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Relating Microclimate to Epiphyte Availability: Edge Effects on Nesting Habitat Availability for the Marbled Murrelet

Abstract

Industrial timber harvesting typically creates forest edges with altered microclimate regimes, causing reduced growth and survival of some canopy epiphytes. This process has implications for the marbled murrelet (*Brachyramphus marmoratus*), a threatened seabird that nests on moss platforms in old-growth forests of the coastal Pacific Northwest in North America. We investigated microclimate and epiphyte availability in old-growth forests of southwestern British Columbia, Canada. We contrasted mean and maximum temperature, mean humidity, mean vapor pressure deficit (VPD) and mean epiphyte cover and platform tree density between forest edge and interior plots at hard edges (recent clearcuts), soft edges (regenerating forest) and natural edges (rivers and avalanche chutes). Differences measured in VPD and epiphyte availability varied due to edge proximity and edge-type. Hard edges had fewer trees with suitable marbled murrelet nest platforms relative to adjacent interiors, and hard-edged patches had the lowest epiphyte cover overall. This suggests that microclimate edge effects and substrate availability can negatively impact epiphyte growth and survival, and may reduce the availability of marbled murrelet nest sites. These negative effects may decrease with time as forests regenerate, as edge effects were lower in magnitude at soft-edged patches. In contrast, natural-edged patches had the greatest levels of epiphyte cover and platform tree density, suggesting that these areas provide an abundant source of potential nest sites. Minimizing the ratio of anthropogenic edge to suitable interior habitat, and maintaining natural edges will limit negative edge effects on moss availability and provide nesting habitat for marbled murrelets.

Introduction

Timber harvesting can create edges that expose the adjacent forest habitat to altered climatic regimes. This can result in "edge effects", in which biotic and abiotic gradients extend from the open edge into the interior of the forest (Harper et al. 2005). Edge environments can experience higher temperatures and solar radiation, lower humidity and stronger winds relative to interior forest (Chen et al. 1995, Stewart and Mallik 2006). Edge environments also have a more variable microclimate, as they are subject to more extreme conditions of longer duration (Fenton and Frego 2005). Microclimate changes can alter the plant community at edges, including that in the forest canopy. In the Pacific Northwest, a lower abundance of canopy trees and decreased canopy cover have been documented at forest edges (Gratowski 1956, Jules et al. 1999, Toms and Lesperance 2003). Epiphytes such as mosses can be particularly susceptible to microclimate edge effects, as they cannot control water uptake or retention, and are limited by water content and evaporation stress (Busby et al. 1978). This has been demonstrated by reduced growth rates in edge habitat due to increased temperature and reduced humidity (Hylander 2005, Stewart and Mallik 2006).

One of the most influential factors affecting the magnitude and spatial extent of edge effects is the structural contrast between habitat patches (Harper et al. 2005). Forest edges adjacent to different stages of regenerating forest may differ in their structural contrast, and therefore in the magnitude

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of edge effects. Edge effects may decline with time after harvesting, as clearcuts regenerate and patch contrast lessens (Matlack 1993, Harper et al. 2005). Patch contrast at natural edges may also be lower than fresh anthropogenic edges. This can result in weaker edge effects at forest-riparian ecotones compared to those at clearcut boundaries (Stewart and Mallik 2006). Considering the effects of different levels of patch contrast is important for environmental management of harvested forest landscapes, where stands of various ages create a patchwork of different edge-types.

Animals that rely upon forest bryophytes may be particularly sensitive to the effects of microclimate on the abundance and availability of mosses and other epiphytes. One example is the marbled murrelet (*Brachyramphus marmoratus),* a threatened sea bird that does not construct a nest, but rather lays a single egg on a mossy platform in old-growth trees (McShane et al. 2004). Murrelets explore forest habitat and choose nesting sites that presumably provide the environment best suited for successfully raising a chick. The widespread loss of epiphyte-rich old-growth habitat resulting from commercial logging is considered to be the major factor responsible for local extirpation and declining murrelet populations along the entire Pacific Northwest coast (Burger 2002, Raphael 2002, McShane et al. 2004). Appropriate tree branch characteristics and bioclimatic conditions are necessary for platform development (Burger et al. 2010). Habitat features on a smaller scale also appear to be important to murrelet nest site selection, including epiphyte cover and thickness, canopy structure and canopy openings (Burger 2002, Silvergeiter 2009). Edge effects on microclimate have the potential to further limit the availability of suitable murrelet habitat by decreasing the availability and thickness of epiphytes in tree canopies. The general effect of forest fragmentation on marbled murrelet nesting biology in British Columbia has been a contentious issue (see "Management Implications").

Although there have been studies investigating edge effects on forest structure and function, microclimate, and moss growth on the forest floor (e.g., Busby et al. 1978, Chen et al. 1992, 1995; Nelson and Halpern 2005, Stewart and Mallik 2006), fewer studies have looked at the influence of canopies on microclimate (see Rambo and North 2009), or compared these effects at different edge-types. The objectives of our study were to: 1) compare microclimate variables between edges and interiors of different edge-types during the summer, 2) compare bryophyte and substrate availability at these locations and 3) relate these findings to marbled murrelet habitat management in southwestern British Columbia.

Study Area

This study was conducted in four regions of southwestern British Columbia, Canada (Figure 1). Regions were selected that had ongoing industrial forestry activity and contained breeding populations of marbled murrelets (Bradley et al. 2004). We sampled microclimate and murrelet nesting habitat variables in the Elaho Valley and surrounding mountains in 2006 (49° 54.0' N 123° 16.8' W), Jordan River on southern Vancouver Island in 2006 (48° 35.4' N 124° 19.8' W), Nimpkish Valley on Northern Vancouver Island in 2005 (50° 12.0' N 126° 37.0' W), and Desolation Sound in 2004 (50° 05.0' N 124° 40.0' W).

These four regions are within the Coastal Western Hemlock (CWH) and Mountain Hemlock (MH) biogeoclimatic zones of British Columbia. The CWH forests are exposed to a mild and wet climate throughout the summer and winter. The tree species that dominate this biogeoclimatic zone are western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), yellow cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), amabilis fir (*Abies amabilis*) and Sitka spruce (*Picea sitchensis*) along valley bottoms. The MH biogeoclimatic zone is characterized by short, cool summers and long, cool winters with heavy snowfall. The tree species that dominate this zone are mountain hemlock (*Tsuga mertensiana*), amabalis fir (*Abies amabilis*) and yellow cedar (*Chamaecyparis nootkatensis*) (Klinka et al. 1991). Table 1 provides environmental descriptions of each region.

