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REVIEW

A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests

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Abstract In contemporary forest management, also of commercial forests, threshold values are widely used for consideration of biodiversity conservation. Here, we present various aspects of dead-wood threshold values. We review published and unpublished dead-wood threshold data from European lowland beech–oak, mixed-montane, and boreo-alpine spruce–pine forests separately to provide managers of European forests with a baseline for management decisions for their specific forest type. Our review of dead-wood threshold data from European forests revealed 36 critical values with ranges of 10–80 m^3 ha^{-1} for boreal and lowland forests and 10–150 m^3 ha^{-1} for mixed-montane forests, with peak values at 20–30 m^3 ha^{-1} for boreal coniferous forests, 30–40 m^3 ha^{-1} for mixed-montane forests, and 30–50 m^3 ha^{-1} for lowland oak–beech forests. We then expand the focus of dead-wood threshold analyses to community composition. We exemplify the two major statistical methods applied in ecological threshold analysis to stimulate forest researchers to analyze more of their own data with a focus on thresholds. Finally, we discuss further directions of dead-wood threshold analysis. We anticipate that further investigations of threshold values will provide a more comprehensive picture of critical ranges for dead wood, which is urgently needed for an ecological and sustainable forestry.

Keywords Thresholds · Conditional inference tree · Maximally selected rank statistic · Logistic regression · Bootstrapping · Variable selection

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Introduction

Dead and dying trees have been shown to be a key habitat feature for a broad range of saproxylic organisms worldwide over the past 20 years (Dickson et al. 1983; Grove 2002b; Davies et al. 2008). The dominant saproxylic groups include fungi (Bader et al. 1995; Heilmann-Clausen and Christensen 2005; Junninen et al. 2006), bryophytes (Ódor et al. 2006), lichens (Ulikzka and Angelstam 2000), beetles (Grove 2002a; Davies et al. 2008), amphibians (DeMaynadier and Hunter 1995), birds (Utschick 1991; Martin and Eadie 1999; Bütler et al. 2004), and small mammals (Sullivan and Sullivan 2001). Other, less dominant groups include mollusks (Kappes 2005; Müller et al. 2005b; Kappes et al. 2009), flat bugs (Jonsell et al. 2005; Möller 2005; Goßner 2006), syrphids (Speight 1989; Reemer 2005; Dziock 2006), and parasitic diptera of wood-inhabiting beetles (Hövemeyer and Schauermann 2003; Hilszczanski et al. 2005). The role of the vertical and horizontal distribution of dead wood as habitat in forests has been considered (Schiegg 2000; Goßner 2004; Müller

2004; Vodka et al. 2009), including underground (Schulz and Ammer 1997) and in rivers and lakes (Hering et al. 2000). Most of the numerous reviews on the relationship of various organisms and dead-wood point to the necessity of an increase in the amount of dead wood in forests, but mostly provide only more or less vague suggestions (Speight 1989; Kirby et al. 1998; Siitonen 2001; Grove 2002c; Grove and Meggs 2003; Christensen et al. 2005; Davies et al. 2008).

Although the great importance of dead wood is well known today, there are no simple and statistically based guidelines on this aspect of forest management. This lack of basic guidelines is often rationalized by the highly complex relationships involved (Grove 2002b; Angelstam et al. 2003; Schlaepfer and Bütler 2004; Stokland et al. 2004), which makes it difficult to come up with simple single-value suggestions for a broad range of taxa (Ranius and Fahrig 2006). Yet, for forest managers, dead-wood conservation is just one small aspect of their work, and, therefore, simple but ecologically meaningful guidelines are required (Müller et al. 2007a).

The simplest guidelines cover critical thresholds for single species, species number, or the community response to habitat alteration, but "simple" does not mean that these thresholds are easy to identify. Thresholds or points or zones of change in the state of matter (May 1973) have been known to exist in the physical sciences since the late 1700s. This concept was introduced to biological conservation during the past 15 years, forced by the accelerating pace of a diminishing biodiversity (Muradin 2001; Huggett 2005). Such a loss process could be slowed down by expanding the use of statistically validated values. However, the dependency of temporal and spatial scales must be considered, which for dead wood can be the micro-scale of a log and the meso-scale of a stand or forest landscape (Grove 2002b; Ranius and Fahrig 2006). There is no question that such robust suggestions for an ecologically sustainable forest management are needed (Ganey 1999; Grove 2002b; Neft 2006; Ranius and Fahrig 2006), but a broader use of thresholds in practice has been limited for the following reasons. First, the diverse threshold values obtained in various studies or the various investigated dependent variables make it questionable whether recommendations based on thresholds can be put into practice (Ranius and Fahrig 2006). Secondly, methods to identify thresholds statistically in forest ecological studies are not widely established. Thirdly, the information on the dead-wood thresholds of different forest types is scattered throughout the scientific literature and therefore hardly available to most forest institutes, which have to develop regional guidelines.

