Factors affecting the availability of thick epiphyte mats and other potential nest platforms for Marbled Murrelets in British Columbia

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Abstract: Nest platforms (mossy pads, limbs, and deformities >15 cm in diameter) are key requirements in the forest nesting habitat of the threatened Marbled Murrelet (*Brachyramphus marmoratus* (J.F. Gmelin, 1789)). Little is known about factors that affect the availability of platforms or the growth of canopy epiphytes that provide platforms. We examined variables affecting these parameters in coastal trees in British Columbia using data from 29 763 trees at 1412 sites in 170 watersheds. Tree diameter (diameter at breast height (DBH)) was the most important predictor of platform availability in the pooled data and within each of six regions. In most regions, platforms become available at DBH > 60 cm, but on East Vancouver Island, DBH needs to be >96 cm and possibly on the Central Coast >82 cm. Other regional predictors of platforms included tree height, tree species, and to a lesser extent elevation, slope, and latitude. Most (72%) trees providing platforms had epiphytes (mainly moss) covering one third or more of branch surfaces and 81% had intermediate or thick epiphyte mats. Mistletoe deformities provided <7% of platforms. Our model predictions help to define and manage suitable habitat for nesting Marbled Murrelets and also contribute to understanding forest canopy ecosystems.

Résumé : Les plateformes de nidification (coussins de mousse, branches et difformités >15 cm de diamètre) constituent des attributs indispensables de l'habitat forestier de nidification de l'alque marbrée (*Brachyramphus marmoratus* (J.F. Gmelin, 1789)), une espèce menacée. On sait peu de choses des facteurs qui affectent la disponibilité des plateformes ou la croissance des épiphytes de la canopée qui fournissent des plateformes. Nous avons examiné les variables qui affectent ces paramètres chez les arbres côtiers de la Colombie-Britannique en utilisant les données de 29 763 arbres répartis dans 1 412 sites et 170 bassins versants. Le diamètre des arbres (le diamètre à la hauteur de poitrine (DHP)) était la meilleure variable prédictive de la disponibilité de plateformes que toutes les données soient regroupées ou dans chacune des six régions d'où provenaient ces données. Dans la plupart des régions, des plateformes devenaient disponibles quand le DHP dépassait 60 cm, mais dans l'est de l'île de Vancouver le DHP devait être >96 cm, et possiblement >82 cm dans la région de la Côte Centrale. Les autres variables prédictives des plateformes dans les modèles régionaux incluaient la hauteur de l'arbre, l'essence et, à un moindre degré, l'altitude, la pente et la latitude. La plupart (72 %) des arbres fournissant des plateformes avaient des épiphytes (surtout des mousses) sur au moins un tiers de la surface des branches et 81 % avaient des coussins d'épiphytes moyens ou épais. Les difformités causées par le gui ont fourni <7 % des plateformes. Les prédictions de notre modèle aident à définir et à aménager des habitats de qualité pour les alques en nidification et elles contribuent aussi à la compréhension des écosystèmes de la canopée forestière.

[Traduit par la Rédaction]

Introduction

Many ecological studies, especially those linked with forest management and habitat mapping, focus on coarse-scale correlates and predictors of an organism's habitat needs (Manly et al. 2002; Scott et al. 2002). Fine-scale analyses are, however, needed to understand the processes that lead to coarser habitat patterns (Huston 2002). Numerous analyses have been applied to understand and predict the forest nesting habitats of the Marbled Murrelet (*Brachyramphus marmoratus* (J.F. Gmelin, 1789)) because loss of nesting habitat is a prime reason for its listing as a threatened species in Canada and the United States (see reviews by Ralph et al. 1995; Burger 2002; McShane et al. 2004; Piatt et al.

2006). These analyses have focused on landscape- and patch-scale predictors and revealed the Marbled Murrelet's dependence, through most of its range, on old (>200 years) coniferous forests. The key requirements provided by large, old trees appear to be a platform of sufficient area to accommodate the nest (which is a simple depression in the moss or duff), sufficient height for the bird to make stall landings and dropoff takeoffs, and gaps in the forest canopy to access the nest sites (see reviews cited above).

Although the importance of potential nest platforms (considered to be structures >15 cm in diameter) is widely recognized in predicting suitable nesting habitat (Waterhouse et al. 2009), the fine-scale factors that affect the availability of such platforms within individual trees remain poorly known. Most nest platforms consist of mossy mats on large canopy limbs, but thick bare limbs, mistletoe infestations (witches brooms), and other deformities also serve as nest sites (Nelson 1997; Burger 2002). In this paper, we analyse factors affecting the availability of canopy platforms and epiphytes, focusing on their potential as nest sites for the Marbled Murrelet, but with the goal of also providing important information on the neglected canopy ecosystem.

Marbled Murrelets are small diving seabirds (family Alcidae) that forage in nearshore coastal waters and usually nest in forests within 30 km of the ocean (Nelson 1997; Burger 2002). Being adapted for underwater locomotion using wing propulsion, Marbled Murrelets have stubby wings, high wing loading, rapid flight, and low maneuverability in flight. These anatomical and behavioral attributes underlie their use of tall old-growth forests as nest sites. Management guidelines for this species focus on the maintenance of existing old seral forests thought to be suitable as nesting habitat (e.g., CMMRT 2003; IWMS 2004). Research has improved knowledge of the forest types used for nesting by Marbled Murrelets, but significant data gaps remain that hinder management compatible with sustainable timber extraction (Burger 2002; McShane et al. 2004). Information on the factors affecting the availability of potential nest platforms at the finest spatial scale (tree or canopy) is scarce. Using a database with samples from most of the species' range in British Columbia, our goal is to explain and predict the availability of platforms and the development of epiphytes that are integral to most platforms. We also investigate the availability of deformities caused by mistletoe. Given the importance of platforms in Marbled Murrelet nesting habitat, our study provides information applicable to field management and conservation policy.

Although we focus on the nesting requirements of the Marbled Murrelet, our work also contributes to a broader understanding of the canopy microhabitat in coastal forests of the Pacific Northwest. These forests are of great economic and cultural importance in both Canada and the United States. Consequently, they have been well studied, but information on the structure and function of the forest canopy in this region remains sparse (Ishii et al. 2004). The development of large mats of epiphytes and accumulated litter is of particular importance in providing physical structure to these canopy ecosystems (McCune 1993; Lyons et al. 2000) as well as providing habitat resources to a wide range of canopy organisms (e.g., Carey 1996; Fagan et al. 2006).
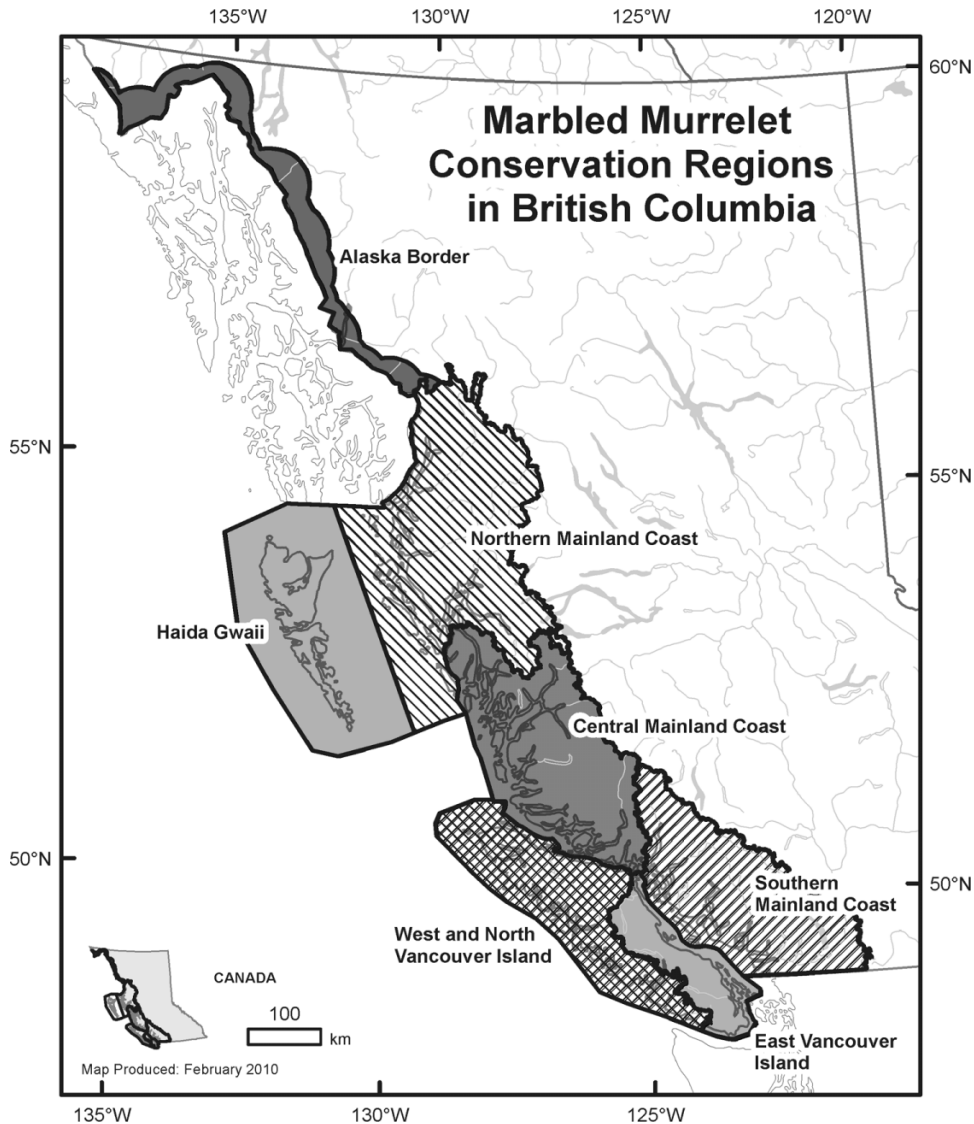
Methods

Regions

For geographical analysis, we used six conservation regions identified by the Canadian Marbled Murrelet Recovery Team (CMMRT 2003) (Fig. 1): Haida Gwaii/Queen Charlotte Islands (hereafter Haida Gwaii (HG)), Northern Mainland Coast (NC), Central Mainland Coast (CC), Southern Mainland Coast (SC), East Vancouver Island (EVI), and West and North Vancouver Island (WNVI). Although based on forestry and wildlife administrative boundaries, the regions provide biologically relevant divisions, including three latitudinal divisions of the mainland coast (NC, CC, and SC, which together span 7° of latitude), division of Vancouver Island into the wetter WNVI and drier EVI, and separation of the biogeographically isolated HG archipelago (Meidinger and Pojar 1991). There were no data from the Alaska Border region where few Marbled Murrelets nest (Fig. 1).

Data sources and sampling randomization

We collated data derived from habitat plots or transects from six sources. Five sources were past studies on the Marbled Murrelet: (i) in Clayoquot Sound (WNVI region) by the British Columbia Ministry of Environment (e.g., Bahn and Newsom 2002; Rodway and Regehr 2002), (ii) on the Sunshine Coast (SC region) by Manley (1999), (iii) on HG by I.A. Manley and A. Cober for the British Columbia Ministry of Environment (McLennan et al. 2000), (iv) in Desolation Sound (SC), Clayoquot Sound (WNVI and EVI), and the Woss landscape unit (WNVI) by a Simon Fraser University (SFU) research team (e.g., Malt and Lank 2009; Silvergieter 2009), and (v) on southwest Vancouver Island (WNVI) and southeast Vancouver Island (EVI) by a University of Victoria research team (e.g., Burger et al. 2000; Burger and Bahn 2004). These samples included all habitat studies with compatible data that were available to us. In 2008, A.E. Burger and M. P. Silvergieter undertook field studies specifically for this project on the NC (Prince Rupert and Kitimat areas), CC (Broughton Archipelago, Knight Inlet, and Bella Coola areas), and EVI (between Sooke and Campbell River). The complete database has been archived with the British Columbia Wildlife Species Inventory (www.env.gov.bc.ca/fia/wsi.htm).

