet responses to ocean condition and fragmentation

Occupancy surveys

We leveraged an extensive previously compiled dataset (Valente, Rivers, et al., 2023) of marbled murrelet breeding season surveys carried out from 1990 to 2020. This encompassed 40,786 sites and 60,633 audiovisual surveys carried out within inland mature and old-growth forests in the Pacific Northwest. Survey data were sourced from federal and state agencies, private timber companies, tribal lands and researchers, with most surveys occurring near proposed timber harvest sites. Standardised protocols adhered to a consistent site size (200-m radius), with surveys carried out by trained observers during a fixed breeding season window (15 April–5 August) using the Pacific Seabird Group (PSG) protocol, which evaluates breeding activity and behaviours at survey sites (see Valente, Gannon, et al., 2023; Valente, Rivers, et al., 2023; Betts et al., 2020 for details). Since our analysis focused in part on climate-driven ocean condition information, which has only been available since 1998 (see below; Peterson et al., 2014), we filtered to surveys sampled after this year when developing occupancy-detection models, leaving us with a total of 20,149 sites and 29,323 audiovisual surveys (the full dataset was available for generating species-distribution models; see below). These sites and surveys were well-distributed across gradients of edge and habitat amount, distance to coast and ocean condition (Figure S2), providing a robust basis for assessing murrelet breeding distributions across the Pacific Northwest.

Occupancy and detection predictor variables

Habitat amount. We calculated the amount of habitat around each murrelet site from a species point-of-view, using previously published year-specific species-distribution models (SDMs) based on Landsat-derived reflectance bands (Betts et al., 2020; Betts et al., 2024). SDMs were generated using MaxEnt and incorporated 2029 occupied sites and 10,000 background locations, with model inputs including raw Landsat reflectance data (1985–2020), continuous change detection (CCDC) for temporal segmentation and topographic and disturbance covariates (Figure S1; see Valente, Rivers, et al., 2023 for details). We defined murrelet habitat as any 30 m pixel (representing the highest resolution scale of Landsat data) with a value ≥45 (range 0–100), which was selected as threshold that maximised the sum of model sensitivity and specificity on the receiver operator characteristic curve (AUCs during SDM model building and validation were between 0.840 and 0.826). Since marbled murrelets may respond to habitat amounts at different scales (Fahrig, 2003; Valente, Rivers, et al., 2023), and since accounting for habitat amount is critical in fragmentation analyses (Fahrig, 2003; Valente, Gannon, et al., 2023), we calculated the proportion of habitat at two spatial scales. These included for 100 m and 2000 m radius buffers around sites, with these scales selected to capture local-scale site features informing nest selection, as well as landscape-level drivers of suitable breeding habitat.

Edge amount. We also used the annual SDMs of murrelet habitat to quantify the proportion of 100 m and 2000 m radius buffers composed of hard edges (hereafter 'edge amount'), since edge dynamics may also operate over different spatial scales (Valente, Gannon, et al., 2023). We identified pixels with open canopies,

consisting of cells with ≤40% canopy cover according to an annual gradient nearest neighbour (GNN) raster product specific to the survey year (Bell et al., 2023; Bell et al., 2024). Murrelet habitat pixels (i.e. those cells with SDM values ≥45) bordering open canopies in any cardinal direction were recategorised as 'hard edges' (Figure S1), and we used the proportional coverage of hard edges (i.e. the number of hard-edge pixels / total pixels in buffer) within buffers to represent the degree of fragmentation at different scales around surveyed sites.

Ocean conditions. We leveraged a long-term regional dataset recording ocean processes and associated marine food webs to provide an annual indication of climate-driven ocean conditions for murrelets (Peterson et al., 2014). This dataset included a suite of 16 marine variables capturing various climate-driven physical and biological processes. Variables included several measures of monthly sea surface temperatures, as well as repeated measures of copepod, salmon and ichthyoplankton biomass (see Table S1 for full details), providing an approximation of at-sea prey abundances for murrelets. Using principal component analysis, these indicators were collapsed into a single variable that has previously been demonstrated to closely track annual terrestrial occupancies of murrelets (Betts et al., 2020). Thus, our measure of ocean climate condition captures both the direct geophysical consequences of climate change on murrelet populations, as well as secondary climate effects via impacts on marine food webs. We used PC1 values in the year prior to murrelet surveys as a lagging predictor for murrelet occupancy, since evidence from radio-tagged individuals suggests murrelets largely avoid inland nesting during severe ocean years (Garcia-Heras et al., 2024), and because incorporating a more extended lag would reduce available sample sizes of surveyed breeding data. We inverted PC1 values so that low values of the first principal component (PC1) represented ocean conditions associated with warm years, and low prey availability and vice versa, categorising 'good' and 'bad' ocean years as the 90th and 10th percentile of observed PC1 values between 1998 and 2023 (Figure S3).

Additional covariates and scaling. We also determined other key predictors known to influence murrelet occupancy and detection for inclusion in detection-occupancy models (see below). To account for differences in detection, we used the day of year that surveys occurred, as well as GNN raster products (Bell et al., 2023; Bell et al., 2024) to calculate canopy cover and conifer density within 100 m radius buffers around murrelet sites, included as both linear and quadratic terms. Since murrelets are more detectable near canopy openings, we included edge amount (within 100 m) as a detection covariate, and we incorporated information on the survey data source to account for differences in land management practices (Valente, Rivers, et al., 2023). Finally, we calculated distance to the coast to include in occupancy models, since murrelets are known to preferentially target more proximate inland forests for breeding (Hamer & Nelson, 1995). All continuous detection and occupancy covariates were regularised by subtracting the mean and dividing by the standard deviation to assist with model convergence, interpretability of coefficients and model comparison.

