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Squeezed by a habitat split: Warm ocean conditions and old-forest loss interact to reduce long-term occupancy of a threatened seabird

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Abstract

Theory predicts that species requiring multiple habitat types simultaneously should have heightened sensitivity to anthropogenic pressures, yet tests of this prediction are especially rare. We tested whether breeding site occupancy of the threatened marbled murrelet (*Brachyramphus marmoratus*) was driven by the synergistic effects of nesting habitat loss in forests, and changing ocean conditions. We paired 70,700 murrelet surveys at 19,837 sites across 20 years from the Oregon Coast Range with annual data on the extent of old forest and biophysical ocean conditions. Dynamic occupancy models indicated that local murrelet colonization rates were strongly reduced during warm ocean conditions with low prey availability. Landscapes that contained more old forest and were closer to the ocean showed reduced rates of local extinction. Given predictions of accelerated ocean warming and increased global timber demand, our results suggest murrelets may continue to be imperiled by deterioration of the two habitats upon which they depend.

KEYWORDS
endangered species, marbled murrelet, ocean conditions, old forest, seabird, threatened

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1 | INTRODUCTION

Species that require two or more habitats during distinct life history stages are considered to have evolved a "habitat-split" strategy. This strategy is found in many vertebrates, such as terrestrial amphibians, which often live in upland habitats most of the year but require wetlands for breeding in spring (Becker et al., 2007; Scheele et al., 2019), and migratory birds that reside in wintering areas that are thousands of kilometers from summer breeding grounds (Webster, Marra, Haig, Bensch, & Holmes, 2002). Species that have evolved a habitat-split strategy are thought to be more sensitive to anthropogenic pressures than those that require a single habitat (Becker et al., 2007). Nevertheless, evaluating whether degradation of multiple habitats leads to synergistic negative effects on populations has been challenging because long-term population data can rarely be coupled with information about changes in habitat quality across multiple habitats.

In relation to species that require multiple habitats at distinct points in the annual cycle, far fewer species exhibit a habitat-split strategy wherein they require two distinct habitats simultaneously during the breeding season. Seabirds exemplify the latter group because they forage in marine habitats that are typically far from breeding colonies where they rear young (Gaston & Jones, 1998). Among seabirds, several species require mainland forests as breeding habitat (e.g. Alcidae, Procellaridae, Laridae) and this is expected to result in heightened sensitivity to anthropogenic change. For example, two *Brachyramphus* murrelets that nest in forests are listed by the IUCN as Near Threatened, with one further classified as Endangered (Bird Life International 2018). The latter species—the marbled murrelet (*Brachyramphus marmoratus*, hereafter murrelet)—is an iconic seabird that typically nests in old-growth and late-successional forest of northwestern North America and forages in nearshore waters of the Pacific Ocean (Nelson, 1997). Because of its association with old forests, which have historically been targeted for timber harvest, this species has been at the center of controversies surrounding management of coastal forests for decades (Thomas, Franklin, Gordon, & Johnson, 2006). In addition to the availability of nesting habitat, murrelet population trends are also thought to be influenced by ocean conditions, particularly the food resources required for successful nesting (i.e., forage fish). In turn, much debate has focused on the relative contributions of terrestrial habitat loss and changing ocean conditions to driving long-term murrelet population declines (Raphael, Shirk, Falxa, & Pearson, 2015).

Murrelets can nest >100 km from marine foraging areas (Lorenz, Raphael, Bloxton, & Cunningham, 2017) and the energetic costs of inland commuting flights are high (Hull et al., 2001), so nesting habitat that is distant from the coastal foraging sites may result in low nest success, particularly during periods of poor ocean conditions. Thus, determining the extent to which changes in forest nesting habitat and ocean conditions drive murrelet population trends has considerable conservation and management implications in the Pacific Northwest. This is particularly true given management activities that promote the creation of early seral ecosystems on federal landownerships via the harvest of old forest (Phalan et al., 2019), and ongoing concerns about the influence of climate change on fish populations (Free et al., 2019). Importantly, the availability of forest nesting habitat and marine foraging areas may result in additive or synergistic effects on murrelet populations, but this idea has yet to be