When applying classification trees (our method of analysis, see below) to ecological distribution data, Edwards et al. (2006) reported that probabilistic (spatially randomized) sampling produced more reliable predictive models than nonprobabilistic purposive sampling (subjectively sampling where the habitat element was expected to occur). Our samples were drawn from studies that included both probabilistic and purposive sampling. Of the 29 763 trees sampled, 19 149 (64.3%) were in plots located using stratified random sampling (Burger et al. 2000; Bahn and Newsom 2002; nonnest SFU data, all new sampling in 2008) and 4293 (14.4%) were in plots associated with audiovisual surveys that were located in a nonrandom manner but were selected for criteria (e.g., visibility) other than the occurrence of platforms or suitable nesting habitat (Manley 1999; Rodway and Regehr 2002; Burger and Bahn 2004). These data (78.8% of trees) could be considered fully random when considering presence or absence of platforms. There might have been some

Fig. 1. Conservation regions recognized by the Canadian Marbled Murrelet Recovery Team (CMMRT 2003). We used the six southern regions for regional analyses; no data were available from the Alaska Border region.

bias towards presence of platforms in the additional 4854 trees (16.3%) sampled in plots at or near nest sites (Manley 1999; SFU nest site plots), but even in these plots, there were always trees with and without platforms. In all of the aforementioned samples (95.1%), the trees were not subjectively sampled because they might have contained platforms and can therefore be considered as nonpurposive in the sense used by Edwards et al. (2006). Only the samples from HG (1467 trees, 4.9%) were from trees selected because they were considered large enough to contain platforms (McLennan et al. 2000). We retained the HG samples in our pooled data because we felt that the effect of sampling bias would be minor and we wished to include this important part of the Marbled Murrelet's range.

Field methods and data extraction

Data extracted covered both site and individual tree descriptions (Table 1). Goals and methods differed among the studies but most sampled habitat using plots (30 m × 30 m square or 25 m radius circular) or, in HG, strip transects (30 m × 200 m; McLennan et al. 2000). With a few minor deviations (see below), all studies used the standardized protocols for evaluating Marbled Murrelet forest habitat (Resources Inventory Committee (RIC) 1997; Resources Information Standards Committee (RISC) 2001). These protocols broadly follow the methods for classifying ecosystems in British Columbia (Luttmerding et al. 1990) but include variables specific to Marbled Murrelets, especially the relative abundance of potential nest platforms, epiphytes (moss, lichens, ferns, and other plants growing on the limbs), and mistletoe infestations (Table 1).

Descriptions of the sites included latitude, elevation, aspect, slope, topographic location in the valley, biogeoclimatic (BEC) subzone, and BEC site series (Table 1). There were too many data gaps to include site index, stand age class, stand height class, and crown closure (all defined by the BEC system: www.ilmb.gov.bc.ca/risc/pubs/teecolo/habitat/). Aspect was simplified to eight cardinal directions plus flat.

Table 1. List of variables and their codes used in the analysis of platform and epiphyte availability.

Variable	Short form	Description
Dependent variables		
Platforms	PLATpa	Presence–absence of platforms (binary 0, 1)
Platform codes	PLATCODE	Rank of number of platforms per tree (0–4) (see Methods)
Epiphyte cover	EpiCOV	% of branch surfaces covered by epiphytes: 0 = none, 1 = trace, 2 = 1%–33%, 3 = 34%–66%, 4 = 67%–100%
Epiphyte thickness	EpiTHICK	Epiphyte thickness code: 1 = sparse, 2 = intermediate, 3 = thick mats
Predictor variables		
Region	Region	Marbled Murrelet management regions: HG, NC, CC, SC, WNVI, EVI (see Methods)
Latitude	UTM	Latitude recorded in Universal Transverse Mercator northing
Elevation	Elev	Elevation (m)
Slope	Slope	Mesoslope code 0–9 following the BC Biogeoclimatic (BEC) codes: www.ilmb.gov.bc.ca/risc/pubs/teecolo/habitat/
Aspect	Aspect	Facing direction of slope: N, NE, E, SE, S, SW, W, NW, Flat
Valley location	ValLoc	Location in valley: B = valley bottom, L = lower one third, M = midslope, U = upper one third, R = ridge top
Biogeoclimatic subzones	BECgrp	22 biogeoclimatic subzones (Meidinger and Pojar 1991) were grouped into nine groups for analysis (see Methods)
Biogeoclimatic site series	Site series	Fine-scale biogeoclimatic description of the forest patch (Meidinger and Pojar 1991; Green and Klinka 1994, p. 71), e.g., CWHwh1-01, CWHxm-04
Productivity	Produnit	Site productivity unit derived from BEC site series (Green and Klinka 1994:197): classes 1 (highest) to 4
Tree species	TreeSp	Species included in analysis: Fir, Hem, Cw, Yc, Ss, Fd, BL (see Methods for species codes)
Tree diameter	DBH	Diameter at breast height (cm)
Tree height	TreeHt	Height (m)
Stratum	Stratum	Stratum reached for the tree: C = canopy, E = emergent, S = subcanopy
Mistletoe infection	Mistletoe	Mistletoe deformities rated 0 (no infection) through 6 (heavy infection) using the Hawksworth (1977) system

BEC zones and subzones (Meidinger and Pojar 1991) were derived from BEC maps and site locations (Banner et al. 1993; Green and Klinka 1994). Most data (92.1% of trees) were from the Coastal Western Hemlock (CWH) zone, which dominates all of the coastal regions, 4.6% were from the higher elevation Mountain Hemlock (MH) zone, and 3.3% (in EVI only) were from the dry Coastal Douglas-fir (CDF) zone. We grouped the 23 BEC subzones sampled into nine groups (BECgrps) based on biogeoclimatic similarities (Banner at al. 1993; Green and Klinka 1994) and sample size as follows: CDFmm (n = 967 trees), CWHd (CWHdm, CWHds1, and CWHds2; n = 2122), CWHm (CWHmm1, CWHmm2, CWHms1, and CWHms2; n = 791), CWHvh (CWHvh1 and CWHvh2; n = 3291), CWHvm1 (n = 11 040), CWHvm2 (n = 6005), CWHw (CWHwh1, CWHwh2, CWHwm, CWHws1, and CWHws2; n = 1670), CWHx (CWHxm, CWHxm1, and CWHxm2; n = 1854), and MHm (MHmh1, MHmm1, and MHmm2; n = 1325).

BEC site series are the fine-scale descriptions of soil, moisture, and vegetation conditions within smaller forest stands and are classified on the basis of soil pits or indicator plant analysis (Banner at al. 1993; Green and Klinka 1994). Our data included 98 site series types, which we grouped into four productivity classes (class 1 having the highest productivity and 4 the lowest), based on predicted capabilities of the site series to grow trees to predetermined heights (Green and Klinka 1994). Previous work on Marbled Murrelet habitat has shown the value in grouping site series by productivity (Burger and Bahn 2004).

Data recorded for each tree included species, diameter at breast height (DBH), tree height, stratum reached, platform availability, and mistletoe infestation (Table 1). In most cases, a clinometer or laser rangefinder was used to measure one to five trees in the plot and the height of the remainder of trees in the plot was estimated using these as a reference; in some cases, all of the tree heights in a plot were estimated by experienced field personnel. A few trees were measured directly by tree climbers using a measured rope. In most studies, all trees ≥10 cm DBH were measured, including subcanopy, canopy, and emergent trees. In the HG sample, however, the trees were selected as those likely to provide platforms (McLennan et al. 2000). As a result, the HG data included few subcanopy and smaller canopy trees and the frequency of platforms per tree was therefore inflated relative to the other regions.

Snags (1653 tree records) were excluded from all analyses, leaving 29 763 live trees (Table 2). To simplify analysis of the most common tree species, the following categories were used with some species pooled as indicated (species codes follow the BEC system; Green and Klinka 1994): Fir = amabilis fir (*Abies amabilis* (Dougl. ex Loud.) (Ba), n = 5224 trees) and grand fir (*Abies grandis* (Dougl. ex D. Don) (Bg) n = 102), Hem = western hemlock (*Tsuga mertensiana* (Bong.) Carr. (Hw), n = 11 630), mountain hemlock (*Tsuga heterophylla* (Raf.) Sarg. (Hm), n = 1464), and unidentified hemlock (n = 54), BL = broadleafed tree species including red alder (*Alnus rubra* Bong. (Dr), n = 431) and bigleaf maple (*Acer macrophyllum* Pursh (Mb), n = 147), Cw = western redcedar (*Thuja plicata* Donn ex D. Don, n = 4876), Fd

Table 2. Summary of sampling effort in the platform database.

Marbled Murrelet Conservation Region (see Fig. 1)	No. of watersheds*	No. of sites	No. of trees (excluding snags)
Haida Gwaii/QCI (HG)	18	65	1467
Northern Mainland Coast (NC)	14	46	1627
Central Mainland Coast (CC)	26	45	1709
Southern Mainland Coast (SC)	44	495	8251
East Vancouver Island (EVI)	35	87	3063
West and North Vancouver Island (WNVI)	33	674	13646
Total all regions	170	1412	29763

*These are minimum numbers because watersheds were not reported in all data sets.

= Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco, n = 1806), Ss = Sitka spruce (*Picea sitchensis* (Bong.) Carr., n = 933), and Yc = yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach, n = 2610). Other species were too infrequent to be considered for specific analysis.

We included scores of mistletoe infestation (Hawksworth 1977) as a variable because a few Marbled Murrelet nests have been found in these deformities in Oregon (Nelson 1997). Infestations of parasitic mistletoe (primarily *Arceuthobium campylopodum* Engelm.) cause deformities (witches brooms) in tree limbs, especially in western hemlock (Pojar and MacKinnon 1994). A few deformities caused by other less common agents (other infections or physical damage) were likely included as mistletoe by field crews.

The availability of potential nest platforms (hereafter platforms) was assessed from the ground. Platforms were defined as limbs or deformities >15 cm in diameter, including any epiphyte growth, and >10 m aboveground. Following protocols (RIC 1997; RISC 2001), each limb that met these criteria was counted as a single "platform", regardless of how many mossy pads or other potential nest sites might be on the limb. The samples obtained by the SFU teams from SC, WNVI, and EVI were obtained to serve other purposes, and platform counts per tree included multiple platforms per limb, if present. To combine the two methods of counting platforms and to compensate for observer differences (which were greatest with large numbers of platforms), we ranked platform counts (PLATCODE; Table 1) as follows: for data following the standard protocols (RIC 1997; RISC 2001), 0 = no platforms, 1 = 1 platform, 2 = 2–5 platforms, 3 = 6–10 platforms, and 4 = >10 platforms; for the SFU data, 0 and 1 were as above but 2 = 2–10 platforms, 3 = 11–20 platforms, and 4 = >20 platforms per tree. We also tested for effects of platform assessment method (RIC/RISC versus SFU) in our statistical analyses (see below). We acknowledge that among the many field observers involved, there would be variation in the assessment of subjective variables such as platform diameter and tree height, but our large sample drawn from multiple studies should reduce the effects of systematic observer bias for any variable.

Statistical analysis

Statistical analyses used SPSS (version 15.0). Classification and regression tree (CART) analysis (De'ath 2002) was used to classify platform availability in trees based on predictor variables. Classification trees were used with PLATpa (presence–absence) as a binary variable and PLATCODE (ranked counts, see Table 1) as an ordinal dependent variable. To improve distribution of sample sizes and improve the fit (percent correct classification) of CART models, PLATCODE scores were grouped as 0, 1–2, and 3–4 for CART analysis but remained ungrouped as raw data for figures. Two advantages of using CART analysis with these data are the ability to classify multiple categorical dependent variables (i.e., multiple platform categories or ranks) and the ability to use cases with missing independent variables (Breiman et al. 1984; De'ath and Fabricius 2000). In SPSS, for cases in which the value for a variable is missing, other independent variables having high associations with the original variable are used as surrogates in CART. Data were filtered to include only selected tree species (above).