This research was part of a broader study investigating edge effects and spatial variation on nest predation risk for marbled murrelets (Malt and Lank 2007, 2009). We selected sites

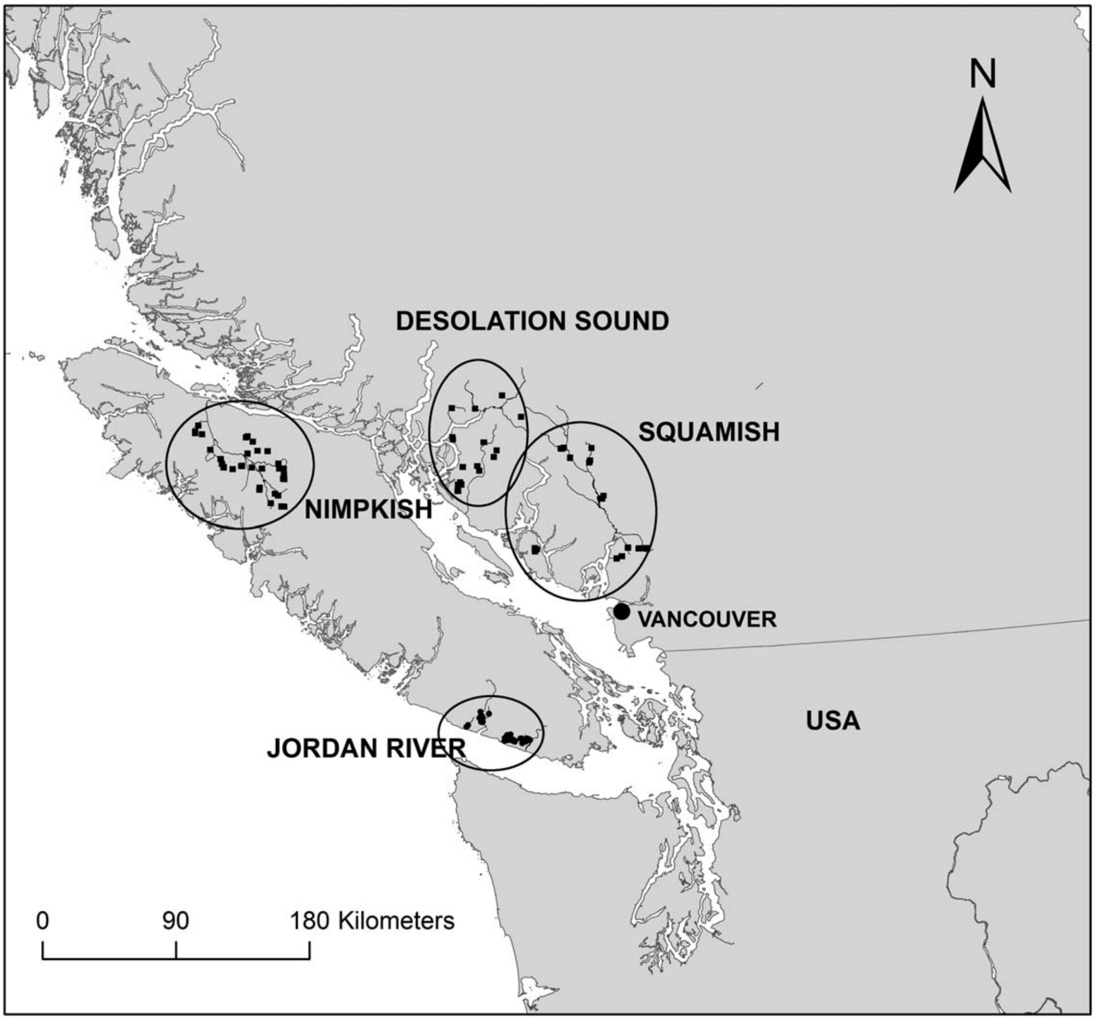

Figure 1. Locations of the four study regions in southwestern British Columbia , Canada, where microclimate and bryophyte availability surveys were conducted (2004 – 2006). Sampling sites and major drainage systems are shown for each region.

that had old-growth forest stands (≥ 250 years old) adjacent to three different edge-types: hard edges (recent clearcuts 5-11 years old), soft edges (regenerating stands 17-39 years old) and natural edges formed by rivers and avalanches. We did not quantify stand structure within the matrix, as we were primarily interested in the availability marbled murrelet habitat within old growth forest patches, and how this varied to different adjacent edge-types. However, we have provided average tree heights of our sampled forest patches (Table 2). Combined with published average tree heights for regenerating forests of these ages within our region (Mitchell and Polsson 1988), this gives a good description of the structural contrast at our edge-types (Table 2).

We selected two trees at both the edge (within 50 m of the edge of interest; Paton 1994), and in the forest interior (≥150 m from any forest openings). We selected trees that contained at least one suitable marbled murrelet platform, defined as being at least 15 m above the ground with a diameter of ≥ 18 cm, including epiphytes (Burger and Bahn 2004).

TABLE 1. Site selection and mean climatic conditions in each of the four regions in which the study was conducted. Edge and interior sampling locations are paired within sites of each edge-type. Values are for the months of May – September.

