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Factors Affecting the Ecological Legacy of Unsalvaged Post-Mountain Pine Beetle Stands

Chan-McLeod, A.[1], X. Zhu[1], and B. Klinkenberg[2]

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[1]Department of Forest Sciences, 3041 - 2424 Main Mall, University of British Columbia, Vancouver, British Columbia, V6T 1Z4
[2]Department of Geography, 1984 West Mall, University of British Columbia, Vancouver, British Columbia, V6T 1Z4

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Natural Resources Canada
Canadian Forest Service
Pacific Forestry Centre
506 West Burnside Road
Victoria, British Columbia V8Z 1M5
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Abstract

The overall objective of this research is to provide information about the short-term ecological legacy of unsalvaged mountain pine beetle-infested stands in the Prince George and Vanderhoof Forest Regions as reflected in the avian community. Our results indicated that in the short term following beetle attack (< 5 years), non-mountain pine beetle factors such as the pre-existing stand structure, pre-existing site features (i.e., presence of a riparian area), and interannual variations resulting most likely from climate and other non-mountain pine beetle factors, were as important or more important than the mountain pine beetle in dictating bird abundance. However, the beetle did have measurable effects on avian abundance, with approximately 64% of individual bird species and 62% of avian community variables responding to the level of beetle infestation within the stand. The type of effect was species- or guild-dependent and generally reflected the natural history of the bird. Time since death of the tree within the first 4-5 years post-attack did not measurably affect most birds, affecting at most only 36% of the species and 12% of the avian community variables measured in this study. The relatively low impact of the mountain pine beetle on avian communities up to 5 years post-attack indicates that there are few ecological reasons for salvage logging immediately post-beetle. The fact that many birds responded significantly to the presence and intensity of beetle attack, but relatively few responded to the time since death of the tree up to 5 years post-attack, strongly underscored the continuing role of the beetle-attacked forest in supporting bird habitat. The potential contradiction between ecological and economic objectives over salvage logging in the short term stresses the importance of clear, explicitly-stated goals. This need is further underscored by the fact that different bird species respond differently to the mountain pine beetle, and management goals must be species- or guild-specific. Because our study results are applicable to only recently attacked stands (<5 years post-beetle), more research is needed to address how the ecological legacy of beetle-killed stands changes over the mid- and long-terms. Although time since death of a tree was not a major determinant of abundance for most species for the first few years post-attack, this will likely change as the stand continues to break up.

Keywords: mountain pine beetle, salvage logging, sustainable forest management, songbirds, ecological value of post-beetle stands, unsalvaged beetle-killed stands, wildlife habitat

Résumé

L’objectif global de l’étude est de fournir de l’information sur les conséquences écologiques à court terme de la non-récupération des étendues forestières infestées de dendroctone du pin ponderosa dans les régions boisées de Prince George et Vanderhoof au regard de l’évolution des populations aviaires. Nos résultats indiquent qu’à court terme, à la suite d’une infestation de coléoptères (< 5 ans), les facteurs étrangers au dendroctone du pin ponderosa, notamment la structure préexistante du peuplement ou les caractéristiques préexistantes du site (p. ex., la présence d’une zone riveraine), ainsi que les variations d’une année sur l’autre probablement dues aux changements climatiques et à d’autres facteurs sans rapport avec le dendroctone du pin ponderosa, influent autant, voire davantage, que la présence du coléoptère sur l’abondance des espèces d’oiseaux. Toutefois, la présence de dendroctone du pin ponderosa s’est avérée avoir des conséquences quantifiables sur l’abondance des espèces d’oiseaux : environ 64 % des espèces d’oiseaux et 62 % des variables associées à la communauté aviaire ont été affectées par le niveau d’infestation des peuplements par le dendroctone du pin. Variables selon les espèces et les guildes, les effets constatés reflètent généralement l’histoire naturelle de l’espèce affectée. Aucune donnée mesurable ne semble indiquer que dans les 4 à 5 années suivant l’infestation, le temps écoulé depuis la mort de l’arbre affecte la plupart des oiseaux : seules 36 % des espèces et 12 % des variables associées à la communauté aviaire mesurées dans cette étude semblent avoir été affectées. L’impact relativement faible du dendroctone du pin ponderosa sur les communautés aviaires dans les 5 ans suivant une infestation indique que sur le plan écologique, il existe peu de raisons de procéder à une coupe de récupération immédiatement après l’infestation d’un peuplement par ce coléoptère. Le fait que de nombreux oiseaux réagissent à la présence et à l’intensité de l’infestation de dendroctones du pin ponderosa, mais que relativement peu soient affectés par le temps écoulé depuis la mort de l’arbre dans les 5 ans suivant l’infestation, souligne fortement le rôle essentiel des peuplements forestiers infestés au regard des habitats aviaires. La contradiction potentielle entre objectifs écologiques et objectifs économiques d’une coupe de récupération rapide démontre l’importance de la définition d’une vision claire et explicite. La nécessité est d’autant plus prégnante que les réactions aux infestations de dendroctone du pin ponderosa diffèrent selon les espèces et les guildes d’oiseaux; les objectifs de gestion de cette question doivent donc être fixés spécifiquement pour chaque espèce ou chaque guilde. Compte tenu de ce que les conclusions de notre étude traitent uniquement de la question des peuplements récemment infestés (< 5 ans suivant l’infestation par le DPP), d’autres recherches seront nécessaires afin de déterminer l’évolution du devenir écologique à moyen et long terme des peuplements forestiers anéantis par le DPP. Bien que le temps écoulé depuis la mort de l’arbre n’apparaisse pas comme un déterminant majeur d’abondance pour la plupart des espèces au cours des premières années suivant une infestation, cette donnée est susceptible d’évoluer au fur et à mesure du démantèlement du peuplement.

Mots-clés : dendroctone du pin ponderosa, ré-exploitation, gestion durable des forêts, oiseaux chanteurs, valeur écologique de peuplements infestés par le DPP, peuplements détruits par le dendroctone et non réexploités, habitat faunique

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1 Introduction

The catastrophic nature of the mountain pine beetle epidemic has resulted in a great push to salvage log beetle-killed stands before declining wood quality renders timber extraction pointless. Unfortunately, however, the rush to salvage log beetle-damaged wood has largely occurred without the benefit of ecological considerations. Although there is ongoing research addressing the effects of beetle-control measures on biodiversity, there is virtually no information on the ecological legacies of the unsalvaged post-beetle stand. These ecological relationships must be identified. If the ecological legacy of beetle-damaged stands is low or ephemeral, then salvage logging should not be hindered by suspected but unproven ecological values. On the other hand, if beetle-infested stands retain high ecological values, then indiscriminate salvage logging would magnify the potentially negative effects of the epidemic.

