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Nesting habitat characteristics of Marbled Murrelets occurring in near-shore waters of the Olympic Peninsula, Washington

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ABSTRACT. Marbled Murrelets (*Brachyramphus marmoratus*) are listed as threatened in the portion of their range extending from British Columbia to California due to loss of nesting habitat. Recovery of Marbled Murrelet populations requires a better understanding of the characteristics of their nesting habitat in this part of their range. Our objective, therefore, was to describe their nesting habitat in Washington State and Vancouver Island, British Columbia. We captured Marbled Murrelets from 2004 to 2008, fitted them with radio transmitters, and followed them to nests ($N = 20$). We used Cohen's unbiased *d* effect size to assess differences between forest plots surrounding nest sites and nearby control sites ($N = 18$). Nest sites had less canopy cover of the dominant conifers and fewer, but larger, trees than control sites. Nest sites also had greater percentages of trees with platforms >10 cm diameter and >15 cm diameter, and more platforms of these sizes than control sites. The mean diameter at breast height of nest trees was 136.5 cm (range = 84–248 cm) and all but one nest was in dominant or co-dominant tree species. At the landscape scale, we used vegetation maps derived from remotely sensed data and found greater canopy cover, higher density of mature trees, more platforms >10 cm/ha, and more old-growth habitat at nest sites than at random sites. Our findings suggest that, at the site scale, nesting Marbled Murrelets selected the most suitable features of forest structure across expansive potentially suitable habitat. Our landscape-scale analysis showed that habitat features in nesting stands differed from those features in available stands in the murrelet's range in Washington. We also found that stands with nests were less fragmented than available forest across murrelet range. All nest sites of radio-tagged birds in Washington were in protected areas in mostly undisturbed forest habitat. Conservation of these areas of inland nesting habitat will be critical to the recovery of Marbled Murrelet populations.

RESUMEN. **Características del hábitat de anidación de *Brachyramphus marmoratus* que ocurren en aguas cercanas a la costa de la península Olímpica, Washington**

Brachyramphus marmoratus esta clasificado como amenazadas en la parte de su área de distribución que se extiende desde la Columbia Británica a California debido a la pérdida del hábitat de anidación. La recuperación de las poblaciones de *B. marmoratus* requiere una mejor comprensión de las características de su hábitat de anidación en esta parte de su área de distribución. Nuestro objetivo, por lo tanto, fue describir su hábitat de anidación en el estado de Washington y la isla de Vancouver, Columbia Británica. Capturamos *B. marmoratus* desde el 2004 hasta el 2008, equipados con transmisores de radio, y se les hizo seguimiento hasta los nidos ($N = 20$). Utilizamos el tamaño del efecto *d* imparcial de Cohen para evaluar las diferencias entre las parcelas de bosque que rodean los sitios de anidación y sitios cercanos de control ($N = 18$). Los sitios de anidación tenían menos cobertura del dosel de las coníferas dominantes y menos, pero más grandes, árboles comparado a los sitios de control. Los sitios de anidación también tenían mayores porcentajes de árboles con plataformas > 10 cm de diámetro y > 15 cm de diámetro, y más plataformas de estos tamaños que en los sitios de control. El diámetro medio a la altura del pecho de los árboles con nido fue 136.5 cm (rango = 84–248 cm) y todos menos uno nido se encontraron en la especies de árbol dominantes o co-dominante. A escala de paisaje, utilizamos mapas de vegetación derivados de los datos de sensores remotos y encontramos una mayor cobertura del dosel, una mayor densidad de árboles maduros, más plataformas > 10 cm/ha, y más hábitat de edad madura en los sitios de anidación que en los sitios al azar. Nuestros resultados sugieren que, a la escala de sitio, *B. marmoratus* durante la anidación selecciona las características más adecuadas de la estructura del bosque a través extensión de hábitat potencialmente adecuado. Nuestro análisis a escala de paisaje mostró que las características del hábitat de anidación en gradas eran diferentes de las características en grada disponibles dentro del rango de *B. marmoratus* en Washington. También encontramos que se colocaron los nidos en bosques menos fragmentado que el bosque disponible en todo el rango de *B. marmoratus*. Todos los sitios de anidación de aves con radio transmisores en Washington estaban en las áreas protegidas del hábitat de

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bosque sin disturbio. La conservación de estas zonas de hábitat de anidación en el interior serán fundamentales para la recuperación de las poblaciones de *B. marmoratus*.

Key words: Brachyramphus marmoratus, Juan de Fuca, old-growth conifer forest, Pacific Northwest, seabird, threatened species, Vancouver Island

Marbled Murrelets (*Brachyramphus marmoratus*) are seabirds found in near-shore waters along the Pacific Coast of North America from the Aleutian Islands, Alaska, south to central California. Marbled Murrelets that breed in the area from British Columbia to California have been listed as threatened, primarily due to loss of nesting habitat in older conifer forests (USFWS 1997, Environment Canada 2014). In the U.S. recovery plan, five Marbled Murrelet Conservation Zones encompass coastal areas in Washington, Oregon, and California (USFWS 1997). Nesting habitat in these areas has been generally described as late-successional conifer forest with varying densities of old-growth and mature forest characteristics. However, given their threatened status, more specific information about nest-site selection by Marbled Murrelets in the northwestern United States is needed.

Radio-tagged birds may provide the most reliable nest-site data for Marbled Murrelets (Burger 2002) because they are followed to nest sites, eliminating possible bias due to investigator search behavior. For example, ~55% of nest sites of radio-tagged birds in British Columbia were inaccessible to ground crews (Silvergieter and Lank 2011a), and nests of radio-tagged birds have been found in inaccessible habitats that are further inland from the coast, at higher elevations, and in steeper terrain than previously documented (Bradley et al. 2004, Barbaree et al. 2014). We used radio-telemetry for locating and studying Marbled Murrelet nest sites in Washington. We compared site-level habitat features (i.e., tree stem composition, size, and abundance, and nesting platform availability and abundance) of nest sites and nearby randomly selected sites. We also used remotely sensed geographical information system (GIS) data for characterizing habitat attributes at nests and comparing them to those of randomly selected sites throughout the nesting range of Marbled Murrelets in Washington.