Region	*N* Hard	*N* Soft	*N* Natural	Temperature (°C)	Humidity (%)	VPD (hPa)	Precipitation (mm)
Squamish	11	13	5	16.1	73.6	6.2	73.1
Jordan River	12	12	11	12.7	94.1	1.8	92.3
Nimpkish	11	11	8	12.6	81.8	2.9	71.5
Desolation Sound	8	4	6	10.2	n/a	n/a	51.6

TABLE 2. Physical and biotic characteristics of hard, soft and natural edge types. DBH, Tree Height (habitat), and Tree spp. composition were calculated from 20 randomly-selected trees, 10 each within one edge and one interior randomly-selected 25 m radius plot from each site. N= 42 hard, 40 soft and 30 natural edged sites. Tree height matrix refers to the regenerating clear-cut area. Elevation effects were controlled for in the data analysis. *P* values correspond to comparisons of variables between edge-types. Acronyms for tree species and biogeoclimatic units are as follows: *T. het. – Tsuga heterophylla, A. ama. – Abies amabilis, T. pli. – Thuja plicata, T. mer. – Tsuga mertensiana, C. noo. – Chamaecyparis nootkatensis,* CWHvm1 – Coastal Western Hemlock, Submontane Very Wet Maritime, CWHvm2 – Coastal Western Hemlock, Montane Very Wet Maritime, CWHms1 – Coastal Western Hemlock, Southern Moist Submaritime, CWHmm1 – Coastal Western Hemlock, Submontane Moist Maritime, CWHds1 – Coastal Western Hemlock, Southern Dry Submaritime, CWHdm – Coastal Western Hemlock, Dry Maritime, CWHxm2 – Coastal Western Hemlock, Western Very Dry Maritime and MHmm1 – Mountain Hemlock, Windward Moist Maritime.

Variable	**Hard**	**Soft**	**Natural**	***P***
DBH (cm)	57.57 ± 1.74	60.89 ± 1.89	60.37 ± 2.10	0.368
Tree Height Habitat (m)	29.15 ± 0.50	29.19 ± 0.49	30.01 ± 0.70	0.498
Tree Height Matrix[1] (m)	<5	27.70 ± 0.40	43.50 ± 0.40	-
Tree Species Composition (%)	40.47± 0.41 *T. het.* 24.12 ± 0.41 *A. ama.* 15.76 ± 0.42 *T. pli.* 9.53 ± 0.42 *T. mer.* 8.47 ± 0.41 *C. noo.*	39.85± 0.41 *T. het.* 25.67 ± 0.41 *A. ama.* 10.51 ± 0.42 *T. pli.* 9.05 ± 0.42 *T. mer.* 13.45 ± 0.41 *C. noo.*	44.72± 0.47 *T. het.* 31.35 ± 0.47 *A. ama.* 12.71 ± 0.47 *T. pli.* 4.62 ± 0.47 *T. mer.* 6.27 ± 0.47 *C. noo.*	0.876
Elevation (m)	680.43	837.16	509.16	-
BEC Composition[2] (%)	57.5 CWHvm1 15 CWHms1 12.5 CWHvm2 5.0 CWHmm1 5.0 MHmm1 2.5 CWHds1 2.5 CWHxm2 2.5 CWHdm	68.4 CWHvm1 2.6 CWHms1 13.2 CWHvm2 2.6 CWHmm1 10.5 MHmm1 2.6 CWHxm2	72.7 CWHvm10.501 3.0 CWHms1 12.1 CWHvm2 3.0 CWHmm1 3.0 MHmm1 6.1 CWHds1	

[1] Mitchell and Polsson (1988), [2] British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests (1998). See methods and references for details.

Methods

Microclimate Sampling

We randomly selected one of the two trees at the edge and the interior of each site to install dataloggers for microclimate sampling. Both the edge and interior of any given site were sampled in the same year during the same summer for the same 14 consecutive day period. These 14 day periods were equally divided between the period of 31 May – 30 June and 1 July – 31 July, to avoid seasonal bias ($P = 0.764$). Each edge-type is equally represented between the two months. The edge and interior at any given site was sampled. The mean installation height was 25.68 m ± 3.22 m at edges and 25.69 m ± 3.12 m at interiors. Dataloggers were left in the edge and interiors of each site for approximately 14 days, during which they simultaneously sampled temperature (°C), dewpoint (°C), relative humidity (%), and absolute humidity (%)**.** Dataloggers began sampling at 1800 h on the day of installation, and recorded variables every 15 minutes until 0600 h on the day of retrieval. We measured microclimate data in Jordan River, Nimpkish and Squamish, but not Desolation Sound.

Because selected trees had murrelet platforms, our microclimate results directly address differences within this habitat stratum. There were no significant differences in branch thickness or height of datalogger placement (both of which could presumably affect microclimate) among our variables of interest (edges vs. interior of hard, soft, and natural edge types; all $P > 0.122$). We were unable to directly control for the bias of interannual climate variability. However, because edge-types and edge proximities were sampled equally within each region during each year, interannual variability should not affect our comparisons of interest. For example, warmer years may affect overall conditions within regions, but they should not affect the relative differences between edges and interiors of different edge-types.

Habitat variables were sampled in randomly selected plots (see below). Ibutton dataloggers (Maxim/Dallas, Sunnyvale, CA) were used at 45 sites and HOBO dataloggers (Onset Computer Corp. Bourne, MA) were used at 50 sites. They are professional grade equipment designed to measure the same variables with a high level of accuracy. The accuracy of both Ibutton and HOBO dataloggers was ± 0.5 °C and ± 2.5%. The Ibutton had a temperature range of -40 °C to 85 °C, the HOBO had a temperature range of 0 °C to 50 °C, and both operated within the range of 0 – 100% humidity.

Habitat Sampling

We sampled habitat predictors of epiphyte availability within randomly-selected 25 m radius plots within the forest edge and interior (see above for edge and interior definitions). Within each habitat plot, we selected 10 canopy/subcanopy trees (≥ 10cm diameter or reaching the canopy of the surrounding forest) using random distances and bearings. For each tree, we recorded species, diameter at breast height (DBH) and tree height. Total epiphyte cover on each tree was scored from zero to four (0 = none, 1 = trace, 2 = 1-33%, 3 = 34-66%, 4 = 67-100%), which has been used previously in similar studies (Newmaster et al. 2003, Fenton and Frego 2005, Nelson and Halpern 2005), and is a relevant component of marbled murrelet habitat (Burger and Bahn 2004). The number of trees within each plot with at least one potential murrelet platform was also recorded ("platform tree density"). All team members were trained together for consistency and each sampled an equal number of edge-types in one region only. Table 2 summarizes habitat variables by edge-type. Although we did not identify specific epiphytes in the canopy, previous research has documented the epiphytic community of this region in detail. Baldwin and Bradfield (2005, 2007), Newmaster et al. (2003) and Pojar and MacKinnon (1994) found the epiphyte community on branches and twigs to be primarily composed of the mosses *Antitrichia curtipendula*, *Neckera douglasii* and *Isothecium myosuroides*, with numerous liverwort species, including *Frullania tamarisci* and *Porella navicularis*; however, many other species of epiphytes were documented.