FIGURE 1 (a) Location of 70,707 marbled murrelet occupancy survey locations (red dots) and old forest (i.e., old and late-successional forest) in western Oregon, USA. (b) Marbled murrelet incubating on its nest located on the branch of a mature Douglas fir tree. Occupancy of murrelets is strongly associated with old forest at landscape scales and cool, productive ocean conditions. Photo of murrelet courtesy of Brett Lovelace/OSU
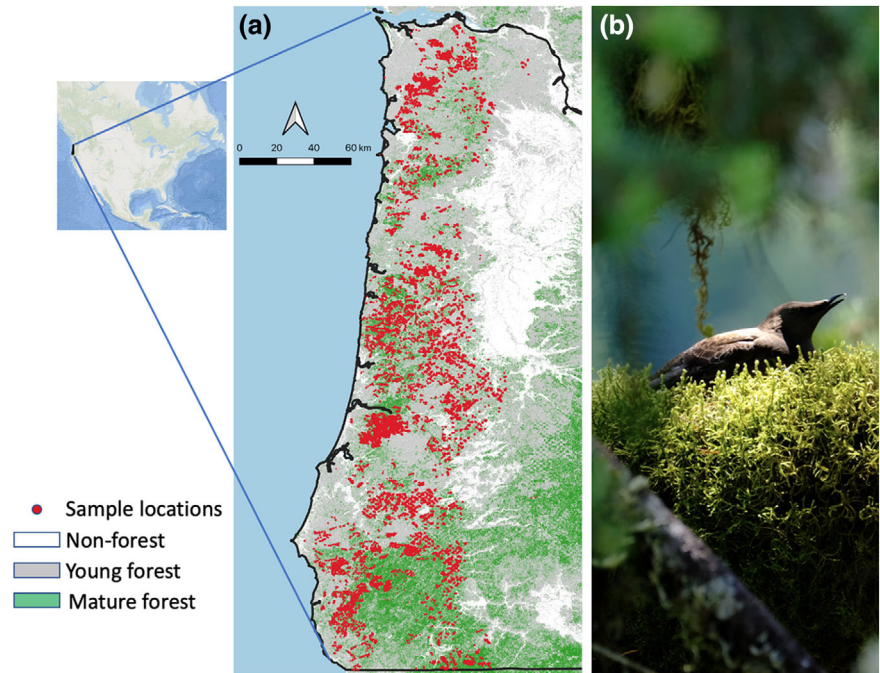
evaluated. Here, we provide the first test of the hypothesis that terrestrial and ocean conditions together interact to drive occupancy dynamics of the murrelet using long-term datasets that represent (a) biophysical indicators of ocean conditions, (b) extent of old forest, and (c) breeding habitat occupancy of murrelets across >19,800 locations in the Pacific Northwestern, USA. We predicted that settlement of previously unoccupied sites would be lowest, and annual local extinction (i.e., vacancy) highest in warm ocean years, and that this effect would intensify in landscapes which have lost a large proportions of nesting habitat.

2 | METHODS

2.1 | Marbled murrelet occupancy surveys

We compiled breeding season audiovisual surveys for murrelets conducted 15 May to 5 August annually as part of research and monitoring efforts and at proposed timber sale sites from a variety of sources in Oregon from 1999 to 2018, including Oregon State University, US Forest Service, Bureau of Land Management, and Oregon Department of Forestry. Our sample totaled 70,700 surveys conducted at 19,837 sites and although it was not drawn at random, it is spatially comprehensive and represents all stand types with the potential to be murrelet habitat (Figure 1). Trained, certified surveyors quantified the number of

