

KEY FACTORS AND CRITICAL THRESHOLDS AT STAND SCALE FOR SAPROXYLIC BEETLES IN A BEECH DOMINATED FOREST, SOUTHERN GERMANY

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RÉSUMÉ. — *Facteurs-clés et seuils critiques à l'échelle du peuplement forestier pour les coléoptères saproxyliques dans une forêt à dominance de hêtre du sud de l'Allemagne.* — Nous avons étudié en hêtre la importance de cinq paramètres structuraux typiques (âge, volume sur pied, diamètre à hauteur de poitrine, surface basale des arbres avec cavités contenant de l'humus, volume de bois mort) pour les coléoptères saproxyliques en relation avec la richesse spécifique et le nombre d'individus en utilisant la recherche directe en temps standardisé et des pièges à vitre dans 69 points-échantillons (0,1 ha). Des statistiques de rang dites «Maximally selected two-sample statistics» ont été utilisées pour identifier les paramètres importants et calculer les seuils critiques. Pour les facteurs spécifiés ci-dessus nous n'avons trouvé des corrélations significatives que pour les espèces menacées et celles indicatrices de conditions naturelles non perturbées. Le seul facteur statistiquement significatif fut la quantité de bois mort. Le seuil critique était de 38 à 58 m³/ha pour les espèces et de 144 m³/ha pour les nombres d'individus.

Mots-clés: Seuils; insectes saproxyliques; hêtraies; quantité de bois mort.

SUMMARY. — We studied the importance of five typical structural parameters (age, growing stock, breast height diameter, basal area of trees with cavities containing humus, dead wood volume) for saproxylic Coleoptera in relation to species richness and numbers of individuals in beech forest, using standard-time direct searches and window traps at 69 sampling plots (0.1 ha). Maximally selected two-sample statistics were used to identify the important parameters and calculate critical thresholds. For the factors specified above we found significant correlations only for endangered species and those indicating pristine conditions. The only statistically significant factor was the amount of dead wood. For species, the critical threshold was found between 38 and 58 m³/ha and for numbers of individuals at 144 m³/ha.

Keywords: Thresholds; saproxylic insects; beech forests; dead wood quantity.

Under natural conditions, most of Germany would be covered by beech dominated forests. As the result of clearance of these for cultivation during the past 2000 years, ancient deciduous forests are rare today (Christensen *et al.*, 2005). Thus the high percentage of endangered saproxylic beetle species is not surprising (Speight, 1989). Some of them are already extinct. Others survive only as small relict populations at a few sites in Germany (Müller, 2005). Due to the fact that a part of the saproxylic species is highly specialized, this group can be used world-wide as a valuable indicator for pristine or close to pristine conditions (Martikainen *et al.*, 1999; Schmidl & Bussler, 2004; Grove, 2002b).

Today, several forest companies are attempting to implement logging practices which are less disruptive to natural systems. For them the main question is: what kind of key structures

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are required by endangered forest species? Accordingly, we have already investigated parts of the fauna and flora of beech-dominated forests in relation to forest structures (Müller, 2005). In this paper we evaluate the importance of five main characteristics of forest structure for saproxylic beetles.

MATERIAL & METHODS

STUDY SITES AND SAMPLING DESIGN

The “Northern Steigerwald” is a forest area of about 10 000 ha, located in northern Bavaria (49°50'N; 10°29'E) which is dominated by hardwoods. The main tree species is beech (*Fagus sylvatica*). Average daily temperatures range from 7 to 8 °C and average annual precipitation from 700 to 800 mm. The predominant plant communities are “*Luzulo-Fagetum*” and “*Galio odorati-Fagetum*”. Some of the stands are well-known for containing the oldest beech trees in Germany; some being 350 years old. The northern parts of this woodland were intensively managed (utilization rates of more than 13 m³/ha/year in some decades) during the last 80 years, resulting in a lack of dead wood and dying trees. Dead wood structures have only been allowed to persist for a short period of 5-10 years. In the southern part, thinning in beech forests was rare during the last century. Clear-cut logging was practised in most cases. Therefore, more natural structures could accumulate in the remaining stands. Since 1972 the stands were logged with special consideration for conservation of dead wood structures. Three sections have been strict forest reserves for the last 25 years, and currently have more than 100 m³ coarse woody debris per hectare. 69 plots in pre-stratified beech stands on sandy soils were randomly selected throughout the whole area using the forest inventory grid. At the selected plots, beech stands grow on Triassic sandstones (so-called “Burgsandstein” and “Coburger Sandstein”).