Data Analysis

Mean temperature, maximum temperature, minimum temperature and relative humidity were calculated as the averaged values of all samples during the ca. two-week exposure period for each edge/interior location of each site. Vapor pressure deficit (VPD) was calculated from the temperature and humidity values for each 15 minute sampling period at each sampling location. An overall site mean was calculated using the VPD values for each 15 minutes at each site. We used the following formula:

$$VPD= (6.1078)[e^{(17.269T/237.3 + T)}](1-RH)$$

where T is the temperature in °C, RH is the relative humidity as a decimal, and VPD is expressed in hPa (from Fenton and Frego 2005). VPD represents the difference between the saturation vapor pressure and the actual vapor pressure in the air at a given temperature. As VPD approaches zero, vapor in the air approaches saturation. 'Platform tree density' was the number of canopy trees per ha with at least one platform, corrected for the area of the plot that was outside of the forest. Epiphyte cover was also included in the analyses (see description above). Other habitat variables sampled, including platform density and epiphyte thickness, were highly correlated with these measures, and we focused our analysis on variables that were most likely to be affected by microclimate and most relevant to marbled murrelet habitat selection.

We ran mixed general linear models using the PROC MIXED procedure in SAS version 9.1 (SAS 2003) to test for individual and combinatorial effects of region, edge proximity (edge/interior) and edge-type (hard/natural/soft) on mean microclimate and habitat variables.

We used a split-plot design, where edge-proximity was the subplot factor (fixed effect), and site the main plot factor, nested within region and edge-type (random effects). In order to avoid over-specifying our models when analyzing data that were separated by edge proximity, we removed the random effects statement from our models. We sequentially removed non-significant interaction terms, only retaining those that were significant at alpha = 0.10.

Elevation has a significant influence on the climate variables we tested and can be represented by a linear relationship (Dodson and Marks 1997). To limit the number of variables in our models and to control for elevation effects and effects of unusually warm or cool periods that might have occurred during the sampling periods, between the sampling years and among regions, we derived regression equations relating region, elevation, edge orientation and julian date to our microclimate variables and output the residuals. We used the same procedure to control for region, elevation and orientation effects in our habitat variables. We analyzed the residuals for edge proximity and edge-type effects.

Results

Microclimate

The effects of edge proximity on mean residual temperature were dependent on edge type at our sample sites ($F_{2,71} = 5.69$, $P = 0.005$; Table 3). Mean residual temperature at hard edges (15.47 ± 0.2 °C) was higher than at hard interiors (15.03 ± 0.2 °C). There was no difference between mean residual temperature at soft edges (15.48 ± 0.3°C) relative to soft interiors (15.47 ± 0.3°C). At natural-edged patches, edges had lower mean residual temperature (14.72 ± 0.3°C) relative to interiors (15.14 ± 0.3°C).

A similar edge proximity*edge-type interaction was observed for mean residual VPD ($F_{2,65} = 5.07$, $P = 0.009$; Table 3). Mean residual VPD at hard edges (2.32 ± 0.74 hPa) was higher than hard interiors (1.91 ± 0.74 hPa) while in contrast soft edges (1.38 ± 0.87 hPa) were lower than soft interiors (1.78 ± 0.87 hPa). At natural-edged patches, edges (1.92 ± 0.83 hPa) had lower residual VPD compared to interiors (2.76 ± 0.87 hPa).

There may have been small differences in maximum residual temperature between sites of different edge-types, but the values were not statistically significant at $\alpha = 0.05$ ($F_{2,77} = 2.87$, $P = 0.06$; Table 3). Natural-edged patches (18.84 ± 0.73°C) had somewhat lower mean maximum residual temperatures than both hard-edged patches (19.68 ± 0.61°C) and soft-edged patches (20.02

TABLE 3. Microclimate variables at edge and interior plots of hard, soft and natural edge types. Values are least-squared means residuals added to standard values ± 95% confidence intervals. Maximum temperature and humidity did not have significant edge proximity*edge-type interactions, therefore values for the edge-type patch are presented. Mean temperature, VPD, maximum temperature and humidity residuals were added to standard values of 15.17°C, 2.0hPa, 19.62°C and 79.17%, respectively. *P* values refer to the edge proximity*edge-type interaction in the models.

	Hard		Soft		Natural				Model
Variable	Edge	Interior	Edge	Interior	Edge	Interior	N	P	Parameters
Temperature	15.47 ± 0.44	15.03 ± 0.45	15.48 ± 0.52	15.47 ± 0.52	14.72 ± 0.54	15.14 ± 0.53	156	0.005	Edge Proximity, Edge-Type
VPD	2.32 ± 0.74	1.91 ± 0.74	1.38 ± 0.87	1.68 ± 0.87	1.92 ± 0.83	2.76 ± 0.83	143	0.009	Edge Proximity, Edge-Type
Maximum Temperature	19.68 ± 0.61		20.02 ± 0.71		18.84 ± 0.73		156	0.063	Edge-Type
Humidity	78.30 ± 2.17		81.31 ± 2.65		78.42 ± 2.63		143	0.179	Edge-Type

TABLE 4. Habitat variables at edge and interior plots of hard, soft and natural edge types. Values for epiphyte cover are least-squared means of residuals added to a standard value of 2.0 ± 95% confidence intervals. Values for platform tree density are means ± 95% confidence intervals, as there was no significant edge proximity*edge-type interaction. *P* values refer to the edge proximity*edge-type interaction in the models. Bold model parameters indicate significant effects in the model.

	Hard		~~Natural~~ -SOFT		~~Soft~~ Natural				Model
Variable	Edge	Interior	Edge	Interior	Edge	Interior	*N*	*P*	Parameters
Epiphyte Cover	1.78 ± 0.25	2.03 ± 0.25	1.90 ± 0.46	2.00 ± 0.27	2.43 ± 0.29	2.21 ± 0.29	204	0.041	**Region,** Edge Proximity, **Edge-Type**
Platform Tree Density	3.76 ± 6.72	15.70 ± 9.29	16.02 ± 5.14	26.80 ± 6.60	31.45 ± 6.80	33.02 ± 6.60	204	-	**Region,** Edge Proximity, **Edge-Type**

± 0.71°C). In contrast, there appeared to be little difference in mean residual humidity between edge-types ($F_{2,72}$ = 1.83, $P = 0.18$; Table 3).