Here, we (1) review dead-wood thresholds as a baseline for management guidelines for European forests, (2) present two widely used statistical methods, following the suggestion of Huggett (2005), to stimulate forest ecologists to analyze their data with a focus on threshold values, (3) expand the threshold analyses to community shifts, and (4) discuss the threshold approach in dead-wood research and future directions needed in this field of conservation biology. To our knowledge, this is the first comprehensive picture of dead-wood thresholds in different forest ecosystems of Europe.

Why is the amount of dead wood important for diversity?

In this review, we will concentrate on the amount of dead wood as a critical environmental variable. From the ecological point of view, there are two major explanations for why an increase in the amount of dead wood increases the number and density of species and diversifies the species composition. First, higher amounts of available dead wood lead to more dead-wood surface area and higher resource availability (Bässler et al. 2010). According to the island theory, we can therefore expect a higher species number on sampling units with a larger "island" (MacArthur and Wilson 1967). Secondly, larger surface areas lead to more different available habitats (Boecklen 1986). Many studies have shown the importance of different types of dead wood, i.e., tree species, decomposition stage, diameter, etc. (Similä et al. 2003; Heilmann-Clausen and Christensen 2004). A critical consideration of most of these studies as well as an analysis of our own data (from beech–oak, beech–fir, and spruce forests in Germany) revealed that in most survey data sets, there is a clear correlation between the amount and the diversity of dead wood. To demonstrate this, we correlated diversity of dead wood with the amount of dead-wood. Here, we defined the diversity of dead wood considering that as more different dead-wood features become available, more habitat niches are offered and therefore the habitat diversity increases (Speight 1989). In one example with 69 sampling plots in beech–oak forests (Müller et al. 2008), we calculated the diversity of dead wood per 0.1 ha plots by summarizing the number of different dead-wood types categorized according to the tree genus (*Fagus*, *Quercus*, *Acer*, *Betula*, *Populus*, *Pinus*, *Picea*), decomposition stage [stages 1–4 according to Albrecht (1991)], diameter class (10–19 to 110–119 cm in 10 cm increments), and type of dead wood (standing or downed) for each object >12 cm in diameter following the method of Siitonen et al. (2000). This example shows a clear relationship between the log(dead-wood amount) and the dead-wood diversity (Fig. 1a). Furthermore, also the number of critically endangered species was correlated with the amount of dead wood (Fig. 1b). These results

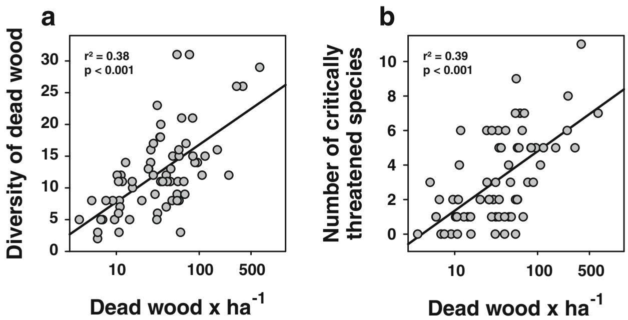

Fig. 1 **a** *Scatter plots*, linear regression, and Spearman correlation statistics of the relationship between log(dead-wood volume m^3 ha^{-1}) in 0.1 ha plots and the diversity of dead wood measured as number of different types of dead wood following Siitonen et al. (2000) in a beech–oak forest (see text). **b** Number of critically threatened saproxylic beetles (Red List of Bavaria 2004, combining the IUCN classifications regionally extinct, critically endangered, and endangered) in the same sampling plots (cf. (Müller et al. 2008)

emphasize that under field conditions, a high diversity of dead wood at a specific site is generally closely linked to a high amount of dead wood. Similar results have been shown also for boreal and tropical forests (Martikainen et al. 1999; Grove 2002b; Similä et al. 2003). This correlation obviates the question whether the amount or diversity is more important. For convincing answers, experimental studies are clearly required. Even though the amount and diversity of dead-wood features are closely related, we are aware that cryptic dead-wood features, such as hollow trees (Ranius 2002), can occur even in forests or parks with a low total amount of dead wood, and nevertheless can be an important habitat for some highly endangered saproxylic species.