Model specification and selection. We used static occupancy models in the R package 'unmarked' (Kellner et al., 2023 using the 'occu()' function) to assess the effects of edge amount and ocean conditions on murrelet occupancy probabilities (ψ), while accounting for habitat amount, distance to coastline and detection probability (p). We used static occupancy models because most sites were surveyed only in one season, precluding dynamic multiseason models, because the species' cryptic behaviour required accounting for variable detectability (Divoky & Horton, 1995), and because survey data focused on single adults attending or leaving nests and so were unsuitable for modelling abundance. As discussed above, detection components across all models used a fixed backbone of covariates likely to affect murrelet detections, including canopy cover, conifer density, day of year, local-scale edge amount and the data source. We then used a structured hypothesis-testing approach with eight nested models to determine drivers of murrelet occupancy. We began with a null, detection-only model (Model 1; for full model structures and syntax see Appendix), which suggested a baseline occupancy of ~0.17. We next sequentially added previous-year ocean condition and distance to coast variables (Model 2), followed by multi-scale (100-m and 2 km-radius) habitat and edge amount variables (Model 3). We tested for habitat-edge amount interactions at both scales (Model 4), but these were not strongly supported and so were excluded from subsequent models. To test our hypothesis that climate-driven ocean conditions modulate fragmentation effects, we next incorporated an ocean condition × landscape edge interaction (Model 5). Then, to accommodate the potential that coastal fragmentation or ocean condition impacts could vary according to their position along murrelets' inland range (Valente, Rivers, et al., 2023), we fit models allowing for interactions between ocean condition and coastal distance (Model 6) and between landscape edge amount and coastal distance (Model 7). Finally, to assess whether there were strong context dependencies between landscape edge amount, ocean conditions and distance to coast—which might manifest if, for instance, the magnifying effects of ocean condition on fragmentation impacts varied along a distance-to-coast gradient—we included a three-way interaction between these covariates (Model 8).

Model performance was compared using Akaike Information Criterion (AIC) scores, ΔAIC values and model weights, which provided a probabilistic ranking of model support. We also performed 10-fold cross-validation to robustly evaluate model performance and ensure generalisability across different subsets of the data while minimising overfitting during model selection. Predictive accuracy was then evaluated across folds by comparing root mean squared error (RMSE) and mean absolute error (MAE). Full model details and performance metrics are included in the Supplementary Materials (Tables S2–S4).

2.1.2 | Alternative production approaches

To test the hypothesis that murrelet populations would benefit more from concentrated instead of extensive and fragmented wood production, with benefits magnified with higher timber demand, we developed a suite of simplified 1 Mha landscape scenarios meeting two overall wood production targets (Figure S4). Our two production targets involved allocating either 30% or 75% of the overall landscape as timber plantations, with the remainder left as unharvested mature forest, which could be used for murrelet nesting. Scenarios assumed that all wood was harvested from equivalently yielding intensively managed plantations with 45-year rotations. We did not consider the potential for production from longer-rotation plantation systems, or from ecological forestry approaches within natural (i.e. non-plantation) forest, since these management systems are historically uncommon in our landscape (and indeed across the murrelet's range), and so their effects on murrelet occupancy could not be empirically tested. We assumed that plantations in scenarios were harvested on a rotational basis across the landscape, thus delivering an even flow of timber annually.

For each production target, we developed 16 landscapes with a fixed plantation area that was configured in increasingly fragmented fashion (see Figure S4), using the LandscapeR (Masante & Murphy, 2024) package in R to allocate plantations as all being concentrated in a single patch, to being grown in increasingly smaller patches across the landscape. Comparing murrelet occupancy across scenarios which generated the same amount of timber allowed us to compare the impacts of landscape-level configuration options without having to consider the consequences of compensating any shortfalls in production through timber harvesting elsewhere (Balmford et al., 2025). Examining across scenarios which delivered different production levels allowed us to explore how the relative performance of management options varied as timber demand increased.

To infer murrelet occupancy for each hypothetical scenario landscape, we computed the edge and habitat amount within 100 m and 2 km buffers (as above) around all mature forest pixels. For simulated landscapes and forests, we could not use our SDM-based approach to categorise murrelet habitat, since this relied on remote-sensing derived metrics to infer habitat suitability. Instead, we assumed that murrelets could not breed within short-rotation plantations (Hamer & Nelson, 1995) and so assigned all plantation pixels as non-habitat (with a value of 0) across the 45-year rotation (0). We also assumed that all forest pixels represented suitable nesting habitat (i.e. with a value of 1). We note that this will overestimate the value of small forest patches within heavily fragmented habitat and so our results are likely to be conservative with respect to the relative value of concentrated production.

2.1.3 | Estimating current and future management and climate impacts

To predict how near-future climate change, fragmentation and forest management across the Pacific Northwest may affect murrelet occupancy, we next uniformly stratified 1,000,000 points (500 m apart) across the murrelets' range. Using a GNN canopy cover product (Bell et al., 2024) for the year 2020, which represented the most recent year for which both murrelet SDM and GNN data (necessary for estimating habitat and edge amount) were available, we excluded points that would not reasonably support closed-canopy forest (e.g. urban areas, lakes, rock and snow-covered zones). We further filtered points to only include those ≤60 km from the coast and <600 m in elevation, since forests outside of these thresholds were not well represented in the murrelet survey data used to fit occupancy models (Figure S2). Murrelet detections are known to drop off substantially at these coastal distances and elevations (Hamer & Nelson, 1995), and so our forecasts of current and future climate and management impacts are likely to represent outcomes in the core terrestrial range of murrelets, though we may not capture dynamics in more marginal habitat or at the species range edge (Valente, Rivers, et al., 2023).

In total, this left 220,816 points for which we extracted 2020 covariates, including edge and habitat amount based on our SDM approach. We then used spatial data describing land-ownership patterns across the PNW (Phalan et al., 2019) to summarise predictions of how current management is likely to be affecting murrelet populations during both good and bad ocean years. Land ownership encompassed six categories including federal (e.g. national parks and forests), state (e.g. state parks and forests), private industrial (mostly industrial plantation lands), private non-industrial (e.g. small family-owned land holdings), tribal and private conservation lands, which largely comprise lands under conservation easements. Next, to investigate the impacts of management or production policies reducing fragmentation into the future, we simulated the consequences of simultaneously reducing both local and landscape-scale edge amounts in 25% intervals, for each of the 220,816 points. These analyses fixed habitat amounts at both local and landscape scales to 2020 levels and so provide an estimation of how future production policies that reduce fragmentation per se would affect murrelet occupancies, while accounting for the often co-occurring confound of habitat amount (Fahrig, 2003; Valente, Gannon, et al., 2023). Nevertheless, it is not straightforward to fully disaggregate the relative contributions of changes in fragmentation and habitat amount in occupancy analyses (Betts et al., 2006).

To identify priority regions where efforts to reduce edge amount would most benefit murrelet populations, we mapped where edge reductions of 50% would lead to the largest (90th percentile) increase in predicted 2020 occupancy levels. We mapped priorities for both good and bad ocean years, or for both—the latter representing areas where efforts to increase murrelet populations are least likely to vary according to at-sea conditions. We explored how priority areas were distributed according to land ownership, and resampled priority areas to 1km^2 spatial scale, as this represents a spatial scale over which management efforts to reduce landscape-level fragmentation could reasonably operate.