audio and visual detections of murrelets during 2-hour surveys following the Pacific Seabird Group (PSG) survey protocol (Evans Mack et al., 2003) which is used to evaluate breeding activity at survey sites. Detections were classified as either murrelets being present (flying over the forest or calling) or exhibiting behavior indicative of nesting (flying below the canopy, landing, and/or circling); otherwise the site was classified as undetected. Areas surveyed were suitable murrelet habitat, primarily mature (>80 years) and old-growth (>200 years) forests that contained at least one potential nest tree that was ≥10 m in height that possessed potential nesting platforms >10 cm in diameter. Multiple surveys were conducted at each site, with an average of one survey per 8–10 ha, unless occupancy was determined before the required number of surveys were undertaken (i.e., minimum of nine surveys required over 2 years; Evans Mack et al., 2003). We reclassified all surveys conducted according to the PSG survey protocol to create a detection/nondetection dataset, with an occupied detection defined as a murrelet exhibiting subcanopy flight behavior, stationary calling, and/or landing in a tree, all of which are considered indicative of nesting (Evans Mack et al., 2003). Since the survey protocol for marbled murrelet occupancy data was not initially designed to support the dynamic occupancy models we implement here, we used data simulations to test whether the temporal structure of surveys could have potentially biased our results in the direction we observed; we found no evidence for such biases (see Appendix, Supporting Simulation Methods and Results).

2.2 | Remote sensing

We obtained Gradient Nearest Neighbor (GNN) map products with annual modeled estimates of vegetation structure from 1998 to 2012 from https://lemma.forestry.oregonstate.edu/data/structure-maps, updated with Global Forest Change data from 2013 to 2018 (Hansen et al., 2013). The GNN method combines vegetation data from Forest Inventory Analysis plots across the region with Landsat Thematic Mapper imagery and other environmental data to predict forest structure and composition at a 30-m pixel resolution (Ohmann & Gregory, 2002). We defined "old forest" using the Old Growth Structure Index (OGSI), following Spies et al. (2007), which is based on the abundance of large live trees, snags, and downed wood, as well as the diversity of tree sizes. We used the broadest definition of old forests available (i.e., OGSI 80; Ohmann & Gregory, 2002) to identify stands >80 years with the structural attributes of old growth (Davis et al., 2015). We summarized the amount of old forest at two spatial scales, one reflecting fine-scale site use in forest habitat surrounding the nest tree (100-m radius, centered on each survey site), and the other quantifying use of broader landscapes (2000-m radius). This broader scale is likely relevant to habitat selection, social attraction (i.e., aggregations of individuals), and potentially dispersal in forest birds of this body size (Betts, Forbes, & Diamond, 2007). We also calculated the density of conifers and canopy cover within a 100-m radius to use as a predictor of detection probability, with the expectation that greater canopy cover and density of conifers reduces murrelet detections.

2.3 | Ocean conditions

There is a paucity of information regarding the distribution and abundance of murrelet prey items, including forage fish that murrelets need for successful reproduction, so we used a long-term dataset on ocean conditions, and the associated marine food web, as a proxy for murrelet prey availability. Although juvenile salmonids (*Oncorhynchus* spp.) are unlikely to be a common prey item for murrelets, they are distributed within the same marine habitat zone over the continental shelf (Bi, Ruppel, Peterson, & Casillas, 2008) and require similar bottom-up trophic processes as murrelets. Juvenile salmonids tend to be positively associated with cooler ocean conditions, and higher copepod availability and biomass (Table S3, Figure S3). A strong link has been found between biological and physical ocean conditions, the survival of juvenile marine salmonids, and the abundance of adult salmonid returns (Pearcy, 1992; Peterson et al., 2014; Burke, Liermann, Teel, &

Anderson, 2013). Therefore, we used a previously derived suite of 16 marine indicators that encompass physical and biological processes and have been shown to have a strong impact on juvenile salmon survival (Peterson et al., 2014) to serve as a proxy for murrelet prey availability (Table S3). We collapsed these indicators into a single explanatory variable using Principal Component Analysis (Table S3). Low values of the first principal component represent ocean conditions associated with warm years, and low prey availability.

