



Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A.

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ABSTRACT

The importance of structural complexity in forest ecosystems for ecosystem diversity has been widely acknowledged. Tree microhabitat structures as indicators of biodiversity, however, have only seldom been the focus of diversity research although their occurrence is highly correlated with the abundance of forest species and ecosystem functions. In this study, microhabitat structures in Douglas-fir (*Pseudotsuga menziesii*) forests were defined and their frequency and abundance in natural stands and stands of varying active management histories and stand ages was compared. Indicator microhabitat structures for natural forests were determined and the relationship of the abundance of microhabitat structures with tree diameter of Douglas-fir trees was analysed.

Most of the investigated microhabitats are indeed indicators of natural mature and natural old-growth stands, e.g., broken tree top, bayonet top, crack or scar, bark loss, hollow chamber, stem cavity with decay, bark pocket with and without decay, bark bowl, burl, heavy resinosis, and bark burst. In Douglas-fir trees, resin drops and heavy resinosis were the dominant microhabitats in trees with >20.0–40.0 cm diameter at breast height (dbh), whereas bark structures such as bowls in the bark, bark pockets, and bark pockets with decay were the most abundant microhabitats in Douglas-fir trees >80.0 cm. Both management history (including no treatment in natural stands) and stand age determined the abundance of microhabitats and microhabitat composition of stands in our study. The observed microhabitat variability was highest in stands that had not been harvested or otherwise treated silviculturally in many years (low treatment history) and the natural stands and lowest in the recently managed stands. Recently managed stands had, on average, 115 microhabitats/ha, stands with a low treatment history had 520 microhabitats/ha, and natural mature and natural old-growth stands had 745 microhabitats/ha.

Active management for microhabitats in silviculturally-treated stands is important if the aim is to create structural complexity for a variety of organisms and ecosystem functions in even-aged Douglas-fir stands. Although the management of microhabitats with respect to biodiversity and economic objectives often seem to be in conflict, we suggest silvicultural measures to reduce the current homogenization of forest stands with relatively minor losses of wood production especially if the reduced timber output is compared with the expected longterm social, economic, and ecological benefits. It may, however, take many decades to obtain stands that approximate the criteria for old-growth according to the interim minimum standards for old-growth Douglas-fir forests in their native western Washington and Oregon.

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1. Introduction

The conservation of biodiversity has become a global concern (*Convention of Biological Diversity – United Nations, 1993*) and the

need to view forest management as complex ecosystem management and its crucial role in biodiversity conservation has become widely accepted (*Kohm and Franklin, 1997*). Increasing structural complexity in forests enhances their ecological complexity and, therefore, is the basis for maintaining a high biodiversity in these ecosystems (*Rapp, 2003*). As a consequence, large studies in the Pacific Northwest of the U.S.A. have begun to investigate a variety of silvicultural systems suggested to increase structural complexity in forest management (*Lindenmayer and Franklin, 2002*;

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Franklin et al., 1997), e.g., CFIRP – College of Forestry Integrated Research Project (Maguire and Chambers, 2005), DEMO – Demonstration of Ecosystem Management Options Study (Halpern and Raphael, 1999), and MASS – Montane Alternative Silvicultural Systems (Beese, 1995).

1.1. The difficulty in monitoring biodiversity

How can biodiversity in a forest ecosystem be measured? There are several approaches to define the term biodiversity. Most often, these include the concepts of genetic, species, and ecosystem diversity or alternatively the concepts of compositional, structural, and functional diversity (Kaennel, 1998; Noss, 1990; Whittaker, 1972). In general, the biodiversity of a specific ecosystem is assessed by determining its species diversity. However, this approach is very labor-intensive, costly, and depends on rare specialists for species determination of various organism groups (Puimalainen, 2001). As a consequence, the need to develop alternative indicators of biodiversity has long been acknowledged. However, newly developed indicators primarily refer to the stand- and landscape level, e.g., forest connectivity, stand heterogeneity, stand complexity, or ecosystem functions (Lindenmayer et al., 2000; Hunter, 1999; Noss, 1990). Although these indicators describing forest health, carbon storage, air pollution, and wildlife habitat have recently been included into the USDA Forest Service – Forest Inventory and Analysis Program (Shaw, 2006), a description of a range of single-tree structures (microhabitats) and an analysis of their role in maintaining biodiversity is still lacking (Spies, 1998).

Especially in highly structured Pacific coastal old-growth forests, biodiversity is expressed through organisms that are generally not easily observed such as fungi (Smith et al., 2002), lichens (McCune et al., 2000), bats (Thomas, 1988), and invertebrates (Addison et al., 2003; Schowalter, 1995). For continual monitoring of these ‘hidden’ organisms, determining the amounts and distributions of microhabitat niches that support this many species on a single-tree basis is crucial. In general, forest structure and more specifically single-tree microhabitats can be regarded as a meaningful alternative to the determination of species of various organism groups because the occurrence of microhabitat structures is highly correlated with the abundance of many forest species and ecosystem functions (Parsons et al., 2003; Remm et al., 2006; Bull et al., 1997; Harmon et al., 1986; Thomas et al., 1979). Although natural Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) forests in the Pacific Northwest differ widely in character with age, geographic location, and disturbance history because of regional differences in climate and fire history, site productivity, and species composition, they share the same general definition and similar structural attributes in their range of occurrence (Franklin et al., 2002; Spies et al., 2002).

1.2. Tree microhabitat structures and their potential use as indicators of biodiversity

Abundance and species diversity often increase with the availability of forest and single-tree structures used for breeding, feeding, and resting (shelter) (Bruce et al., 1985a,b). Often these structures are associated with later stand development stages. For example, large live trees, snags, stumps, logs, down material, and large dead branches in mature or old-growth forests are used as primary or secondary habitat by many vertebrate species including amphibians, reptiles, birds, mammals, and invertebrates (Parks et al., 1997; Blaustein et al., 1995; Harmon et al., 1986; Bruce et al., 1985b; Maser et al., 1979). Hollow snags, often indicated by a bayonet top over the break, or more than one pileated woodpecker (*Dryocopus pileatus*) entrance hole are especially important as nest

and roost sites for Vaux's swifts (*Chaetura vauxi*), roost sites for pileated woodpeckers and northern flickers (*Colaptes auratus*), and rest sites for bushy-tailed woodrats (*Neotoma cinerea*), northern flying squirrels (*Glaucomys*), weasels (*Mustela*), and other small mammals (Parks et al., 1997; Bull, 1995; Bull et al., 1992). A hollow chamber in the butt of a tree can also be used for cover by small animals, for roosting by bats, and as den site by black bears (*Ursus americanus*) (Parks et al., 1997; Noble et al., 1990). Stem cavities in a living tree with decay substrate (mould) are also important for invertebrates and secondary cavity nesters (Winter and Möller, 2008; Remm et al., 2006; Martin et al., 2004).