Finally, to examine trade-offs between reducing fragmentation and supplying wood, and to evaluate the feasibility of concentrating wood production inland to support murrelet recovery, we used a 30 m resolution spatial dataset of potential wood productivity (Weeks

et al., 2023). This layer was derived from over 213,000 USFS Forest Inventory and Analysis (FIA) plots (2014–2018), combined with Landsat 8 OLI vegetation phenology, climatic and topographic data. An ecological ordination model imputed site productivity values, categorised into seven bins ranging from 0 to 225+ cubic feet/acre/year, to unsampled pixels. We analysed how productivity varied by land ownership and distance from the coastline (up to 100 km), fitting relationships using both simple linear models and GAMs (productivity ~ coastal distance).

3 | RESULTS

3.1 | Edge amount interacts with ocean conditions to drive murrelet occupancy

Marbled murrelet occupancy was influenced by a complex interplay of habitat, edge, ocean and coastal distance dynamics (Table S2). To test for the effects of fragmentation per se, it is important to control for habitat amount (Fahrig, 2003), and we indeed found that both local and broader landscape-level habitat amounts (within 100 and 2000 m buffers) positively influenced occupancy, with landscape habitat having a stronger relationship. Based on our best-performing model (Table S3), increasing landscape-level habitat amount by one standard deviation (equivalent to an additional ~280 hectares of habitat in a 2000 m radius buffer [1256 ha]) increased odds of occupancy by 64% [95% CIs: 43%, 87%], whereas a one standard deviation increase in local habitat amount (equivalent to ~1.2 ha of additional habitat in 100 m radius [3.14 ha]) increased odds of occupancy by 46% [20%, 57%]. Distance to coast was also an important driver of occupancy, with the odds of occupancy roughly halved for each additional ~18 km from the coast ($\beta = 0.53$, [0.46,0.60]).

Importantly, after accounting for habitat amount, landscape-level edge amount significantly reduced murrelet occupancy ($\hat{\beta} = -0.546$ [−0.689, −0.404], $p < 0.001$). Critically, this negative edge effect was amplified following poor climate-driven ocean conditions (Figure 1; PC1_t1 × EdgeDens2000: $\hat{\beta} = 0.121$ [0.016,0.226], z = 2.14,

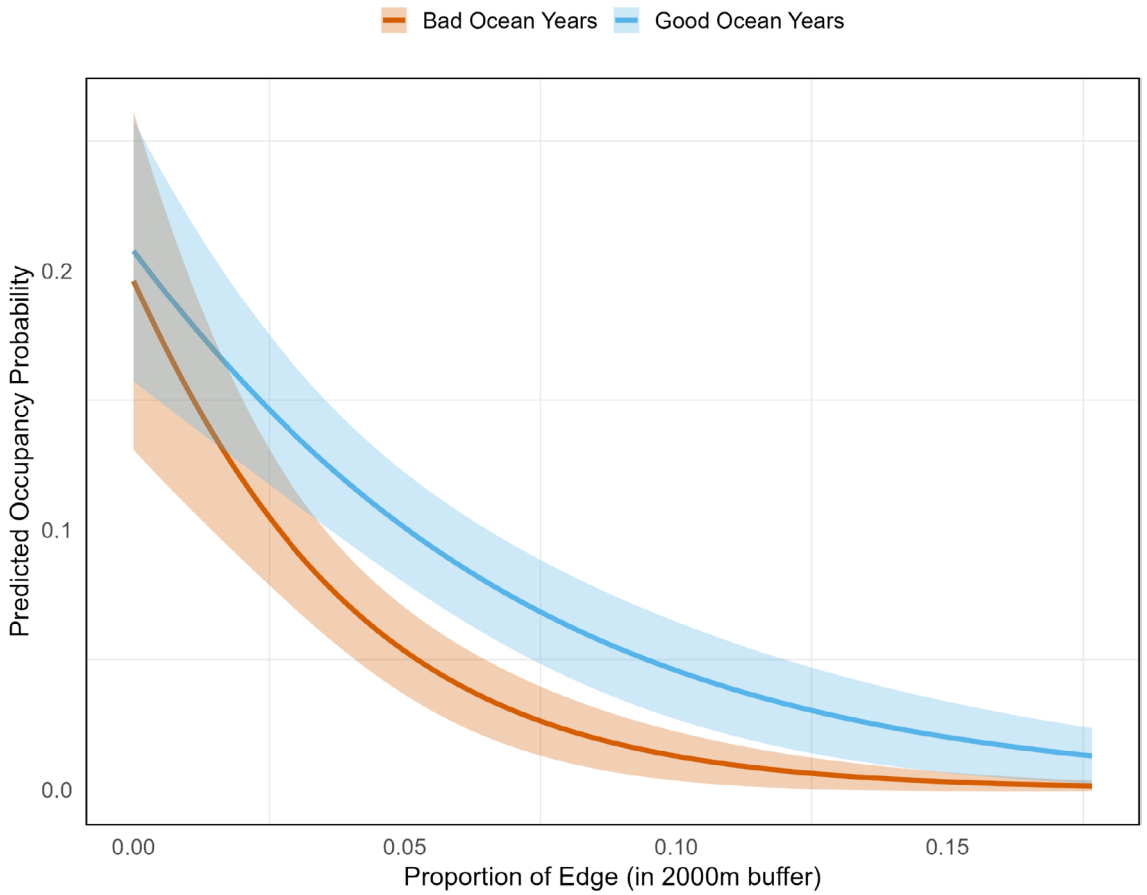


FIGURE 1 Previous-year ocean conditions may amplify landscape-scale edge effects on murrelet occupancy. Negative effects of edge are amplified following years with poor ocean conditions. Predicted occupancies (solid line denotes predicted occupancy with 95% confidence intervals shown by the shaded region) were derived from occupancy analyses that included ocean conditions, edge amount within 100 m and 2000 m radii of survey points, and other occupancy and detection-related predictors (see Model Specification). 'Good' and 'bad' ocean years corresponded to the 10th and 90th percentile of PC1 values recorded between 1998 and 2023, where PC1 was the first principal component of sixteen marine variables capturing various climate-related physical and biological ocean processes (see Table S1). All predictors except ocean conditions, edge proportion and distance to the coast (30 km inland) were held constant at their mean values. The effects of varying distance to coastline are presented in Figure S5.