METHODS

Study site. Our study areas included the Olympic Peninsula, the northwestern Cascades Mountain Range in northwestern Washington, and southwestern Vancouver Island, British Columbia (Fig. 1). The climate in our study area is variably mild, mostly wet maritime that is strongly influenced by a diverse mountainous physiography (Franklin and Dyrness 1988). Franklin and Dyrness (1988) described the forests of our study areas in Washington as the Western Hemlock (*Tsuga heterophylla*) Forest Zone, which extends south from British Columbia through the Olympic Peninsula, Coast Ranges, Puget Trough, and the Cascades physiographic provinces of western Washington. The zone also includes Douglas-fir (*Pseudotsuga menziesii*) and western red cedar (*Thuja plicata*); hardwood trees dominate mostly in recently disturbed sites or riparian areas. Southwestern Vancouver Island is primarily the submontane very wet maritime variant of the Coastal Western Hemlock Zone, which includes western red cedar and Sitka spruce (*Picea sitchensis*). Pacific silver fir trees (*Abies amabilis*) are sometimes locally abundant (Pojar et al. 1991). Murrelet nesting habitat in the Northwest Forest Plan area has been generally described as late-successional conifer forest with varying densities of old-growth and mature forest characteristics; the old-growth stands are 180- to 220-yr-old, and mature forests are generally 80- to 200-yr-old (FEMAT 1993). Franklin and Spies (1991) defined old-growth-sized trees as >81-cm diameter at breast height (dbh), which is the definition we used. They also classified trees >200-yr-old as old growth. Geologically, deeply incised glacial valleys of the Peninsula's Olympic Mountains massif and Vancouver Island Mountain Range fjords form flyways into the river drainages to potential murrelet nesting areas (Burger 2001, Cooper et al. 2001).

Radio tagging birds and locating nest sites. From 2004 to 2008, beginning in early April (prior to nest initiation), we captured birds on the water at night from inflatable boats using dip nets and spotlights (Whitworth et al. 1997, Baker et al. 2006). We radio-tagged birds captured at six locations surrounding the Olympic Peninsula (Fig. 1), including the Strait of Juan de Fuca ($N = 110$), Lopez Island ($N = 2$), Admiralty Inlet ($N = 19$), Hood Canal ($N = 10$), and the Pacific coast

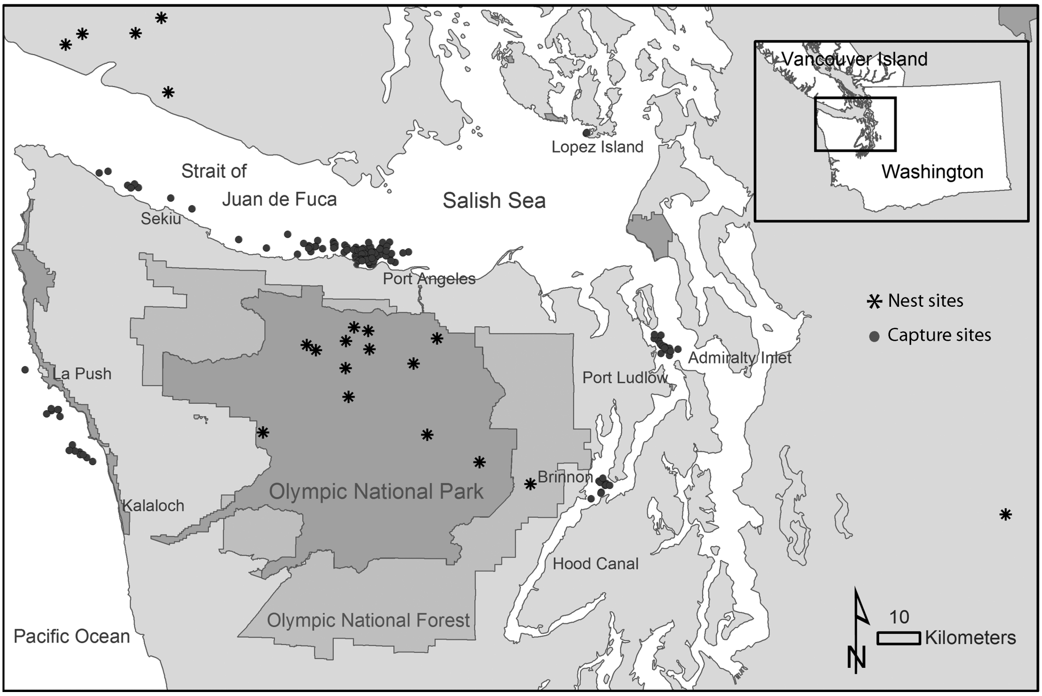

Fig. 1. Study area in Washington State and Vancouver Island encompassing Marbled Murrelet capture and nest locations.

($N = 16$). Most radio-tagged birds (87%) were captured between late April and early June (16% in April, 57% in May, 26% in June, and 1% in July). We attached VHF radio-transmitters (Model A4360, Advanced Telemetry Systems, Isanti, MN) to 157 murrelets using the subcutaneous anchor technique (Newman et al. 1999) without sutures and anesthesia. Units weighed 4.5 g (~1.6–2.6% of body mass) with a life-expectancy of 17–37 weeks. Most radio-tagged birds (96%) were aged as after-second-year (i.e., adult plumage) (Carter and Stein 1995).

We located nest sites of 20 radio-tagged birds using a combination of aerial, boat, and ground telemetry surveys. Aerial surveys were conducted between 17 April and 15 September each year using fixed-wing aircraft with null-peak antenna equipment (Kenward 1987). Tracking effort depended on the number of radio-tagged birds and weather. We attempted to obtain a location at sea as frequently as possible for each bird. When we detected an on–off signal pattern for murrelets, indicating possible incubation (e.g., Bradley et al. 2004), or did not relocate birds at sea on consecutive days, we searched on land to locate nest sites. We systematically flew farther inland, crossing over river drainages to ensure broad coverage. We also tracked birds opportunistically from small boats and ground-based vehicles. Across years, we obtained radio signals on 0–4 d in April, 25–31 d in May, 23–30 d in June, 15–31 d in July, 0–10 d in August, and 0–2 d in September. In May and June, when search effort was most intense, we flew at least every 2 d.

Habitat measurement. We measured habitat features in 25-m-radius (0.2-ha) circular plots centered on nest trees. We also measured habitat features of nearby control sites made up of five ($N = 7$) to seven ($N = 11$) 0.2-ha plots sampled from a larger area of forest near nest sites. In each control plot, we measured the same habitat features as in nest-site plots, and averaged them to determine one metric for each feature in the control plots. Hereafter, the area in the nest plot around the nest tree and the area in the nearby control plots are referred to as sites. All abundance values of habitat features reported are either counts (nest site) or averages of counts (control sites) inside the 0.2-ha plots.

We identified and delimited control areas using digital orthophotos and field assessments. We did not know if murrelets were present in the control sites. Sampling effort was proportional to the number of nest sites and paired control sites. We recorded 71% of all tree stems ≥10 cm dbh on the Olympic Peninsula in 66% of the sampling sites, 24% of tree stems on Vancouver Island in 27% of the sites, and 5% of tree stems in the Cascades in 4% of the sites. Among all sites, we estimated that the maximum distance between any one control subsample site and paired nest sites was 1066 m, and the maximum distance between subsample sites within each control averaged 1.1 ± 0.5 (standard deviation, SD) km (range = 0.8–2.5 km). We recorded habitat data based on protocols in unpublished documents (provided by S. K. Nelson [kim.nelson@oregonstate.edu] entitled "Explanations of measurements of the Marbled Murrelet nest structure form," "PSG Marbled Murrelet nest structure form," "Instructions for filling out the platform data sheet and tally sheet, effectiveness monitoring platform tree data," and "Platform tree data form"; Supplementary Appendices S1–S3).