2.4 | Statistical analysis

Murrelet occupancy surveys represent a time series of spatially referenced detections and nondetections at sites both within and across years, and such data are ideal for fitting dynamic occupancy models (MacKenzie et al., 2018) and allow for assessing the probability of occurrence by breeding murrelets. Dynamic occupancy models account for imperfect detection by capitalizing on multiple visits to the same sites within primary occasions (in this case, years). In addition, they allow for assessing the influence of environmental covariates on the probability of occupancy in the first year of a study (i.e., 1999 in this study, hereafter referred to as "initial occupancy"), the probability of an unoccupied site becoming occupied in the following year (hereafter referred to as "colonization"), and the probability of an occupied site becoming unoccupied in the following year (hereafter referred to as "vacancy," but synonymous with "extinction" in the statistical literature). We modeled the probability of detection as a function of canopy cover and conifer density, as well as land ownership to allow for the possibility that landowner-specific management may have influenced detection probability; we also allowed detection to vary as a quadratic function of the day of the year.

We tested the influence of three factors on murrelet occupancy dynamics: extent of nesting habitat (i.e., old forest), ocean conditions, and distance to the coast. Additionally, we assessed whether the influence of old forest and ocean conditions exhibited time-lag effects on occupancy dynamics. Given that recruitment to the breeding population, and the decision to breed by returning adults in time t is likely driven by food availability in previous years, we modeled colonization and vacancy as either a function of ocean conditions in $t-1$, or the combination of t and $t-1$. Similarly, terrestrial habitat availability in previous years could influence recruitment so we modeled the effects of old forest at the two scales we examined (100, 2,000 m) using forest amount in time t or $t-1$. We also assessed the effect of distance to coast to test the hypothesis that forest

TABLE 1 Coefficient estimates ($\hat{\beta}$), standard errors (SE), and lower and upper confidence limits (LCL and UCL, respectively) from dynamic occupancy models predicting initial occupancy, vacancy, colonization, and detection probability for marbled murrelets. Bold and underlined predictor variables have confidence intervals that do not overlap with zero. Time t or $t-1$ indicates that the variable was measured in either the year that occupancy was estimated or the year prior, respectively. $t+1$ or $t-1$ refers to the year modeled. The model presented is the model with the highest AIC weight

Predictor variables	$\hat{\beta}$	SE	LCL	UCL
Initial occupancy				
Intercept	−2.69	0.16	−3.00	−2.39
Distance tocoast	**−1.34**	**0.17**	**−1.67**	**−1.00**
Mature forest 2 km	−0.09	0.11	−0.30	0.11
Vacancy				
Intercept	−1.45	0.23	−1.90	−1.00
Mature forest 2 km (t–1)	**−0.82**	**0.17**	**−1.16**	**−0.49**
Ocean conditions (t & t–1)	**−0.49**	**0.18**	**−0.85**	**−0.13**
Distance to coast	**0.46**	**0.21**	**0.04**	**0.87**
Mature forest 2 km ($t-1$) × ocean (t & $t-1$)	−0.11	0.11	−0.34	0.11
Settlement				
Intercept	−4.12	0.18	−4.46	−3.77
Mature forest 2 km (t–1)	**0.21**	**0.11**	**0.00**	**0.42**
Ocean conditions (t & t–1)	**0.20**	**0.20**	**0.18**	**0.59**
Distance to coast	**−0.62**	**0.16**	**−0.93**	**−0.31**
Mature forest 2 km (t–1)×ocean (t & t–1)	**−0.53**	**0.11**	**−0.74**	**−0.31**
Detection				
Intercept (Oregon Department of Forestry) land	−2.19	0.10	−2.38	−2.00
Day of year	−0.16	0.12	−0.39	0.08
Day of year2	**0.19**	**0.08**	**0.02**	**0.35**
US Forest Service land	**1.41**	**0.12**	**1.18**	**1.65**
Bureau of Land Management land	**1.76**	**0.11**	**1.54**	**1.98**
Canopy cover	**−0.14**	**0.05**	**−0.24**	**−0.04**
Conifer density	**−0.29**	**0.06**	**−0.41**	**−0.17**

further inland requires greater energetic costs to access and would therefore be less likely to be occupied. We tested for an interaction between distance to coast and ocean conditions to test the hypothesis that murrelets would be less likely to fly further inland during periods of low prey availability. Finally, we tested for the statistical interaction between ocean conditions and old forest amount (model set shown in Table S1, S2, and S4) to evaluate the hypothesis that the effects of poor ocean conditions could be particularly strong and result in low occupancy in landscapes with low amounts of old forest. We fit all models using the statistical program MARK (White & Burnham, 1999) in the R statistical software (R Core Team, 2013) using the "RMark" package (Laake, Johnson, & Conn, 2013). We fit all models by first running three model runs with standard likelihood maximization, all initialized with different values, followed by simulated annealing, initialized with the values estimated through the standard maximization approach. This procedure was used to ensure convergence.