$p = 0.024$). For example, following good ocean years, the odds of occupancy was reduced by 70.2% [51.3%, 81.8%] when going from just 3% to 10% edge within a 2000 m radius, but following bad ocean years, the corresponding reduction was 87.6% [72.3%, 94.5%]. This detrimental landscape-scale effect of edge amount outweighed any small positive effect of local-scale edge on murrelet populations ($\widehat{\beta} = 0.26$ [−0.008, 0.528], $p = 0.057$). Moreover, although on the probability scale it appeared that the magnifying effect of previous-year ocean condition on landscape-scale edge amount also varied by distance to coast (Figure S5), this three-way interaction was not statistically supported (Table S3, compare model 7 vs. model 8), suggesting climate-fragmentation interactions were not mediated by coastal proximity.

3.2 | Spatially concentrated production improves murrelet outcomes following poor ocean conditions

To test whether murrelet populations would benefit more from concentrated versus extensive logging, particularly after bad ocean years, we simulated 1 Mha landscapes with either 30% or 75% allocated to plantations and the remainder left as late-successional forest. For forested pixels across the landscape, we predicted that murrelet occupancy was consistently higher in landscapes where plantation production was spatially concentrated in exchange for conserving contiguous tracts of forest (Figure 2). This pattern persisted following both good and bad climate-driven ocean years, with fragmented landscapes exhibiting both lower median occupancy and a reduced range in occupancy predictions following bad years. Murrelet occupancies were higher in lower-production scenarios (top panel; Figure 2) compared to higher-production scenarios (bottom panel), but we did not find evidence that higher wood production magnified differences between concentrated and fragmented approaches, as steeper occupancy reductions were observed in low-production scenarios. We note that the low variation in occupancy predictions for fully concentrated production landscapes (Figure 2 shaded regions; which represent where all unharvested forest is conserved in one contiguous block) likely reflects the scarcity of large, unfragmented habitat within both the murrelet's terrestrial range and the surveyed data, making it challenging to predict the range of occupancies that would have been typical historically within very large tracts of intact habitat (Phalan et al., 2019).

3.3 | Edge effects strongly reduce the conservation value of key forest areas

Lastly, to explore the consequences of historical and future forest management policies for murrelets, we extracted edge and habitat amount information for 220,816 points uniformly stratified (500 metres apart) across the murrelet's core territory in the Pacific Northwest. For the baseline year of 2020, we found a clear influence of land ownership on forest cover and fragmentation patterns (Figures S6–S9). Habitat amount around points located on private conservation and federal lands was substantially higher at both local and landscape scales (median of 0.35 and 0.9, and 0.5 and 0.5 proportional habitat cover within 100 m and 2000 m buffers, respectively) compared with state, tribal or industrial lands (Figures S7 and S9). However, this higher habitat cover in private conservation and federal lands was accompanied by a greater proportion of lands composed of hard edges, particularly at landscape scales (Figure S8).

Predicted occupancies revealed further differences in how current forest management, climate conditions and fragmentation are likely to shape marbled murrelet populations into the future (boxes at $x = 0$, Figure 3). Across land ownerships (except for tribal lands), we found evidence that current landscape configurations resulting from substantial landscape fragmentation (see Figure S8) are leaving murrelets vulnerable to poor ocean conditions (Figure 3 cf. orange and blue boxplots for 0-values, x-axis). Occupancy predictions across points were generally low (medians between 0.1 and 0.2) in all land ownerships, and highest on private conservation and federal lands (ranges varied considerably; Figure 3). However, when we simulated the consequences of reducing both local and landscape edge amount in the future, holding habitat amount fixed, we found substantial increases in predicted occupancies, especially on private conservation and federal lands, and to a lesser extent on state, private non-industrial and private industrial lands. Importantly, reducing edge amount appears to stabilise occupancy across good and bad ocean years (Figure 3), suggesting edge reduction can mediate the effect of varying ocean conditions. For example, reducing edge amount by 50% increased median occupancy in years following bad ocean conditions to 0.12 and 0.11 in private conservation and federal lands, respectively, up from 0.05 and 0.07. This pattern held generally across all land ownerships: reducing edge amount narrowed (and with large edge reductions removed) the difference between median occupancy in good and bad ocean years (Figure 3).

The opportunity space for edge-reduction efforts to increase murrelet occupancy was not spatially uniform (Figure 4). Using predicted changes in occupancy delivered via a 50% reduction in edge amount, we identified the top 90th percentile priority areas where decreasing edge amount within 1 km^2 cells would yield the greatest occupancy gains for good years (10,091 km^2), bad years (9515 km^2) and for both (4644 km^2; Figure 4). The latter represents areas where edge-reduction would be most beneficial regardless of ocean conditions. Occupancy gains would be maximised by reducing fragmentation in coastal forests including in the Oregon Coast Range around Siuslaw National Forest, in the environs of Olympic National Park in Washington, and in a broad section of the California Coast Range (Figure 4; Figure S10 shows absolute occupancy changes, along with associated uncertainty). Priority areas for reducing fragmentation were generally located where the surrounding habitat suitability was high but interspersed with clear-cut lands or young, open-canopied forest (Figure 4). Overall, priority areas for reducing landscape-scale