The overall objective of our proposed research is to obtain information that will help managers determine what ecological legacies exist in post-beetle forests. The proposed research is designed to 1) provide information about the ecological value of unsalvaged beetle-infested stands; 2) provide understanding of how ecological legacies may vary; and 3) generate information that would contribute to the development of decision support tools for improving ecological integrity in the post-beetle landscape.

2 Material and Methods

2.1 Study Area

This study was conducted in the Canadian Forest Products Timber Supply Area and in provincial parks near Prince George and Vanderhoof, B.C. We selected mature, post-beetle forest stands that would provide as wide a range as possible in the values of the factors being addressed, specifically, the neighbourhood composition, the type and amount of residual green component in the infested stand, stand size, and time since infestation. At the same time, we strove to minimize inter-site variability and hence, confounding from non-study factors. We limited the variability in ecosystem type by selecting only biogeoclimatic zone sub-boreal spruce (BEC SBS) variants SBSdw2 and SBSdw3, and elevations <1000 m. We identified candidate stands that varied widely in size but constrained the lower size limit to an area that would accommodate at least two bird sampling stations (60-m radius circular plots with 80 m between plot boundaries). We included some sites in provincial parks because of their higher incidence of unsalvaged, post-beetle stands. Four provincial parks were included in this study: Dahl Lake, Finger-Tatuk, Francois Lake, and Lower Stuart River.

Forest stands in this study were commonly dominated by lodgepole pine, but some sites were dominated by hybrid spruce or Douglas-fir. Dominant understory species included lodgepole pine, trembling aspen, hybrid spruce and Douglas-fir. Typical shrub species included alder, rose, willow, juniper, kinnikinnick, and Labrador tea.

2.2 Bird Surveys

We used systematic random sampling to lay out the bird stations within each study site. The first bird station was randomized within a forest stand, and subsequent stations were established at the intersection of 200-m grid lines, which allowed for 80 m between the outer circumferences of adjacent stations.

We established 116 bird circular point count stations with 60-m radii at 25 mature forest sites (Table 1). Bird surveys were conducted four times at each site at approximately 2-week intervals between May and June in 2004 and 2005. To control for observer bias, each station was surveyed twice by each of two observers, who were randomly rotated after each round. The sequence in which sites were surveyed was randomized in the first round; subsequent rounds followed the rotation of the first round. To standardize diurnal variation, each point count station within a site was censused in reverse order of the previous round. Censuses began at dawn and ended by 10:00 a.m. Observers waited for one minute following arrival at each count station before beginning the 8-minute survey. We did not conduct surveys on days when it was raining or windy (Beaufort Level 5). We collected data on the species and type (call, visual, song) of bird detection within the 60-m radius plot; habitat type where detection occurred in the plot; structural attribute on which bird was detected; and behaviour of the bird.

2.3 Forest Stand Measurements

Stand structure and vegetation data were collected at each bird station using a protocol modified from the BC Ministry of Forests Site Index by Site Series Sampling and Data Standards. Measured variables included: tree height for the A1 and A2 layers; crown height; tree species; diameter at breast height (dbh); live or dead status; canopy closure; shrub height for the B1 and B2 layers, percentage of cover for the B1 and B2 layers, height and percentage of cover of herbs, and ground cover. Tree and shrub data were measured from variable-sized circular plots with 5.64 m, 7.98 m, or 11.28 m (with 100, 200 or 400 m^2 areas) to include 12 to 24 trees per plot. Herbs and ground cover data were measured from 5.64 m plots.

We recorded the infestation status of all pine trees in the plot. We used three indices to estimate time since death of the tree: 1) foliage colour (Patience Rakochy, personal communications) (Table 2), 2) crown condition (Table 3), and 3) bark retention (Table 4). Although we tried to select stands with widely ranging times since attack, the realized range was generally limited to <5 years because older attacked stands were salvage logged before the epidemic became out of control, or were located in extremely high-elevation, remote sites where trees were relatively more susceptible to beetle attack during endemic years. Additionally, age-since-infestation is confounded by the severity of attack, as earlier infested stands tended to be very localized outbreaks, and by geographic area, as the mountain pine beetle has moved geographically as the epidemic grew. These confounding factors further limited the range of age-since-infestation that we were able to assess. In general, the time since death for the average tree in our stands was less than 5 years, even though there may be occasional instances of beetle-killed trees that pre-date 5 years.

2.4 Data Analyses

We developed Generalized Linear Models (using the poisson family with site as cluster and year effect) relating avian relative abundance to all the independent factors, including time since death (foliage colour, crown condition, and bark retention), stand structural attributes (herb cover, shrub cover, tree height, tree crown depth, canopy closure, mean dbh, maximum dbh, variability of stem size, percentage of pine in stand, deciduous in stand, non-pine coniferous in stand) and severity of mountain pine beetle infestation (percentage of infested pine in stand, and percentage of pine that was infested). Because these standard, full regression models will likely contain both correlated and insignificant factors, the calculated value of percentage explained (i.e., the percent to which the variability in bird abundance can be explained by the variability in the independent factors) will be artificially inflated. The full models will, however, be useful in assessing the general influences of each independent factor on all species and guilds (Manly et al. 2002). We conducted these analyses on all individual bird species with at least 24 detections, and on six guilds: 1) cavity-nesters; 2) deciduous; 3) mature forest dwelling species; 4) species whose primary habitat is in mature forest but secondary habitat includes young forest; 5) edge and open species; and 6) shrub nesters.

To correct for problems of autocorrelation and to identify species- and guild-specific relationships, we generated a set of parsimonious models using backward stepwise poisson regression with the Akaike information criterion (AIC). The AIC measures the goodness of fit of the estimated statistical model, and prevents overfitting of the data by penalizing increases in the number of estimate parameters. The final, most parsimonious model is the model with lowest AIC value, which is considered to explain the data the best using the least number of parameters.

3 Results

3.1 Study Sites and Stand Characteristics

The code names, description, and observed range of values for study variables are shown in Table 5. Frequency distributions of some key variables are illustrated in Figure 1.
The study sites were typically open stands with mean canopy closure of only 22.3% and maximum closure of 60%. Mean tree height for the A1 layer equalled 25.7 m, but mean tree height for the tallest stand was greater than twice as high at 54 m. The average diameter of the trees was 18.9 cm, although much larger trees generally occurred in each plot. The largest tree in each plot averaged 36 cm dbh, and the largest observed tree was 87.4 cm dbh.