Large bark pockets of Douglas-fir are used by bats as roosting sites, e.g., by the silver-haired bat (*Lasionycteris noctivagans*) (Sondenaa, 1991), the California bat (*Myotis californicus*) (Vonhof and Gwilliam, 2007), and by brown creepers (*Certhia americana*) as nesting sites (Parks et al., 1997). If they contain decayed substrate, these bark pockets with decay and bowls in the bark with fresh residue are also important for invertebrates (Winter and Möller, 2008). Small mammals like red tree voles (*Arborimus longicaudus*) and red squirrels (*Tamiasciurus hudsonicus*) build their nests in dense possibly misshapen branches throughout the tree canopy of large Douglas-fir trees where needles provide sufficient cover for the young (Hedwall et al., 2006; Sondenaa, 1991). Such brooms, often caused by dwarf mistletoe (*Arceuthobium* spp.), rust fungi (*Chrysomyxa* spp. or *Melampsorella* spp.), or a needle cast fungus (*Elytroderma deformans*), are also used as food and hiding and nesting habitat for both invertebrates and other vertebrates, e.g., by long-eared owls (*Asio otus*) and great horned owls (*Bubo virginianus*) for nesting, and by American martens (*Martes americana*), fishers (*Martes pennanti*), and porcupines (*Erethizon dorstum*) for cover (Bull et al., 1997; Parks et al., 1997; Forsman et al., 1984; Tinnin et al., 1982; Hawksworth and Wiens, 1972).

Many species depend on old, large trees and their structures to nest, feed, and rear their young, e.g., the pileated woodpecker, the fisher, and the marbled murrelet (*Brachyramphus marmoratus*) (Hartwig et al., 2004; Zielinski et al., 2004; Sondenaa, 1991). Fruiting bodies (conks) of decay fungi are good indicators of softened wood although they do not necessarily appear on decaying trees and logs. Dead or broken tree tops, splintered stems, fire scars, resinosis, burst bark, and other wounds or bark loss are also indicators of beginning tree death or internal decay. Depending on the decay type (internal decay in the heartwood, external decay in the sapwood, or root diseases) a tree will provide characteristic tree structures over time on which different species depend (Parks et al., 1997; Parks and Shaw, 1996). If a tree is not too decayed, it will be used by woodpeckers for nesting, foraging in the bark, and foraging in the interior after carpenter ants which often colonize decaying wood at the base of a living tree (Bull et al., 1997; Parks et al., 1997; McClelland et al., 1979). Trees with a root disease will function only for a short time as snags with associated habitat functions as they may soon fall over after infection with particular fungi (Parks et al., 1997). Broken tree tops or half crowned, partially broken crowns, and broken stems provide nest platforms for e.g., the great gray, great horned, and barred owls (Bull et al., 1997) and the marbled murrelet (Baker et al., 2006). The exceptional role of all of these microhabitats in biodiversity conservation is, therefore, proved by the literature. A quantification of these structures in forest ecosystems, however, has only seldom been the focus of research activities (Winter and Möller, 2008).

Although suggestions for suitable indicators of biodiversity and natural processes of forest ecosystems have been made internationally (e.g., Winter et al., 2004; Spellmann et al., 2002; Larsson, 2001; CIFOR, 1999), clear definitions of microhabitats of different forest tree species and their use as indicators of biodiversity and validations on their practicability have seldom been published

Table 1
Information on study sites, their treatment histories and stand ages.

Experimental study	Number of selected stands (N = 38)	Treatments (Table 2)	Age classes (Table 2)	Geographical location
Natural stands				
H.J. Andrews Experimental Forest (Dyrness and Acker, 1999)	10	6	6.1, 6.2	Oregon Cascade Range
Stands managed primarily for timber production				
DEMO – Demonstration of Ecosystem Management Options Study (Halpern and Raphael, 1999)	6	2, 3, 4, 5	4, 5	Oregon Cascade Range and Southern Washington Cascade Range
CFIRP – College of Forestry Integrated Research Project (Maguire and Chambers, 2005)	5	2, 3, 5	3, 4, 5	Willamette Valley
McDonald-Dunn Forest, Oregon State University (Fletcher et al., 2005)	7	1, 5	1, 2, 3, 5	Willamette Valley
ODF Commercial Thinning Study (Mainwaring et al., 2005)	6	4, 5	2, 3	Oregon Coast Range
Starker Forests Inc. (Internal forest biometrics data, 2006)	4	1, 5	1, 3	Oregon Coast Range

(Winter and Möller, 2008; Franklin et al., 2002; Spies and Franklin, 1991). The objectives of this study were (a) to determine the abundance of such microhabitats on living trees in natural Douglas-fir forests in the Pacific Northwest of the U.S.A. that have been described as important habitat structures in the literature, (b) to define structural indicators of biodiversity by comparing the microhabitat composition in natural mature and natural old-growth Douglas-fir forests with Douglas-fir plantations of various stand ages and treatment histories in Oregon/Washington, and (c) to examine the relationship between tree diameter and microhabitat structures in Douglas-fir.

2. Methods

Thirty-eight stands in Douglas-fir dominated forests in the Pacific Northwest were selected for a variety of past silvicultural treatments, stand ages, and geographical regions (Table 1). Stands were pre-grouped according to either their stand age or past silvicultural overstory treatment (Table 2). Natural stands with no known active management, also called 'virgin stands', were included in the treatment history gradient. Except for four, all stands had already been the focus of recent research activities in Douglas-fir dominated forests of the Pacific Northwest and were determining the design of this study. In addition, four private forest stands owned by Starker Forests Inc., Philomath, OR were selected.

All study plots were randomly selected along the existing study grid in each stand, permanent, circular, and 0.2 ha in size (2×0.1 ha circular plots), except for study plots in the H.J. Andrews Experimental Forest and ODF Commercial Thinning Study which were rectangular and for study plots measured on private forest lands which were non-permanent.

The tree diameter at breast height (dbh) was measured of all living trees with a dbh ≥ 20 cm in each study plot when not

available from regularly collected field data to investigate the relationship between dbh and number of individual tree habitat structures (microhabitats). All trees with a tree diameter ≥ 7 cm in a stand were investigated for the abundance of 21 pre-defined microhabitats that were determined to be typical of Douglas-fir trees and associated tree species (Table 3).

3. Analysis

If not stated otherwise, the significance level in all analyses was set at $\alpha = 0.05$. Mann–Whitney *U*-tests, ANOVA, or Kruskal–Wallis *H*-tests were performed in SPSS 15.0 (SPSS Inc., Chicago) to test for group differences after checking the assumptions of independence, normality, and equal variances visually and with the Kolmogorov–Smirnov and Levene tests. To compare all treatments or stand ages with each other, respectively, the Tukey test with unequal sample sizes (Zar, 1998, p. 213) was performed on three treatment groups and nonparametric multiple comparisons with unequal sample sizes (Dunn, 1964 in Zar, 1998, p. 225) were performed using mean ranks and considering tied ranks on seven stand age groups in MS Excel.

All multivariate analyses were performed with PC-ORD 4.33 (McCune and Mefford, 1999). In Multi-Response Permutation Procedures (MRPP) and Nonmetric Multidimensional Scaling (NMS) a constant of one was added to the abundance of microhabitats to avoid zero values. Furthermore, the abundance of microhabitats was relativized by their maximum to reduce the emphasis on single microhabitats with an extremely high abundance.