Classification trees were grown with the following rules: maximum classification tree depth 5, minimum cases in parent node 100, minimum cases in terminal node 50, and tree pruning (to avoid over fitting) using the 1 standard error rule (Breiman et al. 1984). For ordinal dependent variable models, model fit (percent correct classification) was evaluated with resubstitution (Breiman et al. 1984; De'ath and Fabricius 2000). The importance of individual predictor variables was assessed with normalized importance values, which give 100% importance to the best predictor variable, and contribution of other variables are assessed relative to this variable.

We tested for effects of platform count method (RIC/RISC versus SFU) by including method as a categorical dependent variable in preliminary CART models for the three regions affected. For analysis of PLATCODE, method was the lowest ranked predictor variable for WNVI and EVI (importance values 1.3% and 0.0%, respectively) and thus had no effect. For SC, method ranked as a tertiary predictor variable (47.5% importance) affecting platform classification only for trees <61 cm DBH. This split suggested that for small trees, the standard protocol (RIC 1997; RISC 2001) predicted greater platform counts than the SFU method. Method was not considered to be an important variable in platform prediction and was removed from final models.

We also attempted using the information theoretic methods (Burnham and Anderson 2002) applied to generalized linear models to identify variables and groups of variables that might explain platform availability and epiphyte development, but the occurrence of missing data for some variables made this less suitable than the CART analysis. In addition, our data were more suited to nonparametric analyses (such as CART); many of our variables did not conform to the assumptions required for generalized linear models and similar models, and the large number of possible predictor variables (12) resulted in an unmanageable number of candidate models.

Results

Regional breakdown of data

Overall, we had data from 29 763 trees (snags excluded), 1412 sites, and over 170 watersheds (Table 2). Missing data reduced sample sizes for some parameters. Most data came from the three southernmost regions, SC, EVI, and WNVI. Consequently, in addition to the pooled data set, we analysed each region separately.

Relationships among the predictor variables

Most predictor variables showed significant intercorrelations (Table 3). This is not surprising with environmental variables but also reflects the large sample sizes in the database. Most of the correlation coefficients were, however, small. The strongest and most consistent correlations were between DBH and tree height in all regions. In most regions, slope and elevation also showed strong positive correlations, indicating steeper slopes at higher elevations. Within regions, latitude (northing) showed strong correlations with elevation and slope, reflecting broadscale topographical clines (e.g., steeper and higher elevation terrain to the north of the sampled range on Vancouver Island).

Because DBH was such an important predictor of both platform and epiphyte development (see below), we tested for differences in DBH among categories of each of the categorical predictor variables (all data pooled). One-way ANOVA showed significant ($p < 0.001$) differences among categories in all of the categorical predictor variables. Tukey's post hoc tests for significant differences among groups showed the following homogenous subsets (mean DBH in parentheses). Among the biogeoclimatic groups (BECgrp: $F_{[8,28521]} = 92.69$), DBH was similar for most categories (CWHvm1–CWHx–CWHm–CWHvh–CDFmm–CWHvm2: mean DBH range 46.2–49.6 cm) but smaller in one (CWHd: mean DBH = 39.2 cm) and larger in two (MHm: mean = 55.5 cm, CWHw: mean = 69.1 cm). DBH differed among regions ($F_{[5,29141]} = 265.06$): NC–CC–WNVI–EVI (mean range 43.7–46.6 cm), SC (mean 52.8 cm), and HG (mean 80.3 cm). Each tree species or species group had a mean DBH significantly different from each other ($F_{[6,29140]} = 665.34$), from smallest to largest: broadleafed trees (mean 31.7 cm), firs (38.1 cm), hemlocks (41.7 cm), yellow cedar (59.9 cm), western redcedar (63.6 cm), Douglas-fir (68.0 cm), and Sitka spruce (88.3 cm). There were significant differences in DBH among aspect categories ($F_{[8,28634]} = 18.23$), but no specific north–south or east–west gradient was apparent: N–S (44.1 and 46.1 cm), S–W–NW–E–Flat (range of mean DBH 46.1–49.1 cm), E–Flat–SE (48.3–51.3 cm), and SE–NE–SW (51.3–53.6 cm). As expected, there were large differences in DBH with tree stratum reached ($F_{[2,29125]} = 11 540.8$): subcanopy (mean 25.9 cm), canopy (68.7 cm), and emergent (115.5 cm). Finally, DBH varied with tree location in the valley ($F_{[4,24674]} = 17.17$): Lower–Mid–Bottom (range of means 45.0–47.2 cm), Bottom–Ridge (means 47.2 and 49.0 cm), and Ridge–Upper (means 49.0 and 51.0 cm). In summary, the largest DBH measurements came from CWHw zones, Sunshine Coast and HG, Douglas-fir and Sitka spruce, emergent trees, and in valley bottoms or the upper third of valleys. Thus, the significant role of DBH in all predictive models may, parti-

ally, have resulted from correlations with these categorical predictor variables.

Platform availability: CART results

Classification trees evaluated the ability of the independent variables to classify trees by presence–absence of platforms and into three different platform codes (PLATCODE ranked as 0, 1–2, and 3–4). Figure 2 illustrates an example of a classification tree for data pooled among all regions. The first split identifies that trees with a DBH ≤ 61 cm are unlikely to provide platforms. For example, 19 063 trees with DBH < 61 cm had no platforms (92.9% of trees of this size). Further classification was based on DBH and region; smaller trees (<61 cm DBH in one split and 62–82 cm in another split of larger trees) in HG were more likely to have platforms than similar-sized trees in other regions. In the remaining regions, the presence of mistletoe deformities made a small difference to the availability of platforms. In most models, the number of samples involved in splits after the third (tertiary) node was small, and we therefore focus on the first three variables selected. With samples pooled from all regions, results were identical for presence–absence models and PLATCODE models (Table 4).

Classification trees were also analysed for each region separately (Table 4). For all regions, tree diameter (DBH) was the primary predictor variable. In most regions, DBH of approximately 60 cm was an important threshold distinguishing between trees with and without platforms, but thresholds were larger in the CC and EVI where trees with DBH < 82 cm (CC) and DBH < 96 cm (EVI) were unlikely to have platforms. DBH also reappears as a secondary and tertiary selector in some regions, making finer-scale separations of trees more likely to provide platforms. Other predictors included elevation (in HG, platforms were more likely at lower elevation), slope (in HG, platforms were more likely on slopes at elevations >98 m, but in the same region, platforms were more likely on moderate slopes in hemlock, Sitka spruce, and yellow cedar trees), and latitude within a region (in the large WNVI region, platforms on larger trees were more likely south of Nitinat Lake than in the north). Tree species were selected in the top three CART nodes in only three regions (HG, SC, and EVI), where larger Sitka spruce, yellow cedar, and Douglas-fir were consistently more likely to provide platforms, while western redcedar was consistently less likely to provide them. Firs and hemlocks showed more complex effects: platforms were more likely on larger hemlocks than most other species on HG but less likely in the SC and EVI regions; platforms were more likely on larger firs on EVI but less likely on SC. Larger broadleafed trees provided platforms on SC but not on EVI. Mistletoe deformities seemed important only on EVI, making a minor improvement for large trees of DBH 96–152 cm.

In general, there was a high percentage of cases correctly classified for each region (Table 4), typically >80%. However, closer examination of correct classifications by each of the categories showed that some categories were more easily classified than others (Table 5). In general, PLATCODEs of 0 (no platforms) had the greatest correct classification (mean > 80%) than did presence (mean 60%) or PLATCODEs 1–2 (mean 51%) and 3–4 (mean 18%). This

Table 3. Spearman rank correlations among predictor variables for Marbled Murrelet platforms and epiphyte development.

Region	Variable	DBH	Tree height	Elevation	Slope	Productivity unit	Northing (UTM)	Mistletoe	Region
All data	DBH	—							
	Tree height	0.804**	—						
	Elevation	0.036**	–0.117**	—					
	Slope	–0.024**	–0.111**	0.480**	—				
	Productivity unit	0.026**	–0.148**	0.193**	0.181**	—			
	Northing (UTM)	0.076**	–0.031**	0.079**	0.183**	0.109**	—		
	Mistletoe	0.206**	0.192**	0.011	0.040**	0.039**	0.010	—	
HG	DBH	—	0.851**	–0.143**	–0.037	–0.210**	–0.030	0.069**	NC
	Tree height	0.579**	—	–0.161**	–0.054*	–0.290**	0.003	0.043	
	Elevation	0.119**	–0.030	—	0.505**	0.511**	0.274**	–0.032	
	Slope	0.220**	0.154**	0.656**	—	0.328**	0.242**	–0.041	
	Productivity unit	–0.263**	–0.409**	–0.149**	–0.308**	—	0.044	0.003	
	Northing (UTM)	–0.121**	0.010	–0.400**	–0.269**	0.243**	—	–0.118**	
	Mistletoe	–0.129**	0.109**	–0.157**	–0.136**	–0.044	0.204**	—	
CC	DBH	—	0.725**	0.400**	–0.069**	–0.140**	–0.395**	0.149**	SC
	Tree height	0.875**	—	0.110**	–0.034**	–0.160**	–0.169**	0.108**	
	Elevation	–0.029	–0.004	—	–0.017	0.192**	–0.699**	–0.003	
	Slope	–0.103**	–0.106**	0.320**	—	0.007	0.204**	0.119**	
	Productivity unit	–0.023	–0.072**	0.476**	0.150**	—	–0.065**	–0.180**	
	Northing (UTM)	0.029	0.021	0.266**	0.175**	0.088**	—	0.022	
	Mistletoe	0.031	0.027	–0.034	–0.023	–0.025	–0.101**	—	
WNVI	DBH	—	0.868**	–0.091**	–0.082**	0.022	–0.140**	0.350**	EVI
	Tree height	0.851**	—	–0.132**	–0.134**	–0.061**	–0.216**	0.330**	
	Elevation	–0.054**	–0.135**	—	0.383**	0.044*	0.505**	0.001	
	Slope	–0.010	–0.115**	0.535**	—	0.043*	0.215**	–0.058**	
	Productivity unit	–0.113**	–0.223**	0.136**	0.240**	—	–0.131**	0.138**	
	Northing (UTM)	–0.030**	–0.044**	0.258**	0.159**	–0.097**	—	–0.038*	
	Mistletoe	0.226**	0.224**	–0.010	0.053**	–0.023*	0.051**	—	

Note: Values below the diagonal are for regions listed in the first column and values above the diagonal are for regions listed in the last column. Regions are defined in Table 2. Rank correlations were used because several variables are ranked variables (productivity unit, slope code, mistletoe). Correlations were computed for all continuous and ranked variables ($*p < 0.05$, $**p < 0.01$).

primarily reflects the uneven distribution of sample sizes by category. For example, in HG, there was very poor classification of trees with no platforms because only 20% of the trees in this data set lacked platforms. By contrast, in each of the other regions, 73%–93% of the trees contained no platforms and thus achieved greater classification accuracy. This reflects the difference in sampling method in HG (see Methods).

Table 6 summarizes the relative importance of each independent (predictor) variable in the different CART models. In all models, DBH was the most important predictor. Tree height and stratum reached were the second and third most important predictors in most models. Despite the importance of tree height and stratum, these variables appeared in few classifications, likely because tree height was highly correlated with DBH (Table 3), making tree height a redundant predictor once DBH was included. BECgrp was a relatively important predictor only in the models with data pooled, likely because these biogeoclimatic categories were broadly correlated with general regions in British Columbia. Tree species was a moderately important predictor in most models. There was little support for other predictor variables ex-

cept in the HG region where elevation, slope, aspect, and latitude show complex effects on platform development.