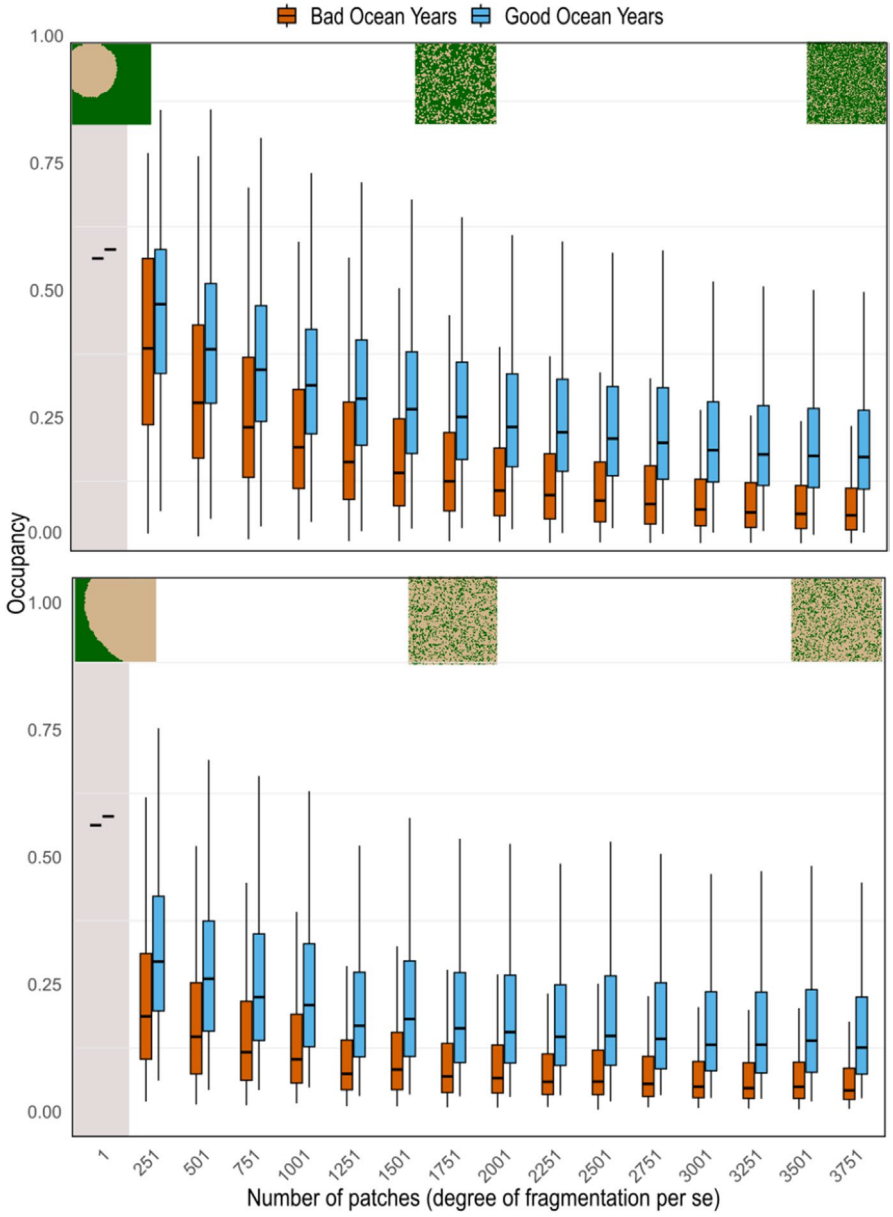


FIGURE 2 Spatially concentrated timber production increases murrelet occupancy during good and bad ocean years. Scenarios represent one-million-hectare landscapes in which proportions of plantation (brown) and temperate forest (green) were held constant at two levels of timber production allocating 30% (top panel) or 75% (bottom panel) of the landscape as plantations. Scenarios encompassed a gradient of production configurations, from concentrated to increasingly fragmented plantation-focused wood production, enabling comparisons of fragmentation impacts per se (i.e. accounting for landscape-level habitat amount). Box plots summarise the median (line), interquartile range (box) and data range within 1.5 × IQR (whiskers) of occupancy estimates for all murrelet survey points within forests across each hypothetical landscape. Occupancy estimates used the same occupancy-detection model as Figure 1, with 'good' and 'bad' ocean years defined in the same way, and with all predictor variables except ocean conditions, edge proportion and habitat amount held constant at their mean values. Note that for the grey shaded region denoting extremely concentrated production (number of patches = 1), only median lines are shown. Our model predictions here showed very little variation in occupancy predictions within forest points, likely because large amounts of zero-edge habitat are highly non-analogous in both our underlying data and across the marbled murrelets terrestrial range, due to historical fragmentation. Hypothetical landscapes can be visualised in Figure S4.

edge amount were disproportionately located around federal and private non-industrial lands, suggesting that these locations—and the lands directly adjacent—offer the greatest opportunities for increasing murrelet occupancies (Figure S11). Nevertheless, substantial, context-specific opportunities also existed on state and private lands (Figure S11).

4 | DISCUSSION

Habitat loss, fragmentation and climate change increasingly threaten forest-dependent biodiversity globally (Betts et al., 2019; Bourgoin et al., 2024; Haddad et al., 2015; Northrup et al., 2019; Sims et al., 2025). We show here that fragmentation and climate can act synergistically,