We visited nest locations between 8 August and 28 September each year after they were no longer active to measure habitat features of nest trees, nest sites, and control sites. Nest tree and nest data were obtained by climbing trees and these data are provided in Supplementary Table S1. We estimated distances from the coast and the topographic elevation for 19 nest sites using GIS and/or topographic maps.

For most nest sites, we recorded (1) species and dbh of all live trees ≥10 cm dbh, (2) a visual estimate of canopy closure of dominant and co-dominant conifers, and total closure (average of plot quadrants), (3) canopy layers as either one or >1, and (4) crown diameter of trees with nest platforms (calculated as the average of two measurements of the crown: drip line to drip line at the widest point, and the measurement perpendicular to that line). We also estimated the number of potential nest platforms in trees because platforms may be the most important characteristic of murrelet habitat, and tree dbh may be the most important predictor of platform availability and size (Burger et al. 2010). Murrelet nests are usually located on large limbs or limb deformities >10 cm in diameter (platforms; in Canada, minimum diameter was defined as >15 cm [Burger et al. 2010]), covered with mats of moss and canopy debris, and generally >10 m above ground (Nelson et al. 2006). Platforms are typically located in large-diameter trees (at least 60 cm dbh), but the dbh of platform trees varies regionally (Burger et al. 2010). Because counting every platform in each tree was not possible, we treated counts as indices of the number of platforms (Hamer 1995). Each branch with ≥1 platform was counted once and limbs at ≥45° angles from horizontal were not counted unless there was ≥0.3 m of level length. We estimated platform height, classified limbs by size, and report platforms as total counts for limbs >10 cm, >15 cm, and >20 cm in diameter because larger platforms may be preferred for nesting. We pooled all trees at nest and control sites to compare average tree dbh within the three size classes of platforms. Pooling was necessary because many nest plots did not have trees in each platform class, resulting in small and/or imbalanced samples that could not be compared in paired-samples tests. These data are presented in Supplementary Table S2.

We also compared landscape metrics around 14 nest sites in Washington (including a cliff nest and excluding one unconfirmed nest tree) to those of a random sample of about 10,000 forest sites capable of supporting forest structure with the potential to provide murrelet nesting habitat (Raphael et al. 2011). Habitat-capable forest excluded high elevation, rock, developed land, and water. The forests extended from the coast to the eastern boundary of the murrelet range (see map Fig. 2 in Raphael et al. 2011). We obtained habitat data from predictive vegetation maps of forest attributes with pixels of 30-m resolution (0.28-ha) created using the gradient nearest neighbor method (GNN data) (Ohmann and Gregory 2002, Davis et al. 2015). Hereafter, one pixel is one landscape-scale site (GNN site), either a nest or random site. Habitat features compared were (1) platform density (derived from tree density by tree species, dbh class, and average platform abundance from large samples of trees from plots scattered throughout the range of murrelets; Raphael et al. 2011), (2) conifer tree canopy cover (%), (3) hardwood tree canopy cover (%), (4) quadratic mean diameter (QMD) of dominant conifer trees (the diameter of the tree of average per tree basal area), (5) number of conifer trees with dbh ≥100 cm/ha, (6) stand height, (7) old-growth structure index,

(8) percent slope, (9) tree diameter diversity index (higher values for more forest structural diversity and canopy heterogeneity; no units) (see Table 1 in Raphael et al. 2011, 2015a), and (10) three patch-fragmentation metrics (core area, core area as a percentage of land area, and patch-cohesion index; see "Analysis" section). Old-growth structure index is a composite variable computed from the density of large live trees, diversity of live tree size classes, density of large snags, and percent cover of downed woody material. Low index values represented younger, less structurally complex forests, and high index values represented older, more structurally complex forests (no units) (Raphael et al. 2015a). Classification accuracy of the GNN data in classifying vegetation as large conifer (class 10) and giant conifer (class 11) was 44% and 58%, respectively, lending these data more to general regional applications (Ohmann and Gregory 2002). We developed this novel approach to supplement the murrelet nest habitat studies of Raphael et al. (2011, 2015a) where GNN nest sites of radio-tagged murrelets were a subset.

Analysis. We paired data from each nest site with its control for analysis of 18 nest sites, including 13 in Washington (cliff nest and one other site were not measured) and five on Vancouver Island. We pooled all sites and used paired-samples *t*-tests with Cohen's *d* effect-size confidence intervals (CIs) to assess differences between nest and control sites. For features with non-normal data distributions, we present summary statistics. We also summarize data for the three geographic regions where nests were located, including the Olympic Peninsula ($N = 12$ nest sites), Vancouver Island ($N = 5$) and Western Cascade Mountains ($N = 1$).

We used paired-samples *t*-tests because they controlled for the possible confounding effects of nest-site elevation and distance from the ocean. Criteria for these tests were satisfied based on proximity and habitat homogeneity of contiguous forest in nest and control sites. We compared species composition, canopy cover, abundance, and dbh of all trees ≥10 cm dbh, and the subset of old-growth-sized trees (dbh >81 cm dbh), basal area, crown area, percentages of trees with platforms, and total platforms by size class. We also compared nest-tree metrics to the averages of neighboring trees within nest plots. We were interested in effect size (effect size) and thus did not report traditional *P*-values because they do not show the size of an effect (Sullivan and Feinn 2012). We categorized effect size as either consistent (i.e., CI excluded zero) or variable (i.e., CI included zero). We quantified effect size for each feature in the paired sites using Cohen's *d*, which is the mean difference between a compared feature in paired-samples sites divided by the pooled SDs adjusted for small sample size to provide an unbiased estimate (d_{unb}) of the population effect size, Cohen's δ: for $d_{unb} < \sim 0.2$ = no measurable effect, $d_{unb} \sim 0.2$ = small effect size, $d_{unb} \sim 0.5$ = medium effect size, and $d_{unb} \geq \sim 0.8$ = large effect size (d_{unb} values can be + or –) (Nakagawa and Cuthill 2007, Cumming 2012). Because *d* values are not *sine qua non*, and there is no precedent for their use, the interpretation of biological significance of the results is important (Nakagawa and Cuthill 2007). Because *d* has a non-central *t*-distribution, CIs for δ cannot be precisely computed, so an iterative or successive approximations method is required that often results in asymmetric CIs (Cumming 2012).

To determine normality of data on the differences between paired sites, we converted skewness and kurtosis values into *z*-scores then divided them by their standard errors (Field 2013). We considered an absolute value of >1.96 to be significant ($\alpha \sim 0.05$). Because effect-size CIs were too imprecisely computable for non-normal data (Cumming 2012), we compared these data (e.g., platforms/tree) using summary statistics. Between paired-samples sites, for effect-size point-estimates ≥∼0.2, we also report the probability that a randomly chosen nest site (*n*) has a greater value (i.e., lies to the right of) than a randomly chosen control site (*c*), denoted as *Prob* [$n > c$] (Cumming 2012).