The level of beetle infestation, when expressed as percentage of stems in the stand that was infested, was relatively uniformly distributed (Figure 1). However, the level of beetle infestation, when expressed as percentage of pine basal area that is infested, was skewed to high infestation rates, with 100% infestation being the most common class (Figure 1). Thus, the pine infestation was bi-modal at the two extreme situations, with either no pine trees infested in green stands, or with virtually all trees attacked in infested stands. Time since infestation, as indexed by the foliage code, was primarily represented by the stages between the yellow-red foliage phase and the completely defoliated grey phase. Nonetheless, we were able to evaluate all foliage codes, although more recently attacked stands were represented at lower frequencies.

Large, non-conifer snags were highly uncommon, although the ones that were present tended to be quite large, with a maximum dbh of up to 92.6 cm. Large lodgepole pine snags were relatively more common, but with a maximum dbh of up to 49.5 cm. Riparian areas were also uncommon. Given the rarity of non-conifer snags and riparian areas, we did not analyse their abundance but instead classified them as binary variables.

We found that the four indices of time since death (foliage colour, tree condition, crown condition, and bark retention) correlated well with each other throughout the range of observed values. With exception of bark retention, which had a relatively limited range in values and therefore varied less with time since death, the indices appeared to be fairly comparable indicators of time since death.

3.2 Bird Communities

We detected a total of 1480 birds in 2005 and 1783 birds in 2006 that represented 50 and 55 species respectively (Table 6). Golden-crowned kinglet and yellow-rumped warblers were the two most common species in both years, representing 39% and 29% of all bird detections in 2005 and 2006 respectively. Other relatively common species included dark-eyed junco, ruby-crowned kinglet, dusky and Hammond’s flycatcher, and winter wren. Many species were detected only rarely – in both years, 24 species were each detected fewer than six times.

3.3 Effects of Mountain Pine Beetle and Stand Structure

3.3.1 Full regression models

We conducted poisson regression analyses for 11 avian species that had sufficiently large sample sizes (≥24 per year) to be analysed on an individual basis. We developed full regression models for 9 of the 11 species, but the assessed independent variables generally accounted for < 30% of the variability in bird abundance. We did not identify significant factors other than year for ruby-crowned kinglet and Swainson’s thrush.

The full models revealed that although the level of beetle infestation (as percentage of pine basal area, or as percentage of all trees in stand) was a significant determinant of abundance for some bird species (i.e., brown creeper, dark-eyed junco, and gray jay), the time since infestation (for the timeframe evaluated in this study) was not a significant factor for any bird species. Thus, neither foliage code nor crown condition were significant factors when the other independent factors had already been accounted for. The effects of level of infestation were species-dependent. Whereas brown creepers and gray jays increased with increasing levels of infestation, dark-eyed junco declined with increasing levels of infestation. The density of large pine snags contributed to the variability in the abundance of golden-crowned kinglet and western tanager.

Significant model factors typically included critical habitat elements for the species, such as tree height, shrub cover, herb cover, large snags, mean diameter at breast height, large trees, and deciduous trees. Other important factors included the occurrence of riparian areas, and for three species (i.e., golden-crowned kinglet, ruby-crowned kinglet, and Swainson's thrush) the year of the study. Detections of golden-crowned kinglet and Swainson's thrush increased between the two study years independent of the other study factors, whereas detections of ruby-crowned kinglet decreased from 2005 to 2006.

Poisson regression analyses of avian community variables produced similar results to those of individual avian species. However, neither level of beetle infestation nor time since infestation (for the timeframe evaluated) was a significant factor in any community variable. Similar to the results for individual species, significant model factors typically included critical habitat elements for the guild, with for example, cavity-nesters being sensitive to the availability of large trees, and deciduous-requiring species sensitive to the availability of deciduous trees. The year of the study was a significant factor for all six guilds, with the cavity-nesters and mature forest-dwelling guilds increasing between the two study years, and the open-edge and mature and young forest-dwellers decreasing from 2005 to 2006.

3.3.2 Akaike information criterion models

We developed parsimonious models using the Akaike information (AIC) criterion for 11 avian species and 9 community variables (Tables 7 and 8). All models were highly significant but sometimes explained only small percentages of the variation in bird abundance. The western tanager model had the highest percentage of deviance explained at 29.2%. However, models for the American robin, dark-eyed junco, and ruby-crowned kinglet models had percentage of deviance explained values of only 5 to 6%. The parsimonious models were better at explaining the abundances of guilds rather than individual species. For example, approximately 63% of variability in the abundance of the primarily mature forest-dwelling guild was explained by the study factors.

The parsimonious models concurred with the standard full regression models on the importance of the beetle infestation rate in dictating avian abundance (Tables 7 and 8). In fact, the level of beetle attack on pine trees (expressed as percentage of pine basal area) was one of the most frequently selected independent variables, affecting 7 of 11 individual bird species. The level of beetle attack (expressed either as percentage of all trees in the stand, or as percentage of pine basal area) was also included in five of the eight community variable models. The direction and magnitude of the beetle infestation rate varied depending on the species or the community variable. Bird species that responded negatively to increasing infestation rate included dark-eyed junco, Swainson's thrush, warbling vireo, and western tanager. Guilds that declined with increasing level of infestation included the edge and open habitat guild, the deciduous guild, the mature forest guild, and the shrub guild. Bird species and guilds that responded positively to increased level of infestation included the golden-crowned kinglet, gray jay, and the cavity-nesting guild. Pine infestation rate (percentage of pine in stand that is infested) and stand infestation rate (percentage of all trees in stand that are infested) had opposing effects on the abundance of brown creeper and winter wren. Brown creeper correlated positively with the stand infestation rate (expressed as percentage of tree stems), but correlated negatively with pine infestation rate (percentage of pine basal area). The degree to which bird species and guilds were affected by the level of beetle infestation ranged from a 2.2% decline in population size with each percent increase in the infestation rate, to a 2.7% increase in population size with each percent increase in the infestation rate.

In contrast to the standard full regression models, time since beetle attack (as expressed by the foliage condition code or the crown index) was a significant factor in some of the parsimonious models when stand structural characteristics had been accounted for (Tables 7 and 8). Brown creeper increased 15.3 % with each unit increase in the foliage condition code while the edge and open-habitat guild increased 5.9% with each unit increase in the crown code. In contrast, gray jay, western tanager, and yellow-rumped warbler declined with increasing deterioration of the foliage. Western tanager was most sensitive to changes in the foliage, declining 14% with each unit increase in the foliage condition code.

Similar to the results for standard regression analyses, important model factors typically included critical habitat elements for the species, such as tree height, herb cover, non-pine conifers, large snags, mean diameter at breast height, large trees, and deciduous trees (Tables 7 and 8). The presence of water had large and significant effects on seven species and two guilds. Winter wren, which was most responsive to the presence of water, increased by more than 300% in the presence of water. The effects of riparian areas on other species were somewhat less pronounced, but were still marked, affecting individual species by >40% and guilds by >40%. Interannual variation was also an important factor for all guilds and for golden-crowned kinglet, ruby-crowned kinglet, and Swainson's thrush.