For detecting differences between stands of different management histories (including natural stands) and of different ages with regard to their microhabitats, MRPP was used. MRPP is a nonparametric procedure for testing for group differences of

Table 2
Groups of different treatment alternatives and stand ages.

Age class	1: Clearcut (0–1 years) (n = 4)	2: Young (20–50 years) (n = 4)	3: Middle-age (51–80 years) (n = 9)	4: Mature (81–120 years) (n = 4)	5: Old (121–250 years) (n = 7)	6.1: Natural mature ^a (<250 years) (n = 5)	6.2: Natural old-growth ^a (>250 years) (n = 5)
Treatment (six groups, detailed)	1: Clearcut (recent, no new plantings) (n = 4)	2: Gaps (stands with gaps of different shapes and sizes) (n = 3)	3: Two-story, seed-tree (heavy reduction in overstory density) (n = 4)	4: Even thinning (even and medium reduction in overstory density) (n = 4)	5: Low (low management level over the years, probably some prior thinning, but none recent) (n = 13)	6: Natural stand (no silvicultural treatment ever, only natural disturbances in the past) (n = 10)	
Treatment (three groups)	1–4: Recent overstory density reduction (within the last 20 years) (n = 15)				5: Low (s.a.) (n = 13)	6: Natural stand (s.a.) (n = 10)	

^a A distinction between natural mature and natural old-growth Douglas-fir forests can be made because forest age describes the time after the last major natural disturbance. Therefore, a Douglas-fir forest can be young but still be a virgin forest.

Table 3

Definition of microhabitats. The recorded variable 'dead tree top' was often difficult to determine in the forest and for that reason not included in the analysis. The recorded variable 'stem breakage of a live tree' was also omitted from the final data set because it occurred only twice in all stands.

Microhabitat	Definition
Broken tree top	At least 50% of the crown broke off
Partially broken crown	Less than 50% of the crown, including primary branches, broke off
Bayonet top	After stem breakage, creation of a new crown with an upturned leader
Cracks or scars	Reaching into the wood and at least 2 cm wide and at least 25 cm long
Bark loss	Loss of bark at least 5 cm × 5 cm in size
Splintered stem after stem breakage	Many splinters with a length of at least 50 cm after stem breakage
Woodpecker foraging/excavations deep into the bark	Woodpecker foraging into the bark with a size of at least 2 cm × 3 cm or many woodpecker drillings
Woodpecker cavity	Woodpecker hole in the wood that indicates a cavity
Hollow chamber in butt of tree	Natural cavity at the base of the tree stem of at least 10 cm in height, width, and depth without decay
Stem cavity with decay	Cavity at the base of the tree or on the stem in an advanced decay stage and with mould
Bark pockets	Space between loose bark of at least 5 cm in width and 2 cm deep
Bark pockets with decay	Same as above but with mouldy substrate
Bowls in bark	Bowl structure in bark at least 3 cm wide collecting litter
Burls	Cancerous growth at least 5 cm × 5 cm in size
Heavy resinosis	Fresh heavy flow of resin at least 30 cm long or >5 flows of resin of smaller size
Resin drops	Only few resin drops indicating only a minor injury
Witch broom	Dense agglomeration of branches from a parasite or epicormic branching
Burst bark	Black burst of bark often with resin indicating injury/disease
Conks	Fungi indicating stem decay

a-priori defined groups of a multivariate data set (Mielke and Berry, 2001 in McCune and Grace, 2002). From a calculated distance matrix, the average of a group-size weighted mean within-group distance (δ) was calculated for each group and compared to the expected δ under the null hypothesis of no difference between groups providing a p -value. The effect size independent of the sample size was then given by the chance-corrected within-group agreement (A). This statistic describes within-group homogeneity compared to random expectation.

For detecting relationships between stands by treatment or age, respectively, and microhabitats in ordination space and assessing the dimensionality of the data, NMS (Mather, 1976) was used. The NMS autopilot in PC-ORD was applied with Sørensen distance as the distance measure, the setting 'slow and thorough' with random starting configurations, and 40 runs with real data. The dimensionality of the data set was assessed with a scree plot and by tabulating final stress in relation to dimensionality. In the NMS ordination, when comparing all stands according to their microhabitat composition, two major gradients captured most of the variance in the community of microhabitats, the first two dimensions containing 71.1% and 16.0%, respectively, of the information in the analytical data set (cumulative = 87.1%). Higher dimensions improved the model very little. The number of randomized runs in a Monte Carlo test was 50 and the probability that a similar final stress could have been obtained by chance was low ($p = 0.02$). The number of iterations for the final solution was 400 with a final instability of 0.01 and final stress of 15.36 (Figs. 4–6).

Indicator Species Analysis follows MRPP and answers the question of how well each microhabitat separates among treatment or stand age groups (Dufrêne and Legendre, 1997 in McCune and Grace, 2002). It provides indicator values for each microhabitat in each group of stands depending on how 'faithful' to that group (always present) this structure is and how 'exclusive', i.e., never occurring in other groups (McCune and Grace, 2002). Although primarily used for species data, its concept of including both abundance in particular groups and relative frequency within a group can be applied to microhabitats in groups of stands equally well.

As there was no convincing difference between the abundance of microhabitats in natural mature and natural old-growth stands

(Figs. 1, 3 and 6), they were combined into one treatment group representing natural stands in the analyses of treatment effects and into one age group in the indicator analysis.

4. Results

4.1. Natural mature and natural old-growth stands

Natural mature and natural old-growth stands statistically differed in their composition of microhabitats ($p = 0.02$, MRPP). However, stands within each group were fairly similar (chance-corrected within-group agreement $A = 0.043$, MRPP) and the variability was much higher in the natural mature stands (Fig. 1). The data were only weakly structured and no useful NMS ordination was found. Natural mature and natural old-growth stands did not differ statistically significant in any single one of the investigated microhabitats ($p > 0.05$, Mann–Whitney U -tests). Only the abundance of signs of woodpecker foraging and trees with a bayonet top were close to the significance level ($p = 0.06$ and 0.10 , respectively, from a Mann–Whitney U -test).