Epiphyte Habitat

We detected significant edge proximity*edge-type effects ($F_{2,101}$ = 6.36, $P = 0.003$; Table 4) on mean residual epiphyte cover score. The difference between hard edges (1.78 ± 0.25) and interiors (2.03 ± 0.25) was much larger compared to soft edges (1.90 ± 0.46) and interiors (2.00 ± 0.27). Natural edges (2.43 ± 0.29) and interiors (2.21 ± 0.29) had the highest scores.

Mean residual platform tree density varied significantly by edge proximity ($F_{1,96}$ = 10.40, P = 0.002; Table 4) and edge-type ($F_{2,101}$ = 6.50, P = 0.002; Table 4). Hard edges (3.76 ± 6.72) and interiors (15.70 ± 9.29) had substantially lower mean residual platform tree densities relative to both soft edges (16.02 ± 5.14) and interiors (26.80 ± 6.6) and natural edges (31.45 ± 6.8) and interiors (33.02 ± 6.6).

Discussion

Patch-Level Variation in Microclimate and Habitat Variables

Our results demonstrate significant anthropogenic edge effects on epiphyte availability in old-growth forests in four regions of south-western British Columbia. Despite only small differences in microclimate measured between treatments, habitat variables varied significantly with respect to both edge proximity and edge-type. Both hard and soft edges had less epiphyte cover compared to adjacent interiors, whereas natural edges had a higher epiphyte cover relative to interiors. Moreover, natural-edged sites had the highest density of platform trees overall, while hard-edged sites had the lowest. These results suggest that the creation of artificial edges by forest fragmentation will have negative consequences for epiphyte colonization, growth and survival in western forests, and has the potential to reduce the availability of marbled murrelet nesting habitat.

We observed substantially higher VPD and slightly higher temperatures at hard edges relative to interiors. This finding is consistent with Heithecker and Halpern (2007) and Stewart and Mallik (2006), who documented higher temperatures, higher VPD, and lower humidity at forest edges relative to interiors. These differences have been related to reduced growth, vitality, and survival of mosses at forest edges (Hylander et al. 2002, Hylander 2005, Stewart and Mallik 2006). Reduced epiphyte cover near anthropogenic edges may be related to lower survival associated with dry conditions (Proctor 1990). Also, anthropogenic edges are subject to higher wind speeds (Chen et al. 1995), which may decrease epiphyte cover through damage and removal of epiphytes. In addition, these winds can cause limb breakage and blow-down of trees at the forest edge (Chen et al. 1992, Harper and MacDonald 2002, Esseen 2006), which reduces the amount of suitable substrate available for epiphyte development. As such, it appears that the edge effects on epiphyte habitat we observed at hard edges resulted from the combination of changes to microclimate conditions and substrate availability.

Although edge effects on epiphyte habitat did occur at soft edges, the magnitude of this edge effect appeared to be lower than those occurring at hard edges. For instance, although there was less epiphyte cover at soft edges relative to interiors, this difference was smaller than that at hard edges. Platform tree density was also higher overall at soft-edged sites relative to hard-edged sites, and VPD was actually lower at soft edges compared to interiors. More platform trees at soft-edged patches suggest that microclimate conditions improved sufficiently at these locations for epiphytes to recruit and grow to establish new platforms. Indeed, it has been shown that significant re-colonization of tree branches in similar regions can occur within four years of epiphyte removal (Sillett et al. 2000). It is possible that the dense canopy of regenerating forest at soft edges buffers the negative impacts of altered microclimate at forest edges, and detrimental edge effects at recent clearcuts may decline as forests regenerate (i.e., Didham and Lawton 1999, Malt and Lank 2009). However, the buffering effects of soft edges observed in our study areas may be lower in magnitude compared with eastern forests, where regenerating forests can develop a sidewall of vegetation that limits edge effects (Matlack 1993). Nonetheless, it is possible that regenerating western forests older than those sampled in this study (11-30 years) may act as buffers to anthropogenic edge effects.

Compared to hard and soft-edged patches, forest patches containing natural edges were less affected by detrimental edge effects on moss availability. Epiphyte cover was higher at natural edges relative to interiors, and platform tree density was highest overall at natural-edged sites. Natural edges also had considerably lower VPD compared to interiors. This is consistent with Rambo and North (2009), who documented the lowest summer night-time temperatures and VPD at all heights in the canopy in riparian areas relative to upland areas.

A large portion of natural edges in this study were river and stream channels, which supply cool air and moisture to the surrounding forest (Brosofske et al. 1997). In addition, the smaller forest openings present at natural edges likely limits damage caused by exposure to extreme weather. As such, natural edges appear to provide excellent conditions for moss growth in these landscapes, and have the potential to act as refugia for canopy bryophytes in fragmented landscapes.

Potential Influence of Microclimate on Epiphytes

Our observation of overall decreases in epiphyte cover and platform tree density with increased VPD at forest edges suggests that fluctuations in temperature, humidity, and wind have greater influence on bryophyte growth and welfare in edge habitat, whereas in interior forests, availability of suitable substrates and more prominent radiation exposure may be dominant (Fenton and Frego 2005). These potential correlations are consistent with our observations of edge-types with low epiphyte cover and corresponding high VPD. Indeed, others have also suggested that evaporation stress influences the growth of bryophytes (Busby et al. 1978, Stewart and Mallik 2006, among others) and the magnitude of this stress can limit recovery (Proctor 1990). This is especially important for epiphytic bryophytes, which are completely dependent on air moisture, precipitation, and stem flow as water sources. Slower growth rates, reduced ability to colonize branches, and reduced sporophyte production could provide the mechanism through which microclimate influences epiphyte cover and platform tree density at forest edges (Sillett et al. 2000, Muir et al. 2006). This gives support to our previous suggestion that VPD may be influencing our habitat results.