4 Discussion

Our results indicated that in the short term (<5 years) following beetle attack, non-mountain pine beetle factors such as the pre-existing stand structure, pre-existing site features (i.e., presence of a riparian area), and interannual variations resulting most likely from climate and other non-mountain pine beetle factors, were as important or more important than the mountain pine beetle in dictating bird abundance. However, the mountain pine beetle did have measurable effects on avian abundance, with approximately 64% of individual bird species and 62% of avian community variables responding to the level of beetle infestation within the stand. The type of effect was species- or guild-dependent and reflected the natural history of the bird. Species that declined with increasing levels of infestation were generally foliage gleaners (e.g., Swainsons' thrush, warbling vireo, and western tanager) that were likely responding to the rapid deterioration in the foliage. Dark-eyed junco, a non-foliage gleaning species, also declined with increasing levels of infestation. This species feeds primarily by gleaning from the ground surface and may be responding to the lack of seed supply, as its diet comprises mainly of seeds. The mature forest guild, which prefers closed canopy habitats, was also negatively impacted by high infestation rates. In contrast, cavity-nesters increased with increased intensity of beetle attack, probably in response to the increased supply of suitable nest sites in dead and dying trees. Paradoxically, the golden-crowned kinglet, which is a foliage-gleaner and which is commonly found in closed-canopy coniferous forests, also increased with increased levels of beetle infestation. A possible explanation for these results may relate to the sap feeding habits of this species. Although golden-crowned kinglets feed primarily on insects, they may be capitalizing on the easy access to pine sap during the beetle epidemic, and their populations may have responded to the increase in this food source.

The two variables of infestation rate (stand infestation rate, pine infestation rate) had opposing effects on the abundance of brown creeper and winter wren. This apparent discrepancy may perhaps be attributed to the fact that stand infestation rate reflected not just the prevalence of attacked trees, but also the prevalence of non-pine trees. In contrast, pine infestation rate, which measures only the infestation rate of susceptible trees, was bi-modally distributed, with either no pines being attacked in green stands, or virtually all pines being attacked in infested stands. Thus, brown creeper, a bark gleaner that would have benefited from the increased food supply from the beetle epidemic, correlated positively with the stand infestation rate. At the same time, brown creeper may have declined with increased basal area of infested pine, because high values of this variable corresponded to high compositions of pine within the stand, and large non-pine conifers are critically important to brown creeper. Another possible explanation for the apparent discrepancy is that extensive debarking sometimes characterizes extremely heavy infestations (Otvos 1979). In such situations, particularly in the absence of non-pine conifers, there would be a lack of feeding substrate for bark gleaning species such as the brown creeper.

Time since death of the tree within the first 4-5 years post-attack did not measurably dictate the abundance of most individual bird species or avian community variables in this study. None of the time-since-death indices were significant factors in the standard regression models for any species or guild. Time-since-death indices were included as factors in parsimonious models for only 36% of the species and 12% of the guilds. Cavity-nesters and brown creeper increased with increased time since death, up to 5 years post-attack. These increases were likely in response to the increased availability of suitable nesting sites, as cavity-nesters would have benefited from the relative ease of cavity excavation in softened wood, while brown creepers would have benefited from loosened bark as that is where they typically nest. Time since death of attacked trees was a negative factor for gray jay, western tanager, and yellow-rumped warbler. These results are probably food related, as western tanager and yellow-rumped warbler are foliage gleaners, and likely responding to the rapid deterioration of the foliage. Similarly, gray jay is an omnivorous ground gleaner, and may be responding to decreased supplies in seeds and insects in primarily dead, opened stands.

Although time since death of a tree was not a major determinant of abundance for most species for the first few years post-attack, this will likely change as the stand continues to break up (Chan-McLeod 2006). Negative effects of the mountain pine beetle on wildlife species that depend on the forest for cover become more apparent when the dead trees drop their foliage and the stand opens up. When this happens, there may be a ripple effect in the food chain, with predators preying on the impacted species also experiencing declines. As successive waves of beetle attacks pass through a stand, suitable brood trees become unavailable, and the temporary spike in the food supply for woodpeckers and for insectivores that feed on the adult beetle is concluded. The fall-down of beetle-killed lodgepole pine trees is expected to begin 3 to 5 years after tree death, with 25 to 50% of the snags down within 10 years (Lewis and Hartley 2005). Waterhouse and Armleder (2004) determined that fall rates for dead trees in the Williams Lake area to be equivalent to approximately 7.5% stand attrition by year 5, while Bull (1983) noted that more than 90% of beetle-killed lodgepole pines were standing 3 years after being killed, but only 38% remained after 8 years. After 8 to 10 years, as the stand opens up significantly from the falldown of snags, beneficial effects accrue to wildlife species that thrive in open conditions, and to a lesser extent, to wildlife species that have requirements for mature forest attributes, such as adequately decayed snags and down wood.

The relatively low impact of the mountain pine beetle on avian communities up to 5 years post-attack indicates that there are few ecological reasons for salvage logging immediately post-beetle. The schedule for timber recovery is more urgent for economic reasons, given the rapidity at which production opportunities and timber quality are lost due to snag dehydration, checking, and the bluestain fungi (Lewis and Hartley 2006). On the other hand, salvage logging shortly after beetle attack may be more detrimental than beneficial to forest-dwelling species in the majority of situations. The fact that many birds responded significantly to the presence and intensity of beetle attack, but that relatively few responded to the time since death of the tree up to 5 years post-attack, strongly underscored the continuing role of the beetle-attacked forest in supporting bird habitat. This is because at least in the short term, much of the pre-existing habitat structure is still intact, and include, in addition to the mostly intact dead trees, living components of understory and in some ecosystems, a regenerating tree layer. In fact, pure pine stands constitute only a minority of the mountain pine beetle-affected landscape (Burton 2006). Moreover, 40% of lodgepole pine stands have sufficiently restocked understories (Burton 2006). Thus, there may be some contradiction between ecological and economic objectives over the short term. Alternatively, the fact that different bird species respond differently to the mountain pine beetle underscores the importance of clear management goals that are species- or guild-specific.

Many avian models developed in this study explained only modest proportions of the total variability in bird abundance. Much of the variability in bird abundance was due to non-beetle factors such as interannual variation and stand structure. Because we conducted site selection to maximize mountain pine beetle factors (such as intensity of attack and time since attack) while minimizing inter-site variability, the range of stand structural conditions was relatively homogeneous among sites and therefore represented relatively uniform habitat conditions. Thus, much of the variability in detection rates was likely stochastic. This is especially true as we limited our study to unsalvaged stands, and therefore did not provide the range in habitat conditions to which strong responses would be expected from open or edge dwelling species. For this reason, the primarily mature forest-dwelling guild had the strongest model, because they would be most sensitive to nuances in mature forest structure. In contrast, ubiquitous and generalist species that inhabit a wide range of forest types would be insensitive to such nuances.