We used graphical Tukey box plots to display the GNN nest and random site comparisons of all features in the landscape analysis. For GNN random sites, we used the approximate 5% trimmed mean to be compared with GNN nest site 95% CIs. We trimmed means by removing the upper and lower 5% of the values to exclude outliers. For comparisons of landscape fragmentation between GNN nest and random sites, we used the patch-cohesion metrics in Fragstats (McGarigal et al. 2012). We used a moving window approach (see Raphael et al. 2015b) to compare amounts of forest classified as large conifer and giant conifer within a 150-ha area around each nest, based on an estimate of ecological density of murrelets calculated by Raphael et al. (2002). We first looked at nest patch core area size, which is the interior area of patches after edge-effect buffering, using a 90-m buffer. Core area integrates patch size, shape, and edge effect distance into a single measure. All other things being equal, smaller patches with greater shape complexity have less core area (McGarigal et al. 2012). Second, we computed core area size as a percentage of land area in the large conifer and giant conifer classes inside the 150-ha area. Third, we computed a patch-cohesion index, which is the physical connectedness of the corresponding patch type. This index increases as the patch type becomes more clumped or aggregated in its distribution (value range = 0–100) (McGarigal et al. 2012). Because computing time was long for patch-metrics processing, we limited our sample to 890 GNN random sites to compare with the GNN nest sites.

We expected few differences, that is, where effect sizes would be $\geq\sim 0.2$, between habitat features in paired sites because of the similarity and the contiguity of habitat surrounding the sites, and the possibly high SDs due to the small sample size of nest sites. However, our approach allowed for robust results (i.e., consistent or variable effect sizes) open to biological interpretation. We expected large differences (i.e., nest site 95% CIs vs. control trimmed $\bar{x}$) when comparing mapped GNN sites because of the uneven distribution of forest types across the forested landscape. We used IBM SPSS software (v. 23 IBM Corp., released 2015) for general data processing and box-plot graphics, and Exploratory Software for Confidence Intervals (ESCI, Cumming 2012) for the paired-samples effect size analyses. Values are presented as means ± 1 SD.

RESULTS

Locations of nest sites. We located 20 nest sites, including 14 on the Olympic Peninsula, one in the northern West Cascades, and five on southwestern Vancouver Island, British Columbia (Fig. 1). We measured characteristics of 18 nest sites and 17 nest trees; we were unable to locate a nest in one suspected nest tree in British Columbia and were unable to obtain habitat data at two other sites. In Washington, 13 sites were in Olympic National Park, including the first known cliff nest south of British Columbia. We confirmed the cliff nest by observing an adult murrelet flying from the cliff at dawn and later finding a dead nestling at the base of the cliff; the estimated elevation of this nest was 1280 m. One nest site was located in the Brothers Wilderness Area within the Olympic National Forest, and one in the Alpine Lakes Wilderness Area, Mt. Baker Snoqualmie National Forest (Cascades) (Fig. 1). Three nest sites on Vancouver Island were in Carmanah/Walbran Provincial Park and Crown Lands murrelet wildlife habitat areas. Two sites were on Crown Lands not regulated for habitat protection (M. Mather, pers. comm.).

Distances of nest sites from the coast averaged 19 ± 5 (90% CI) km (range = 4–58 km) ($N = 19$). Average distances from the coast were 22 ± 5 km (range = 9–58 km, $N = 14$) in Washington, and 8 ± 3 km (range = 4–15 km, $N = 5$) on Vancouver Island. Overall, elevation of nest sites averaged 669 ± 126 m (range = 150–1280 m) ($N = 19$). Average elevations were 729 ± 154 m (range = 235–1280 m) in Washington and 502 ± 171 m (range = 150–760 m) on Vancouver Island. On the Olympic Peninsula, average distance of nest sites from the coast was 21 ± 6 km and the mean elevation was 708 ± 173 m. The elevation of the Cascades nest was 780 m (Supplementary Table S3).

Habitat of paired sites at the stand scale: percent tree stem composition. Western hemlock was the most common tree species in our study area, followed by Douglas-fir and western red cedar, and most forests had ≥2-layer canopies (89% of plots). Hemlock trees were also the most prevalent among old-growth stems across the study area (Table 1). Trees of old-growth size made up about one-third (32–36%) of the stem composition at both nest sites and control sites, but stem composition varied among regions. For example, whereas Douglas-fir trees were co-dominant on the Olympic Peninsula, red cedar trees were the co-dominant species on Vancouver Island and in the Cascades (Table 1). Douglas-fir trees were nearly absent from Vancouver Island plots and were absent from Cascades plots. Pacific silver fir trees were present on Vancouver Island and in the Cascades sites, but only a small percentage was in old-growth.

Hemlock tree stem composition was lower at nest sites than control sites (absolute $\bar{x}$ difference

Table 1. Species composition (% of stems) of five important conifer trees in eighteen 0.2-ha paired nest and control sites (N) across three geographic regions.

	Olympic Peninsula		Vancouver Island		Western Cascades		Total	
	Nest (12)	Control (12)	Nest (5)	Control (5)	Nest (1)	Contro (1)	Nest (18)	Control (18)
Douglas-fir	32.0 ± 28.9	39.3 ± 27.1	–	3.2 ± 3.5	–	–	21.4 ± 28.0	26.9 ± 28.3
Old growth[a]	20.2 ± 6.2	20.6 ± 16.5	–	0.4 ± 0.3	–	–	13.4 ± 19.8	13.5 ± 16.5
Western Hemlock[a]	31.4 ± 27.2	36.8 ± 16.0	42.1 ± 23.9	54.4 ± 19.4	50.0	63.8	35.4 ± 25.5	40.5 ± 17.3[b]
Old growth	10.2 ± 18.7	9.2 ± 9.3	13.9 ± 17.3	16.1 ± 15.8	27.8	11.3	12.2 ± 17.8	10.5 ± 10.9
Western red cedar[a]	14.6 ± 16.5	8.8 ± 8.4	29.8 ± 31.3	35.6 ± 27.9	27.8	18.9	19.5 ± 21.4	15.4 ± 18.7[b]
Old growth[a]	3.2 ± 6.0	1.8 ± 2.1	8.9 ± 9.5	14.4 ± 13.8	27.8	15.6	6.2 ± 9.0	5.3 ± 8.8
Sitka spruce	4.8 ± 16.5	2.9 ± 9.9	–	–	–	–	3.2 ± 13.5	1.9 ± 8.1
Old growth	3.6 ± 12.4	2.2 ± 7.8	–	–	–	–	2.4 ± 10.1	1.5 ± 6.3
Pacific silver fir[a]	11.1 ± 18.6	8.2 ± 11.7	23.5 ± 20.0	23.8 ± 14.5	22.2	17.3	15.2 ± 18.8	11.4 ± 12.7[b]
Old growth	1.6 ± 4.5	1.3 ± 1.9	2.3 ± 2.1	1.9 ± 1.8	11.1	3.9	2.3 ± 4.3	1.5 ± 1.9

Average values (±SD) per species are shown for all trees ≥10 cm dbh and for old-growth trees >81 cm dbh.