4.2. Total abundance of microhabitats

The four recent overstory reduction treatments (clearcut, gaps, two-story, and even thinning) did not differ from each other in their total abundance of microhabitats/ha ($p > 0.05$, nonparametric multiple comparison test with unequal sample sizes, Dunn 1964). For this reason and to examine the difference in general between recently managed stands, stands with a low treatment, and natural stands, the treatments: clearcut, gaps, two-story, and even thinning were combined into one group of recent overstory reduction treatments. The three resulting groups (1–4: recent overstory reduction treatments, 5: low treatment level, 6: natural stands) were not equal in their total abundance of microhabitats/ha ($p < 0.001$, ANOVA F -test) (Fig. 2). Natural stands had developed on average about 1.4 times more microhabitats (745 microhabitats/ha) than stands that have not been harvested or otherwise treated silviculturally in many years (low treatment) (520 microhabitats/ha) and about 6.6 times more microhabitats than stands with a relatively recent overstory reduction treatment (105 microhabitats/ha). All three groups differed significantly from each

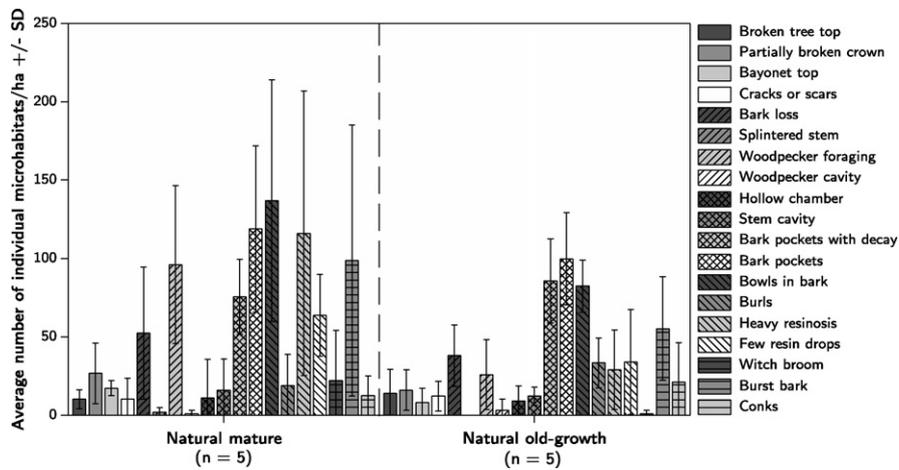


Fig. 1. Average number of individual microhabitats/ha (±standard deviation) in natural mature and natural old-growth stands.

other in their total number of microhabitats (Tukey test with unequal sample sizes).

Of the seven groups with different stand ages at least one differs significantly from the others in its total number of microhabitats/ha ($p < 0.001$, Kruskal–Wallis H -test). A statistically significant difference regarding the total number of microhabitats/ha was only found between the clearcut stands and the managed young, natural mature, and natural old-growth stands, respectively ($p < 0.05$, nonparametric multiple comparison test with unequal sample sizes, Dunn 1964). The high number of microhabitats in young stands results from trees with heavy resinosis or resin drops (Fig. 3).

4.3. Microhabitat composition

If considering the frequency and abundance of all single microhabitats, stands of alternative treatments differed from each other and they were very homogenous within when focusing on six pre-defined treatment groups ($p < 0.001$, $A = 0.287$, MRPP) and, after summarizing all recent overstorey reduction treatments, on

only three pre-defined treatment groups ($p < 0.001$, $A = 0.255$) (Fig. 4).

The stands of the six pre-defined stand treatments are fairly well grouped in the ordination (circles with solid line), i.e., each treatment group has a relatively distinctive microhabitat composition (Fig. 4). The variability between stands within one treatment group increased from recent overstorey treatments (1: clearcut, 2: gaps, 3: two-story, and 4: even thinning) to the low treatments (5) and the natural mature and natural old-growth stands (6). A good distinction can also be made between the three pre-defined treatment groups (circles with dotted lines): natural stands (6), stands with a low treatment (5), and stands that were recently managed (1–4). Only few stands do not follow these pre-defined groupings. Natural stands were the only grouping for which some of the microhabitats are representative in the ordination space (Fig. 5). For example, the microhabitats bark pockets and bark pockets with decay showed the highest correlation with axis 1, following the sequence of treatment groupings more than stand

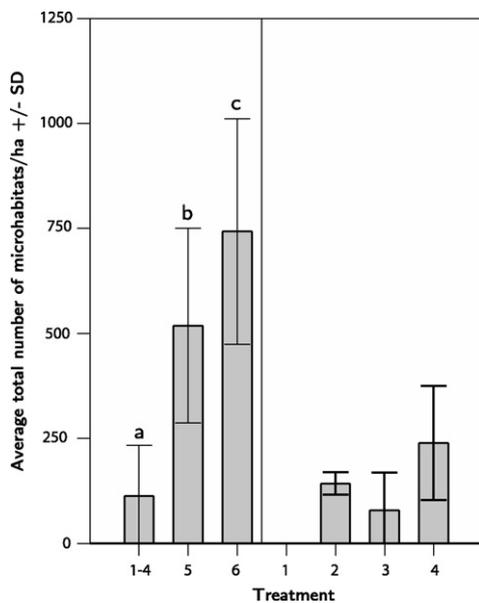


Fig. 2. Average total number of microhabitats/ha (±standard deviation) in treatment groups according to the three pre-defined treatment groups (1–4: 1 – clearcut ($n = 4$), 2 – gaps ($n = 3$), 3 – two-story ($n = 4$), 4 – even thinning ($n = 4$); 5: low management ($n = 13$); 6: natural stand ($n = 10$)). Different letter indicates significant difference at $p < 0.05$, from Tukey tests with unequal sample sizes.

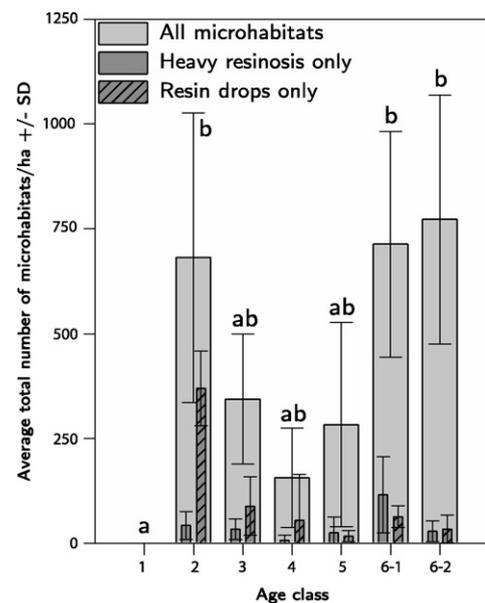


Fig. 3. Average total number of microhabitats/ha ± standard deviation in stand age groups according to the seven pre-defined age groups (1: clearcut ($n = 4$), 2: young ($n = 4$), 3: middle-age ($n = 9$), 4: mature ($n = 4$), 5: old ($n = 7$), 6.1: natural mature ($n = 5$), 6.2: natural old-growth ($n = 5$)). The microhabitats heavy resinosis and resin drops are also drawn separately to emphasize their significance in the young stands. Different letter indicates difference at $p < 0.05$, from nonparametric multiple comparison tests with unequal sample sizes using mean ranks, Dunn 1964.