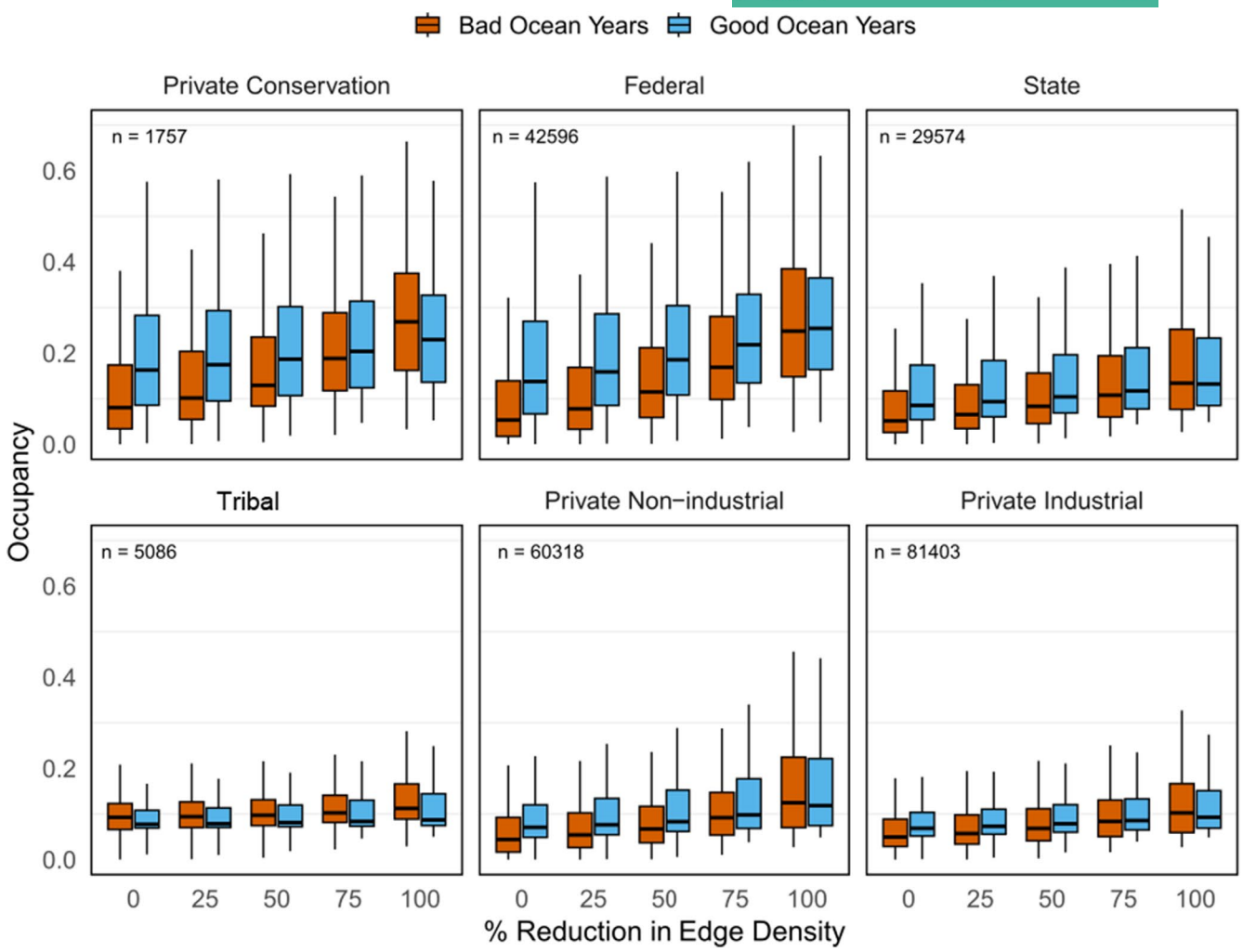
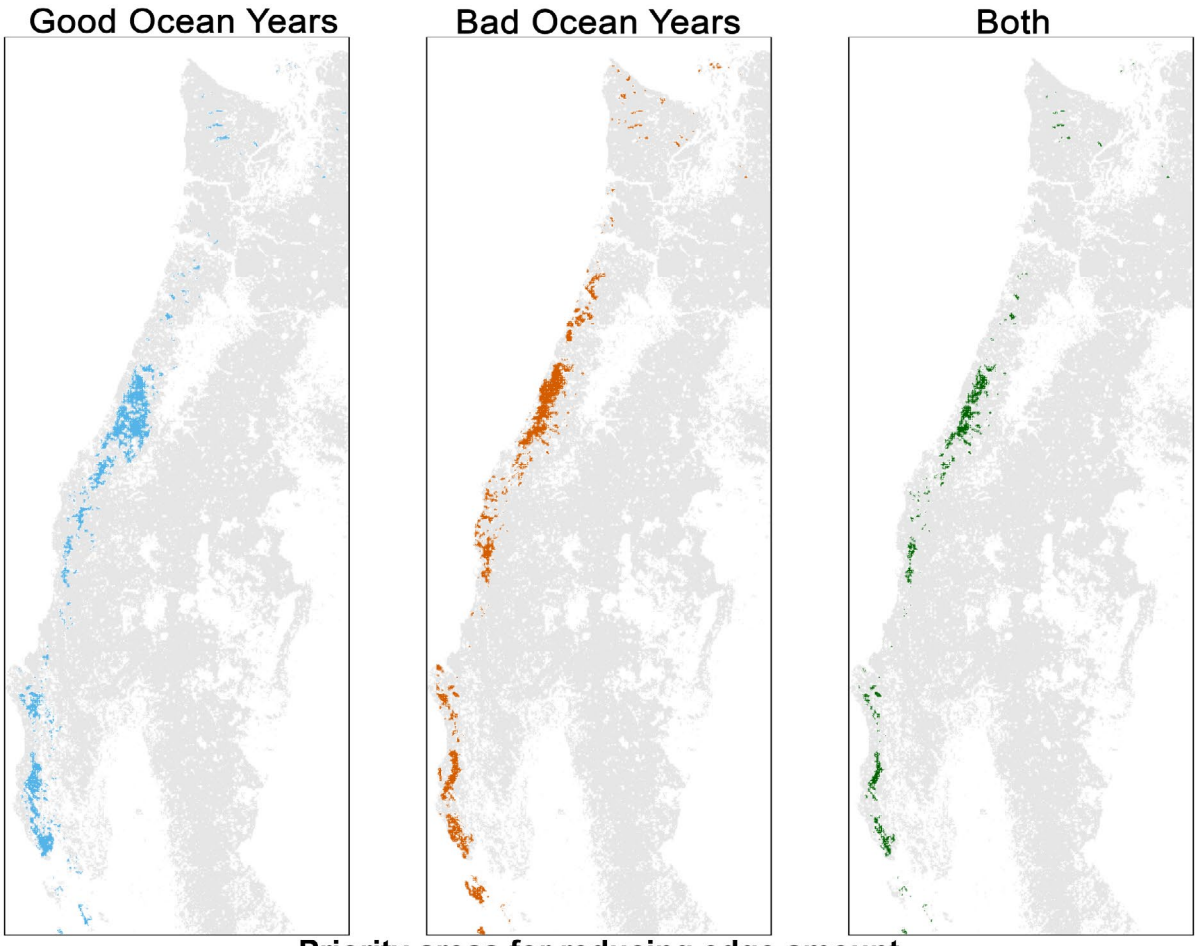


FIGURE 3 Reducing edge amount, without additional habitat gain, boosts occupancy and negates negative effects of bad ocean conditions on occupancy. For each of 220,816 points stratified uniformly (each 500 m) across the Pacific Northwest, we calculated edge and habitat amounts for the year 2020 (0-values on x-axis) and then simulated the effects of reducing the proportion of hard edges (25, 50, 75 and 100% in both 100 m and 2000 m radii buffers), while holding habitat amount fixed. Occupancy estimates used the same occupancy-detection model as Figure 1, with 'good' and 'bad' ocean years defined in the same way, and with all predictor variables except ocean condition, edge proportion and habitat amount held constant at their mean values. Note that while point centroids were within specified land ownerships, habitat metrics were calculated within buffers that could overlap adjacent ownerships. Figures S6–S9 show the distribution of habitat and edge amount at different scales around points. Plots were filtered to only include points <60 km from the coast and <600 m, excluding urban areas, bare rock and snow lands, reflecting the range of data for which our models were fitted.

with edge amount and climate-driven ocean conditions as key interacting drivers of murrelet occupancy. Concentrated timber production would therefore seem to better reconcile murrelet conservation with growing wood demands than spatially extensive harvests, reflecting findings made for other forest-dependent species in temperate and tropical biomes worldwide (Cerullo, França, et al., 2023; Edwards et al., 2014; Harris & Betts, 2023; Runting et al., 2019). However, we additionally demonstrate that the potential conservation gains from concentrated production may grow as climate conditions are exacerbated, due to previously hypothesised climate-magnified negative impacts of fragmentation (Travis, 2003). Our results underscore the need for integrated, landscape-scale timber harvesting policies in the Pacific Northwest and have at least three broad implications for navigating production-conservation trade-offs in the 21st century.