FIELD METHODS

Data on forest structure (Tab. I) were collected using fixed-radius ($r = 17.82$ m) point counts measured with GPS. All pieces of dead wood >11 cm diameter were included, even dead wood attached to living trees. Diameters of trees with humus-filled cavities were measured at breast height (dbh). Stand age, growing stock and maximum dbh were taken from forest inventory data. The range of values is given in Table 1. For a more detailed description of methods see Müller (2005).

TABLE I
Variables measured from each of the 69 sampling plots

Variable code	Description	Range of value
<i>Independent</i>		
AGE	Age of oldest tree	100-350 years
DBH	Diameter at breast height of the 3 largest trees in plot	0-88 cm
GRS	Growing stock as the amount of all living woody debris per hectare larger than 7 cm	0-854 m ³ /ha
DWA	Total dead wood volume	3-562 m ³ /ha
HOT	Basal area of hollow humus trees	0-14 m ² /ha
<i>Dependent</i>		
SPEC	Number of saproxylic beetle species	12-52
IND	Individuals of saproxylic beetles	16-1713
ESPEC	Number of endangered saproxylic beetle species	0-11
EIND	Individuals of endangered saproxylic beetles	0-95
ISPEC	Number of indicator saproxylic beetle species	0-14
IIND	Individuals of indicator saproxylic beetles	0-106

At each point we conducted three standard-time direct searches for saproxylic beetles (Bussler *et al.*, 2004): one in spring, one in summer, and one in autumn 2005. One flight interception trap was also used at each of the 69 plots for beetle inventory (Grove, 2000). The results of both techniques were used in the final analysis. Nomenclature of saproxylic beetles follows the list by Schmidl & Bussler (2004). Endangered species data was obtained from the Bavaria Red Data Book 2003, which includes all saproxylic beetle species. Classification of indicator species for pristine conditions has been carried out previously (Müller 2005).

DATA ANALYSIS

We applied recursive partitioning with maximally selected rank statistics (Müller & Hothorn, 2004) for modelling the relationship of the dependent and independent variables. This method separates two groups of observations with maximal discrepancy of the response values by a simple cut-point defined with respect to the independent variable. Therefore, the procedure allows a multivariate approach which can be applied in the presence of several independent variables. The best predictor ("key factor") for high and low densities can then be selected from a group of habitat parameters. The statistical analysis is based on implementations of the above procedures using the add-on package "party" within the R system for statistical computing (version 2.2.1, R Development Core Team, 2005).

RESULTS

A total of 9301 individuals belonging to 283 species of saproxylic Coleoptera were found in the plots. Of these, 64 are endangered species (Schmidl & Bussler, 2003) and 63 are indicators for nearly pristine conditions (Tab. II).

TABLE II

Saproxylic beetle species found at 69 plots using windows traps and standard-time manual searches