Although we detected significant edge effects on our habitat variables, our study design is retrospective, and therefore we cannot unequivocally determine causal mechanisms. Indeed, other researchers have found contrasting results. Muir et al. (2006) found that *Anritrichia curtipendula*, an old-growth epiphytic moss common in our regions (Pike et al. 1975), grew better in open areas and patch cuts relative to unthinned forest. However, their study was conducted close to the forest floor, rather than in the canopy, where microclimate differences are often more extreme (Rambo and North 2008, 2009). Indeed, Sillett (1995) found that the cover of *A. curtipendula* was lower in the canopies of edge trees relative to interior trees, and Sillett et al. (2000) demonstrated reduced branch colonization by the same species in open habitat. Our observation of lower epiphyte cover at hard and soft edges is consistent with these findings.

We conducted our study during the summer, the driest time of year in these regions, when desiccation was most likely to be an issue. Despite substantial differences observed in epiphyte cover and platform tree density in relation to edge-type and edge proximity, differences in microclimate variables between these treatments were relatively small. The differences in mean temperature were only 0.4 °C and 0.6 °C for edges and interiors of hard and natural patches respectively, and differences in maximum temperature were not statistically significant. Given that some moss species are able to withstand long periods of temperature extremes (Proctor 2000), it is possible that VPD and solar radiation, rather than extremes in temperature, contribute to limiting moss growth in these regions (Proctor 1990). Indeed, we did observe greater differences in VPD between treatments relative to other microclimate variables. Alternatively, our inability to detect extremes in microclimate may have been influenced by our placement of dataloggers underneath large branches, where microclimate conditions might not have reached the same extremes as conditions above the branch, where mosses are exposed to direct solar radiation. Future researchers may wish to experiment with different placement of dataloggers in order to sample a wider range of microclimate conditions that may influence bryophyte growth and survival. Finally, extremely dry, cold, and windy winter periods can also occur in these regions, which may also stress bryophytes differentially with respect to edge proximity.

Potential Impact to the Availability of Marbled Murrelet Habitat

The patterns of variation in epiphyte cover and nest platform availability by edge proximity and edge-type show a negative initial effect of forest fragmentation on marbled murrelet nest site availability that appears to decrease with time as replanted forests regenerate. In contrast, forest stands associated with natural edges appear to have the highest levels of moss and platform availability. Rodway and Regehr (2002) suggest habitat preferences for murrelet habitat close to stream channels. Murrelets use watercourses as inland flyways (Peery et al. 2004), their nesting behaviour is positively associated with stream channels (Rodway and Regehr 2002), and they nest closer to streams than expected by chance at the landscape scale (Zharikov et al. 2006). The abundance of potential nest sites associated with the prolific moss growth at natural edges may contribute towards murrelets' selection of these areas.

The physical and stand level characteristics of bryophytes that were measured in our study are directly related to specific habitat variables that are selected by marbled murrelets (Burger and Bahn 2004). However, the relevance of these findings to murrelet conservation and management depends on whether these differences in moss availability are large enough to significantly impact marbled murrelets. We observed an average of 27 platform trees/ha in natural-edged patches, versus 9 platform trees/ha in hard-edged patches. In comparison, marbled murrelet nesting density can be as low as 0.11 nests/ha (Conroy et al. 2002). Therefore, it appears that even the relatively low density of platform trees at hard-edged patches could provide sufficient habitat availability for murrelets. In British Columbia, the presence of mossy platforms is an important criterion for ranking potential murrelet habitat suitability based on helicopter over flights (Waterhouse et al. 2009). However, availability of mossy platforms is only one component of habitat suitability. Murrelets appear to incorporate many factors into nest site selection, including access, overhead foliage cover and proximity to feeding areas at multiple scales (Manley 1999, Waterhouse et al. 2002, Zharikov et al. 2006). Consequently, if only small subsets of the available platforms are suitable based on the combination of all these criteria, edge effects have the potential to reduce the availability of platforms below thresholds required by marbled murrelets (e.g., Burger and Waterhouse 2009). These thresholds are most likely to be exceeded in highly fragmented landscapes, where a large proportion of habitat area is influenced by edge effects.

Conclusions

The influence of forest fragmentation on marbled murrelet habitat suitability in southwestern British Columbia has been a contentious issue, with contradictory conclusions being drawn by investigators using different approaches to study different phenomena (radar indices, potential or real usage, breeding success, apparent nest risk from predators) in regions of the province with different harvest histories, topographies, and microclimates (e.g. Burger 2001, 2002; Burger et al. 2004; Burger and Page 2007; Zharikov et al. 2006, 2007a,b; Malt and Lank 2007, 2009). Most of this discussion involves potential negative edge effects driven by higher nest predation at edges and potential positive effects due to easier nest site accessibility. In contrast, our study strengthens the case that the actual availability of potential nesting platforms is decreased at edges, and that microclimate is a mechanism partly responsible this. A reduction in epiphyte cover by reduced growth, survival, and colonization of mosses at hard and soft edges, and through the loss of substrate as a result of wind damage are measurable. These negative effects apparently persist for 20-30 years, and then decrease as adjacent clearcut forests regenerate.

Harvest planners can better preserve canopy bryophytes in several ways (Burger 2002, Malt and Lank 2009). The ratio of anthropogenic edge to suitable interior habitat can be minimized by creating larger, more circular forest reserves (Burger 2002), and the creation of canopy gaps should be avoided as they significantly increase the risk of wind damage (Zeng et al. 2010). Aggregated patterns of retention coupled with the retention of stable tree species, such as western red cedar, can reduce windthrow damage (Franklin et al. 1997). It is also important for managers to consider the structure of retention trees, as they can buffer the canopy microclimate (Parker et al. 2004, Dynesius et al. 2008); and the placement of forest edges in topographic locations that are not susceptible to extreme wind events (Gratowski 1956). Natural edges should be considered to have high potential for suitable habitat and accordingly the creation of other edges near these areas should be limited in order to maintain the beneficial effects that the natural edge provides. Finally, when selecting the location of new protected areas, choosing forest patches surrounded by regenerating forest may minimize edge effects occurring in these areas.

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Literature Cited

Baldwin, L. K., and G. E. Bradfield. 2005. Bryophyte community differences between edge and interior environments in temperate rain-forest fragments of coastal British Columbia. Canadian Journal of Forest Research 35:580-592.