First, many studies conclude that habitat fragmentation has relatively little impact on biodiversity, with total habitat amount the principal driver of species outcomes (Fahrig, 2003; Valente, Gannon, et al., 2023). However, holding forest amounts constant and analysing species-level edge responses across multiple spatial scales, we find the opposite: increasing fragmentation drives pronounced occupancy declines. Encouragingly, this suggests that efforts to reduce fragmentation by altering landscape configurations could boost species persistence considerably, without reducing overall wood production—an advantage that expanding habitat area typically cannot deliver alone (especially since it risks merely displacing wood production elsewhere; Balmford et al., 2025; Cerullo, Barlow, et al., 2023; Wear & Murray, 2004). Yet our findings also indicate that studies overlooking fragmentation impacts risk markedly underestimating



Priority areas for reducing edge amount

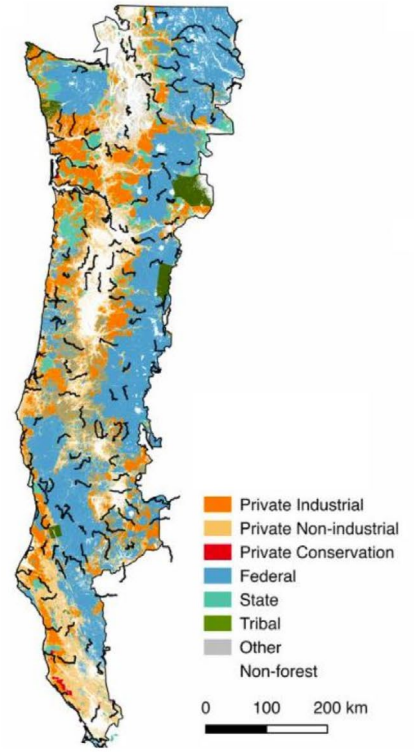


FIGURE 4 Priority 1 km^2 areas where reducing edge amount by 50% would result in the greatest occupancy increase from current (2020) levels. Priority areas are shown for good ocean years, bad ocean years or for both, representing intersecting areas where occupancy would be increased most regardless of ocean condition. Priority regions represent the 90th percentile of absolute occupancy change values from current levels. Variation in absolute occupancy increases along with associated uncertainty around values are shown in Figure S10. Grey backgrounds show areas with some amount of forest canopy coverage. Insets show the distribution of land ownerships in the Pacific Northwest, a marbled murrelet nesting on a mossy platform and recently clear-cut plantation in the Oregon Coast Range. Murrelet photo from Brett Lovelace, plantation photo from Megan Eldred, land ownership map from Phalan et al. (2019).

logging's ecological costs. Second, extensive logging approaches remain favoured globally due to societal preferences (Ribe, 2006), merchantable timber distributions (Cerullo, França, et al., 2023) and environmental policies including certification standards and clear-cut size restrictions (Betts et al., 2021). In the Pacific Northwest, for instance, splintered land-ownership and plantation adjacency rules have forced small (<50 ha), scattered clear cuts, fragmenting murrelet habitat across broad spatial scales and eroding the conservation value of key remaining habitat patches on federal, state and private reserves (Valente, Rivers, et al., 2023). Similar effects may also be undermining forest-dependent biodiversity in other harvested systems and regions worldwide, meriting urgent study. Third, we provide to our knowledge some of the strongest evidence for how alternative logging layouts may affect biodiversity under climate change, finding that climate change may amplify logging-driven occupancy declines; something that concentrated harvests could mitigate. As wood demand grows potentially >50% by 2050 (Peng et al., 2023), spatial aggregation of timber harvests could thus be a critical strategy for protecting other climate-sensitive, forest-dependent species beyond the Pacific Northwest. Ensuring any such benefits of concentrated harvests in practicewill require active mechanisms and safeguards to ensure any rebound effects are avoided (i.e. that intensified production does not merely incentivise higher levels of extraction elsewhere). Strong land-zoning mechanisms already in place in the Pacific Northwest, which restrict plantation expansion to clearly demarcated land areas, provide one key instrument for avoiding perverse outcomes associated with plantation concentration (Nagel et al., 2025).

Multiple mechanisms may explain murrelets' stronger preferences for contiguous habitat following poor ocean conditions. Lower at-sea prey availability could reduce parental nest attendance due to longer foraging demands (Cheung & Frölicher, 2020; Martin, 1995), potentially leading to higher predation rates at forest edges (Malt & Lank, 2007; Martin, 1995). Alternatively, poor ocean conditions might create filtering effects that alter population-level nest-site selection. For example, previous research shows that poor ocean conditions drive substantial at-sea movement of murrelets (Garcia-Heras et al., 2024) and both higher parasite loads and reduced nesting attempts (Michlanski et al., 2025). Our results could therefore be explained by a biasing of remaining nesters toward higher-fitness individuals that consistently select less-fragmented habitat, with lower-condition individuals either abstaining from or reducing nesting attempts. While previous research has identified some evidence of terrestrial-ocean interactions in driving murrelet population outcomes (e.g. Becker et al., 2007), our analyses consider a more comprehensive suite of ecologically meaningful ocean variables beyond ocean temperatures, also encompassing climate-mediated impacts on marine food webs (Betts et al., 2020; Peterson et al., 2014). Nevertheless, an important limitation is that we do not account for the potentially compounding effects of consecutive poor ocean years on murrelet occupancy. Our results are thus likely to be conservative and may underestimate future ocean impacts on murrelet populations, especially as 'bad' ocean years become more frequent or severe with exacerbating climate change (Cheung & Frölicher, 2020; Ren et al., 2023). Climate change is also likely to further threaten core murrelet habitat in other ways not quantified here, including by increasing insect outbreaks and the frequency, extent and severity of forest fires (Halofsky et al., 2020; Parks et al., 2019). These exacerbating pressures can degrade core nesting habitat directly and amplify edge effects beyond those caused by timber harvests (Parkins et al., 2018), underscoring the need to understand how climate- and ocean-driven climate-associated events jointly shape murrelet populations. Future studies could also revisit sites that have experienced changes in edge amount to obtain before–after estimates of occupancy responses and to enable modelling across seasons, rather than relying solely on space-for-time substitutions as we do here (Christie et al., 2019; França et al., 2016; Lovell et al., 2023).