Taxa	Red Data Book	Indicator for naturalness	Specimens	Frequence
<i>Tachya nana</i>			11	4
<i>Plegaderus dissectus</i>	endangered	X	4	1
<i>Abraeus granulum</i>	endangered	X	7	2
<i>Abraeus perpusillus</i>			30	7
<i>Paromalus flavigornis</i>			9	6
<i>Anisotoma humeralis</i>			1	1
<i>Anisotoma castanea</i>			4	1
<i>Anisotoma orbicularis</i>			2	2
<i>Agathidium nigripenne</i>			4	4
<i>Euthiconus conicicollis</i>	endangered	X	3	3
<i>Stenichnus godarti</i>			5	4
<i>Microscydmus minimus</i>		X	9	4
<i>Ptenidium gressneri</i>	endangered	X	32	6
<i>Ptenidium turgidum</i>	endangered	X	13	6
<i>Pteryx suturalis</i>			1	1
<i>Scaphidium quadrimaculatum</i>			3	2
<i>Scaphisoma agaricinum</i>			33	11
<i>Phloeocaris subtilissima</i>			45	14
<i>Acruia inflata</i>			5	4
<i>Phyllodrepa melanocephala</i>	almost end.		2	2
<i>Hapalaraea pygmaea</i>	endangered	X	3	2
<i>Phloeonomus punctipennis</i>			1	1
<i>Nudobius latus</i>			11	8
<i>Atrecus affinis</i>			6	5
<i>Hesperus rufipennis</i>	endangered	X	1	1
<i>Gabrius splendidulus</i>			17	9
<i>Velleius dilatatus</i>	almost end.		1	1
<i>Quedius truncicola</i>	almost end.	X	1	1
<i>Quedius microps</i>	almost end.		2	1
<i>Quedius brevicornis</i>	endangered	X	1	1
<i>Quedius maurus</i>			4	1
<i>Quedius xanthopus</i>			31	17
<i>Sepedophilus testaceus</i>			10	3
<i>Gyrophaena minima</i>			4	3
<i>Gyrophaena strictula</i>			11	3
<i>Gyrophaena boleti</i>			1816	6
<i>Agaricochara latissima</i>	X		1	1
<i>Placusa depressa</i>			8	1
<i>Placusa tachyporoides</i>			1	1

Taxa	Red Data Book	Indicator for naturalness	Specimens	Frequence
<i>Anomognathus cuspidatus</i>			10	4
<i>Leptusa pulchella</i>			4	3
<i>Leptusa fumida</i>			75	20
<i>Euryusa castanoptera</i>			11	4
<i>Euryusa optabilis</i>			3	1
<i>Bolitochara obliqua</i>			21	7
<i>Bolitochara lucida</i>			1	1
<i>Dinaraea aequata</i>			6	1
<i>Dadobia immersa</i>			1	1
<i>Atheta picipes</i>	X		1	1
<i>Phloeopora testacea</i>			1	1
<i>Phloeopora corticalis</i>			4	1
<i>Phloeopora scribae</i>			1	1
<i>Ischnoglossa prolixa</i>			1	1
<i>Bibloporus bicolor</i>			21	7
<i>Euplectus nanus</i>			5	3
<i>Euplectus karsteni</i>			7	6
<i>Euplectus fauveli</i>			2	2
<i>Plectophlaeus fischeri</i>			1	1
<i>Dictyopterus aurora</i>			2	2
<i>Pyropterus nigroruber</i>			1	1
<i>Platycis minutus</i>			1	1
<i>Platycis cosnardi</i>	endangered	X	1	1
<i>Malthinus punctatus</i>			83	37
<i>Malthinus seripepunctatus</i>			7	4
<i>Malthinus facialis</i>	almost end.	X	5	4
<i>Malthodes guttifer</i>			1	1
<i>Malthodes mysticus</i>			4	3
<i>Malthodes spathifer</i>			61	31
<i>Malthodes holdhausi</i>	almost end.	X	1	1
<i>Malthodes brevicollis</i>			2	1
<i>Malachius bipustulatus</i>			7	6
<i>Aplocnemus impressus</i>			1	1
<i>Aplocnemus nigricornis</i>			2	2
<i>Dasytes cyaneus</i>			25	18
<i>Dasytes plumbeus</i>			25	10
<i>Tillus elongatus</i>			31	20
<i>Thanasimus formicarius</i>			1	1
<i>Nemosoma elongatum</i>			4	4
<i>Thymalus limbatus</i>	endangered	X	1	1
<i>Hylecoetus dermestoides</i>			107	27
<i>Ampedus balteatus</i>			7	2
<i>Ampedus sanguineus</i>			1	1
<i>Ampedus pomorum</i>			31	23
<i>Ampedus nigrinus</i>			1	1
<i>Melanotus rufipes</i>			8	7
<i>Melanotus castanipes</i>			42	23
<i>Anostirus purpureus</i>			13	9
<i>Anostirus castaneus</i>			6	4
<i>Calambus bipustulatus</i>			1	1
<i>Hypoganus inunctus</i>	almost end.	X	2	1
<i>Denticollis rubens</i>	endangered	X	25	12
<i>Denticollis linearis</i>			34	19
<i>Melasis buprestoides</i>			19	15
<i>Eucnemis capucina</i>	endangered		8	3
<i>Dirhagus pygmaeus</i>	endangered	X	8	6
<i>Dirhagus lepidus</i>	endangered	X	3	3
<i>Hylis olexai</i>	endangered		5	4
<i>Hylis cariniceps</i>			2	2
<i>Hylis foveicollis</i>			2	1
<i>Anthaxia quadripunctata</i>			1	1