In summary, the CART models indicated that DBH was the important predictor of platforms in trees in all regions. Threshold values suggest that trees must have a DBH > 60 cm for platform development but larger on EVI (>96 cm) and possibly on CC (>82 cm). Depending on the region, other predictors of platforms in trees included tree height, tree species, and to a lesser extent elevation, slope, and latitude.

Trends in the platform data

Plots of raw data are useful to visualize modeling results and help interpret parameter estimates. Figure 3 shows the relationships between DBH and platform occurrence (PLATCODE) for each tree species and region. As predicted in the CART models, platforms generally appear in trees >60 cm DBH. One noticeable trend includes higher platform ranking and platforms in smaller trees for HG relative to other regions, in part an artifact of the sampling method (see Methods), but possibly also reflecting more favorable conditions for canopy epiphyte development in that region. Also,

Fig. 2. Classification tree for presence and absence of potential nest platforms using all data pooled across six regions: Haida Gwaii (HG), North Coast (NC), Central Coast (CC), Southern Mainland Coast (SC), East Vancouver Island (EVI), West and North Vancouver Island (WNVI). The first split (node 2) shows that trees with a DBH > 61 cm are more likely to have platforms present.
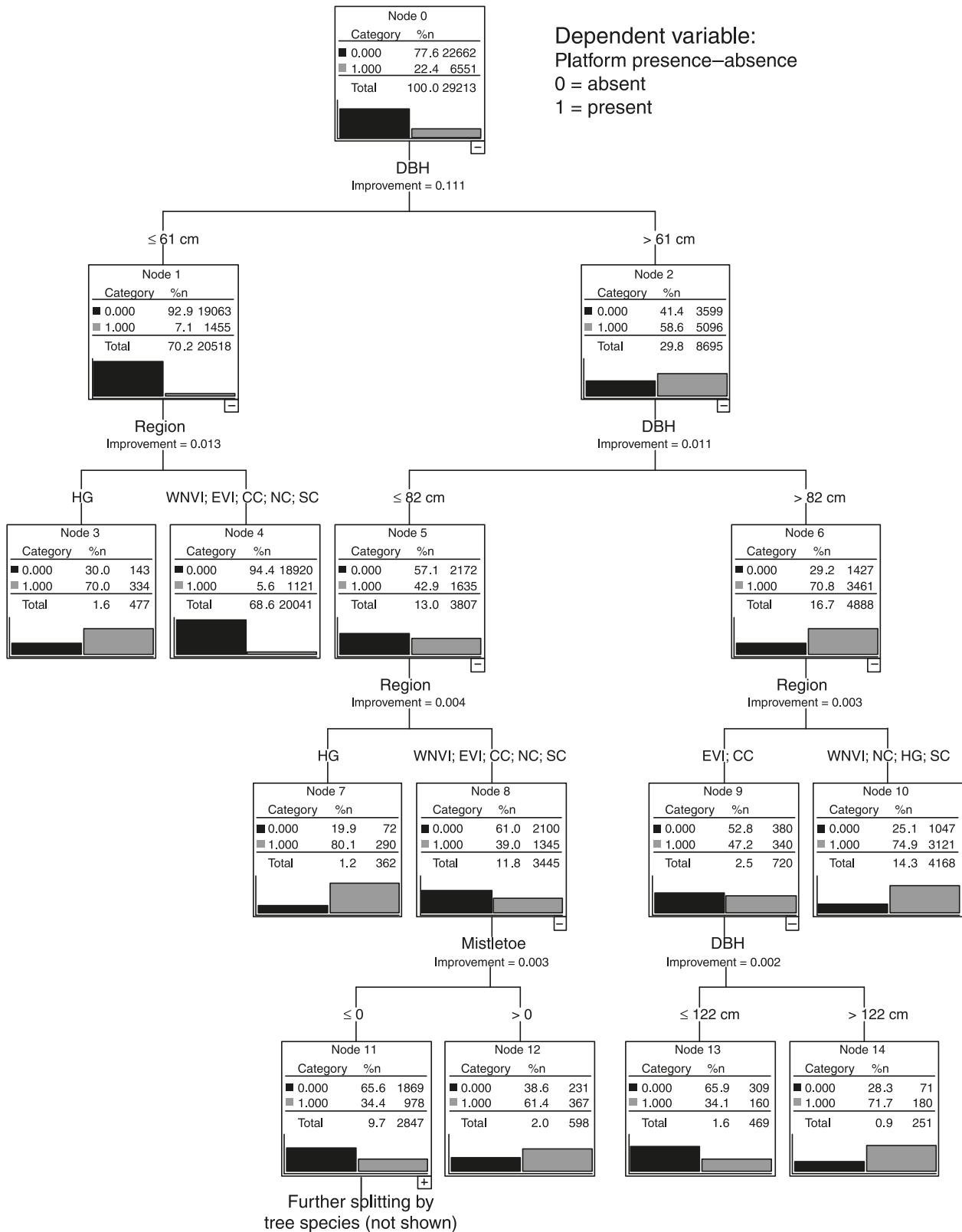
Table 4. Factors influencing the occurrence and number of platforms in trees in British Columbia.

Data set	n	% correct classification	Primary variable	Secondary variable	Tertiary variable
Platform (presence–absence)					
All data	29213	87.1	DBH (>61 cm)	If DBH < 61 cm, then Region (HG > others)	If DBH > 61 cm, then DBH (>82 cm)
HG	1440	81.0	DBH (>58 cm)	If DBH < 58 cm, then Elev (<98 m)	If Elev > 98 m, then Slope code (>0)
NC	1627	87.0	DBH (>60 cm)	DBH (>76 cm)	
CC	1665	94.5	DBH (>82 cm)	DBH (>130 cm)	If DBH > 130 cm, then Aspect (E, SW, W, S, NE > SE, N, Flat)
SC	8069	85.2	DBH (>61 cm)	DBH (>80 cm)	If DBH < 80 cm, then TreeSp (Yc, Fd, BL, Ss > Hem, Fir, Cw)
WNVI	13433	89.0	DBH (>61 cm)	DBH (>85 cm)	If DBH < 61 cm, then Stratum (C, E > S)
EVI	2977	91.8	DBH (>96 cm)	TreeSp (Fd, Fir, Yc > Hem, BL, Cw)	
PLATCODE (ranked 0, 1–2, 3–4)					
All data	29213	83.1	DBH (>61 cm)	If DBH < 61 cm, then Region (HG > others)	If DBH > 61 cm, then DBH (>82 cm)
HG	1440	64.6	DBH (>79 cm)	TreeSp (Ss, Hem, Yc > Cw)	If TreeSp Ss, Hem, Yc, then Slope code (<5)
NC	1627	84.4	DBH (>60 cm)	DBH (>76 cm)	
CC	1665	94.5	DBH (>82 cm)	DBH (>130 cm)	If DBH < 130 cm, then TreeHt (<26 m)
SC	8069	82.0	DBH (>61 cm)	DBH (>80 cm)	If DBH < 80 cm, then TreeSp (Yc, Fd, BL, Ss > Hem, Fir, Cw)
WNVI	13433	84.8	DBH (>61 cm)	DBH (>85 cm)	UTM northing (South > North); split at northing 5394834
EVI	2977	90.1	DBH (>96 cm)	DBH (>153 cm)	If DBH < 153 cm, then Mistletoe (>0)

Note: Classification trees were used to classify platform presence–absence and coded number of platforms per tree (PLATCODE). Parentheses indicate thresholds in classification. For example, the primary variable for platform presence–absence classification with all data showed platforms to be more likely for trees with DBH > 61 cm (primary variable), but if DBH was <61 cm, then platforms were more likely in HG than in other regions (secondary variable). Unless indicated by an "if", the secondary and tertiary predictors are branches off the preceding split that indicated greater platform development. Fir, amabilis and grand fir; Hem, western and mountain hemlock; BL, broadleafed species; Ss, Sitka spruce; Fd, Douglas-fir; Yc, yellow-cedar; Cw, western redcedar. Other variables are defined in Table 1.

Table 5. Summary of model fit for CART models classifying trees by presence–absence and into three categories (PLATCODE 0, 1–2, 3–4) of platform abundance.

	% correct classification							
	All data	HG	NC	CC	SC	WNVI	EVI	Average
Platform								
Absent (0)	92.2	16.9	93.1	99.7	91.0	95.8	98.5	83.9
Present (1)	69.4	97.6	56.6	21.8	69.2	59.0	45.5	59.9
Overall	87.1	81.0	87.0	94.5	85.2	89.0	91.8	87.9
Platform code								
0	94.0	0.0	93.1	99.6	92.1	95.8	98.7	81.9
1–2	55.1	98.2	52.6	25.5	60.5	38.6	24.6	50.7
3–4	12.7	15.4	0.0	0.0	13.9	33.1	51.1	18.0
Overall	83.1	64.6	84.4	94.5	82.0	84.8	90.1	83.4

Note: See Table 2 for region abbreviations.

Table 6. Summary of importance values of each independent (predictor) variable in the CART models for platform availability.

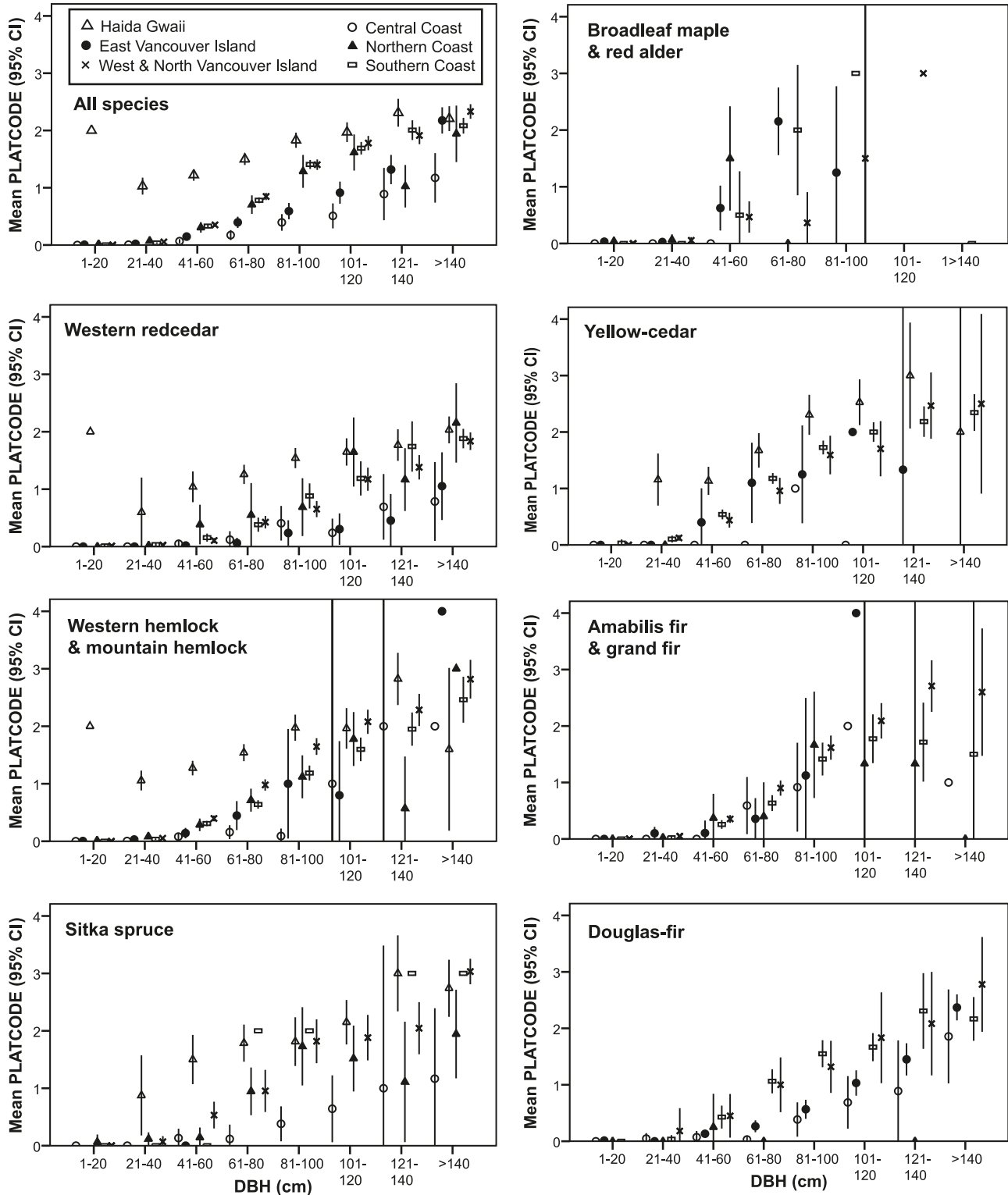|		Normalized importance values of independent variables in CART models						
Dependent variable	Independent variable	All data	HG	NC	CC	SC	WNVI	EVI
Platform (presence–absence)	DBH	100	100	100	100	100	100	100
	Stratum	58	53	25	12	59	30	38
	Region	44	na	na	na	na	na	na
	TreeHt	43	69	63	47	37	52	57
	BECgrp	26	6	0	3	4	0	0
	Mistletoe	11	1	1	0	0	15	42
	TreeSp	6	19	15	7	48	10	0
	UTM northing	3	33	5	4	12	10	1
	Elev	1	85	5	10	9	1	1
	Aspect	0	58	5	10	8	1	2
	ValLoc	0	0	0	11	5	0	1
	Slope	0	28	0	10	2	0	0
	Produnit	0	14	0	4	2	3	6
PLATCODE (ranked 0, 1–2, 3–4)	DBH	100	100	100	100	100	100	100
	Stratum	59	16	24	18	60	27	36
	Region	51	na	na	na	na	na	na
	TreeHt	44	63	63	47	37	51	54
	BECgrp	31	0	0	3	5	1	0
	TreeSp	9	56	16	16	51	10	0
	Mistletoe	9	9	1	0	0	15	43
	UTM northing	4	10	4	5	13	10	2
	Elev	3	6	5	15	10	0	1
	Slope	1	30	0	9	0	1	0
	Produnit	1	10	0	6	1	3	6
	ValLoc	1	0	0	13	4	2	3
	Aspect	0	13	5	12	5	1	4