[a]Paired-samples t-tests and effect-size statistics performed on data. Other data sets were not normally distributed and were not tested.

[b]A small, variable (95% CI includes zero) effect size (d_{unb} = 0.20–0.22).

[diff.] = 5.1%, d_{unb} = −0.22, −0.60 to 0.14 [95% CI], $Prob$ [$n > c$] = 0.44) (Table 1). However, more red cedar (diff. = 4.1%, d_{unb} = 0.20, −0.02 to 0.43, $Prob$ [$n > c$] = 0.56) and silver fir trees (diff. = 3.8%, d_{unb} = 0.22, −0.06 to 0.52, $Prob$ [$n > c$] = 0.57) were found at nest sites than control sites (Table 1).

Tree size, canopy closure, abundance, and crown area. We found that average dbh was greater at nest sites than control sites for trees ≥10 cm diameter (diff. = 4.5 cm, d_{unb} = 0.27, −0.01 to 0.66 [95% CI], $Prob$ [$n > c$] = 0.58), and for old-growth-sized trees (diff. = 10.7 cm, d_{unb} = 0.40, −0.12 to 0.95, $Prob$ [$n > c$] = 0.62) (Table 2). Dominant conifer canopy cover (diff. = 9.3%, d_{unb} = −0.79, −1.48 to −0.16, $Prob$ [$n > c$] = 0.28) and total canopy cover (diff. = 5.7%, d_{unb} = −0.51, −1.09 to 0.03, $Prob$ [$n > c$] = 0.35) were smaller at nest sites than control sites (Table 2). Tree abundance was lower at nest than control sites (diff. = 3.5 trees, d_{unb} = −0.63, −1.11 to −0.19, $Prob$ [$n > c$] = 0.32). Old-growth tree abundance was similar between nest and control sites. Nest sites also had smaller crown areas than control sites (diff. = 1.7 m^2, d_{unb} = −0.42, −0.78 to −0.06, $Prob$ [$n > c$] = 0.38) (Table 2).

Platforms. We found higher percentages of trees with platforms >10 cm (diff. = 6.8%, d_{unb} = 0.45, −0.05 to 0.98 [95% CI], $Prob$ [$n > c$] = 0.63) and more platforms >10-cm diameter (diff. = 14.8 platforms, d_{unb} = 0.42, −0.15 to 1.03, $Prob$ [$n > c$] = 0.62) at nest sites than control sites. There were also higher percentages of trees with platforms >15-cm diameter (diff. = 3.6%, d_{unb} = 0.30, −0.08 to 0.71, $Prob$ [$n > c$] = 0.59) and more platforms >15-cm diameter (diff. = 5.4 platforms, d_{unb} = 0.28, −0.23 to 0.81, $Prob$ [$n > c$] = 0.58) at nest sites than control sites (Tables 2 and 3). Trees of larger average size had larger platforms than trees of smaller size among the common nest tree species (Supplementary Table S2). Data on platforms/tree are presented in Supplementary Table S4.

Nest trees. We found that murrelets used nest trees larger than other trees at nest sites. We found nests in four species of trees and their average size ($\bar{x}$ = 136.5 ± 48.2 cm dbh) exceeded the averages of all other trees at the nest sites (Table 4) (diff. = 61.6 cm, d_{unb} = 1.6, 0.89–2.50 [95% CI], $Prob$ [$n > c$] = 0.89, N = 17) (Supplementary Table S5). Crown areas of nest trees were also greater than those of neighboring trees with platforms (diff. = 1.5 m^2, d_{unb} = 0.28, −0.13 to 0.71, $Prob$ [$n > c$] = 0.58). Nest trees also had more platforms >15-cm diameter than other trees at nest sites (diff. = 1.4 platforms, d_{unb} = 0.35, 0.05–0.68, $Prob$ [$n > c$] = 0.60).

Limb diameters of nest trees at the nest averaged 30 cm and only three of 15 nest limbs measured were <20 cm in diameter (Supplementary Table S1). However, there was no difference between the average number of trees with platforms >20-cm diameter, and the percentage of trees with platforms >20-cm diameter (Table 2). When we excluded nest trees from platform comparisons, the overall average for total platforms >10-cm diameter was smaller in nest that control sites (diff. = 1.1 platforms) and in nest plots, represented an overall reduction of ∼25%

Table 2. Canopy cover, number and size of trees (dbh), basal area, number of trees and percentage of trees with platforms, crown area of trees ≥10 cm dbh with platforms, and number and size (dbh) of old-growth trees (>81 cm dbh) ($\bar{x}$ ± SD) in 18 0.2-ha paired nest sites of Marbled Murrelets and control sites (*N*).

	Olympic Peninsula		Vancouver Island		Western Cascades		Total	
	Nest (12)	Control (12)	Nest (5)	Control (5)	Nest (1)	Control (1)	Nest (18)	Control (18)
Canopy cover (%)								
Dominant conifer	39.9 ± 12.4	49.6 ± 10.1	36.5 ± 15.5	49.6 ± 6.6	45.0	31.3	**39.3 ± 12.4**	**48.6 ± 9.8**[c]
Co-dominant conifer	30.0 ± 19.4	30.2 ± 11.7	41.3 ± 15.8	41.1 ± 10.2	18.8	40.0	32.5 ± 18.4	33.8 ± 11.8
Total cover	60.1 ± 14.5	65.5 ± 7.9	61.3 ± 12.4	68.6 ± 5.0	55.0	56.8	60.2 ± 13.2	65.9 ± 7.3[b]
Trees (*N*)	21.4 ± 5.9	25.2 ± 6.0	26.4 ± 2.7	29.3 ± 4.1	18.0	21.8	**22.6 ± 5.6**	**26.1 ± 5.6**[b]
dbh (cm)	79.0 ± 17.6	75.6 ± 13.2	68.2 ± 10.8	68.0 ± 11.8	114.8	75.9	78.0 ± 18.4	73.5 ± 12.6[a]
Basal area (m^2)	12.6 ± 4.5	13.4 ± 6.2	11.6 ± 4.3	13.1 ± 4.0	25.6	13.9	13.0 ± 5.2	13.3 ± 5.4
With platforms >10 cm (*N*)	8.7 ± 4.7	8.5 ± 3.8	8.0 ± 4.6	6.6 ± 2.6	9.0	8.0	8.5 ± 4.4	8.0 ± 3.4
With platforms >15 cm (*N*)	5.1 ± 3.0	5.7 ± 2.0	6.6 ± 3.8	5.3 ± 2.7	9.0	7.6	5.7 ± 3.2	5.7 ± 2.1
With platforms >20 cm (*N*)	2.6 ± 1.6	2.7 ± 1.4	2.8 ± 2.3	3.5 ± 2.2	6.0	3.8	2.8 ± 1.9	3.0 ± 1.6
With platforms >10 cm (%)	40.0 ± 18.3	33.7 ± 9.9	29.9 ± 16.9	23.0 ± 8.4	50.0	36.7	37.7 ± 17.7	30.9 ± 10.3[b]
With platforms >15 cm (%)	24.7 ± 12.1	23.3 ± 8.4	24.9 ± 14.3	18.4 ± 8.4	50.0	22.6	26.2 ± 13.4	22.6 ± 8.7[a]
With platforms >20 cm (%)	14.2 ± 11.2	12.3 ± 9.6	10.7 ± 9.2	12.2 ± 6.8	33.3	17.4	14.3 ± 11.2	12.5 ± 8.5
Crown area (m^2)	15.0 ± 5.4	16.8 ± 3.6	13.4 ± 3.2	15.2 ± 2.6	17.0	16.6	**14.6 ± 4.7**	**16.3 ± 3.2**[b]
Old growth (*N*)	8.3 ± 5.8	9.4 ± 5.9	6.8 ± 4.6	7.4 ± 3.5	12.0	6.6	8.1 ± 5.3	8.7 ± 5.2
Old growth dbh (cm)	126.3 ± 38.4	109.5 ± 10.7	108.0 ± 18.5	112.1 ± 12.7	146.7	135.2	122.3 ± 33.8	111.6 ± 12.1[a]