5 Conclusions

This study documented the short-term ecological legacy of unsalvaged post-beetle forest stands in the Prince George and Vanderhoof Forest Regions. Our results indicated that in the short term (<5 years) following beetle attack, non-mountain pine beetle factors such as the pre-existing stand structure, pre-existing site features (i.e., presence of a riparian area), and interannual variations resulting most likely from climate and other non-mountain pine beetle factors, were as important or more important than the mountain pine beetle in dictating bird abundance. However, the mountain pine beetle did have measurable effects on avian abundance, with approximately 64% of individual bird species and 62% of avian community variables responding to the level of beetle infestation within the stand either positively or negatively. The type of effect was species- or guild-dependent and generally reflected the natural history of the bird. Time since death of the tree within the first 4-5 years post-attack did not measurably dictate the abundance of most individual bird species or avian community variables in this study. The relatively low impact of the mountain pine beetle on avian communities up to 5 years post-attack indicates that there are few ecological reasons for salvage logging immediately post-beetle. The schedule for timber recovery may be more urgent for economic reasons, given the rapidity at which production opportunities and timber quality are lost due to snag dehydration, checking, and the bluestain fungi. On the other hand, salvage logging shortly after beetle attack may be more detrimental than beneficial to forest-dwelling species in the majority of situations. The fact that many birds responded significantly to the presence and intensity of beetle attack, but that relatively few responded to the time since death of the tree up to 5 years post-attack, strongly underscored the continuing role of the beetle-attacked forest in supporting bird habitat. The apparent contradiction between ecological and economic objectives over the short term underscores the importance of clear goals in salvage logging prescriptions. The need for clear management goals that are species- or guild-specific are further underscored by the fact that different bird species respond differently to the mountain pine beetle. Our study results are applicable to only recently attacked stands (<5 years post-beetle). Future research needs to address how the ecological legacy of beetle-killed stands changes over the mid- and long-terms. Although time since death of a tree was not a major determinant of abundance for most species for the first few years post-attack, this will likely change as the stand continues to break up.

6 Acknowledgements

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7 Literature Cited

Bull, E.L. 1983. Longevity of snags and their use by woodpeckers. Pages 64-6 *in* J.W. Davis, G.A. Goodwin and R.A. Ockenfels (Technical Coordinators). Snag habitat management: proceedings of the symposium. USDA Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report RM-99.

Burton, P. J. 2006. Restoration of forests attacked by mountain pine beetle: Misnomer, misdirected, or must-do? BC Journal of Ecosystems and Management 7(2):1-10.

Chan-Mcleod, A.; Allaye, C. 2006. A review and synthesis of the effects of unsalvaged mountain pine beetle stands on wildlife and implications for forest management. BC Journal of Ecosystems and Management 7(2):119-132.

Lewis, K.J.; Hartley, I. 2005. Rate of deterioration, degrade and fall of trees killed by mountain pine beetle: a synthesis of the literature and experiential knowledge. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Mountain Pine Beetle Initiative Working Paper 2005-14. 21 p.

Lewis, K.J.; Hartley, I.D. 2006. Rate of deterioration, degrade, and fall of trees killed by mountain pine beetle. BC Journal of Ecosystems and Management 7(2):11-19.

Manly, B.F.J.; McDonald, L.L.; Thomas, D.L.; McDonald, T.L.; Erickson, W.P. 2002. Resource selection by animals – statistical design and analysis for field studies. Second Edition. Kluwer Academic Publishers, Norwell, MA, USA.

Otvos, I.S. 1979. The effects of insectivorous bird activities in forest ecosystems: an evaluation. Pages 341-374 *in* Dickson, J.G., R.N. Connor, R.R. Fleet, J.A. Jackson, and J.C. Kroll, eds. The role of insectivorous birds in forest ecosystems. Academic Press, New York, N.Y.

Waterhouse, M.; Armleder, H. 2004. Windthrow in partially cut lodgepole pine forests in west-central British Columbia. Extension Note 70. British Columbia Ministry of Forests Research Branch. Victoria, BC.

Contact: Ann Chan-McLeod. (604) 822-8287, ann.chan-mcleod@ubc.ca

8 Tables and Figures

Table 1. BEC variants and site information for study stands.

	# of stations	BEC variant	Age	Elev (m)
Canfor Sites				
Barton	3	SBS dw 2	120	817
Bobtail A	6	SBS dw 3	135	920
Bobtail B	6	SBS dw 3	144	856
Bobtail C	5	SBS dw 3	134	872
Eulatazella	6	SBS dw 3	87	835
Kenney	6	SBS dw 3	79	888
Kluskus A1	6	SBS dw 3	122	916
Kluskus A2	6	SBS dw 3	122	869
Norman A	6	SBS dw 3	85	897
Norman B	6	SBS dw 3	85	956
Tagai	5	SBS dw 2	140	898
Tory	3	SBS dw 2	154	761
Park Sites				
Dahl D	6	SBS dw 3	172	891
Finger-Tatuk D	6	SBS dw 2	145	965
Finger-Tatuk E	6	SBS dw 2	124	981
Finger-Tatuk F	6	SBS dw 2	124	960
Francois A	6	SBS dw 3	119	815
Francois D	6	SBS dw 3	144/174	875
L. Stuart C	6	SBS dw 3	84	766
L. Stuart E	6	SBS dw 3	84	736
L. Stuart G	4	SBS dw 3	120	777

Table 2. Foliage colour codes used in the study (modified from Rachoky, pers. comm.)

Code	Year of attack	Foliage Condition
0	Year 0	No Pitch Tubes
1	Year 1	Foliage green, pitch tubes present
2	Year 1	Foliage Green/Yellow mixture
3	Year 1-2	Foliage Yellow/Red mixture
4	Year 2-3	Foliage mostly red
5	Year 2-4	Foliage completely red, partial defoliation
6	Year 3-5	Complete Defoliation, Grey Tree

Table 3. Crown condition classes used in the study.

Code	*Description*
1	All foliage, twigs and branches present
2	1-25% Foliage lost; possibly some twigs lost; all branches usually present; possible broken top
3	26-50% Foliage lost; possibly some twigs lost; all branches usually present; possible broken top
4	51-75% Foliage lost; possibly some twigs lost; all branches usually present; possible broken top
5	76-99% Foliage lost; possibly some twigs lost; all branches usually present; possible broken top
6	No foliage present; up to 50% of twigs lost; most branches present; possible broken top
7	No foliage or twigs present; up to 50% of branches lost; top usually broken
8	Most branches gone; some sound branch stubs remain; top broken
9	No branches present; some sound and rotting branch stubs; top broken

Table 4. Bark retention classes used in the study.