Note: Importance values are normalized such that the most important predictor receives 100% importance and the contributions of other predictors are gauged relative to this most important predictor. See Table 1 for explanation of codes and Table 2 for region abbreviations. na, not applicable.

within regions, some species show greater platform development relative to tree size than other species (e.g., Sitka spruce and hemlocks relative to western redcedar). The low number of platforms on western redcedar is striking: even very large cedars fail to provide more than five platforms per tree (PLATCODE > 2), especially on EVI and the CC. Yellow cedar, which tends to have more horizontal thicker limbs than western redcedar, provided higher numbers of platforms than western redcedar. Large firs and hemlocks provide more platforms on WNVI than on NC and SC. Douglas-fir provides more platforms in WNVI and SC than on EVI and CC (the species is not found on NC or HG).

Although not selected in CART models because of correlations with DBH, tree height and stratum were also important indicators of platform occurrence and abundance (Table 6). Apart from the divergent HG data, platforms begin to appear regularly in trees >30 m tall and continue to increase with increasing height (Fig. 4). Platforms are rare in subcanopy trees and are most abundant in the large emergent trees, although less so on CC (Fig. 4).

Fig. 3. Effects of region and tree diameter (DBH) on PLATCODE (ranks 0–4) for seven tree species or species groups.
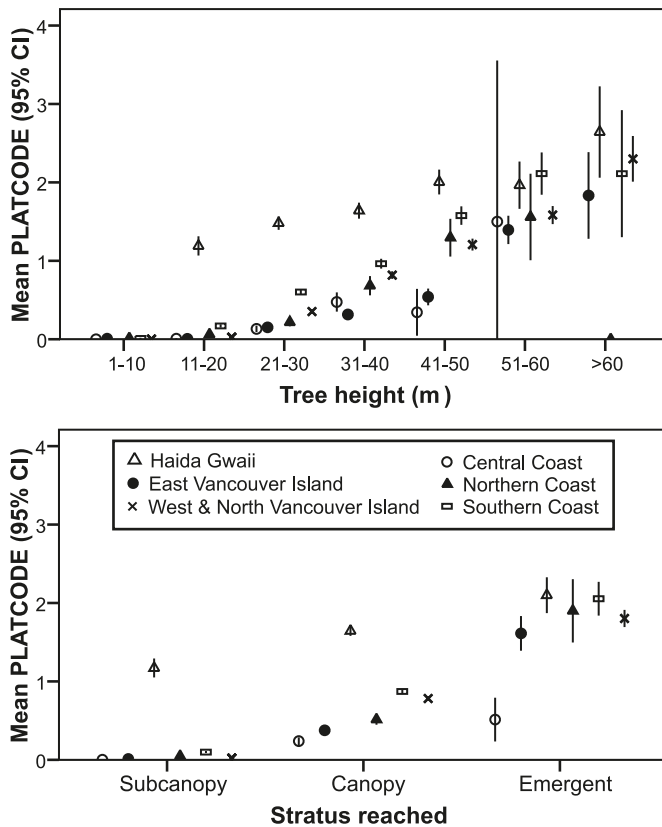

Epiphyte development

Epiphytes (mossy pads) are important in providing potential nest platforms for nesting murrelets, but this paper is the first to analyse the proportion of platforms provided by epiphytes and whether epiphytic growth varies with region, tree species, and other habitat features. Epiphyte development on branches was measured as epiphyte cover (percentage of branch surfaces covered) and by epiphyte thickness rank (Table 1). As expected, most platforms were provided by thick, mossy mats that developed on the limbs of canopy trees: out of 5088 trees with one or more platforms that had epiphyte data, most (72%) had epiphyte cover higher than

Fig. 4. Effects of tree height and tree stratum reached on PLATCODE (ranks 0–4) for each of six regions.

generally, valley bottom and lower slopes provided more epiphyte growth than mid and upper slopes or ridge tops (Table 8). Aspect was important only on HG (epiphyte cover higher on Flat and northerly aspects) and NC (higher on Flat, W, E, N, and NE). Elevation was a selected predictor in two regions, showing somewhat different effects on CC (epiphyte cover higher in larger trees below 186 m) and on SC (epiphyte thickness higher in smaller trees on slopes when above 440 m; Table 8). Latitude, site productivity, and BECgrp were also selected as predictors in one or two regions (Table 8) with moderate to low importance values in other regions (Table 9).

Role of mistletoe deformities

Mistletoe deformities were recorded in 20.2% of all canopy and emergent trees (n = 12 832, subcanopy trees and snags excluded) and were most common in western hemlock (this species made up 56% of the trees with mistletoe, mistletoe was found in 31% of all trees of this species) followed by Douglas-fir (11%, 22%), amabilis fir (11%, 17%), yellow cedar (10%, 21%), and mountain hemlock (3%, 15%). Although mistletoe deformities were not rare in canopy trees, it is unlikely that they provide an important source of potential nest platforms in British Columbia. Most trees showing these deformities also had high to moderate scores of epiphyte cover and thickness on their limbs (Table 7). Of the 4787 canopy trees with platforms that had data on mistletoe deformities and epiphyte cover, only 42 (0.9%) had mistletoe but lacked epiphyte cover or had only traces (Table 7). Similarly, considering epiphyte thickness, 894 (19.7%) of the 4530 trees with platforms lacked thick or intermediate epiphyte pads. Of these trees lacking epiphyte pads, 324 (7.2%) had mistletoe deformities but 570 (12.6%) did not (Table 7), and platforms were therefore provided by thick limbs and other structures (e.g., broken tops and limb forks). Because most mistletoe deformities were too flimsy or thin (<15 cm) to provide a nest platform for Marbled Murrelets (authors' personal observations), fewer than 7% of all platforms could be attributed to mistletoe or similar infestations.

Discussion

Application of classification trees to our data

As explained in the Methods, we found classification trees (De'ath and Fabricius 2000; De'ath 2002) to be the most applicable and robust method to derive explanations and predictions from our large data set. Edwards et al. (2006) found differences in the accuracy of classification tree models between spatially randomized and nonrandom (purposive) sampling. Although some of our sample plots were not spatially randomized, 95% of all trees (all except those in HG) were in plots selected for criteria other than availability of platforms (see Methods). Furthermore, we focused on occurrence of platforms within individual trees and not sample plots, and all plots contained trees with and without platforms. The great majority of our samples (95%) cannot therefore be considered purposive in the sense used by Edwards et al. (2006). As reported by Edwards et al. (2006), we found that models based on subjectively sampled purposive sampling (our HG samples) produced lower predictive

33% and only 153 (3%) had minimal traces or no epiphyte cover (Table 7). In these latter few trees, platforms were provided by exceptionally thick limbs or mistletoe deformities. Similarly, 81% of trees with platforms had epiphyte thickness scored as intermediate or thick mats (n = 4811 trees) (Table 7). Canopy trees with one or more platforms were significantly more likely to have higher scores of moss cover (χ^2 = 1752, df = 4, $p < 0.001$) and moss thickness (χ^2 = 2894, df = 3, $p < 0.001$) than those with no platforms, and the difference was accentuated in trees with multiple platforms (Fig. 5).

Classification trees (CART) evaluated each epiphyte measure separately (Table 8) and provided the relative importance values of each predictor variable (Table 9). DBH was an important predictor of epiphyte cover and thickness in the pooled data and in all but two of the regions. When DBH was the primary CART variable, epiphyte cover and thickness were generally higher above DBH thresholds of 40–50 cm. Tree height (>18 m) was the primary predictor of epiphyte coverage for CC and affected cover or thickness on WNVI and EVI regions. Thus, tree size (DBH and (or) height) appears to be a primary determinant of epiphyte development for all regions except HG (where samples were restricted to larger trees thereby minimizing the size effect). Tree species was the secondary variable in the pooled data for both epiphyte cover and thickness and was also important in three regions (Tables 8 and 9). Douglas-fir and, less consistently, western redcedar and yellow cedar showed less epiphyte growth than other tree species. Location in the valley was important in the pooled data and in four regions;

Table 7. Numbers of canopy and emergent trees showing epiphyte cover and thickness and mistletoe deformities relative to epiphyte occurrence.

Variable	Trees with platforms	Trees with no platforms	All trees	All canopy trees*		Trees with platforms*	
				No mistletoe	Mistletoe	No mistletoe	Mistletoe
Epiphyte cover (%)							
0	42	349	391	366	12	30	11
<1 (trace)	111	1071	1182	966	112	80	31
1–33	1291	3228	4519	3598	721	865	364
34–66	1772	2261	4033	2930	791	1112	485
67–100	1872	903	2775	1963	699	1258	551
Total	5088	7812	12900	9823	2335	3345	1442
Epiphyte thickness score							
0 (no epiphytes)	44	351	395	366	12	30	11
1 (sparse)	876	4695	5571	4388	833	540	313
2 (intermediate)	1789	1790	3579	2668	798	1196	538
3 (thick mats)	2102	839	2941	2082	615	1391	511
Total	4811	7675	12486	9504	2258	3157	1373

Note: Snags and subcanopy trees were omitted.

*Sample sizes differ among columns because not all trees had mistletoe data.

accuracy than those from randomized data (our other regions). The trends and predictions derived from the HG data were generally similar to those from other regions, reflecting the importance of DBH even though small trees had not been included. Further sampling is needed to determine if some of the differences between HG and other regions were due to nonrandomized sampling or genuinely reflect the conditions affecting platform availability on HG.