Evidence of dead-wood thresholds for saproxylic organisms

We identified relevant threshold studies dealing with dead-wood amount by searching the electronic databases ISI Web of Knowledge and Google Scholar. Couplets of the following key terms were used for searching: dead wood, coarse woody debris, threshold, cutpoint, and logistic regression. We also included our own data and the gray literature of researchers investigating dead-wood thresholds. All results were filtered before being accepted into the final data set. We included only those articles that provided recommendations, implications, or derivations of threshold values considering dead wood. Therefore, studies that demonstrated only a dependency of an organism on dead wood without threshold values were not considered. Our final data set yielded 37 thresholds for dead wood using the occurrence of single species, the number of species of a certain taxonomical group, or the density of a certain taxonomical group as dependent variable (Table 1). When we searched the databases without biogeographical restrictions, all values except one from Canada were from European forests. We further divided the 36 European values into three coarse forest types: boreo-alpine spruce–pine forests, montane-mixed (beech–fir–spruce) forests, and lowland beech–oak forests. Histograms classified according to the three forest types showed values with ranges of 10–70 m^3 ha^{-1} for boreal forests and 10–150 m^3 ha^{-1} for lowland forests and mixed-montane forest (Fig. 2). We found a peak at 20–30 m^3 ha^{-1} for boreal coniferous forests, 30–40 m^3 ha^{-1} for mixed-montane forests, and 30–50 m^3 ha^{-1} for lowland forests. The values for the boreo-alpine forests tended to be somewhat lower, while some values for montane forests >100 m^3 ha^{-1} were found. Considering the amount of dead wood in natural forests of these three types (Fig. 2), the trend of lower thresholds is in line with the generally lower amounts of living wood. The general picture of values is less comprehensive for mixed-montane forests, underlined by several gaps along the gradient in the histogram (Fig. 2b).

We found 14 threshold values for single species (Table 1), with several instances of the woodpecker species *Picoides tridactylus* and *Picoides leucotos*. In contrast to the high numbers of species related to dead wood (around 25–30% of forest inhabitants; Schmidt 2006; Stokland et al. 2004), the results obtained reveal that our knowledge of the response of single species is still rather low. We found 18 dead-wood threshold values for a higher species richness of particular saproxylic communities and 5 threshold values for the density of saproxylic communities. When we visually summarized the range of values reported, we concluded that at local values >30–50 m^3 ha^{-1} for broadleaf forests and 20–30 m^3 ha^{-1} for boreo-alpine forests, the majority of species and communities seem to be present. However, for long-term sustainability, it is also of importance to consider the spatial and temporal configuration of dead-wood habitats. To date, only a few studies in this area are available (i.e., Jönsson et al. 2008; Penttilä et al. 2006), and only one deals with thresholds (Okland et al. 1996).

Statistical methods used to identify thresholds

A review of methods used to identify ecological thresholds, cutpoints, and regime shifts in general has been recently published by Andersen et al. (2008). The aim of their review was partly similar to ours, namely to reduce the gap between the prominence of current theoretical frameworks involving ecological thresholds and regime shifts, and the paucity of efforts to conduct simple tests and quantitatively

Table 1 A summary of the characteristics and results of 37 studies investigating threshold values of the occurrence or number of species in relation to dead-wood volume