Emboldened numbers indicate d_{unb} 95% CIs exclude zero (consistent effect size); footnoted not emboldened indicates d_{unb} CIs include zero (variable effect size).
[a]Small effect size (d_{unb} = 0.27–0.40),
[b]Medium effect size (d_{unb} = 0.42–0.63; + and – values),
[c]Large effect size (d_{unb} = −0.79).

Table 3. Number of platforms ($\bar{x}$ ± SD) by platform limb diameter classes in 18 0.2-ha paired nest sites of Marbled Murrelets and control sites (*N*).

	Olympic Peninsula		Vancouver Island		Western Cascades		Total	
	Nest (12)	Control (12)	Nest (5)	Control (5)	Nest (1)	Control (1)	Nest (18)	Control (18)
Total platforms >10 cm	60.7 ± 41.5	50.9 ± 18.8	65.6 ± 54.5	41.5 ± 23.4	83.0	55.0	63.3 ± 42.9	48.5 ± 19.4[b]
Nest tree excluded	48.1 ± 34.4	–	38.5 ± 33.3	–	75.0	–	47.4 ± 33.0	–
Total platforms >15 cm	27.4 ± 26.9	22.3 ± 8.6	25.6 ± 18.6	22.1 ± 14.7	47.0	29.0	28.0 ± 24.0	22.6 ± 10.1[a]
Nest tree excluded	19.2 ± 17.4	–	16.3 ± 13.8	–	41.0	–	19.8 ± 16.6	–
Total platforms >20 cm	10.3 ± 13.0	7.7 ± 5.5	5.8 ± 5.5	8.8 ± 6.6	16.0	7.2	9.3 ± 11.0	8.0 ± 5.5
Nest tree excluded	6.2 ± 6.9	–	3.5 ± 3.4	–	13.0	–	5.9 ± 6.3	–

[a]Small variable effect size (d_{unb} = 0.28).
[b]Low–medium variable effect size (d_{unb} = 0.42).

(Table 3). For platforms >15-cm (diff. = 2.8 platforms) and >20-cm diameter (diff. = 2.1 platforms), reductions were ~29 and ~37%, respectively.

Habitat of mapped sites at landscape scale. Comparison of GNN data at nest sites and random sites in Washington indicated that the GNN nest sites had higher values than random locations (indicated by 95% CI [nest] vs. trimmed $\bar{x}$ [random]) for all features except for hardwood tree canopy cover (Figs. 2–4). GNN nest sites also had larger average core areas and higher patch cohesion than random sites (Fig. 5).

DISCUSSION

Locations of nest sites. We found all nests of Marbled Murrelets in protected areas in federal reserves in Washington. Half of the nest locations were in northern Olympic National Park and in Conservation Zone 1 (British Columbia nests excluded). Protected areas on the Olympic Peninsula have previously been identified as important nesting habitat for murrelets (Raphael et al. 2011). Indeed, Raphael et al. (2015b) demonstrated the importance of the proximity of these nesting areas to marine areas where murrelets were abundant. We found nest sites in old conifer forests with large trees,

Table 4. Mean diameter at breast height (dbh) (± SD) of 17 Marbled Murrelet nest trees compared to all trees ≥10 cm dbh recorded in nest and control sites.

	Olympic Peninsula	Vancouver Island	Western Cascades
Douglas-fir			
Nest tree dbh (cm) ($N = 8$)	134.4 ± 33.9	–	–
Nest tree dbh range (cm)	98–193	–	–
All trees dbh (cm)	88.2 ± 32.8	58.5 ± 21.6	–
All trees dbh range (cm)	17–233	32–118	–
Western Hemlock			
Nest tree dbh (cm) ($N = 5$)	99.0 ± 11.4 ($N = 3$)	114.0 ± 19.8 ($N = 2$)	–
Nest tree dbh range (cm)	86–107	100–128	–
All trees dbh (cm)	64.7 ± 26.4	67.3 ± 27.2	59.3 ± 27.5
All trees dbh range (cm)	25–175	25–180	28–169
Western red cedar			
Nest tree dbh (cm) ($N = 3$)	–	127.0 ± 60.8 ($N = 2$)	248.0 ($N = 1$)
Nest tree dbh range (cm)	–	84–170	–
All trees dbh (cm)	62.1 ± 26.3	74.0 ± 42.6	164.4 ± 56.3
All trees dbh range (cm)	25–172	25–236	70–248
Sitka spruce[a] ($N = 1$)	219.0	–	–
Total	132.6 ± 41.8 ($N = 12$)	120.5 ± 37.7 ($N = 4$)	248.0 ($N = 1$)

[a]We recorded this species in only 1% of sites and only on the Olympic Peninsula (mean dbh = 150.1 ± 61.2 cm, range = 28–242 cm).

which is similar to the results of studies conducted in Alaska (Barbaree et al. 2014), Vancouver Island (Silvergieter and Lank 2011a, b), Washington (Hamer 1995, Hamer and Nelson 1995, Nelson 1997), Oregon (Ripple et al. 2003), and California (Baker et al. 2006). Nest trees in our study were characterized by large size, large limbs, and numerous large platforms.