Baldwin, L. K., and G. E. Bradfield. 2007. Bryophyte responses to fragmentation in temperate coastal rainforests: a functional group approach. Biological Conservation 136:408-422.

Bradley, R. W., F. Cooke, L. W. Lougheed, and W. S. Boyd. 2004. Inferring breeding success through radiotelemetry in the marbled murrelet. Journal of Wildlife Management 68:318–331.

British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests. 1998. Field Manual for Describing Terrestrial Ecosystems. Research Branch, Victoria, British Columbia.

Brosofske, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in Western Washington. Ecological Applications 7:1188-1200.

Burger, A. E. 2001. Using radar to estimate populations and assess habitat associations of marbled murrelets. Journal of Wildlife Management 65:696–715.

Burger, A. E. 2002. Conservation assessment of marbled murrelets in British Columbia: a review of the biology, populations, habitat associations and conservation. Technical Report Series No. 387. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia. http://www.sfu.ca/biology/wildberg/bertram/mamurt/PartA.pdf

Burger, A. E., and V. Bahn. 2004. Inland habitat associations of marbled murrelets on southwest Vancouver Island, British Columbia. Journal of Field Ornithology 75:53-66.

Burger, A. E., M. M. Masselink, A. R. Tillmanns, A. R. Szabo, M. Farnholtz, and M. J. Krkosek. 2004. Effects of habitat fragmentation and forest edges on predators of marbled murrelets and other forest birds on southwest Vancouver Island. *In* T. D. Hooper (editor), Proceedings of the Species at Risk 2004 Conference, March 2-6, 2004, Victoria, British Columbia. Pp. 1-19.

Burger, A. E., and R. E. Page. 2007. The need for biological realism in habitat modeling: a critique of Zharikov et al. (2006). Landscape Ecology 22:1273–1281.

Burger, A. E., and F. L. Waterhouse. 2009. Relationships between habitat area, habitat quality, and populations of nesting Marbled Murrelets. British Columbia Journal of Ecosystem Management 10:101–112. Available online at http://www.forrex.org/publications/jem/ISS50/vol10_no1_art10.pdf. (accessed on 31 October, 2011).

Burger, A. E., R. A. Ronconi, M. P. Silvergieter, C. Conroy, V. Bahn, I. A. Manley, A. Cober, and D. B. Lank. 2010. Factors affecting the availability of thick epiphyte mats and other potential nest platforms for Marbled Murrelets in British Columbia. Canadian Journal of Forest Research 40:727-746.

Busby, J. R., L. C. Bliss, and C. D. Hamilton. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses *Tomenthypnum nitens* and *Hylocomuim splendens*. Ecological Monographs 48:95-110.

Chen, J. Q., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-Fir forests. Ecological Applications 2:387-396.

Chen, J. Q., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-Fir forests. Ecological Applications 5:74-86.

Conroy, C. J., V. Bahn, M. S. Rodway, L. Ainsworth, and D. Newsom. 2002. Estimating nest densities for marbled murrelets in three habitat suitability categories in the Ursus Valley, Clayoquot Sound. *In* A. E. Burger and T. A. Chatwin (editors), Multi-scale Studies of Populations, Distribution and the Habitat Associations of Marbled Murrelets in Clayoquot Sound, British Columbia. British Columbia Ministry of Water, Land and Air Protection, Victoria, British Columbia. Pp. 121-137.

Didham, R. K., and J. H. Lawton. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31:17-30.

Dodson, R., and D. Marks. 1997. Daily air temperature interpolated at high spatial resolution over a large mountainous region. Climate Research 8:1-20.

Dynesius, M., M. Astrom, and C. Nilsson. 2008. Microclimatic buffering by logging residues and forest edges reduces clear-cutting impacts on forest bryophytes. Applied Vegetation Science 11:345-354.

Esseen, P. A. 2006. Edge influence on the old-growth indicator lichen *Alectoria sarmentosa* in natural ecotones. Journal of Vegetation Science 17:185-194.

Fenton, N. J., and K. A. Frego. 2005. Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests. Biological Conservation 122:417-430.

Franklin, J. F., D. Rae Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. *In* K. A. Kohm and J. F. Franklin (editors), Creating a Forestry for the 21st Century. Island Press, Washington, D.C. Pp. 111-139.

Gratowski, H. J. 1956. Windthrow around staggered settings in oldgrowth Douglas-fir. Forest Science 2:60–74.

Harper, K. A., and S. E. MacDonald. 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. Journal of Vegetation Science 13:535-546.

Harper, K. A., S. E. MacDonald, P. J. Burton, J. Q. Chen, K. D. Brosofske, S. C. Saunders, E. S. Euskirchen, D. Roberts, M. S. Jaiteh, and P. A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology 19:768-782.

Heithecker, T. B., and C. B. Halpern. 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. Forest Ecology and Management 248:163-173.

Hylander, K. 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. Journal of Applied Ecology 42:518-525.

Hylander, K., B. G. Jonsson, and C. Nilsson. 2002. Evaluating buffer strips along boreal streams using bryophytes as indicators. Ecological Applications 12:797-806.

Jules, E. S., E. J. Frost, S. L. Mills, and D. A. Tallmon. 1999. Ecological consequences of forest fragmentation in the Klamath region. Natural Areas Journal 19:368–378.

Klinka, K., J. Pojar, and D. V. Meidinger. 1991. Revision of biogeoclimatic units of coastal British Columbia. Northwest Science 65:32-47.

Malt, J. M., and D. B. Lank. 2007. Temporal dynamics of edge effects on nest predation risk for the marbled murrelet. Biological Conservation 140:160-173.

Malt, J. M., and D. B. Lank. 2009. Marbled murrelet nest predation risk in managed forest landscapes: dynamic fragmentation effects at multiple scales. Ecological Applications 19:1274-1287.

Manley, I. A. 1999. Behaviour and habitat selection of marbled murrelets nesting on the Sunshine Coast. M.S. Thesis. Simon Fraser University, Burnaby, British Columbia.

Matlack, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66:185-194.