Taxa	Red Data Book	Indicator for naturalness	Specimens	Frequence
<i>Chrysobothris affinis</i>		1	1	
<i>Agrilus obscuricollis</i>		1	1	
<i>Agrilus olivicolor</i>		1	1	
<i>Agrilus viridis</i>		5	3	
<i>Prionocyphon serricornis</i>		X	2	2
<i>Megatoma undata</i>	endangered	X	7	5
<i>Cerylon fagi</i>		X	19	14
<i>Cerylon histeroides</i>			1	1
<i>Cerylon ferrugineum</i>			58	21
<i>Carpophilus sexpustulatus</i>			2	2
<i>Epuraea neglecta</i>			1	1
<i>Epuraea longula</i>			1	1
<i>Epuraea variegata</i>		X	7	4
<i>Cycharamus variegatus</i>		X	60	19
<i>Cycharamus luteus</i>			120	29
<i>Glischrochilus quadriguttatus</i>			9	9
<i>Rhizophagus depressus</i>			1	1
<i>Rhizophagus perforatus</i>	endangered		3	3
<i>Rhizophagus dispar</i>			85	24
<i>Rhizophagus bipustulatus</i>			116	28
<i>Rhizophagus nitidulus</i>	endangered		53	9
<i>Rhizophagus parvulus</i>	endangered		1	1
<i>Silvanus unidentatus</i>			2	2
<i>Silvanopus fagi</i>			1	1
<i>Uleiota planata</i>			111	15
<i>Tritoma bipustulata</i>			32	9
<i>Triplax russica</i>	endangered	X	7	5
<i>Triplax lepida</i>	endangered	X	47	6
<i>Dacne bipustulata</i>			3	3
<i>Diplocoelus fagi</i>	almost end.		2	2
<i>Pteryngium crenatum</i>	endangered	X	2	1
<i>Cryptophagus labilis</i>	endangered	X	2	2
<i>Cryptophagus dorsalis</i>	endangered		2	2
<i>Micrambe abietis</i>			11	7
<i>Atomaria turgida</i>			1	1
<i>Laemophlaeus monilis</i>	endangered	X	1	1
<i>Placonotus testaceus</i>			14	3
<i>Cryptolestes duplicatus</i>			1	1
<i>Latridius hirtus</i>	endangered	X	4	4
<i>Enicmus brevicornis</i>	endangered	X	3	3
<i>Enicmus fungicola</i>		X	1	1
<i>Enicmus atriceps</i>	endangered	X	1	1
<i>Stephostethus alternans</i>			63	21
<i>Stephostethus rugicollis</i>			1	1
<i>Litargus connexus</i>			47	22
<i>Mycetophagus quadripustulatus</i>			1	1
<i>Mycetophagus atomarius</i>			14	10
<i>Mycetophagus quadriguttatus</i>		X	1	1
<i>Mycetophagus multipunctatus</i>	endangered	X	19	4
<i>Mycetophagus fulvicollis</i>	endangered	X	1	1
<i>Cicones variegatus</i>	endangered		21	12
<i>Bitoma crenata</i>			46	4
<i>Orthoperus atomus</i>			3	1
<i>Arpidiphorus orbiculatus</i>	endangered		14	1
<i>Octotemnus glabriculus</i>			27	9
<i>Ropalodontus perforatus</i>	endangered	X	4	2
<i>Sulcaxis affinis</i>			174	9
<i>Sulcaxis fronticornis</i>			2	2
<i>Cis nitidus</i>			163	9
<i>Cis jacquemartii</i>	endangered	X	3	2
<i>Cis glabratus</i>			36	2