Most nest sites in our study were relatively close to the coast ($\bar{x}$ = 19 km). This may have been due to the local topography and the proximity of suitable nesting habitat to the coast. For example, Washington has little suitable nesting habitat more than 100 km from the coast (Huff 2006). Although most murrelets appear to nest within 60 km of the coast, a grounded chick was discovered 100 km inland in British Columbia (Nelson 1997). In Alaska, the median distance inland of murrelet nests was 10 km (Barbaree et al. 2014), and nests are generally located within 16 km of the coast (Nelson et al. 2006). In addition, nest sites of radio-tagged murrelets in our study were more than twice the average elevation of previously known nest sites in Washington ($\bar{x}$ = 348 m, Hamer and Nelson 1995). Within the area of the Northwest Forest Plan, most nesting habitat is below 1036 m in elevation (Nelson et al. 2006), but, elsewhere, some nesting habitat has been identified at elevations between 1280 and 1530 m (Burger 2002). Other investigators have reported nest sites of Marbled Murrelets at elevations ranging from a median of 376 m (Barbaree et al. 2014) to an average of 886 m (Manley 1999).

Habitat. Most nest sites in our study were on the Olympic Peninsula, possibly because we captured most murrelets from nearby waters (Raphael et al. 2015b). Productive marine feeding areas located near suitable nesting habitat have also been reported in southern Oregon, southwestern British Columbia, and Alaska (Meyer and Miller 2002, Zharikov et al. 2006, Barbaree et al. 2015). In British Columbia, Manley et al. (1999) found that the main difference between nest sites and paired, randomly selected unused sites was the availability of large trees with large numbers of platform limbs in areas with lower tree densities, and we also found this to be the case in our study. Our results also suggest a more open structure around nest sites than in other areas of the forest (control sites). For example, in addition to fewer trees, nest sites in our study had less dominant conifer cover, less total canopy cover, and smaller non-nest-tree crown areas of platform trees. This open

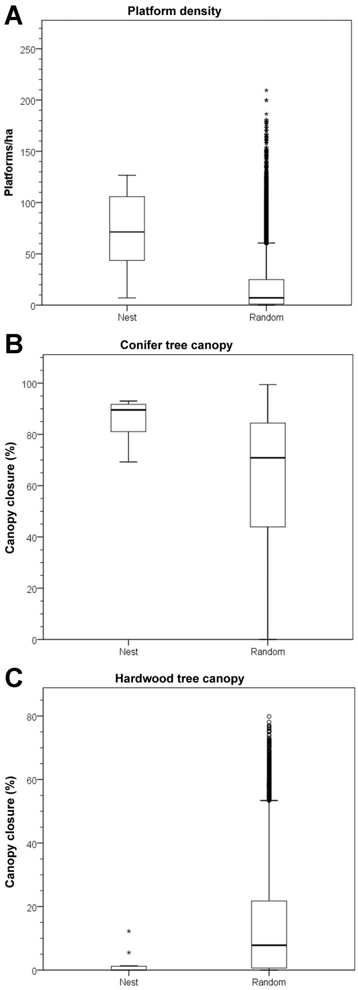

Fig. 2. Tukey box-plot graphs for (A) platform density, and percent canopy cover of (B) conifer and (C) hardwood trees for 14 Marbled Murrelet nest sites (Nest) compared to 10,094 random sites (Random) in Washington State. Boxes show the central 50% of the data (interquartile range). Solid lines are medians. Medians falling toward either end of box show data are skewed to left (top of box) or right (bottom). Whiskers attached to top and bottom of box are minimum and maximum values that are not outliers. Symbols outside whiskers are outliers (open circles) and extreme outliers (stars). Stars and dashed lines inside "Nest" boxes are mean ± 95% confidence intervals (CIs). Stars inside "Random" boxes are 5% trimmed means and are different from nest sites if they fall outside nest feature CIs. Note that for random sites, the trimmed mean is compared to nest site 95% CIs because CIs were indiscernibly narrow (most ≤1% between upper and lower limit values) when plotted on graphs.

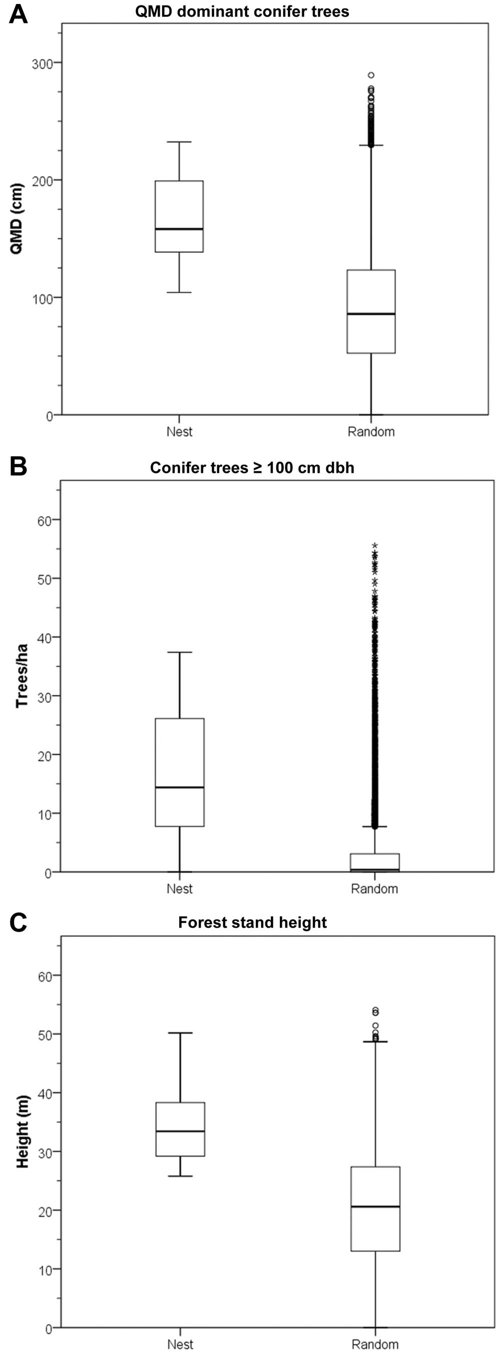

Fig. 3. Tukey box-plot graphs for quadratic mean diameter (QMD) of (A) dominant conifer trees, (B) conifer trees ≥100 cm dbh/ha, and (C) forest stand height for 14 Marbled Murrelet nest sites (Nest) compared to 10,094 random sites (Random) in Washington State (see Fig. 2 for explanation of box-plot symbols).