We compared candidate models using AICc, and standardized all continuous covariates by subtracting the mean and dividing by the standard deviation to allow for direct comparison of model coefficients.

3 | RESULTS

Murrelet occupancy was low across all surveyed sites with <10% predicted occupancy in all years. We did not find a strong influence of mature forest on initial occupancy, but occupancy tended to decrease with increasing distance from the coast (Table 1).

We found that loss of old forest interacted with ocean conditions to influence occupancy dynamics; models containing interaction terms between old forest and ocean conditions were well supported (cumulative AICc weight = 0.68), but that was not the case for models lacking an interaction term (cumulative AICc weight = 0.32,
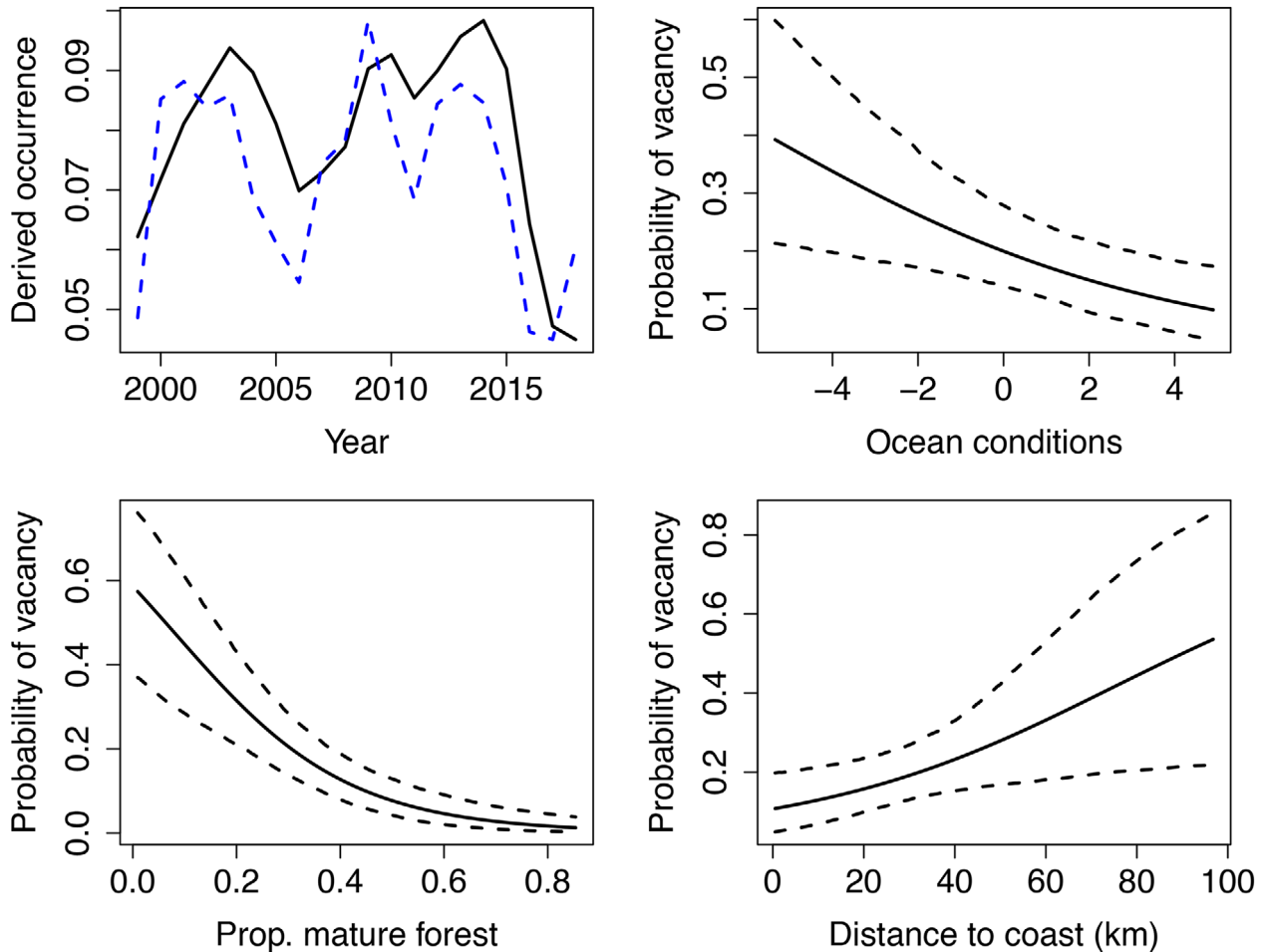
FIGURE 2 (a) Mean estimated marbled murrelet occurrence (solid black line), as derived from a dynamic occupancy model that takes into account imperfect detection, in relation to ocean conditions (blue dashed line). High values of ocean conditions reflect cool, productive conditions and low values warm years with reduced prey availability. (b) Estimated probability of murrelet colonization as a function of ocean conditions, with ocean conditions measured by PC1 in year $t-1$ from a multivariate analysis that includes physical and biological indicators (see Section 2); high values of PC1 indicate cooler conditions with more prey. (c) Probability that an occupied site becomes unoccupied ("vacancy") in relation to the proportion of old forest at the landscape-scale (2-km radius around survey site). (d) Probability of murrelet vacancy as a function of the distance of survey site from the Pacific coast. Dotted black lines represent 95% confidence intervals in (a)–(c)