Taxa	Red Data Book	Indicator for naturalness	Specimens	Frequence
<i>Cis hispidus</i>			12	8
<i>Cis micans</i>			17	7
<i>Cis boleti</i>			62	15
<i>Cis rugulosus</i>			4	3
<i>Cis castaneus</i>			18	7
<i>Cis bidentatus</i>			4	3
<i>Orthocis alni</i>			4	4
<i>Orthocis festivus</i>			2	2
<i>Ennearthron cornutum</i>			11	6
<i>Hedobia imperialis</i>			25	21
<i>Xestobium plumbeum</i>			23	15
<i>Xestobium rufovillosum</i>		X	1	1
<i>Ernobius abietis</i>			2	2
<i>Gastrallus immarginatus</i>			1	1
<i>Anobium nitidum</i>			1	1
<i>Anobium costatum</i>			169	47
<i>Ptilinus pectinicornis</i>			106	37
<i>Dorcatoma dresdensis</i>	endangered		9	6
<i>Dorcatoma robusta</i>	endangered	X	3	3
<i>Calopus serraticornis</i>			1	1
<i>Ischnomera sanguinicollis</i>	endangered	X	1	1
<i>Ischnomera cyanea</i>			5	5
<i>Rabocerus foveolatus</i>			1	1
<i>Sphaeriestes castaneus</i>			1	1
<i>Vincenzellus ruficollis</i>			44	27
<i>Salpingus planirostris</i>			27	14
<i>Salpingus ruficollis</i>			18	15
<i>Pyrochroa coccinea</i>			234	30
<i>Schizotus pectinicornis</i>			203	24
<i>Cyrtanaspis phalerata</i>	endangered	X	1	1
<i>Anaspis frontalis</i>			34	20
<i>Anaspis marginicollis</i>	endangered	X	1	1
<i>Anaspis thoracica</i>			5	4
<i>Anaspis ruficollis</i>	endangered	X	5	5
<i>Anaspis rufilabris</i>			29	20
<i>Anaspis flava</i>			1	1
<i>Aderus populeus</i>	endangered	X	5	2
<i>Tomoxia bucephala</i>			3	2
<i>Variimorda villosa</i>			2	2
<i>Mordellistena neuwaldeggiana</i>			1	1
<i>Mordellochroa abdominalis</i>			5	4
<i>Hallomenus binotatus</i>			1	1
<i>Orchesia minor</i>			1	1
<i>Orchesia fasciata</i>	endangered	X	6	3
<i>Orchesia undulata</i>			22	16
<i>Abdera flexuosa</i>	endangered	X	2	2
<i>Phloiotrya rufipes</i>	endangered		5	5
<i>Melandrya caraboides</i>			3	1
<i>Melandrya barbata</i>	endangered	X	2	2
<i>Conopalpus testaceus</i>			1	1
<i>Conopalpus brevicollis</i>	endangered	X	2	2
<i>Tetratoma fungorum</i>			62	3
<i>Tetratoma ancora</i>	endangered	X	9	4
<i>Allecula morio</i>	endangered	X	6	6
<i>Allecula rhenana</i>	endangered	X	1	1
<i>Mycetochara linearis</i>			21	7
<i>Bolitophagus reticulatus</i>	endangered	X	143	11
<i>Platydema violaceum</i>		X	2	1
<i>Corticeus unicolor</i>			362	27
<i>Stenomax aeneus</i>			1	1
<i>Dorcus parallelipipedus</i>		X	13	4