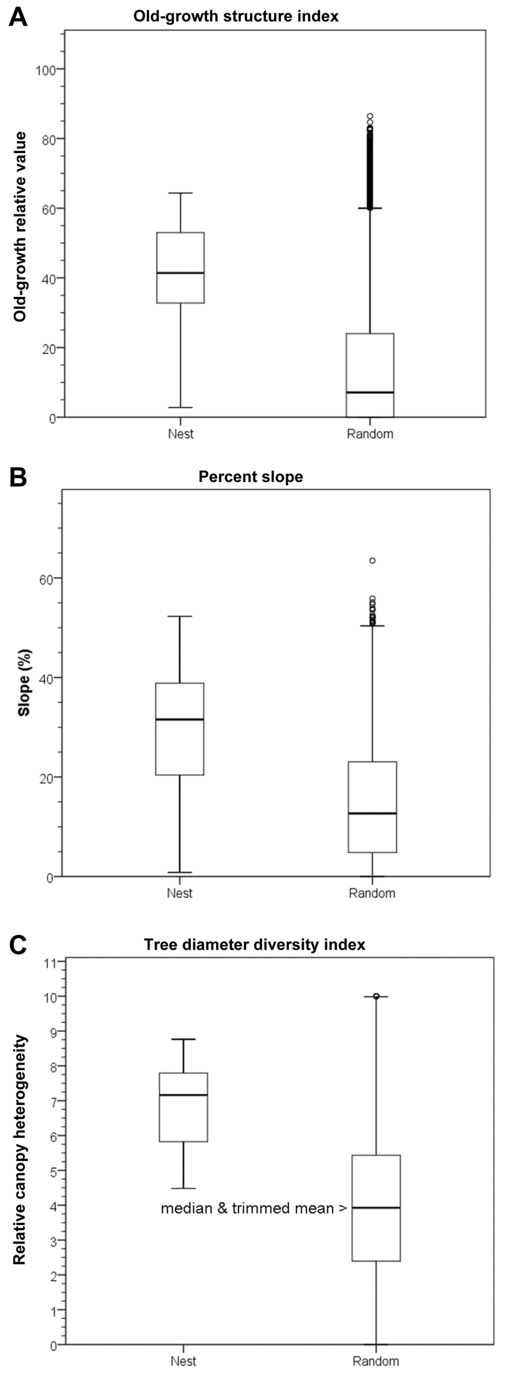

Fig. 4. Tukey box-plot graphs for (A) old-growth structure index, (B) percent slope, and (C) tree diameter diversity index for 14 Marbled Murrelet nest sites (Nest) compared to 10,094 random sites (Random) in Washington State (see Fig. 2 for explanation of box-plot symbols).

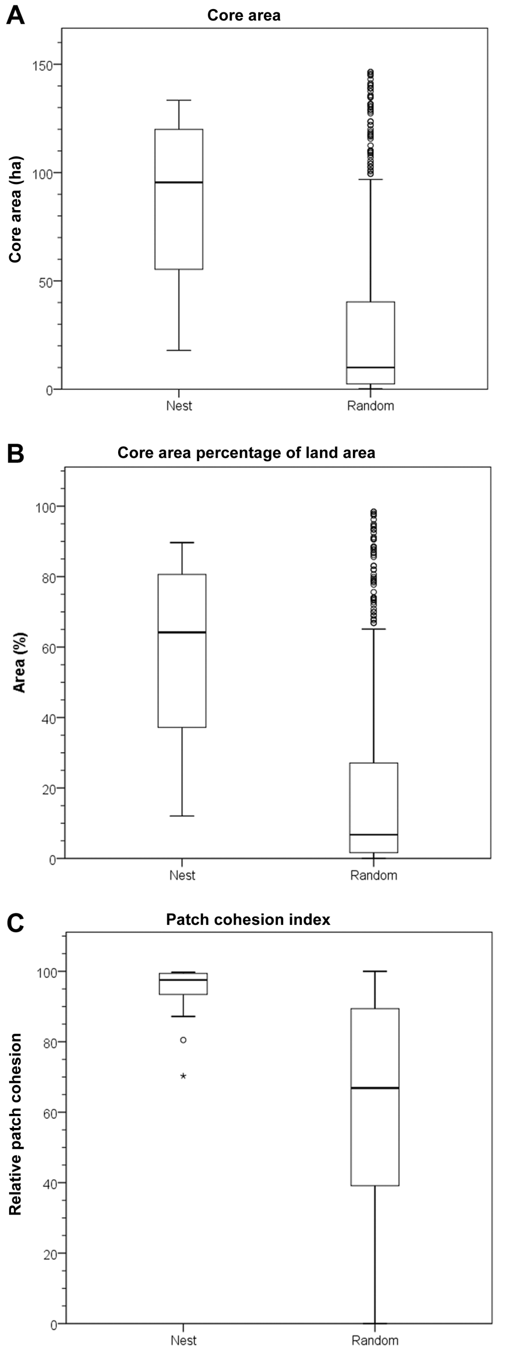

Fig. 5. Tukey box-plot graphs for three patch fragmentation metrics, including (A) core area, (B) core area percentage of land area, and (C) patch-cohesion index for 14 Marbled Murrelet nest sites (Nest) compared to 890 random sites (Random) in Washington State (see Fig. 2 for explanation of box-plot symbols).

structure may provide easier access to their nest sites for murrelets (Nelson et al. 2006).

We found that nest sites had more trees with platforms, and more total platforms >10 cm and >15 cm in diameter than control sites. Nest trees had more platforms than surrounding trees, particularly platforms >15 cm, and nest tree limbs were exceptionally large. Similarly, in Washington and Oregon, nest platforms were larger in diameter and nest trees had more platforms >15 cm than non-nest trees (Nelson et al. 2006). In Clayoquot Sound, British Columbia, nest trees also had more platforms than non-nest trees (Conroy et al. 2002) and, on the Sunshine Coast of British Columbia, nest trees had more platforms than other available platform trees (Manley et al. 1999). Because of the similarity of forest habitats compared, our results suggest that, at the stand or site level, nesting murrelets selected the most suitable features of forest structure across expansive potentially suitable habitat, as exemplified by the differences we found between nest and control sites.

We did not compare the smallest two levels of nest selection available to murrelets, the nest tree and nest limb scales. If murrelets select nest trees based on something unique about those trees, or select nest platforms based on size, nest cover, or some other feature, then site-level attributes may not be that important to murrelets. For example, in west-central Vancouver Island and the nearby mainland, Silvergieter and Lank (2011a) suggested that murrelets selected individual platforms, rather than platform trees *per se*. These investigators also asserted that nest trees were usually distinctive because they averaged 15–20% taller, had larger stem diameters, more potential nest platforms, and more moss than other trees in surrounding 25-m-radius patches. We also found that nest trees had larger diameters and more platforms than nearby trees. Such results seem to demonstrate the nexus between distinctive trees and platform quality, which our findings infer in the absence of platform-scale paired-site comparisons.

Conservation of inland nesting habitat is critical to the recovery of Marbled Murrelet populations (Raphael et al. 2015a). Our GNN landscape-scale analysis showed that important murrelet habitat features in stands where nests were found were less common, and stands with nests were less fragmented than habitat-capable forest across murrelet range. All nest sites of radio-tagged birds in Washington were in protected areas in mostly undisturbed pristine forest habitat. Much of the remaining suitable nesting habitat is fragmented and surrounded by immature forest resulting from both logging and natural disturbance (Raphael 2006). Developing larger areas of contiguous forest will take many decades and depend on the slow process of tree growth in these disturbed patches.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1.

Table S2.

Table S3.

Table S4.

Table S5.

Appendix S1.

Appendix S2.

Appendix S3.