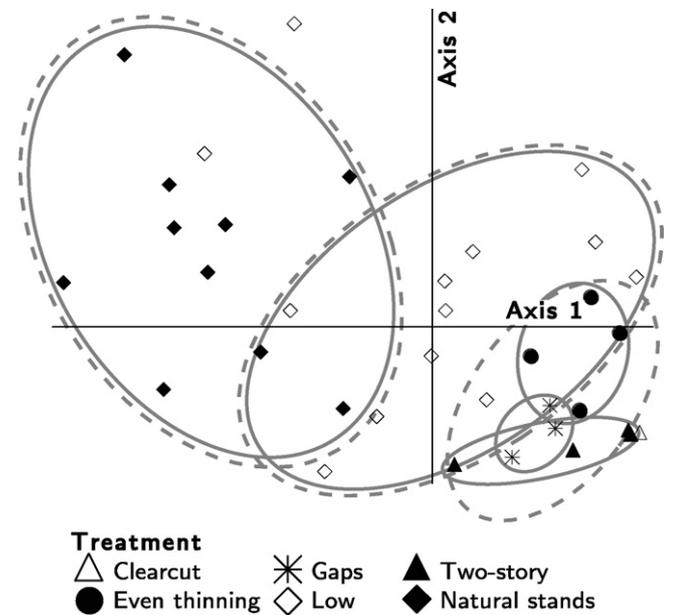


Fig. 4. Two-dimensional ordination of microhabitats with different symbols representing stands with alternative treatment histories. Distances between stands approximate dissimilarity in composition of all microhabitats. Lines were drawn to capture most of the stands within the same 6- (solid lines) and 3-level (dotted lines) treatment group. The empty triangle represents four clearcut stands.

ages in the ordination. No microhabitats could be visually distinguished to represent any other of the treatment groups in the ordination.

According to the frequency and abundance of all single microhabitats, stands of alternative stand ages differed from each other and they were relatively homogenous within when focusing on pre-defined age groups ($p < 0.001$, $A = 0.259$, MRPP). However, in the ordination, stands of similar stand ages could not as clearly be grouped as stands with different treatment histories (Figs. 4 and 6). Two groups could be visually distinguished: (a) natural mature and natural old-growth stands (except one), and (b) clearcut, young (except one), middle-age, and managed mature stands. Old stands were found in both groups.

4.4. Indicator microhabitats of natural forests

Microhabitats that are indicators of natural forests are: broken tree top, bayonet top, crack or scar, bark loss, hollow chamber,

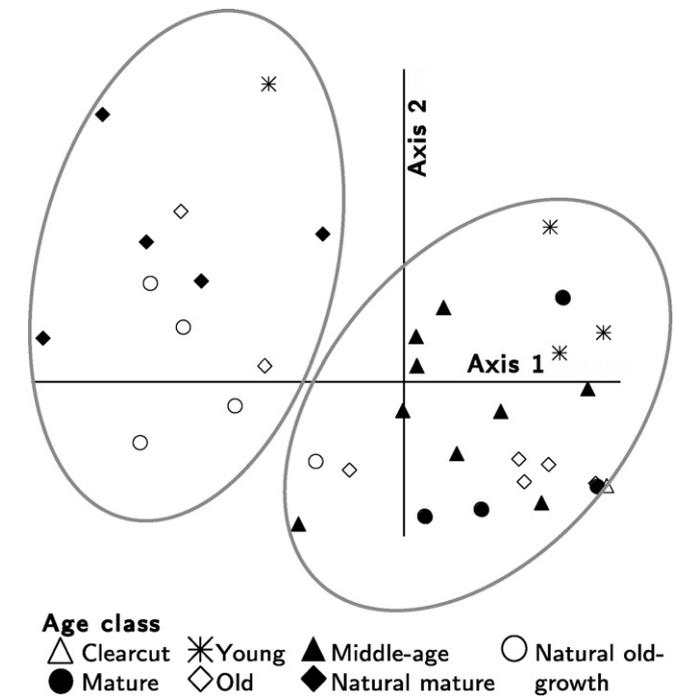


Fig. 6. Two-dimensional ordination of microhabitats with different symbols representing stands with alternative stand ages. Distances between stands approximate dissimilarity in composition of all microhabitats. Lines were drawn to separate visually distinct groups in the ordination. The empty triangle represents four clearcut stands.

stem cavity with decay, bark pocket with and without decay, bark bowl, burl, heavy resinosis, and bark burst (Table 4). Only drops of resin are an indicator structure for stands with a low level of management. No microhabitat was characteristic of a recent overstory reduction treatment.

As there were no convincing differences between natural mature and natural old-growth stands in a direct comparison (Fig. 1) and they could not be clearly distinguished in ordination space (Fig. 6), both groups were combined to determine indicator structures of stand ages. The following microhabitats are indicators of natural stands in comparison to clearcut, young, middle-age, mature, and old managed stands: broken tree top, stem cavity with decay, bark pocket, bark pocket with decay, bark pocket, bowl in bark, burl, heavy resinosis, and burst bark (Table 5). Trees with resin drops are an indicator microhabitat in young stands.

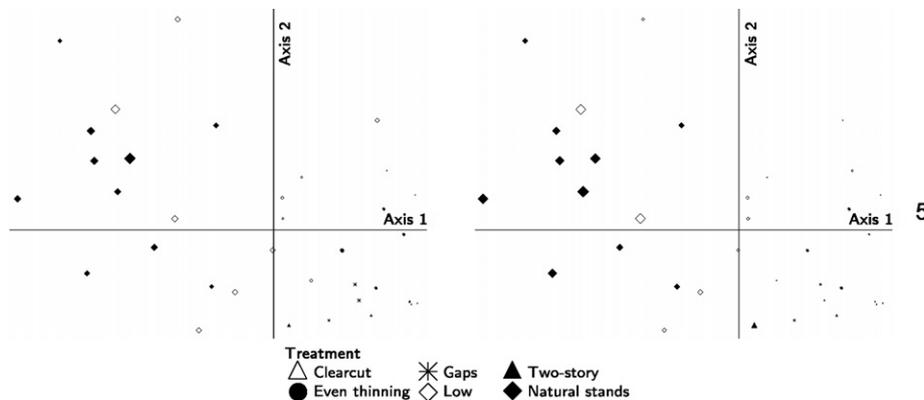


Fig. 5. Two-dimensional ordination of microhabitats with different symbols representing stands of alternative treatments. Overlay with sizes of symbols proportional to the abundance of trees with bark pockets (left, $r = -0.86$ with axis 1) and bark pockets with decay (right, $r = -0.89$ with axis 1), respectively. Distances between stands approximate dissimilarity in composition of all microhabitats.

Table 4

Indicator values (IV; % of perfect indication, based on combining values for relative abundance and relative frequency) of each microhabitat for each treatment group of stands, rounded to the nearest whole percentage. The indicator values range from zero (no indication) to 100 (perfect indication).