Table S1). Even in models without an interaction, these two variables strongly influenced either colonization or vacancy rates over the 18-year period (Figure 2b, c, Table 1, Table S2). Murrelet colonization rates were influenced by an interaction between ocean conditions and mature forest (Table 1). During years of warm ocean conditions with low prey availability, colonization was effectively zero in areas containing low amounts of old forest (Table 1). In contrast, during good ocean conditions, areas with reduced amounts of old forest had higher rates of colonization (Table 1).

We did not find strong support for a statistical interaction between mature forest and ocean conditions on vacancy, but landscape-scale mature forest alone had a strong buffering effect on vacancy rates (Figure 2c); for example, a 1 SD increase in old forest reduced local vacancy by >2 times (95% CI: 1.5, 2.95; Table 1). Models including old forest at broad scales (2000 m) had greater support than those with old forest at fine scales (100 m; ΔAIC > 40). Warm ocean conditions substantially increased murrelet vacancy rates in the following year; vacancy rates following the poorest ocean conditions (mean = 0.38 [95% CI: 0.32, 0.45]) were 4 times higher than the period with the best ocean conditions (mean = 0.09 [95% CI: 0.04, 0.23]). Models with time-lagged effects of ocean condition (i.e., $t-1$) were better supported than those also including ocean conditions in the year of breeding (AICc weight 0.68–0.85; Table S1).

Among all models, murrelets exhibited increased rates of vacancy and decreased rates of colonization as the distance between survey site and ocean increased, a pattern presumably related to the energetic cost of commuting

flights. For example, sites ~100 km from the coast were five times more likely to become locally vacant than sites within 500 m of the ocean, with the latter sites being 20 times more likely to be colonized (Figure 2d). Murrelet detectability was highest in surveys conducted on federal land (Bureau of Land Management) and lowest on state land (Oregon Department of Forestry, Table 1). Detectability decreased at sites with high canopy cover and dense conifers, although it was not strongly influenced by day of year.