Taxa	Red Data Book	Indicator for naturalness	Specimens	Frequence
<i>Platycerus caraboides</i>			12	10
<i>Sinodendron cylindricum</i>	endangered	X	50	20
<i>Prionus coriarius</i>			1	1
<i>Tetropium castaneum</i>			1	1
<i>Rhagium bifasciatum</i>			10	5
<i>Rhagium mordax</i>			355	24
<i>Rhagium inquisitor</i>			12	3
<i>Oxymirus cursor</i>			2	2
<i>Grammoptera ruficornis</i>			3	2
<i>Alosterna tabacicolor</i>			23	8
<i>Leptura maculata</i>			15	10
<i>Leptura aethiops</i>			1	1
<i>Anoplodera sexguttata</i>	endangered	X	2	2
<i>Corymbia maculicornis</i>			8	1
<i>Corymbia rubra</i>			1	1
<i>Corymbia scutellata</i>	endangered	X	6	6
<i>Pachytodes cerambyciformis</i>			14	3
<i>Stenurella melanura</i>			29	6
<i>Stenurella nigra</i>			1	1
<i>Pyrrhidium sanguineum</i>			12	6
<i>Phymatodes testaceus</i>			2	2
<i>Phymatodes pusillus</i>	endangered	X	1	1
<i>Clytus arietis</i>			3	1
<i>Anaglyptus mysticus</i>			2	2
<i>Pogonocherus hispidulus</i>			1	1
<i>Leiopus nebulosus</i>			18	11
<i>Exocentrus adspersus</i>	endangered	X	2	1
<i>Saperda populnea</i>			1	1
<i>Stenostola dubia</i>			3	3
<i>Platyrhinus resinosus</i>	endangered	X	6	4
<i>Dissoleucas niveirostris</i>			1	1
<i>Anthribus albinus</i>			10	5
<i>Scolytus intricatus</i>			23	15
<i>Hylastes opacus</i>			1	1
<i>Hylastes cunicularius</i>			1	1
<i>Hylurgops palliatus</i>			49	34
<i>Tomicus piniperda</i>			6	5
<i>Leperisinus fraxini</i>			7	5
<i>Dryocoetes autographus</i>			1	1
<i>Dryocoetes villosus</i>			1	1
<i>Cryphalus abietis</i>			10	10
<i>Ernporicus fagi</i>			52	29
<i>Pityophthorus pityographus</i>			1	1
<i>Taphrorychus bicolor</i>			365	34
<i>Pityogenes chalcographus</i>			11	9
<i>Ips cembrae</i>			250	1
<i>Xyleborus dispar</i>			23	13
<i>Xyleborus saxeseni</i>			30	8
<i>Xyleborus monographus</i>			3	3
<i>Xyleborus germanus</i>			1068	49
<i>Xyleborus peregrinus</i>			37	17
<i>Xyloterus domesticus</i>			471	61
<i>Xyloterus signatus</i>			125	46
<i>Xyloterus lineatus</i>			14	10
<i>Phloeophagus lignarius</i>			4	4
<i>Stereocorynes truncorum</i>			5	4
<i>Pissodes piceae</i>			1	1
<i>Magdalis phlegmatica</i>			1	1
<i>Magdalis duplicita</i>			2	1
<i>Hylobius abietis</i>			1	1
<i>Acalles hypocrita</i>		X	1	1

For the sum of all species and the total numbers of individuals, none of the five parameters was significant, but for the contingent of endangered species a threshold value of $38.2 \text{ m}^3/\text{ha}$ dead wood volume was found ($p < 0.001$). Using the number of indicator species as a dependent variable, a threshold of $58.5 \text{ m}^3/\text{ha}$ dead wood could also be derived. With respect to specimen numbers of endangered and indicator species, the amount of dead wood was similarly found to be the key factor. However, the threshold value was much higher at $144.4 \text{ m}^3/\text{ha}$ for both of these groups (both $p < 0.001$), although a second significant threshold ($p < 0.001$) was identified at $57.9 \text{ m}^3/\text{ha}$ (Fig. 1).