We used resubstitution as the method for estimating the accuracy of our classification trees because this gave us greater flexibility in pruning the trees with the SPSS software used. Edwards et al. (2006) found that cross-validation gave more realistic estimates of classification tree accuracy than resubstitution, but in their tests with randomized nonpurposive samples (which most closely resemble our sampling mix), the differences in model accuracy they reported were <10%. Differences in accuracy between these two methods were also around 10% in tests done by De'ath and Fabricius (2000). The accuracy of our predictions might therefore be slightly overestimated. Of course, the accuracy of our models would best be tested by applying our predictions to an independent fully randomized data set (Scott et al. 2002; Edwards et al. 2006), but that was not possible with the resources of our study and remains an important future goal.
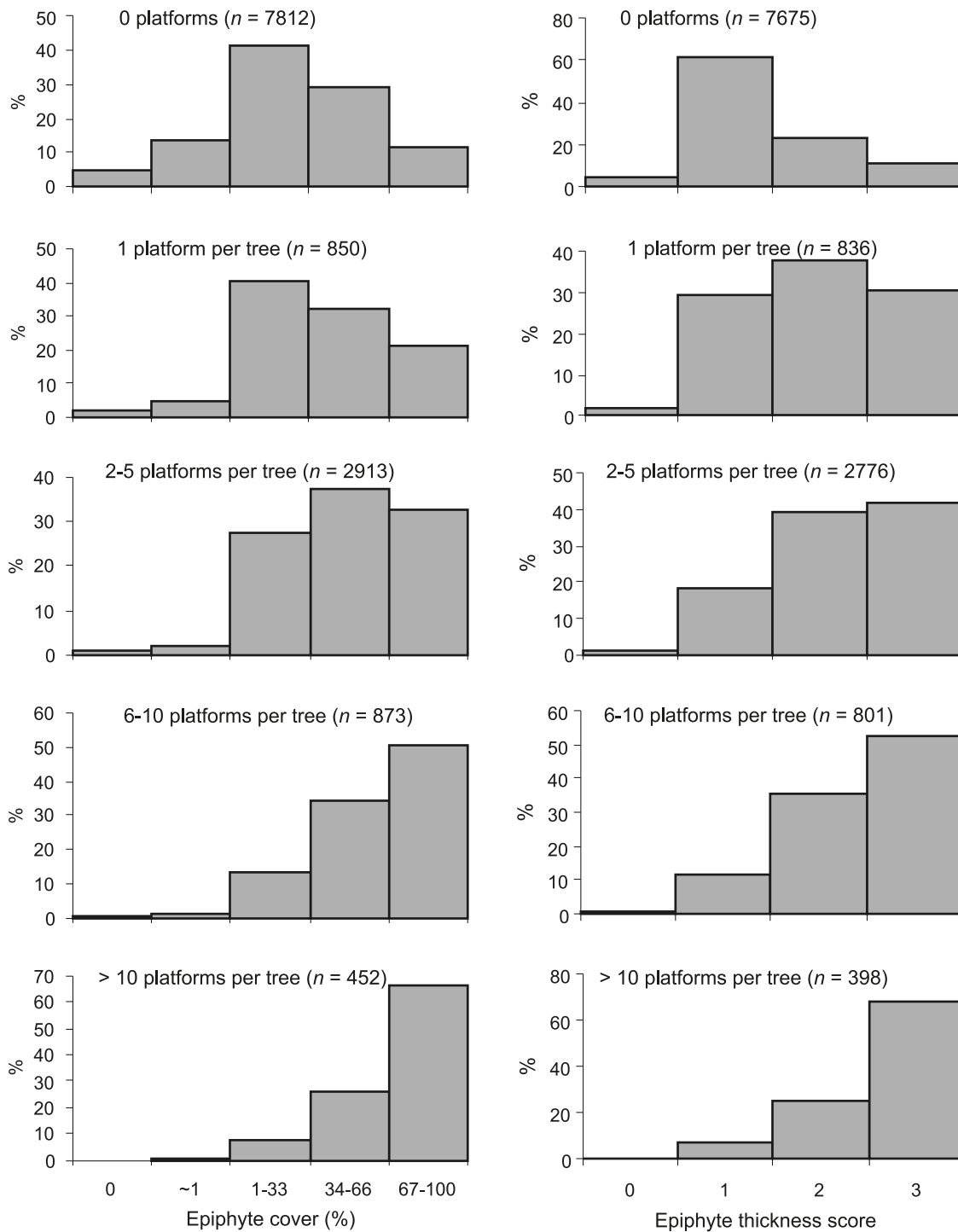
How many platforms are needed?

Although a pair of nesting Marbled Murrelets requires only a single platform for each nesting attempt, most nests are in trees with multiple platforms and stands with trees providing multiple platforms are more likely to be used by nesting Marbled Murrelets than those with few platforms (Burger 2002; Silvergieter 2009). Multiple platforms providing alternative nesting sites are important because Marbled Murrelets frequently switch nest sites (Burger et al. 2009) and there are theoretical reasons to expect lower nest predation in habitat that offers a large number of potential nest sites (i.e., platforms) to confound a predator (Chalfoun and

Martin 2009). The classification of a potential nest platform used in British Columbia (RIC 1997; RISC 2001) is based on limb diameter (including epiphytes if present) and makes no assumptions about suitability for Marbled Murrelets. An unknown but likely substantial proportion of our potential platforms would not be suitable for nesting Marbled Murrelets, e.g., not sufficiently level or lacking canopy gaps for access (Nelson 1997; Burger 2002). For these reasons, we focus not only on the presence and absence of platforms in a tree but also the approximate number of platforms in the tree as indicators of suitability for nesting Marbled Murrelets. The numbers of platforms would also be a good indicator of the structural complexity and community diversity of canopy ecosystems.

Factors affecting platform availability: tree and stand age

From a management perspective, availability of potential nest platforms relative to tree age would be very valuable information. One could then begin to address the question of how old stands have to be to provide platforms and suitable nesting habitat in each region and in various landscape situations affected by tree species, biogeoclimatic conditions, elevation, slope, and aspect. Unfortunately, it was not practical to core each tree to measure its age in the Marbled Murrelet habitat studies that provided our samples, and stand age was rarely given in the data. Although we expect general correlations between tree size (DBH and height) and age, the rate of tree growth is strongly affected by a wide range of environmental factors and there is no simple age–size relationship. In western hemlock, the numerically dominant tree species across the British Columbia coast, tree age is a poor predictor of tree size and epiphyte cover (Lyons et al. 2000). Although epiphyte biomass in the canopy (which contributes to platforms) tends to increase with stand age in the Pacific Northwest (McCune 1993), tree size and structure were better predictors of epiphyte biomass than tree age (Lyons et al. 2000; Pipp et al. 2001).

Fig. 5. Frequency distributions of canopy and emergent trees showing the relationships between epiphyte cover (left graphs) and epiphyte thickness (right graphs) and numbers of potential nest platforms per tree. Trees with platforms generally had some epiphyte cover and those with multiple platforms almost invariably had thick mossy mats.

Our continuing study will investigate the size–age relationships in our data in an effort to provide predictions on platform availability relative to stand and tree age, but until these complex relationships are resolved, we focus on DBH, mediated by regional and local conditions and tree species, as the most reliable predictor of platform availability. Since

DBH is readily and accurately measured, we recommend that this also be the primary management measure for ground-based management of habitat at the stand level. Tree height, which is the standard measure of tree size in forest cover mapping (Green and Klinka 1994) and in assessing Marbled Murrelet habitat using aerial photographs

Table 8. Factors influencing epiphyte development on trees in British Columbia.

Data set	n	% correct classification	Primary variable	Secondary variable	Tertiary variable
Epiphyte cover (ranked 0–4)					
All data	26878	44	DBH (>41 cm)	TreeSp (Fir, Hem, Ss, BL, Yc > Fd, Cw)	ValLoc (B, L > M, U, R)
HG	1440	58	Aspect (Flat, NW, N, NE > W, SW, S, SE, E)	If Aspect Flat, NW, N, NE, then UTM northing (S > N at UTM 5973326)	If Aspect W, SW, S, SE, E, then UTM northing (N > S at UTM 5916222)
NC	1594	49	DBH (>36 cm)	If DBH <36 cm, then Aspect (Flat, W, E, N, NE > NW, SW, S, SE)	If Aspect Flat, W, E, N, NE, then DBH (>16 cm)
CC	1654	59	TreeHt (>18 m)	If TreeHt > 18 m, then Elev (<186 m)	If TreeHt < 18 m, then TreeSp (Hem, Fir, Ss, BL > Yc, Cw, Fd)
SC	5900	52	Produnit (≤2)	If Produnit > 2, then DBH (>52 cm)	If DBH < 52 cm, then ValLoc (B, L > M, U, R)
WNVI	13312	44	DBH (>44 cm)	If DBH < 44 cm, then ValLoc (B, L > M, U, R)	If DBH > 44 cm, then TreeSp (Fir, Hem, Ss, BL > Cw, Yc, Fd)
EVI	2978	61	TreeHt (>28 m)	If TreeHt < 28 m, then Produnit (≤2)	If Produnit ≤ 2, then ValLoc (L, B > M)
Epiphyte thickness (ranked 0–3)					
All data	26139	63	DBH (>46 cm)	TreeSp (Fir, Hem, Ss, Cw, BL, Yc > Fd)	If DBH < 46 cm, then ValLoc (B, L > M, U, R)
HG	1440	66	UTM (N > S at UTM 5975755)	If UTM S, then UTM (N > S at UTM 5957294)	If UTM S, then UTM (N > S at UTM 5863508)
NC	1627	64	DBH (>40 cm)	DBH (>84 cm)	If DBH < 84 cm, then BECgrp (MHm, CWHvm1, CWHw > CWHvh)
CC	1654	74	ValLoc (B > U, L, M)	If ValLoc B, then TreeHt (>21 m)	If ValLoc U, L, M, then DBH (>46 cm)
SC	5304	65	DBH (>52 cm)	If DBH < 52 cm, then ValLoc (B, L > M, U, R)	If ValLoc M, U, R, then Elev (>440 m)
WNVI	13139	65	DBH (>51 cm)	TreeHt (>40 m)	DBH (>85 cm)
EVI	2975	72	Produnit (≤2)	If Produnit ≤ 2, then ValLoc (L, B > M)	If Produnit > 2, then TreeSp (Fir, Hem, BL, Cw, Yc, Ss > Fd)

Note: Classification and regression trees (CART) were used to classify epiphyte cover (ranked 0–4) and epiphyte thickness (ranked 0–3). Parentheses indicate thresholds in classification. Unless indicated by an "if", the secondary and tertiary predictors are branches off the preceding split that indicated greater platform development. For abbreviations, see Tables 1 and 2.

Table 9. Summary of importance values of each independent (predictor) variable in the CART models for epiphyte development (Table 8).

Dependent variable	Independent variable	Normalized importance values of independent variables in CART models						
		All data	HG	NC	CC	SC	WNVI	EVI
Epiphyte cover (ranked 0–4)	DBH	100	14	100	78	60	100	78
	TreeHt	78	19	83	72	51	86	65
	BECgrp	58	40	10	26	51	47	44
	Region	56	na	na	na	na	na	na
	Stratum	51	6	56	63	29	58	49
	ValLoc	42	0	6	46	47	56	94
	TreeSp	41	77	17	54	32	50	59
	Produnit	34	24	10	40	73	63	52
	Elev	30	69	10	58	92	46	100
	UTM northing	26	100	28	46	100	42	100
	Slope	22	38	6	57	63	34	57
	Aspect	20	76	20	100	49	35	90
	Mistletoe	20	24	3	3	12	21	30
Epiphyte thickness (ranked 0–3)	DBH	100	1	100	82	100	100	50
	TreeHt	71	15	65	64	54	84	36
	Stratum	65	3	47	67	46	69	6
	Region	46	na	na	na	na	na	na
	BECgrp	39	24	11	34	16	3	4
	UTM northing	28	100	27	38	59	13	100
	TreeSp	24	14	34	57	21	22	41
	Produnit	15	3	11	67	95	4	45
	Elev	15	26	17	49	55	4	72
	ValLoc	12	0	0	100	48	8	73
	Mistletoe	11	8	6	10	7	17	6
	Slope	8	14	1	21	31	5	8
	Aspect	7	41	2	47	38	8	86

Note: Importance values are normalized such that the most important predictor receives 100% importance and the contribution of other predictors are gauged relative to this most important predictor. See Table 1 for explanation of codes and Table 2 for region abbreviations. na, not applicable.

or low-level aerial surveys (Burger 2004), is strongly correlated with DBH (Table 3) and could serve equally well when DBH is impractical.