Code	*Description*
1	All bark present
2	Bark lost on damaged areas only (<5% lost)
3	Most bark present; bare patches; some bark may be loose (5-25% lost)
4	Bare sections; firm and loose bark remains (26-50% lost)
5	Most bark gone; firm and loose bark remains (51-75% lost)
6	Trace of bark remains (76-99% lost)
7	No bark (100% lost)

Table 5. Description of study variables, including minimum, maximum, and mean values.

Variable Name	Variable Description	Units	Min	Max	Mean
Foliage	Foliage colour	code	0	6	3.45
tree_class	Tree class	code	1	4	2.80
crown	Crown condition	code	1	9	3.74
bark	Bark retention	code	1	6	2.68
snagspl	DBH of pine snags > 20cm	cm	20.4	49.5	27.86
snagsnonpl	DBH of non-pine snags > 20cm	cm	22.3	92.6	40.70
moss	Ground cover: moss	%	5	97	70.76
lichen	Ground cover: lichen	%	0	10	0.88
grass	Ground cover: grass	%	0	25	2.18
rock	Ground cover: rock	%	0	10	0.19
bare	Ground cover: bare ground	%	0	25	0.35
litter	Ground cover: litter	%	0	89	19.50
water	Ground cover: water	%	0	20	0.75
cwd	Ground cover: coarse wood	%	0	25	5.30
herbs_ht	Herb height	cm	0	80	19.68
herbs	Herb cover	%	0	70	20.91
b1ht	B1 shrub height	cm	0	600	214.48
b1cov	B1 shrub cover	%	0	75	10.73
b2ht	B2 shrub height	cm	0	180	81.53
b2cov	B2 shrub cover	%	0	60	18.54
a1ht	A1 Tree height	m	0	54	25.70
a1crown	A1 Tree crown depth	m	0	30.98	8.00
a2ht	A2 Tree height	m	0	31.95	16.04
a2crown	A2 Tree crown depth	m	0	31.95	6.18
canopy	Canopy closure	%	3	60	22.30
dbhavg	Mean DBH: All trees	cm	7.4	36.18	18.88
dbhmax	Maximum DBH: All trees	cm	18.6	87.4	35.97
stems	Tree density	stems/ha	250	4000	1366.55
ba_all	Basal area: All trees	m^2 / ha	8.92	158.02	43.07
ba_pl	Basal area: Pine	m^2 / ha	0	62.9	20.89
ba_plinfst	Basal area: Infested pine	m^2 / ha	0	62.9	17.74
ba_decid	Basal area: Deciduous	m^2 / ha	0	70.74	3.86
ba_conif	Basal area: Non-pine conifers	m^2 / ha	0	138.99	18.14
pl_ba	Pine in stand	% of basal area	0	100	51.08
stinfest_ba	Stand infestation rate	% of basal area	0	100	43.12
plinfest_ba	Pine Infestation rate	% of basal area	0	100	67.15
decid_ba	Deciduous in stand	% of basal area	0	93.99	8.09
nonplcon_ba	Non-pine conifers in stand	% of basal area	0	100	40.46
stinfest_sh	Stand infestation rate	% of stems/ha	0	100	29.59
plinfest_sh	Pine infestation rate	% of stems/ha	0	100	61.33

Table 6. Bird species detected during the breeding season in the study area, 2005-2006.

Common Name	Scientific Name	Code	2005 # Detections	2006 Total Detections
Chickadee, Black-capped	*Poecile atricapilla*	BCCH	22	12
Chickadee, Boreal	*Poecile hudsonica*	BOCH	0	12
Chickadee, Mountain	*Poecile gambeli*	MOCH	1	12
Cowbird, Brown-Headed	*Molothrus ater*	BHCO	1	0
Creeper, Brown	*Certhia americana*	BRCR	25	25
Crossbill, Red	*Loxia curvirostra*	RECR	1	53
Crow, American	*Corvus brachyrhynchos*	AMCR	4	0
Crossbill, White-winged	*Loxia leucoptera*	WWCR	0	12
Duck Species		DUCK SP	0	2
Eagle, Bald	*Haliaeetus leucocephalus*	BAEA	1	0
Finch, Purple	*Carpodacus purpureus*	PUFI	0	9
Flicker, Northern	*Colaptes auratus*	NOFL	1	1
Flycatcher, Alder	*Empidonax alnorum*	ALFL	1	
Flycatcher, Dusky	*Empidonax alnorum*	DUFL	28	8
Flycatcher, Hammond's	*Empidonax oberholseri*	HAFL	11	68
Flycatcher, Dusky or Hammond's		DUHA	62	30
Flycatcher, Olive sided	*Contopus cooperi*	OSFL	3	1
Flycatcher, Least	*Empidonax minimus*	LEFL	1	0
Flycatcher, Pacific-Slope	*Empidonax difficilis*	PSFL	2	0
Grosbeak, Evening	*Coccothraustes vespertinus*	EVGR	3	0
Grouse, Ruffed	*Bonasa umbellus*	RUGR	0	2
Hawk, Cooper's	*Accipiter cooperii*	COHA	0	1
Hawk, Red-tailed	*Buteo jamaicensis*	RTHA	0	2
Hawk, Sharp-shinned	*Accipiter striatus*	SSHA	0	1
Hummingbird Species		HU SP	1	0
Jay, Gray	*Perisorius canadensis*	GRJA	38	44
Junco, Dark-Eyed	*Junco hyemalis*	DEJU	129	145
Kinglet, Golden crowned	*Regulus satrapa*	GCKI	344	216
Kinglet, Ruby crowned	*Regulus calendula*	RCKI	94	169
Kinglet Species		KI SP	1	0
Loon, Common	*Gavia immer*	COLO	1	1
Nuthatch, Red-breasted	*Sitta canadensis*	RBNU	6	69
Owl, Great grey	*Junco hyemalis*	GGOW	0	1
Pewee, Western-wood	*Contopus sordidulus*	WWPE	1	3
Pipit, American	*Anthus rubescens*	AMPI	0	14
Raven, Common	*Corvus corax*	CORA	7	6
Robin, American	*Turdus migratorius*	AMRO	25	40
Sandpiper Species		USAND	1	0
Sandpiper, Solitary	*Tringa solitaria*	SOSA	0	5
Sapsucker, Red-breasted	*Ficedula parva*	RBSA	5	12
Siskin, Pine	*Carduelis pinus*	PISI	35	20
Snipe, Common	*Gallinago gallinago*	COSN	2	1