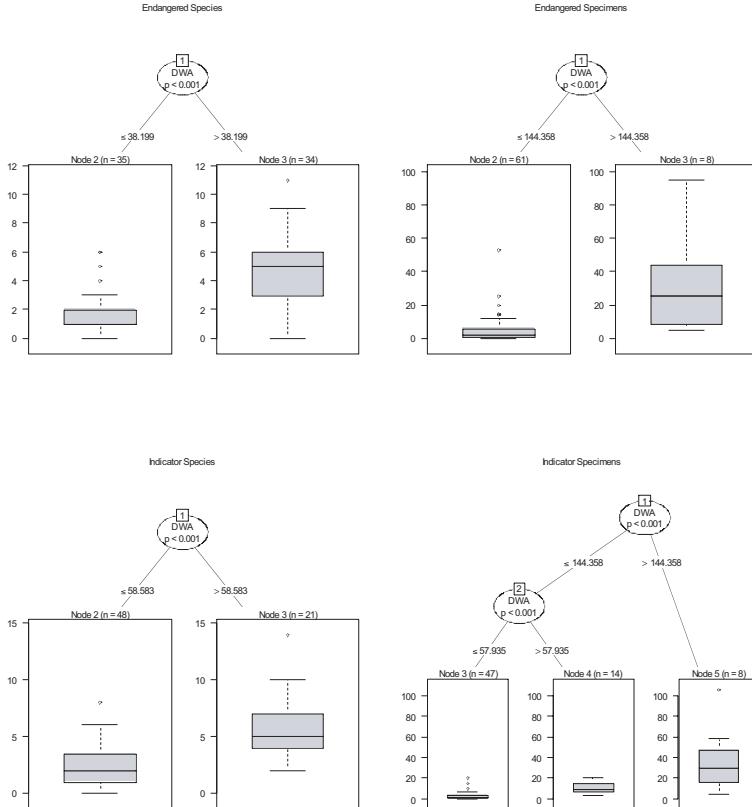


Figure 1. — Thresholds for different independent variables (DWA=Dead wood amount per hectare). Number of plots per group and p-values are given.

DISCUSSION

The fact that total species numbers and numbers of individuals do not relate to dead wood amount or age would have been surprising 15 years ago. Today, as a result of a series of standardized investigations conducted in recent years, it is generally accepted that forest utilization does not lead automatically to a reduced number of species (Bader *et al.*, 1995; Ammer, 2001; Lammertink, 2004; Winter *et al.*, 2005). However, the total number of saproxylic species seems unsuitable for the assessment of naturalness of beech-forests. This is because of beneficial effects for some species due to forest activities, for example the introduction to beech forest of non-indigenous species such as spruce. As a consequence of this, 30 of the 283 species found at the plots in our investigation depend on spruce. These are not species of the natural beech forest communities.

In forest management, structural descriptions and guidelines are in most cases based on parameters such as breast height diameter, growing stock and age. Whilst these parameters have an obvious economic significance, our results do not indicate that they are important for endangered forest species. The outstanding factor was simply the amount of dead wood. With respect to the whole saproxylic beetle community this factor proves to be an even better

predictor than the number of trees with cavities. Nevertheless, cavities are very important, especially for endangered species in beech forests (Jarzabek, 2006). Regarding new objectives in forest management, such as a higher degree of naturalness, these findings shift the role of main indicator value to the amount of dead wood.

A volume of 40-60 m³ of dead wood/ha seems to be high, when compared with the usual amount of dead wood in commercial forests today. However, the results of our present study and for groups of organisms such as molluscs or fungi, as well as for previous investigations on other groups, all indicate the requirement for such a large quantity of dead wood by rare, endangered and highly specialized species.

Hardly any literature is available which addresses the question of dead wood quantity in forest with potential donor populations (high numbers of individuals). Our results with thresholds of over 100 m³/ha of dead wood correspond with data from virgin beech forests and old forest strict conservation areas (Christensen *et al.*, 2005) where indicator species can be found in much higher numbers than in commercial forest (Müller *et al.*, 2005).

We should not forget the fact of impoverished beetle communities in our Central European forest landscape. All results can only be implemented in forest management for species that still persist as viable populations, and cannot assist extinct or nearly extinct species. Studying the requirements of the latter for particular forest structures in beech forests needs further research in the large virgin forests of Eastern Europe, where a complete saproxylic fauna can still be found (Bussler *et al.*, 2005).