Country or area	Threshold value of range	Dependent variable	Taxonomical group	Forest type	Methodology	Year	Reference
Germany	5–10 $m^3\ ha^{-1}$ adequate 10–20 $m^3\ ha^{-1}$ high	Number of species	Wood-inhabiting species	Temperate deciduous forest	Expert assessment	1991	(Ammer 1991)
Germany	5–10 m^3 ha (>20 cm DBH) adequate 20–60 $m^3\ ha^{-1}$ optimal	Number of species	Forest birds	Spruce-dominated commercial forests	Statistical (Regression analysis)	1991	(Utschick 1991)
Norway	24–29 $m^3\ ha^{-1}$	Occurrence of single species	Five saproxylic beetles	Boreal spruce forests with pine	Statistical (minimum amount of dead wood required for the occurrence of single species)	1996	(Okland et al. 1996)
Germany	>10 $m^3\ ha^{-1}$ (>20 cm DBH)	No target	Saproxylic organisms	Beech forests	Expert assessment (commercial forests)	1997	(Erdmann and Wilke 1997)
Germany	40 $m^3\ ha^{-1}$	Number of species	Saproxylic beetles	Oak forests	Expert assessment (theoretical implications from beetle breeding)	1998	(Haase et al. 1998)
Great Britain	20–40 $m^3\ ha^{-1}$ medium (fallen only) >40 high (fallen only)	No target	Saproxylic organisms	Mixed deciduous woodland	Expert assessment (comparison of managed/unmanaged forests)	1998	(Kirby et al. 1998)
Scandinavia	>50 $m^3\ ha^{-1}$	Number of species	Saproxylic beetles	Boreal spruce forests	Statistical (regression analysis)	2000	(Martikainen et al. 2000)
Scandinavia	>70 $m^3\ ha^{-1}$	Occurence	*Pytho kolwensis*	Boreal spruce forests	Statistical (minimum amount of dead wood in occupied stands)	2000	(Siitonen and Saaristo 2000)
Austria	58 $m^3\ ha^{-1}$	Occurrence	White-backed woodpecker (*Dendrocopos leucotos*)	Montane beech fir forests	Statistical (amount of dead wood in occupied territories)	2002	(Frank 2002)
Scandinavia	10–20 $m^3\ ha^{-1}$	Occurrence	White-backed woodpecker (*Dendrocopos leucotos*)	Boreal spruce forests	Expert assessment	2003	(Angelstam 2002)
Germany	11–30 $m^3\ ha^{-1}$	Occurrence	Three-toed woodpecker (*Picoides tridactylus*)	Norway-Spruce forests	Expert assessment	2004	(Pechacek and D'Oleire-Oltmanns 2004)
Finland	>20 $m^3\ ha^{-1}$ to >100 $m^3\ ha^{-1}$	Number of species	Threatened polypore wood-decaying fungi	Norway-Spruce-dominated forests	Expert assessment (polypore occurrence)	2004	(Penttilä et al. 2004)
Switzerland, Sweden	>15 $m^3\ ha^{-1}$ (standing only) 33 $m^3\ ha^{-1}$	Occurrence	Three-toed woodpecker (*Picoides tridactylus*)	Alpine and boreal Norway-Spruce-dominated forests	Statistical (logReg)	2004	(Bütler et al. 2004)
Germany	30–50 $m^3\ ha^{-1}$	Number of individuals of woodpecker, saproxylic beetles, polypore species	Xylobiontic birds; wood-inhabiting fungi; saproxylic beetles	Lowland beech forests	Expert assessment	2005	(Winter et al. 2005; Flade et al. 2004)
Germany	70 $m^3\ ha^{-1}$	Number of species	Endangered saproxylic beetles	Lowland beech forests	Statistical (CIT)	2005	G. Möller, (unpublished data)
Germany	30 $m^3\ ha^{-1}$	No target	Forest insects	Forest	Expert assessment	2005	(Loser et al. 2005)