Table 6 continued…

Common Name	Scientific Name	Code	2005 # Detections	2006 Total Detections
Solitaire, Townsend's	*Myadestes townsendi*	TOSO	1	2
Sparrow, Chipping	*Spizella passerina*	CHSP	6	14
Sparow, Lincoln's	*Melospiza lincolnii*	LISP	10	5
Sparrow, Song	*Melospiza melodia*	SOSP	1	3
Sparrow, White-throated	*Zonotrichia albicollis*	WTSP	0	1
Tanager, Western	*Piranga ludoviciana*	WETA	31	46
Thrush Species		THRU SP	0	2
Thrush, Hermit	*Catharus guttatus*	HETH	6	34
Thrush, Swainson's	*Catharus ustulatus*	SWTH	54	97
Thrush, Varied	*Ixoreus naevius*	VATH	14	14
Vireo, Cassin's	*Vireo cassinii*	CAVI	20	27
Vireo, Warbling	*Vireo gilvus*	WAVI	30	31
Warbler Species		WARB SP	0	2
Warbler, MacGillivray's	*Oporornis tolmiei*	MGWA	14	7
Warbler, Orange-crowned	*Vermivora celata*	OCWA	8	9
Warbler, Tennessee	*Vermivora peregrina*	TEWA	0	1
Warbler, Townsend's	*Dendroica townsendi*	TOWA	37	22
Warbler, Wilson's	*Wilsonia pusilla*	WIWA	8	6
Warbler, Yellow-rumped	*Dendroica coronata*	YRWA	233	292
Waterthrush, Northern	*Seiurus noveboracensis*	NOWA	12	5
Woodpecker Species		WOOD SP	31	12
Woodpecker, Black-backed	*Picoides arcticus*	BBWO	2	5
Woodpecker, Downy	*Picoides pubescens*	DOWO	0	3
Woodpecker, Hairy	*Picoides villosus*	HAWO	1	14
Woodpecker, Pileated	*Dryocopus pileatus*	PIWO	2	1
Woodpecker, Three-Toed	*Picoides tridactylus*	TTWO	16	71
Wren, Winter	*Troglodytes troglodytes*	WIWR	49	50
Yellowlegs, Lesser	*Tringa flavipes*	LEYE	7	0
Yellowlegs, Greater	*Tringa melanoleuca*	GRYE	0	2
Yellowthroat, Common	*Geothlypis trichas*	COYE	4	0
Unknown Species		UNKN	26	8
Total Species 2005 =	**50**		1480	1783
Total Species 2006 =	**55**			
Total Number Species (05/06) =	**64**			

Table 7. Effect size of study factors on avian species abundance, as measured by the percent change in abundance with each unit change in study factors entered in AIC parsimonious models.

Variable	AMRO	BRCR	DEJU	GCKI	GRJA	RCKI	SWTH	WAVI	WETA	WIWR	YRWA
Treecon		15.28			-8.28				-14.00		-4.79
Crown										11.43	
Water		-100.00				50.83	-54.41	161.68	-91.60	327.30	-40.32
Herbs			0.72		0.01						0.58
B1cov				-0.66						-4.79	0.92
A1ht			-2.55	1.63	-2.89					6.09	
Dbhavg			3.09		4.00			-12.01	8.84	-5.66	2.80
Dbhmax	-2.38	4.44			0.64	-1.42	1.23	3.62			-1.00
Plinfest_ba	0.67	-0.93		0.36	1.82			-1.40	-0.81	0.99	
Decid_ba			-1.18		2.28			2.83	1.68		-0.68
Nonplcon_ba	1.72		-0.73	0.78	2.99	0.40			1.55	-0.95	
Stinfest_sh		1.72	-0.77		2.74		-0.86			-2.16	
Snagspl				-0.60	0.09	1.26	1.32	3.47	3.82	-0.90	
Snagsnonpl					-47.89					8.47	
Year				-46.51	-0.78	38.71	51.85			-17.87	
% deviance explained	5.9	15.3	5.4	23.7	13.7	5.1	8.8	22.5	29.2	17.8	13.2
Whole model P-value	0.0209	0.0000	0.0005	0.0000	0.0000	0.0246	0.0000	0.0000	0.0000	0.0000	0.0000

Table 8. Effect size of study factors on avian community variables, as measured by the percent change in community values with each unit change in study factors entered in AIC parsimonious models.

Variable	CN_GLD	DECID_GLD	EDGOPN	GEN_OTHER	MAT_YNG	MATGUILD	SHRUB_G	SPPRICHNESS	TOTALDETECT
Treecon	-15.35			-2.31					
Crown	8.16		5.94	1.69					
Water	45.73			-10.07		-29.52			
Herbs	0.43		0.61	0.20	0.31	0.29	1.27	0.26	0.41
B1cov			-0.66	-0.51		-0.32			
A1ht				0.45		-1.35			
Dbhavg				-1.91		1.70			
Dbhmax	-2.19		-0.76	0.70					
Plinfest_ba	0.70	-0.47							
Decid_ba	1.01	2.66		0.28	-0.26		-0.53	0.38	0.20
Nonplcon_ba	1.43	1.91		0.58	0.25	0.29		0.44	0.48
Stinfest_sh	0.68		-0.53			-0.66	-0.82		
Snagspl	1.68	3.37			0.42	1.31		0.56	0.49
Snagsnonpl				-36.60					
Year	289.56	329.41	-64.35	81.23	-14.52	1788.00	-60.62	28.04	
% deviance explained	29.2	39.5	18.8	17.0	62.7	8.8	19.2	27.7	17.5
Whole model P-value	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0002