Factors affecting platform availability: tree size

Tree size, as indicated by diameter (DBH), was the dominant factor in separating trees with platforms from those without and in determining the relative abundance of platforms within trees. This applied to the pooled data from all regions and within each region. DBH was often a secondary and tertiary factor as well, indicating that other variables had relatively little influence in some regions. Tree height did not appear in any CART models, undoubtedly because it was significantly correlated with DBH, but when investigated independently, tree height and stratum were also important predictors of platform abundance. Obviously, it is the overall size and age of trees that is important here and not only diameter, but DBH appears to be the most reliable and consistent measure of tree size.

In the pooled data and in four of the six regions, tree diameter of about 60 cm appeared to be the primary factor affecting platform availability. The plots of platform abundance compared with DBH (Fig. 3) indicate that there was, indeed, a threshold response at about 60 cm for most species of trees in most regions. In other words, epiphyte growth exceeds the defined threshold for potential nest platforms (15 cm diameter) when most trees are above 60 cm in diameter. There were some important variations around this general trend. In the CC and EVI regions, the CART models indicate the need for somewhat larger trees (82 and 96 cm, respectively), which is also seen in the graphs (Fig. 3). The requirement for larger trees in CC is not clear because this region falls geographically and climatically between the SC and NC regions where larger trees are not indicated. Most of EVI falls within the drier leeward side of Vancouver Island in the Coastal Douglas-fir (CDF) or Coastal Western Hemlock – Very Dry Maritime (CWHxm) subzones (Green and Klinka 1994). Consequently, epiphyte growth in tree canopies is slower than in the moister parts of the British Columbia coast, explaining the requirement for larger trees to provide platforms.

Our data indicate some differences in platform availability relative to tree size in HG. The CART models showed differences between this region and the other five regions. Overall and for most tree species, platform counts were higher on HG than in other regions, especially for smaller trees (Figs. 3 and 4). This result was largely due to an artifact in the sampling methods. Sampling on HG was focused on trees that might provide platforms (McLennan et al. 2000); consequently, many smaller trees lacking platforms were omitted, thereby inflating the mean platform counts. Further research is needed to see if this isolated region does differ from the rest of coastal British Columbia in platform availability.

Factors affecting platform availability: tree species

Tree species was an important factor affecting platform availability in the HG, SC, and EVI regions and was selected in the less important outer branches of CART models (not shown in Table 4) for the pooled data (Fig. 2) and in some regions too. In regions where these species were common, Sitka spruce, Douglas-fir, and yellow cedar were consistently more likely to provide platforms and western redcedar consistently less likely to provide platforms than the other tree species. In part, this is related to the canopy microstructure. Branches in the first three species tend to be fairly horizontal and thick, providing a wide base and promoting epiphyte retention and the development of thick mossy mats. In contrast, the thin downward-sweeping boughs of western redcedar retain relatively little moss or other epiphytes, and in this species, potential platforms were often provided by deformities related to leader death ("chandelier growth"). Fir species (mostly amabilis fir with a smaller sample of grand fir) and hemlocks (mostly western hemlock with some mountain hemlock at higher elevations) were inconsistent in providing platforms. Firs provided more platforms than other species of similar size on EVI but fewer on SC. Likewise, hemlocks provided more platforms on HG but fewer on SC and EVI. Hemlocks were the most common species in most regions (>40% of the sampled trees in all regions except EVI where they comprised 27% of trees) and grow in a wide range of edaphic and microclimatic conditions (Pojar and MacKinnon 1994). In some situations, epiphytic development is evidently rapid on hemlock trees, promoting development of platforms, whereas in drier conditions such as on EVI and parts of SC, this ubiquitous species will have little epiphyte growth and few platforms.

One interesting result is that the small sample of broadleafed deciduous trees (red alder and bigleaf maple) showed quite high numbers of platforms (for trees >60 cm DBH on EVI and SC and >80 cm for WNVI) (Fig. 3). Out of more than 200 Marbled Murrelet nests found in British Columbia by telemetry and other means (Burger 2002; D.B. Lank, unpublished data), only one has been in a broadleafed tree (a red alder on the SC region; Bradley and Cooke 2001). Clearly, there are factors other than availability of platforms that influence the selection of nest sites by Marbled Murrelets. The structure of the canopy is likely important too, and the thick summer foliage of broadleafed trees might hinder access to flying Marbled Murrelets.

Factors affecting platform availability: epiphytes

The Marbled Murrelet habitat sampling protocols (RIC 1997; RISC 2001) did not provide information on the specific structures that provide the platforms in each tree (e.g., mossy mats, bare limbs, broken limbs, mistletoe deformities); this should be included in future revisions of the protocol. It is clear from our data, however, that the overwhelming majority of platforms were provided by epiphyte growth, specifically thick mossy mats that might also include minor amounts of ferns, lichens, and a few vascular plants. All Marbled Murrelet nests located in British Columbia except one on a thick bare limb were depressions on mossy pads, whether in trees or on cliffs (Bradley and Cooke 2001; Burger 2002; D.B. Lank and M.P. Silvergieter,

unpublished data). This is also the most common nest substrate throughout the species range, although a few nests in Washington, Oregon, and California have been found in duff on thick limbs in drier areas and on mistletoe deformities (Nelson 1997; McShane et al. 2004). In our data, most (72%) trees providing platforms had epiphytes covering one third or more of branches and 81% had epiphyte thickness scored as intermediate or thick mats (thickness score 2 or 3). Canopy trees with one or more platforms were significantly more likely to have higher scores of moss cover and moss thickness than those with no platforms, and nearly all trees with multiple platforms had both high epiphyte cover (usually >67%) and intermediate or thick mossy pads.

As expected, because most platforms were provided by epiphytes, the predictors of epiphyte cover and thickness were similar to those predicting platforms, including a strong effect of tree size (DBH and height) and less consistent effects of tree species, latitude, elevation, aspect, location in the valley, and site productivity. There was more diversity in the primary, secondary, and tertiary predictors in CART models for epiphyte cover and thickness than for the platform models, and the percent correct classification was often lower for epiphytes (44%–74%) than for platforms (65%–95%). This is in part because epiphyte cover (five categories) and thickness (four categories) were more finely classified than platform presence–absence (two categories) and the modified PLATCODE (three categories). In addition, high epiphyte cover and thickness could occur on smaller trees with narrow limbs (notice the lower DBH thresholds in CART models for epiphytes compared with those for platforms) so that many trees heavily covered with epiphytes might not have provided platforms. It is clearly the combination of large trees (with thicker limbs) and thick epiphyte cover that provides optimal conditions for potential nest platforms.

In general, the effects of tree species on epiphyte cover and thickness mirrored their effects on platforms. Relative to most other species, yellow cedar had higher epiphytic cover and thickness, while western redcedar had less. By contrast, Douglas-fir, which provided higher numbers of platforms than expected in EVI and SC, was among the species showing less epiphytic growth than other species of comparable size in the pooled, WNVI, and EVI samples. This apparent paradox is likely due to the thick limbs of Douglas-fir providing platforms without the need for thick epiphytic growth and to the prevalence of large trees of this species in the drier EVI and SC regions where epiphyte growth is often inhibited.

Our finding that tree size (DBH or height) is the most consistent predictor of epiphyte cover and thickness is consistent with other studies from the Pacific Northwest. McCune (1993) showed that epiphyte biomass increased with stand age but tree size was the strongest predictor within stands. He also suggested that bryophyte biomass in the canopy (the greatest contributor to Marbled Murrelet nest platforms) would only increase in late succession and in trees >200 years old. Lyons et al. (2000) found that canopy height and tree size were the main influences on epiphyte cover in western hemlock trees in Washington; large trees (>37 m tall) had twice the epiphyte cover found in medium-sized trees (12–37 m) and three times that of small

trees (<12 m). They also concluded that tree size was a better predictor of epiphyte cover than tree age.

Factors affecting platform availability: mistletoe deformities

Eighteen Marbled Murrelet nests have been found in mistletoe deformities (witches brooms) in Oregon, some in trees 66–150 years old, younger than typical old-growth (Nelson 1997; Nelson and Wilson 2002). It is therefore relevant to know to what extent mistletoe infestations might provide potential nest platforms in British Columbia and serve as alternative sites to the typical mossy platforms on large late-seral trees. Although mistletoe deformities were not uncommon (found in 20% of all canopy and emergent trees and in all regions), most trees with these deformities also had intermediate or thick mossy pads on their limbs that would be more likely to provide a nest platform. Our data indicate that mistletoe or similar infestations provide fewer than 7% of potential platforms for Marbled Murrelets in British Columbia. Unfortunately, the standard mistletoe scoring system used (Hawksworth 1977) provides no information on the size of the deformities or their suitability as potential nest platforms to refine this estimate. No Marbled Murrelet nests have been found in a mistletoe deformity in British Columbia (Burger 2002; D.B. Lank, unpublished data), and although we do not rule out the possibility of such deformities providing a small number of nest sites, their role in management of nesting habitat must be considered negligible.

Management implications

Our results provide important benchmarks in the management of nesting habitat for the Marbled Murrelet. In particular, our results should help to ensure that forests maintained as habitat (e.g., Wildlife Habitat Areas; IWMS 2004) include adequate platforms and a suitable proportion of those tree species that are most likely to provide platforms, to develop policies and field practices for partial-retention cutting that ensure retention of suitable trees with platforms so that murrelets might still nest, and to facilitate the recruitment of older second-growth forests to provide future habitat in areas where old forests are severely depleted.

Throughout most of the range in British Columbia, managers should not expect habitat to be suitable until a substantial proportion of the trees in a stand exceed 60 cm in diameter. The threshold is larger (90–100 cm DBH) on EVI and perhaps also on CC (~80 cm). For EVI, this difference is important. Within British Columbia, this coastal region has experienced the greatest loss of likely forest nesting habitat due to logging, urbanization, and agriculture (probably >75% of the preindustrial habitat; Burger 2002), and the Canadian Marbled Murrelet Recovery Team has recommended retention of 95% of the remaining habitat with recruitment required to increase habitat area (CMMRT 2003). If trees take longer to reach the threshold for providing potential nest platforms on EVI, then recovery of the Marbled Murrelet in this region can be expected to be more protracted and require more careful management and selection of habitat for recruitment.

In addition to DBH, our CART models provide managers with simple guidelines to the regional factors likely to be important in providing platforms and promoting epiphyte growth. The large samples of trees used in our analyses and the high proportion of correct classification in our models give reasonable confidence in the application of these data to management in British Columbia, although extrapolation of our results outside our study area (e.g., in the Alaska Border region in British Columbia and in the United States) requires caution and additional testing.

Our data indicate that Sitka spruce (generally on floodplains and lower slopes), Douglas-fir (in drier BEC subzones), and yellow cedar (generally in higher elevations) should provide potential nest platforms more often than other species, whereas the widespread western redcedar is consistently poor. Hemlock and fir species frequently provide platforms, but local research is needed to determine whether they are a preferred species or not. Species composition should therefore be considered when selecting stands for maintaining Marbled Murrelet habitat and in developing regional algorithms for identifying suitable habitat for Marbled Murrelets (e.g., McLennan et al. 2000; Hobbs 2003). Species composition might be particularly important where managers are selecting regenerating immature forest for future recruitment of Marbled Murrelet habitat.