McShane, C., T. Hamer, H. Carter, G. Swartzman, D. Friesen, D. Ainley, R. Tressler, K. Nelson, A. Burger, L. Spear, T. Mohagen, R. Martin, L. Henkel, K. Prindle, C. Strong, and J. Keany. 2004. Evaluation report for the 5-year status review of the marbled murrelet in Washington, Oregon and California. Unpublished report. http://www.earthjustice.org/library/reports/MAMU_EDAW_summary.pdf (accessed on 31 October 2011).

Mitchell, K. J., and K. R. Polsson. 1988. Site index curves and tables for British Columbia: coastal species. FRDA Report 037. British Columbia Ministry of Forests, Research Branch, Victoria, British Columbia.

Muir, P. S., T. R. Rambo, R. W. Kimmerer, and D. B. Keon. 2006. Influence of overstory removal on growth of epiphytic mosses and lichens in western Oregon. Ecological Applications 16:1207-1221.

Nelson, C. A., and C. B. Halpern. 2005. Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Canadian Journal of Botany 83:610-620.

Newmaster, S. G., R. J. Belland, A. Arsenault, and D. H. Vitt. 2003. Patterns of bryophyte diversity in humid coastal and inland cedar-hemlock forests of British Columbia. Environmental Reviews 11:S159-S185.

Parker, G. G., M. E. Harmon, M. A. Lefsky, J. Chen, R. van Pelt, S. B. Weiss, S. C. Thomas, W. E. Winner, D. C. Shaw, and J. F. Franklin. 2004. Three-dimensional structure of an old-growth *Pseudotsuga-tsuga* canopy and its implications for radiation balance, microclimate and gas exchange. Ecosystems 7:440-453.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17-26.

Peery, M. Z., R. Beissinger, S. H. Newman, B. H. Becker, E. Burkett, and T. D. Williams. 2004. Individual and temporal variation in inland flight behaviour of marbled murrelets: implications for population monitoring. Condor 106:344-353.

Pike, L. H., W. C. Denison, D. M. Tracy, M. A. Sherwood, and F. M. Rhoades. 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in Western Oregon. The Bryologist 78:389-402.

Pojar, J., and A. MacKinnon. 1994. Plants of Coastal British Columbia including Washington, Oregon and Alaska. B.C. Ministry of Forests and Lonepine Publishing, Vancouver, British Columbia.

Proctor, M. C. F. 1990. The physiological basis of bryophyte production. Botanical Journal of the Linnean Society 104:61-77.

Proctor, M. C. F. 2000. Physiological ecology. *In* J. A. Shaw and B. Goffinet (editors), Bryophyte Biology. Cambridge University Press, Cambridge, UK. Pp. 225-247.

Rambo, T. A., and M. P. North. 2008. Spatial and temporal variability of canopy microclimate in a Sierra Nevada riparian forest. Northwest Science 82:259-268.

Rambo, T. A., and M. P. North. 2009. Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. Forest Ecology and Management 257:435-442.

Raphael, M. G., D. Evans Mack, J. M. Marzluff, and J. M. Luginbuhl. 2002. Effects of forest fragmentation on populations of the marbled murrelet. Studies in Avian Biology 25:221-235.

Rodway, M. S., and H. M. Regehr. 2002. Inland activity and forest structural characteristics as indicators of marbled murrelet nesting habitat in Clayoquot Sound. *In* A. E. Burger and T. A. Chatwin (editors), Multi-scale studies of populations, distribution and the habitat associations of marbled murrelets in Clayoquot Sound, British Columbia. British Columbia Ministry of Water, Land and Air Protection, Victoria, British Columbia. Pp. 57–87.

SAS. 2003. SAS 9.1 for Windows. SAS Instutute Inc., Cary, N.C.

Sillett, S. C. 1995. Branch epiphyte assemblages in the forest interior and on the clearcut edge of a 700-year-old Douglas-Fir canopy in Western Oregon. The Bryologist 98:301-312.

Sillett, S. C., B. McCune, J. E. Peck, and T. R. Rambo. 2000. Four years of epiphyte colonization in Douglas-Fir forest canopies. The Bryologist 103:661-669.

Silvergieter, M. P. 2009. Multi-scale analyses of nest site selection and fledging success by marbled murrelets (*Brachyramphus marmoratus*) in British Columbia. M.S. Thesis, Simon Fraser University, Burnaby, British Columbia.

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Stewart, K. J., and A. U. Mallik. 2006. Bryophyte responses to microclimate edge effects across riparian buffers. Ecological Applications 16:1474-1486.

Toms, J. D., and M. L. Lesperance. 2003. Piecewise regression: a tool for identifying ecological thresholds. Ecology 84:2034–2041.

Waterhouse, F. L., R. Bradley, F. Markila, F. Cooke, and L. Lougheed. 2002. Use of airphotos to identify, describe, and manage forest structure of marbled murrelet nesting habitat at a coastal British Columbia site. Technical Report TR-016. Research Station, Vancouver Forest Region, B.C. Ministry of Forests, Nanaimo, British Columbia.

Waterhouse, F. L., A. E. Burger, D. B. Lank, P. K. Ott, E. A. Krebs, and N. Parker. 2009. Using the low-level aerial survey method to identify marbled murrelet nesting habitat. British Columbia Journal of Ecosystem Management 10:80–96. Available Online at http://www.forrex.org/publications/jem/ISS50/vol10_no1_art8.pdf (accessed 31 October 2011).

Zeng, H., J. Garcia-Gonzalo, H. Peltola, and S. Kellomaki. 2010. The effects of forest structure on the risk of wind damage at a landscape level in a boreal forest ecosystem. Annals of Forest Science 67:111.

Zharikov, Y., D. B. Lank, F. Huettmann, R. W. Bradley, N. Parker, P. P. -W. Yen, L. McFarlane Tranquilla, and F. Cooke. 2006. Habitat selectivity and breeding success in a forest-nesting alcid, the marbled murrelet, in two landscapes with different degrees of forest fragmentation. Landscape Ecology 21:107–120.

Zharikov, Y., D. B. Lank, and F. Cooke. 2007a. Influence of landscape structure on breeding distribution and success in a threatened alcid, the marbled murrelet: model transferability and management implications. Journal of Applied Ecology 44:748–759.

Zharikov, Y., D. B. Lank, F. Huettmann, and F. Cooke. 2007b. Interpreting habitat distribution models of an elusive species, the marbled murrelets: a response to Burger and Page. Landscape Ecology 22:1283–1289.