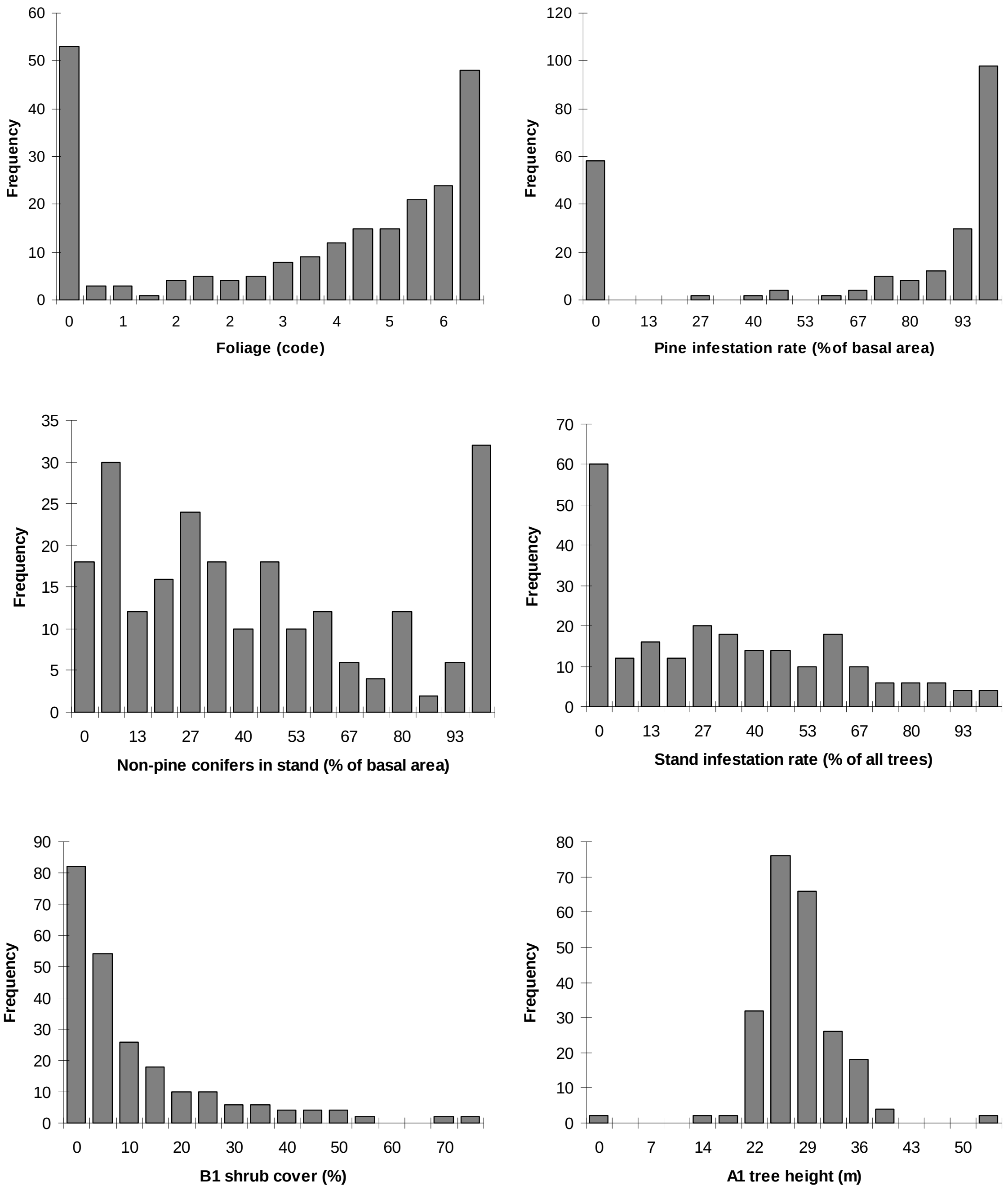

Figure 1. Frequency distribution of some of the independent variables that were included in standard poisson regression analyses and in parsimonious model development using the Akaike Information Criterion.

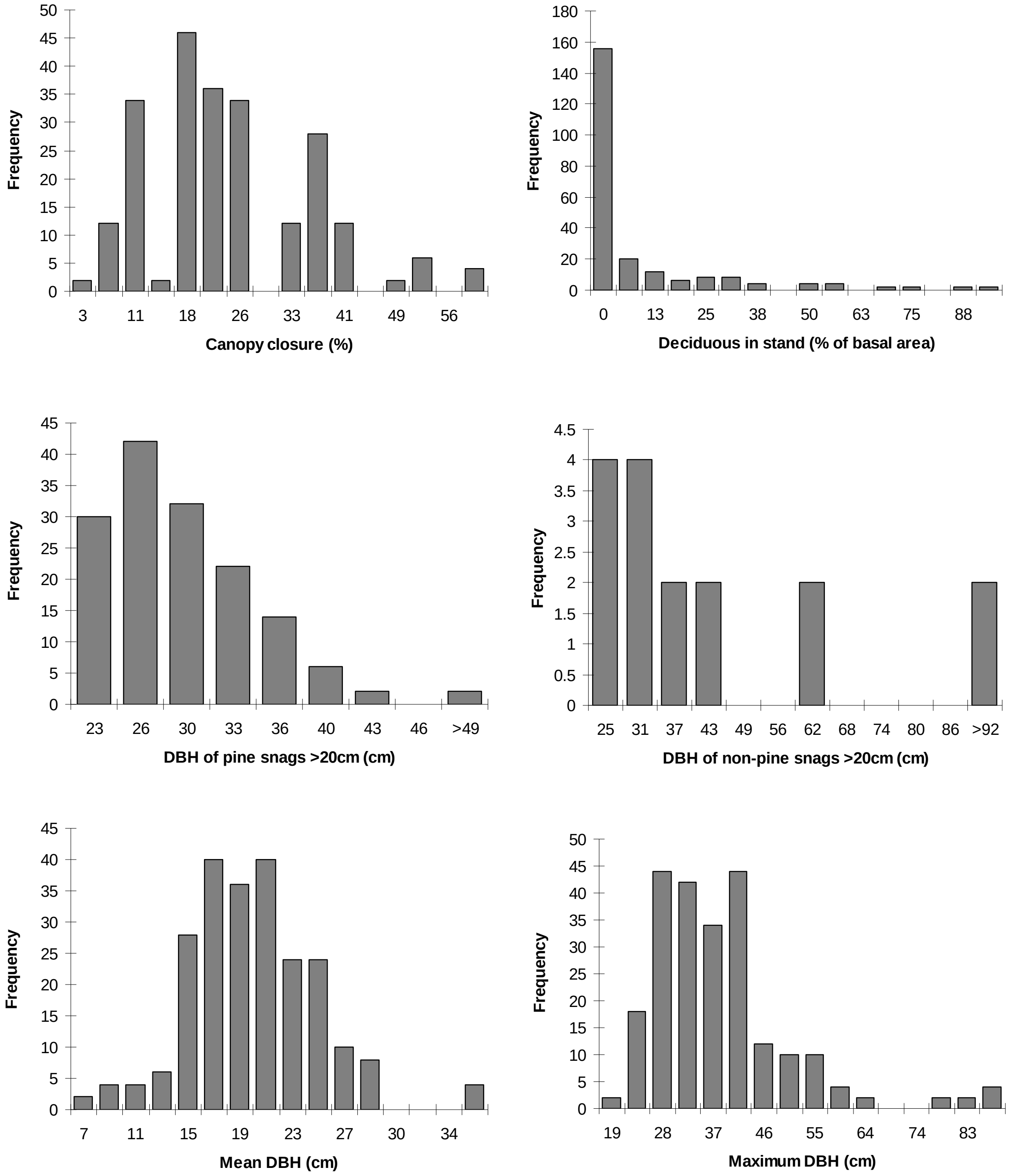

Figure 1 continued. Frequency distribution of some of the independent variables that were included in standard poisson regression analyses and in parsimonious model development using the Akaike Information Criterion.