Microhabitat	Treatment group			1: Clearcut (n = 4)	2–4: Recently managed (n = 11)	5: Low (n = 13)	6: Natural (n = 10)	p*
	Avg IV	Max IV	Maxgrp	Indicator values (IV)				
Broken tree top	23	87	Natural	0	0	3	87	0.0010
Partially broken crown	20	39	Natural	0	3	36	39	0.0990
Bayonet top	18	47	Natural	0	0	24	47	0.0220
Cracks or scars	15	42	Natural	0	0	19	42	0.0380
Bark loss	20	49	Natural	0	12	18	49	0.0170
Splintered stem	4	14	Natural	0	0	2	14	0.3460
Woodpecker foraging	22	44	Low	0	4	44	39	0.0940
Woodpecker cavities	6	13	Low	0	6	13	7	0.7060
Hollow chamber	11	41	Natural	0	0	4	41	0.0340
Stem cavity w decay	18	67	Natural	0	0	5	67	0.0020
Bark pockets w decay	24	64	Natural	0	8	22	64	0.0010
Bark pockets	24	55	Natural	0	12	29	55	0.0010
Bowls in bark	23	65	Natural	0	6	20	65	0.0010
Burls	20	67	Natural	0	1	10	67	0.0010
Heavy resinosis	22	57	Natural	0	9	21	57	0.0090
Resin drops	22	61	Low	0	9	61	19	0.0030
Witch broom	9	14	Natural	0	9	14	14	0.8380
Burst bark	23	92	Natural	0	0	1	92	0.0010
Conks	18	43	Natural	0	1	27	43	0.0520
Averages	18	51		0	4	20	48	

* p-values are from a Monte Carlo test of significance of observed maximum indicator values (IV) for each microhabitat, based on 1000 randomizations; significance level $\alpha = 0.05$; Maxgrp = group identifier for group with maximum observed IV.

4.5. Effect of Douglas-fir diameter on microhabitat abundance

On average, a Douglas-fir tree has developed at least one microhabitat after it has reached a dbh of at least 30 cm, two different microhabitats after it has reached a dbh of at least 70 cm, and three different microhabitats after it has reached a dbh of at least 90 cm (Fig. 7). For trees with ≥ 110 cm dbh, the mean number of microhabitats/tree remains near four with a decreasing standard deviation.

Many microhabitat structures on Douglas-fir depend on tree diameter. The percentage of Douglas-fir trees in three tree diameter classes (>20.0–40.0 cm, >40.0–80.0 cm, >80.0 cm) on

which a specific microhabitat was found was not equal for the following ten out of 19 investigated microhabitat structures ($p < 0.05$, Kruskal–Wallis H -test): woodpecker foraging, hollow chamber, stem cavity, bark pockets, bark pockets with decay, bowls in bark, burls, heavy resinosis, resin drops, and witch broom (Fig. 8). The most abundant microhabitat on Douglas-fir trees with >20.0–40.0 cm dbh was drops of resin. This microhabitat occurred on 50% of the trees. Heavy resinosis was found on 12% and other microhabitats occurred on only less than 10% of the trees in that diameter class. Microhabitats that occurred on at least 10% of the trees with 40.1–80.0 cm dbh were resin drops (40%), bowls in bark (33%), heavy resinosis (27%), and bark pockets (19%). On trees with

Table 5

Indicator values (IV; % of perfect indication, based on combining values for relative abundance and relative frequency) of each microhabitat for each age group of stands, rounded to the nearest whole percentage. The indicator values range from zero (no indication) to 100 (perfect indication).

Microhabitat	Age group			1: Clearcut (n = 4)	2: Young (n = 4)	3: Middle-age (n = 9)	4: Mature (n = 4)	5: Old (n = 7)	6: Natural (n = 10)	p*
	Avg IV	Max IV	Maxgrp	Indicator values (IV)						
Broken tree top	13	75	Natural	0	2	0	1	3	75	0.0010
Partially broken crown	10	24	Natural	0	7	8	6	14	24	0.4520
Bayonet top	9	31	Natural	0	15	7	2	2	31	0.0910
Cracks or scars	8	27	Natural	0	8	2	2	6	27	0.2190
Bark loss	13	34	Natural	0	24	13	0	10	34	0.0910
Splintered stem	3	12	Natural	0	0	0	0	6	12	0.7530
Woodpecker foraging	14	27	Young	0	27	20	1	11	24	0.4170
Woodpecker cavity	6	25	Old	0	0	5	3	25	5	0.1880
Hollow chamber	7	30	Natural	0	8	0	0	2	30	0.1720
Stem cavity w decay	12	58	Natural	0	0	8	3	0	58	0.0040
Bark pockets w decay	15	49	Natural	0	2	11	8	22	49	0.0010
Bark pockets	16	39	Natural	0	15	16	3	24	39	0.0010
Bowls in bark	14	49	Natural	0	7	14	3	10	49	0.0020
Burls	12	48	Natural	0	17	2	4	1	48	0.0070
Heavy resinosis	14	40	Natural	0	18	19	1	6	40	0.0380
Resin drops	15	64	Young	0	64	14	2	3	8	0.0010
Witch broom	7	14	Mid-age	0	0	14	9	11	10	0.8000
Burst bark	15	85	Natural	0	1	0	0	2	85	0.0010
Conks	10	30	Natural	0	3	17	6	4	30	0.1330
Averages	11	40		0	11	9	3	9	36	

* p-values are from a Monte Carlo test of significance of observed maximum indicator values (IV) for each microhabitat, based on 1000 randomizations; significance level $\alpha = 0.05$; Maxgrp = group identifier for group with maximum observed IV.

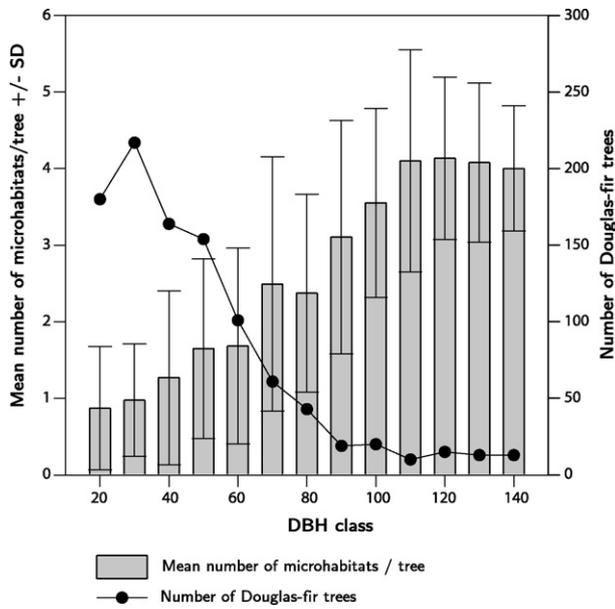


Fig. 7. Mean number of different microhabitats (\pm standard deviation) per Douglas-fir tree depending on tree diameter. Tree diameter classes were defined in the following way: e.g., the class ‘=20’ equals trees with a dbh between >20.0 cm and 30.0 cm. Because of the lack of trees in higher diameter classes, all trees with a diameter >140 cm were combined in the diameter class ‘140’.

a dbh larger than 80.0 cm, the most common microhabitats were bowls in bark (84%), bark pockets (78%), bark pockets with decay (61%), heavy resinosis (29%), resin drops (27%), and burls (15%).

The most characteristic microhabitats in large diameter trees were bark features such as bark pockets, bark pockets with decay, and bowls in the bark in which litter is collected (Fig. 8). These three different structures were found on more than 75% of the trees with a dbh of ≥ 100 cm and their abundance was strongly increasing on trees with ≥ 70 cm dbh (Fig. 9). Yet, at least one more microhabitat/tree on average was found on trees with a dbh of 110 cm or more (Fig. 7). These were most often resinosis, resin drops, or burls. Although of high ecological importance, other microhabitats occur only in less than 10% of the investigated Douglas-fir trees in any diameter class (Fig. 8).