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REFERENCES

- AMMER, U. (2001). — Vergleichende waldökologische Untersuchungen in Naturwaldreservaten und Wirtschaftswäldern unterschiedlicher Naturnähe in Mittelschwaben - Schlussfolgerungen für die forstliche Praxis. *LWF-Bericht*, 33: 50-58.
- BADER, P., JANSSON, S. & JONSSON, B.G. (1995). — Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. *Biol. Cons.*, 72: 355-362.
- BUSSLER, H., MÜLLER, J. & DORKA, V. (2005). — European Natural Heritage: The saproxylic beetles in the proposed parc national Defileul Jiului. *Analele ICAS*, 18: 55-71.
- BUSSLER, H., MÜLLER, J. & SIMON, U. (2004). — Erfassung xylobionter Käfer in Waldökosystemen. *NUL*, 36: 197-201.
- CHRISTENSEN, M., HAHN, K., MOUNTFORD, E.P., ÓDOR, P., STANDÓVAR, T., ROZENBERGAR, D., DIACI, J., WIJDEVEN, S., MEYER, P., WINTER, S. & VRSKA, T. (2005). — Dead wood in European beech (*Fagus sylvatica*) forest reserves. *For. Ecol. Manage.*, 210: 267-282.
- GROVE, S. (2000). — Trunk window trapping: an effective technique for sampling tropical saproxylic insects. *Mem. Queensland Mus.*, 46: 149-160.
- GROVE, S. (2002b). — Saproxylic insect ecology and the sustainable management of forests. *Ann. Rev. Ecol. Syst.*, 33: 1-23.
- JARZABEK, A. (2006). — Schatztruhen im Buchenwald. *LWF aktuell*, 53: 4-5.
- LAMMERTINK, M. (2004). — A multiple-site comparison of woodpecker communities in Bornean lowland and hill forests. *Cons. Biol.*, 18: 746-757.
- MARTIKAINEN, P., SIITONEN, J., KAILA, L., PUNTTILA, P. & RAUH, J. (1999). — Bark beetles (Coleoptera, Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *For. Ecol. Manage.*, 116: 1-3.
- MÜLLER, J. (2005). — *Waldstrukturen als Steuergröße für Artengemeinschaften in kollinen bis submontanen Buchenwäldern*. Dissertation, Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt. Technische Universität München, <http://mediatum.ub.tum.de>.
- MÜLLER, J., BUSSLER, H., BENSE, U., BRUSTEL, H., FLECHTNER, G., FOWLES, A., KAHLEN, M., MÖLLER, G., MÜHLE, H., SCHMIDL, J. & ZABRANSKY, P. (2005a). — Urwald relict species - Saproxylic beetles indicating structural qualities and habitat tradition. *Waldökologie Online*, 2: 106-113.

- MÜLLER, J., BUSSLER, H. & DORKA, V. (2005b). — Karpatenwälder als Bezugsflächen für mitteleuropäische Urwälder. *AFZ/Der Wald*, 9: 482-484.
- MÜLLER, J. & HOTHORN, T. (2004). — Maximally selected two-sample statistics as a new tool for the identification and assessment of habitat factors with an application to breeding-bird communities in oak forests. *Eur. J. For. Res.*, 123: 219-228.
- SCHMIDL, J. & BUSSLER, H. (2004). — Ökologische Gilden xylobionter Käfer Deutschlands. *NUL*, 36: 202-218.
- SCHMIDL, J., BUSSLER, H. & LORENZ, W. (2003). — Die Rote Liste gefährdeter Käfer Bayerns im Überblick. Pp. 99-101 in: J. Voith (ed.), *Schriftenreihe Bayer. Landesamt für Umweltschutz* 166.
- SPEIGHT, M.C.D. (1989). — *Saproxylic invertebrates and their conservation*. Council of Europe, Nature and environment series, 42, Strasbourg.
- WINTER, S., FLADE, M., SCHUMACHER, H., KERSTAN, E. & MÖLLER, G. (2005). — The importance of near natural stand structures for the biocoenosis of lowland beech forests. *For. Snow Landsc. Res.*, 79: 127-144.