Reducing edge amount within wood production landscapes emerges as a key strategy for enhancing climate resilience for forest-dependent murrelets. We find that edge reduction could substantially improve the conservation value of federal and private conservation lands, with our spatial analyses identifying where interventions would yield the greatest occupancy benefits. More generally, our findings highlight the critical role that intact forest patches could play in buffering murrelet populations against adverse ocean conditions, and these areas would benefit from explicit policies that actively reduce landscape fragmentation (Betts et al., 2019). Opportunities to increase occupancy through edge reduction are not uniformly distributed across landholders or spatial locations, with the greatest potential concentrated around key remaining habitat patches, particularly on federal and private non-industrial lands. These landholders, along with those driving fragmentation in adjacent areas, represent critical stakeholders for securing murrelet populations under climate change. Yet ultimately, meaningful edge reduction will require integrated land-use planning coordinated across multiple partners, as fragmentation generated, for example, on private industrial lands directly undermines habitat quality in adjacent potential nesting habitat. For instance, in forests adjacent to murrelet habitat, incentives could be provided to private landowners

to engage in silvicultural activities that decrease the availability of open-canopy forest edges.

Targeted management approaches, including extending logging rotation lengths near high-quality habitat to reduce edge frequency, or encouraging dense plantings around existing habitat patches to rapidly seal edges, could be key strategies for conserving murrelet populations and other forest interior-associated species. Forestry incentives or land swaps could also promote concentrated production in inland areas, where fewer murrelets nest; a preliminary analysis suggests this would incur minimal wood losses, as timber productivity remains stable within 100 km of coast (Figure S12). Nevertheless, any murrelet policies that do reduce local wood production risk displacing harvest into other key habitats unless losses are offset and so must be carefully evaluated (Balmford et al., 2025; Cerullo, Barlow, et al., 2023; Wear & Murray, 2004). Murrelet-focused management plans must also consider the habitat requirements of early-seral species dependent on naturally regenerating open lands (Phalan et al., 2019), though such species may also benefit from efforts to concentrate plantation forestry if this enables larger tracts of young broadleaf habitat (Betts et al., 2010; Phalan et al., 2019). Meanwhile, concentrated forestry policies could consider wood production strategies that are both resilient to exacerbating climate, pathogen and wildfire risks and that minimise highly localised disturbances including soil compaction and erosion (Fahey et al., 2018; Messier et al., 2021). 'Ecological forestry' approaches in native, non-plantation forests, which our analyses do not consider, could potentially reduce conservation–production trade-offs while rendering wood supply more resilient to escalating climate-driven threats, especially in comparison to monoculture plantations (Franklin et al., 2018). However, any benefits of such forestry (which can include practices such as selection cuts or retention harvests) should be quantified and not assumed; insofar as these increase the footprint of production via lower yields or lead to greater landscape-level fragmentation, our findings suggest limited benefits.

Our results also have policy implications in the context of recent proposals for both rapid expansion of timber production on federal lands (Betts et al., 2025) and Northwest Forest Plan revisions targeting old-growth patch protection without considering landscape-scale contexts (Northwest Forest Plan & Amendment, Forest Service). To support murrelets and other forest-dependent species, policies could support strategic concentration of harvests, maintaining large unfragmented areas of high-quality habitat as climate refugia, and incorporating consideration of landscape-scale processes into production and conservation planning. More broadly, while ecological theory predicts lower fragmentation impacts in temperate versus tropical systems due to historical extinction filters (Betts et al., 2019), our findings demonstrate that pervasive forest fragmentation can still substantially reduce populations of sensitive temperate species. As shown here for marbled murrelets in the Pacific Northwest, fragmentation effects may be expected to be most severe for habitat specialists in regions where anthropogenic disturbances dramatically exceed natural historical baselines. Future research examining climate-fragmentation interactions across other old-forest species will help elucidate whether they are facing similar pressures from rising global wood demand.

AUTHOR CONTRIBUTIONS

Gianluca Cerullo and Mathew Betts conceptualised the study. Mathew Betts supervised the research. Gianluca Cerullo and Mathew Betts designed the methodology, with support from Jennifer Bailey Guerrero, Emily Conklin, Dusty Ganon, Anna Kohlberg, Jonathon Valente and Zhiqiang Yang. Gianluca Cerullo undertook the investigation, led the writing of the manuscript and was responsible for visualisations. Funding acquisition was by Mathew Betts, James W. Rivers and Kim Nelson. All authors reviewed and edited the manuscript draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code available at https://doi.org/10.5281/zenodo.18432151 (Cerullo & Betts, 2026). Code can also be accessed at https://github.com/gcerullo/MarbledEdges.

ETHICS STATEMENT

The manuscript did not require ethical approval and used pre-existing data sources.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Workflow for defining edge and habitat amount for marbled murrelets.

Figure S2. The distribution of predictor variables within 29,323 sites surveyed for murrelets between 1998 and 2023.

Figure S3. Variation in ocean conditions through time.

Figure S4. Configurations for 1 Mha hypothetical landscapes in Figure 2 in the main text.

Figure S5. Mean estimated effect (solid line) of previous-year ocean condition and edge amount on marbled murrelet occupancy, shown for different distances from the coast.

Figure S6. The distribution of edge amounts in 100 m radius buffers surrounding 220,816 points uniformly distributed in 500 m intervals across the Pacific Northwest.

Figure S7. The distribution of the habitat amounts in 100 m radius buffers surrounding 220,816 points uniformly distributed in 500 m intervals across the Pacific Northwest.

Figure S8. The distribution of the edge amount in 2000 km radius buffers surrounding 220,816 points uniformly distributed in 500 m intervals across the Pacific Northwest.

Figure S9. The distribution of habitat amounts in 2000 km radius buffers surrounding 220,816 points uniformly distributed in 500 m intervals across the Pacific Northwest.

Figure S10. Change in absolute occupancy from reducing edge amount 50% in priority areas.

Figure S11. The distribution of 1 km^2 priority areas for reducing edge amount across land ownerships.

Figure S12. Potential timber productivity with distance to coastline, shown for different landownerships across the Pacific Northwest.

Table S1. Ocean Conditions methods.

Table S2. Parameter estimates from the top-ranked occupancy model (Model 7), including 95% confidence intervals.

Table S3. Model comparison table showing AIC-based support for candidate occupancy models.

Table S4. Ten-fold cross-validation results from occupancy models showing root mean square error (RMSE) and mean absolute error (MAE) with standard deviations (SD).

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