5. Discussion

5.1. Different management histories, including natural stands, and stand ages

Although Spies and Franklin (1991) have found a relationship of several measures of forest structure with stand age in natural forests, the abundance and composition of tree microhabitat structures in this study did not vary convincingly in natural mature and natural old-growth Douglas-fir stands (less and more than 250 years of age, respectively) given the natural processes that create

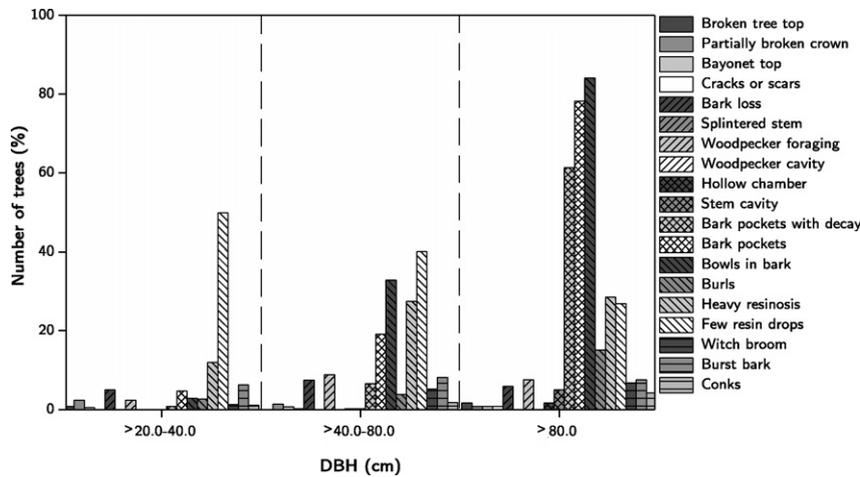


Fig. 8. Percentage of Douglas-fir trees with specific microhabitats in three tree diameter classes. Sample sizes were $n = 383$ in diameter class >20.0–40.0 cm, $n = 444$ in diameter class >40.0–80.0 cm, and $n = 119$ in diameter class >80.0 cm.

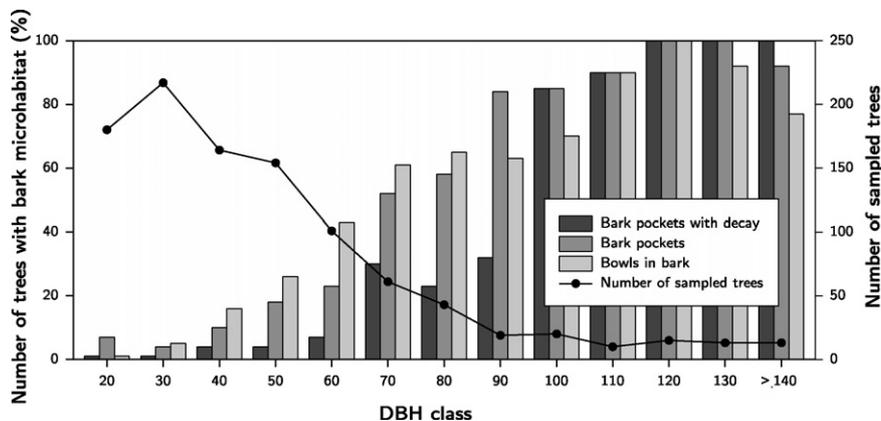


Fig. 9. Percentage of Douglas-fir trees in diameter classes with bark pockets, bark pockets with decay, and bowls in bark. Tree diameter classes were defined in the following way: e.g., the class ‘=20’ equals trees with a dbh between >20.0 cm and 30.0 cm. Because of the lack of trees in higher diameter classes, all trees with a diameter >140 cm were combined in the diameter class ‘>140’.

and maintain them over time beginning at around age 80–100. At this age, live Douglas-fir trees begin to develop a high number of various signs of decadence such as multiple tops, dead tops, bole and top rots, cavities, and brooms (Franklin et al., 2002). In the natural mature stands, a higher stand density in combination with remnant trees that have already reached an age or diameter at which microhabitat structures develop, may have caused this lack of differentiation with age in the natural stands of our study.

Combining natural and non-natural stands, both stand age and management history determined the microhabitat abundance and composition in our study. Microhabitat abundance and composition in the natural stands differed from other treatment groups with the low treatment intermediate between recently managed stands and unmanaged natural stands. The objective of traditional forest management is to produce stands that are mostly uniform in tree species, size, and spacing (Hansen et al., 1991). For this reason, many large and/or potential habitat trees are removed from the stand for their economic value or, if damaged, to reduce the number of competitors in order to increase future stand value. The intermediate position of low treatment stands could be explained by the longer time period without active management. Although microhabitats may have been removed at an early stand age in these stands, they may have again developed over the years.

Natural mature and old-growth stands differed from other age groups although not as convincingly as from other treatment groups. In their microhabitat composition, age groups were significantly different but only two groups of stands could be clearly distinguished: (a) the natural stands and (b) clearcut, young, middle-age, and managed mature stands. Old stands were found in both groups with some already resembling natural stands in their composition of microhabitats and some still lacking a high diversity of structures and being more similar to the younger age classes. The total abundance of microhabitats was significantly lower only on the clearcuts compared to the natural mature and natural old-growth stands. Except for the young stands, the abundance was lower in all other age groups compared to the natural stands although this difference was not statistically significant with the used test. The young stands had nearly as many microhabitats/ha as the natural stands only because of the high number of trees with signs of resin. Trees exude resin as a result of a high stand density and associated natural pruning and as defense mechanisms of trees with low vigor or Swiss needle cast. This disease has gained much attention in the Pacific Northwest lately and is caused by the ascomycete fungus *Phaeocryptopus gaeumannii* (Hansen et al., 2000).

Differences between actively managed stands and stands of different stand ages in comparison with natural forests have also been found in investigations of forest structure, including a few microhabitats (Bingham and Sawyer, 1992; Spies and Franklin, 1991), of arthropods on the forest floor (Addison et al., 2003) and canopy (Schowalter, 1995) in Douglas-fir dominated forests in the Pacific Northwest, and of microhabitats, ground vegetation, mosses, carabidae, and saproxylic beetles in European beech forests (Winter, 2005; Winter et al., 2005). In more than 100 years unmanaged beech forests, the number of microhabitats was approximately half of the microhabitat number in Douglas-fir forests in our study (Winter and Möller, 2008). This difference can be explained by species specific bark characteristics and resin flow which is typical of most coniferous trees. Both bark characteristics and resinosis were the most abundant microhabitats on Douglas-fir trees in our study. The bark of European beech is relatively thin and smooth compared to the thick (up to >30 cm) and rough bark of Douglas-fir. Therefore, bark structures such as bark pockets with and without decay and bowls in the bark are much more abundant in Douglas-fir than in European beech forests.