4 | DISCUSSION

Quantifying the cumulative importance of distinct habitats has hindered the development of comprehensive conservation approaches for declining species that exhibit habitat-split strategies. Here we provide the first evidence that ocean conditions combined with broad-scale old forest nesting habitat influence long-term occupancy dynamics of an endangered seabird. In particular, we found that ocean conditions appear to be a key driver of occupancy dynamics. This finding is particularly relevant to current policy, which classifies a site on state land in Oregon without murrelet detections in two successive years as unoccupied (Evans Mack et al., 2003) thereby by allowing it to be harvested for timber. Our data indicate that poorer than average ocean conditions may persist for >2 successive years (Figure 2a), which could lead to a scenario where sites used for breeding in good ocean years might go unoccupied for multiple years and thereby be available for harvest. If ocean conditions continue to deteriorate over the long term, breeding habitat could be "ratcheted" down, and due to habitat loss, prevent site recolonization even following good ocean years. These results suggest that to maximize confidence that a site is not suitable murrelet nesting habitat, prospective timber harvest locations should be surveyed only in years following good ocean conditions, or for periods that exceed the maximum length of poor ocean conditions (i.e., potentially >2 consecutive years).

We found that the amount of old forest habitat had a strong positive influence on vacancy rates. The negative effect of old forest loss appeared to be stronger at broad (2000-m radius) than fine spatial scales (100 m). Given that murrelets need only a single large nesting tree in any given year, this result might seem counter-intuitive, but we hypothesize that murrelets may favor nesting near conspecifics as is the case for other seabirds, including auks (Rolland, Danchin, & de Fraipont, 1997). Thus, larger stands of contiguous forest habitat may be especially valuable nesting habitat, particularly if murrelets rely on conspecific attraction when selecting nest sites (Danchin, Giraldeau, Valone, & Wagner, 2004).

Taken together, our results indicate that sites are most likely to be occupied by murrelets if they occur in landscapes with larger amounts of old forest that are closer to the coast, and when foraging conditions are of high quality (i.e., cool ocean temperatures). Therefore, continued conservation of contiguous old forest closer to the ocean, in addition to maintaining all occupied sites, will likely provide the greatest benefit toward recovering murrelet populations. For instance, efforts to create early seral forest within the geographic scope of the Northwest Forest Plan should focus on cutting younger plantations farther inland rather than old forest near the coast (Phalan et al., 2019) if conservation of murrelet populations is the goal. Including inland habitat and adjacent optimal foraging habitat in a reserve design (to reduce habitat split) could also be of high value to murrelet conservation (Hazlett, Martin, Sampson, & Arcese, 2010). Given continued increases in global timber demand (FAO, 2016) and accelerated warming (Cox, Huntingford, & Williamson, 2018), we speculate that murrelet populations may come under increased pressure from a reduction in the quality and extent of the two habitats upon which they depend. Unfortunately, murrelets are not alone in being impacted by a degradation of multiple habitats; a sizable proportion of vertebrates depend on multiple habitats throughout the annual cycle (fish: Price et al., 2019; birds: Ferraz et al., 2007; amphibians: Becker et al., 2007; dragonflies: Nagy et al., 2019), many of which are currently due to anthropogenic activities. Nevertheless, obtaining data that allow for the assessment of the relative contribution of different habitats is a challenging, but necessary step toward a comprehensive conservation planning. We suggest that "habitat split" be considered a risk factor that affects species' sensitivity to global change and, as studies similar to ours accumulate, the generality of this hypothesis will be formally tested across taxa. We suspect that for many species, as in the case of murrelets, concurrent conservation measures will need to be taken in multiple habitats to ensure populations persist into the future.

AUTHORS' CONTRIBUTIONS

MGB, JMN, JABG, LJA, KM, DDR, and JWR conceived of the paper; JMN, BDG, ZY, JLF, and MGB conducted data analysis; and MGB led the writing of the manuscript. All authors contributed to the writing and gave final approval.

ETHICS STATEMENT

The authors adhered to all laws, regulations and protocols in conducting this research. Authors also adhered to Wiley's "Publishing Ethics Guidelines."

DATA ACCESSIBILITY STATEMENT

Data and code used in analysis have been deposited at Figshare: https://figshare.com/articles/dataset/Squeezed_by_a_habitat_split_warm_ocean_conditions_and_old-forest_loss_interact_to_reduce_long-term_occupancy_of_a_threatened_seabird_data_and_code_/12743762

CONFLICT OF INTEREST

The authors declare no conflict of interest

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SUPPORTING INFORMATION

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

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