Habitat recruitment is not a major focus of management in British Columbia at present, but the dearth of available old-seral habitat in the southern mainland (SC) and EVI (Burger 2002; CMMRT 2003) means that recruitment of regenerating forest as nesting habitat is likely to be an important option in the near future. Similarly, partial-retention cutting is not a recommended forestry practice in Marbled Murrelet habitat at present (IWMS 2004) and it is not known whether removal of some canopy trees affects the probability of Marbled Murrelets nesting. But this form of logging is becoming more common in British Columbia and our data will assist in determining the size and species of trees to leave standing to maximize the probability of retaining nesting capability for Marbled Murrelets.

Relevance of our data to canopy ecosystems

Because they are hard to access, canopy communities in tall forests remain poorly understood but are often important components in the overall forest ecosystem (Lowman and Rinker 2004). Although focused on potential nest sites for Marbled Murrelets, our data and classification models provide much-needed information on the development of epiphytes and occurrence of mistletoe deformities, which both contribute to the physical structure and habitat complexity of the coastal forest canopies in the Pacific Northwest. The large mats of epiphytes and litter that accumulate on the canopy boughs are important habitat for a wide range of canopy plants (McCune 1993; Lyons et al. 2000) as well as invertebrates (Fagan et al. 2006) and arboreal mammals (Carey 1996). Our data show the size of trees and other factors affecting epiphyte development and could be used in predictive models for canopy organisms in the same way as in our Marbled Murrelet analysis.

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References

Bahn, V., and Newsom, D. 2002. Can marbled murrelet use of nesting habitat be predicted from mapped forest characteristics? *In* Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia. *Edited by* A.E. Burger and T.A. Chatwin. British Columbia Ministry of Water, Land and Air Protection, Victoria, B.C. pp. 89–99.

Banner, A., MacKenzie, W.H., Haeussler, S., Thomson, S., Pojar, J., and Trowbridge, R.L. 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region. Land Management Handbook 26. British Columbia Ministry of Forests, Victoria, B.C. Available from www.for.gov.bc.ca/hfd/pubs/Docs/Lmh/Lmh26.htm.

Bradley, R.W., and Cooke, F. 2001. Cliff and deciduous tree nests of Marbled Murrelets in southwestern British Columbia. Northwest. Nat. **82**(2): 52–57. doi:10.2307/3536786.

Breiman, L., Friedman, J.H., Olshen, R.A., and Stone, C.J. 1984. Classification and regression trees. Wadsworth International Group, Belmont, Calif.

Burger, A.E. 2002. Conservation assessment of Marbled Murrelets in British Columbia: review of the biology, populations, habitat associations, and conservation. Technical Report Series No. 387. Canadian Wildlife Service, Delta, B.C. Available from www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm.

Burger, A.E. (*Editor*). 2004. Standard methods for identifying and ranking nesting habitat of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia using airphoto interpretation and low-level aerial surveys. British Columbia Ministry of Water, Land and Air Protection, Victoria, B.C. Available from www.env.gov.bc.ca/wld/documents/fia_docs/mamu_standard.pdf.

Burger, A.E., and Bahn, V. 2004. Inland habitat associations of marbled murrelets on southwest Vancouver Island, British Columbia. J. Field Ornithol. **75**: 53–66.

Burger, A.E., Bahn, V., and Tillmanns, A.R.M. 2000. Comparison of coastal fringe and interior forests as reserves for Marbled Murrelets on Vancouver Island. Condor, **102**(4): 915–920. doi:10.1650/0010-5422(2000)102[0915:COCFAI]2.0.CO;2.

Burger, A.E., Manley, I.A., Silvergieter, M., Lank, D.B., Jordan, K.M., Bloxton, T.D., and Raphael, M.G. 2009. Re-use of nest sites by Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia. Northwest. Nat. **90**(3): 217–226. doi:10.1898/NWN08-50.1.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Carey, A.B. 1996. Interactions of Northwest forest canopies and arboreal mammals. Northwest Sci. **70**: 72–78.

Chalfoun, A.D., and Martin, T.E. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. J. Anim. Ecol. **78**(3): 497–503. doi:10.1111/j.1365-2656.2008.01506.x. PMID:19040684.

CMMRT. 2003. Marbled Murrelet Conservation Assessment 2003, Part B — Marbled Murrelet Recovery Team advisory document on conservation and management. Canadian Wildlife Service, Delta, B.C. Available from www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm.

De'ath, G. 2002. Multivariate regression trees: a new technique for modeling species–environment relationships. Ecology, **83**: 1105–1117. doi:10.2307/3071917.

De'ath, G., and Fabricius, K.E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology, **81**(11): 3178–3192. doi:10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2.

Edwards, T.C., Jr., Cutler, D.R., Zimmermann, N.E., Geiser, L., and Moisen, G.G. 2006. Effects of sample survey design on the accuracy of classification tree models in species distribution models. Ecol. Model. **199**(2): 132–141. doi:10.1016/j.ecolmodel.2006.05.016.

Fagan, L.L., Didham, R.K., Winchester, N.N., Behan-Pelletier, V., Clayton, M., Lindquist, E., and Ring, R.A. 2006. An experimental assessment of biodiversity and species turnover in terrestrial vs. canopy leaf litter. Oecologia (Berl.), **147**(2): 335–347. doi:10.1007/s00442-005-0262-6.

Green, R.N., and Klinka, K. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. Land Management Handbook No. 28. British Columbia Ministry of Forests, Research Branch, Victoria, B.C.

Hawksworth, F.G. 1977. The 6-class dwarf mistletoe rating system. U.S. For. Serv. Gen. Tech. Rep. RM-48.

Hobbs, J. 2003. Marbled murrelet nesting habitat in the mid coast forest district: an assessment of the mid coast model. Available from British Columbia Ministry of Water, Land and Air Protection, Victoria, B.C.

Huston, M.A. 2002. Critical issues for improving predictions. *In* Predicting species occurrences: issues of accuracy and scale. *Edited by* J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, and F.B. Samson. Island Press, Washington, D.C. pp. 7–21.

Ishii, H.T., Van Pelt, R., Parker, G.G., and Nadkarni, N.M. 2004. Age-related development of canopy structure and its ecological functions. *In* Forest canopies. 2nd ed. *Edited by* M.D. Lowman and H.B. Rinker. Academic Press, New York. pp. 102–117.

IWMS. 2004. Identified Wildlife Management Strategy. Accounts and measures for managing identified wildlife: Marbled Murrelet *Brachyramphus marmoratus*. British Columbia Ministry of Water, Land and Air Protection, Victoria, B.C. Available from www.env.gov.bc.ca/wld/frpa/iwms/accounts.html.

Lowman, M.D., and Rinker, H.B. (*Editors*). 2004. Forest canopies. 2nd ed. Academic Press, New York.

Luttmerding, H.A., Demarchi, D.A., Lea, E.C., Meidinger, D.V., and Vold, T. 1990. Describing ecosystems in the field. British Columbia Ministry of Environment and Forestry, Victoria, B.C.

Lyons, B., Nadkarni, N.M., and North, M.P. 2000. Spatial distribution and succession of epiphytes on *Tsuga heterophylla* (western

hemlock) in an old-growth Douglas-fir forest. Can. J. Bot. **78**(7): 957–968. doi:10.1139/cjb-78-7-957.

Malt, J.M., and Lank, D.B. 2009. Marbled murrelet nest predation risk in managed forest landscapes: dynamic fragmentation effects at multiple scales. Ecol. Appl. **19**(5): 1274–1287. doi:10.1890/08-0598.1. PMID:19688934.

Manley, I.A. 1999. Behaviour and habitat selection of Marbled Murrelets nesting on the Sunshine Coast. M.Sc. thesis, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., and Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Kluwer Academic, Dordrecht, The Netherlands.

McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga–Tsuga* forests of different ages in western Oregon and Washington. Bryologist, **96**(3): 405–411. doi:10.2307/3243870.

McLennan, D., Veenstra, V., and Manley, I.A. 2000. Preliminary landscape-level habitat suitability algorithms for Marbled Murrelet and Queen Charlotte Goshawk on the Queen Charlotte Islands/Haida Gwaii. British Columbia Ministry of Environment, Lands and Parks, Smithers, B.C., and Oikos Ecological Services Ltd., Smithers, B.C.

McShane, C., Hamer, T., Carter, H., Swartzman, G., Friesen, V., Ainley, D., Tressler, R., Nelson, K., Burger, A., Spear, L., Mohagen, T., Martin, R., Henkel, L., Prindle, K., Strong, C., and Keany, J. 2004. Evaluation report for the 5-year status review of the Marbled Murrelet in Washington, Oregon and California. Available from EDAW Inc., Seattle, Wash. Prepared for the U.S. Fish and Wildlife Service, Region 1, Portland, Oreg.

Meidinger, D., and Pojar, J. (*Editors*). 1991. Ecosystems of British Columbia. B.C. Minist. For. Spec. Rep. Ser. 6.

Nelson, K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). *In* Birds of North America. No. 276. *Edited by* A. Poole and G. Gill. Academy of Natural Sciences, Philadelphia, Pa., and American Ornithologists' Union, Washington, D.C.

Nelson, S.K., and Wilson, A.K. 2002. Marbled Murrelet habitat characteristics on state lands in western Oregon. Report to Oregon Department of Forestry. Available from Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, Ore.

Piatt, J.F., Kuletz, K.J., Burger, A.E., Hatch, S.A., Friesen, V.L., Birt, T.P., Arimitsu, M.L., Drew, G.S., Harding, A.M.A., and Bixler, K.S. 2006. Status review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia. U.S. Geol. Surv. Open-File Rep. 2006-1387. Available from pubs.usgs.gov/of/2006/1387/.

Pipp, A.K., Henderson, C., and Callaway, R.M. 2001. Effects of forest age and forest structure on epiphytic lichen biomass and diversity in a Douglas-fir forest. Northwest Sci. **75**: 12–24.

Pojar, J., and MacKinnon, A. 1994. Plants of coastal British Columbia. Lone Pine, Vancouver, B.C.

Ralph, C.J., Hunt, G.L., Jr., Raphael, M.G., and Piatt, J.F. (*Editors*). 1995. Ecology and conservation of the Marbled Murrelet in North America. U.S. For. Serv. Gen. Tech. Rep. PSW-GTR-152. Available from www.fs.fed.us/psw/rsl/projects/wild/gtr152/.

RIC. 1997. Standardized inventory methodologies for components of British Columbia's biodiversity: Marbled Murrelets in marine and terrestrial habitats. Version 1.1. Publ. No. 208. Ministry of Environment, Lands and Parks, British Columbia Resources Inventory Committee, Victoria, B.C.

RISC. 2001. Inventory methods for Marbled Murrelets in marine and terrestrial habitats. Version 2.0. Standards for components of British Columbia's biodiversity. No. 10. Ministry of Environment, Lands and Parks, Resources Inventory Branch, Victoria, B.C. Available from archive.ilmb.gov.bc.ca/risc/pubs/tebiodiv/.

Rodway, M.S., and Regehr, H.M. 2002. Inland activity and forest structural characteristics as indicators of Marbled Murrelet nesting habitat in Clayoquot Sound. *In* Multi-scale studies of populations, distribution and habitat associations of Marbled Murrelets in Clayoquot Sound, British Columbia. *Edited by* A.E. Burger and T.A. Chatwin. British Columbia Ministry of Water, Land and Air Protection, Victoria, B.C. pp. 57–87.

Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A., and Samson, F.B. (*Editors*). 2002. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C.

Silvergieter, M.P. 2009. Multi-scale analyses of nest site selection and fledging success by marbled murrelets (*Brachyramphus marmoratus*) in British Columbia. M.Sc. thesis, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C.

Waterhouse, F.L., Burger, A.E., Lank, D.B., Ott, P.K., Krebs, E.A., and Parker, N. 2009. Using the low-level aerial survey method to identify Marbled Murrelet nesting habitat. B.C. J. Ecosyst. Manag. **10**: 80–96. Available from www.forrex.org/publications/jem/ISS50/vol10_no1_art8.pdf.