A higher variability in microhabitat composition in the natural stands and in stands that have not been treated silviculturally in many years can be explained by multiple pathways in stand development of natural Douglas-fir forests with low- and high-severity natural disturbances such as fire, insect outbreaks, diseases, and wind damage. These natural disturbances create a highly variable mosaic of vertical and horizontal structures. As a consequence and as is shown in this study, natural stands generally offer more structural features than traditionally managed stands regardless of their age because of the carryover of large snags, logs, and live trees that often persist after a disturbance and remain in a decay stage for a long time (Hansen et al., 1991). Only a variety of silvicultural treatments may be able to mimic at least some of the variation similar to the effects of natural disturbances (McComb et al., 1993). Compared to a traditionally managed forest stand, a natural, unmanaged forest can, therefore, generally be characterized by a higher structural complexity and ecological diversity (Winter and Möller, 2008; Franklin et al., 2002; Spies et al., 2002; McComb and Lindenmayer, 1999; Bull et al., 1997; Franklin and Spies, 1991; Hansen et al., 1991; Harmon et al., 1986).

5.2. Indicator microhabitats of natural forests

Indicator microhabitats are tree structures that are significantly more frequent and abundant in one group of stands of a certain treatment history or stand age. Except for one, all of the significant indicator microhabitats were found in natural mature and natural old-growth stands. Indicator microhabitats were primarily microhabitats that depend on large diameter trees: broken tree top, stem cavity, bark pocket with and without decay, bark bowl, burl, heavy resinosis, and bark burst. Additional indicator microhabitats were found only when comparing groups of different treatment histories: bayonet top, crack or scar, bark loss, and hollow chamber. Some of these microhabitats were also found by Bingham and Sawyer (1992) and Spies and Franklin (1991) to discriminate old-growth against mature and young Douglas-fir dominated stands in the Pacific Northwest. For example, the microhabitats broken tree top, resinosis, conks, and root and stem cavity increased with stand age in the study by Bingham and Sawyer (1992) and broken top, resinosis, root and stem cavity in the study by Spies and Franklin (1991). In both studies, however, no detailed microhabitat descriptions were given (compare with Table 3).

As expected, none of the investigated microhabitat structures was an indicator of recently managed stands. Resin drops were characteristic of young stands and stands with a low level of management, again, probably as a result of a high stand density and associated natural pruning and defense mechanisms of trees with low vigor or Swiss needle cast.

5.3. Relationship between tree diameter and the abundance of microhabitats in Douglas-fir

In general, structural attributes at the tree level, especially of the bole and crown, increase with tree age (Winter and Möller, 2008; Winter, 2005; VanPelt in Spies, 2004; Spies et al., 2002). The abundance of different microhabitats on a Douglas-fir tree in this study strongly increased on trees with ≥ 70 cm dbh up to an average of four different microhabitats/tree on trees ≥ 110 cm dbh. The most abundant microhabitats on large diameter trees were bark structures such as bark pockets, bark pockets with decay, and bowls in the bark in which litter is collected. These bark structures were found to be extremely important for invertebrates on beech trees (Winter and Möller, 2008) and are assumed to be as important for Douglas-fir communities (Franklin et al., 2002). A study by Michel and Winter (submitted for publication) confirms this significant relationship between tree diameter in Douglas-fir

and the occurrence of several bark microhabitat structures. Other microhabitats were not as abundant in this study presumably because, e.g., in contrast to bark features, many crown structures only occur on trees with an age of many 100 years (Van Pelt in Spies, 2004; Franklin et al., 2002). Even in the investigated old-growth forests, trees of that age were not very abundant on a per hectare basis. The low abundance of cavities in Douglas-fir has also been found by Martin et al. (2004) in British Columbia and can be explained by the high decay-resistant and resinous wood of Douglas-fir. Only live trees were analysed in our study and many microhabitats, especially cavities or hollow chambers, are created primarily in recently developed snags and on available tree species other than Douglas-fir (Martin et al., 2004; Bull et al., 1997; Parks et al., 1997).

6. Conclusions

Microhabitats are a key component of natural stands with larger trees and a higher complexity of structures, although little research has quantified their amount and composition (Winter, 2005; Franklin et al., 2002; Bingham and Sawyer, 1992; Spies and Franklin, 1991). In our study, we have confirmed that many of the investigated microhabitats are indeed indicators of natural mature and natural old-growth Douglas-fir dominated stands and especially of large diameter trees with a dbh of at least 70 cm. Old stands and stands that have not been harvested or otherwise treated silviculturally in many years have begun to resemble this microhabitat composition but have still not reached the same level of complexity.

As a consequence of our findings, active management for microhabitats in silviculturally-treated stands is important if the aim is to create structural complexity for more compositional diversity during timber harvest in even-aged Douglas-fir stands in the future (Franklin et al., 2002; Lindenmayer and Franklin, 2002). In order to increase structural complexity while resembling natural disturbances and stand development processes, proposed silvicultural practices include: e.g., the retention of biological legacies such as large diameter snags, logs, and old decadent trees, increasing the rotation length above the 40–50-year rotations used by many non-federal owners, harvesting by group selection and creating small openings, thinning, maintaining hardwood species, or creating snags by topping or intentionally killing single trees (Franklin et al., 2002; Muir et al., 2002; DeBell et al., 1997; Tappeiner et al., 1997; Curtis, 1995). With these measures, the current homogenization of forest plantations can be reduced with relatively minor losses of wood production especially if the reduced timber output is compared with the expected longterm social, economic, and ecological benefits (Curtis, 1995; Hansen et al., 1991; Franklin et al., 1986).

Following the extensive loss of natural stands of all ages and their structural complexity in the Pacific Northwest, forest reserves to enhance their natural development in the future or management studies in young Douglas-fir plantations to quickly develop these structures have been implemented within the last decades (e.g., Muir et al., 2002). Although most of the investigated stands in this study have been managed as part of alternative management studies with the aim to improve stand complexity, the time after study implementation may have been too short to already find a diverse array of structures in these stands. It may, therefore, take many decades to obtain Douglas-fir forests that approximate the criteria for old-growth according to the interim minimum standards for old-growth Douglas-fir forests in their native western Washington and Oregon (Old-Growth Definition Task Group, 1986). The preservation of the remaining natural Douglas-fir forests in addition to active management, therefore, is crucial for

maintaining a high biodiversity in the Pacific Northwest of the U.S.A.

While the existing network of forest reserves is small and a major expansion unlikely, the conservation of biological diversity highly depends on the acceptance of silvicultural practices in timber-oriented forest management that provide many of the microhabitats found in natural stands (McComb et al., 1993; Wilcove, 1989). A major step towards a higher awareness of the ecological importance of tree microhabitat structures would be to include these in forest inventory programs as has been the case in the German state of Brandenburg. There, microhabitats are monitored based on a study on the diversity of microhabitats in natural beech forests (Winter and Möller, 2008).

Future research may include the influence of abiotic variables, such as soil and microclimatic conditions, on the development of microhabitats, the dependence of these variables on forest structure, and a mechanistic approach to the functional role of each microhabitat in a forest ecosystem.

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