Table 1 continued

Country or area	Threshold value of range	Dependent variable	Taxonomical group	Forest type	Methodology	Year	Reference
Germany	57 m^3 ha^{-1}	Density	Land snails (individuals)	Colline-submontane beech forests	Statistical (CIT)	2005	(Müller et al. 2005b)
Germany	38–58 m^3 ha^{-1}	Number of species	Saproxylic beetles (indicator of naturalness)	Colline-submontane beech forests	Statistical (CIT)	2005	(Müller 2005)
Germany	98–140 m^3 ha^{-1}	Density	Saproxylic beetles (indicator of naturalness)	Colline-submontane beech forests	Statistical (CIT)	2005	(Müller 2005)
Germany	61 m^3 ha^{-1}	Density	Wood-inhabiting fungi	Colline-submontane beech forests	Statistical (CIT)	2006	(Müller et al. 2007b)
Germany	29 m^3 ha^{-1}	Number of species	Red-listed saproxylic species	Colline-submontane beech forests	Statistical (CIT)	2006	(Müller and Bussler 2008)
Europe	8–17 m^3 ha^{-1} snags ($\sim$ 36 m^3 ha^{-1} dead wood)	Occurrence	White-backed woodpecker (*Dendrocopos leucotos*)	Temperate deciduous forests of the hemiboreal zone	Statistical (logReg)	2008	(Roberge et al. 2008)
Germany	74 m^3 ha^{-1}	Occurrence	Three-toed woodpecker	Norway-Spruce-dominated forests	Statistical (CIT)	2008	(Kratzer 2008)
Europe	>20 m^3 ha^{-1} downed dead wood (=30 m^3 ha^{-1} total volume)	Density	Clausilidae, litter dwelling fauna	Colline-submontane beech forests	Statistical (ANOVA among classes of dead-wood amount)	2009	(Kappes et al. 2009)
Germany	141 m^3 ha^{-1}	Number of species	Cavity-breeding birds	Montane mixed spruce–beech–fir forests	Statistical (CIT)	2009	(Moning and Müller 2008)
Germany	17 m^3 ha^{-1} (coniferous trees)	Number of species	Mosses	Montane mixed spruce–beech–fir forests	Statistical (CIT)	2009	(Moning et al. 2009)
Germany	37 m^3 ha^{-1}	Number of species	Red-listed saproxylic beetle species and Urwald relict species	Montane mixed spruce–beech–fir forests	Statistical (CIT)	2009	(Moning et al. 2009)
Germany	127 m^3 ha^{-1}	Number of species	Lichens	Montane mixed spruce–beech–fir forests	Statistical (CIT)	2009	(Moning et al. 2009)
Canada	35 m^3 ha^{-1}	Occurrence	Black-backed woodpecker (*Picoides arcticus*)	Boreal spruce forest	Statistical (amount of dead wood in occupied territories)	2009	(Tremblay et al. 2009)
Germany	123 m^3 ha^{-1}	Occurrence	*Antrodiella citrinella*	Montane mixed spruce–beech–fir forests	Statistical (CIT)	2009	(Bässler and Müller 2010)

Values are given as the volume of dead wood >12 cm in total. For studies that gave only the volume of standing dead wood, we used the general proportions of 1/3 standing and 2/3 downed dead wood for estimating the corresponding total dead-wood volume. Thresholds implicated from general studies and not derived directly from data were expertly assessed. CIT, conditional inference tree; logReg, logistical regression; DBH, diameter at breast height

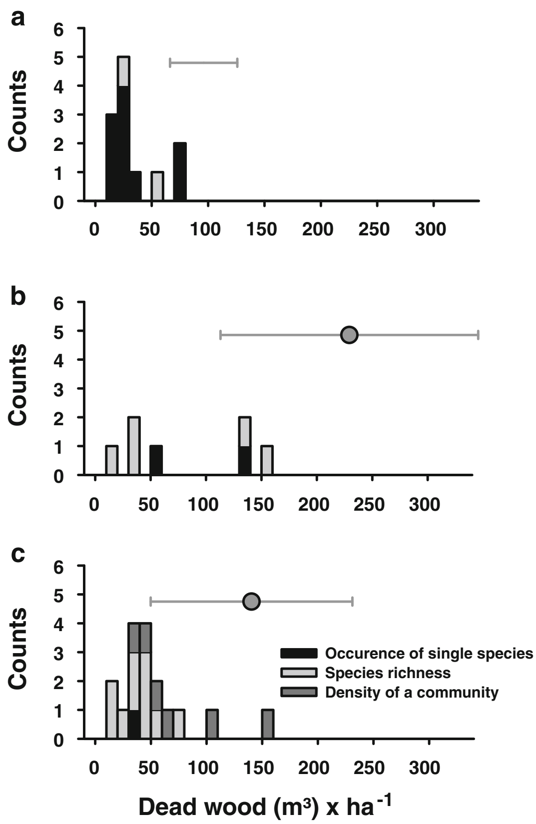

Fig. 2 Histograms of 36 threshold values from European forests (Table 1) for the occurrence of single species, species richness of a specific community, or density of a community dependent on the amount of dead wood (m^3 ha^{-1}). The *horizontal lines* indicate the range of dead-wood amount in long-term nature reserves for (**a**) boreal forests according to Siitonen (2001), where pine and spruce forest reserves averaged 60–120 m^3 dead wood ha^{-1}, and for (**b**) montane-mixed forests and (**c**) lowland beech–oak forests, showing the mean and standard error according to Christensen et al. (2005). For ranges of values from the literature, we only used the mean in this analysis (see Table 1)

infer ecological data. In contrast to several approaches in biological conservation, which were dominated by the approach of logistic regression (Angelstam et al. 2003; Bütler et al. 2004; Guénette and Villard 2004), Andersen et al. (2008) expand the view to a broad set of methods of analysis that provide inferential approaches.

Here, we present an application-oriented description of two methods that seem to be very useful in conservation analysis of threshold (synonymous to ‘cutpoint’ in this study) values. We compare the two methods and provide a cookbook-like recipe, such as using R script, to allow researchers in the field of forest ecology to analyze their data with a focus on thresholds (see Supplementary material). Of the 36 threshold values presented, 12 used conditional inference trees, 11 used a more descriptive statistic than mean values in occupied territories, 2 used logistic regression, and 11 were implicated on the basis of expert assessments, i.e., they were derived from studies, but not directly from data.

The most widely distributed method to derive thresholds (but not in dead-wood studies; Table 1) is logistic regression, which is a member of the family of generalized linear models (GLMs; Quinn and Keough 2002). In our context, logistic regression is used to predict the probability of occurrence of a species in relation to the amount of dead wood by fitting data to a logistic curve. In the first step, the user correlates the dependent variables of the occurrence data (0/1) multivariate with several predictors. In our context, if this multivariate method shows a clear relationship to a dead-wood predictor variable, a logistic function for the probability (y) can be fit to the amount of dead wood (x). Basically, the problem of all GLM models is the selection of the predictors for the final model. Three applications are possible: (a) using univariate *t*-tests for continuous variables, which have to be adjusted in multiple testings; (b) using a simultaneous GLM and a selection using the *P*-values, although selection control is then missing; and (c) using the AIC criterion, which selects the variables with the best linear explanation (Burnham and Anderson 2002; Quinn and Keough 2002) but does not automatically reveal the best threshold. After fitting the logistic regression against the predictor variable amount of dead wood, the researcher has the full responsibility and ability to select a threshold dependent on the desired probability for the occurrence of the species. From a statistical point, the most objective values would be a probability of $y = 0.5$, which could be too risky in some conservation approaches, where extinction should be avoided (see Bütler et al. 2004). To overcome the difficulty in determining the threshold value in logistic methods, especially in curves with little change in slope, application of receiver-operating characteristic (ROC curve) analysis has been suggested. This allows searching for the point of maximum sensitivity and specificity (Guénette and Villard 2004).

A second major set of methods is provided by the framework of classification or regression trees with many algorithms, most of which follow a simple general rule: first partition the observations by univariate splits recursively and then fit a constant model in each cell of the resulting partition (for an overview, see Murthy 1998). Owing to several methodological advantages for practical users, we selected and present the conditional inference tree method from the family of recursive partitioning, which is based on maximally selected rank statistics (Hothorn and Zeileis 2008), available as the function *ctree* in the add-on package *party* in R (R Core Development Team 2008). The algorithm roughly works as follows: (1) The global null hypothesis of independence between any of the input variables, such as the amount of dead wood and other variables, and the response, i.e., occurrence or species richness per observation, are tested. If this hypothesis cannot be rejected, the calculation stops. Otherwise, it selects the predictor variable with the strongest association to the response variable (Müller and Hothorn 2004; Hothorn et al. 2006). This association is measured by a *P*-value corresponding to a test for the partial null hypothesis of a single-input variable and the response (this clear criterion for developing a tree is one advantage over other *classification and regression tree* applications). (2) The method implements a binary split in the selected input variable. (3) This calculation is recursively repeated for each subset, created by the binary split (threshold). This statistical approach ensures that an appropriate-sized tree in a statistical sense is grown and no form of pruning or cross-validation or whatsoever is needed. The selection of the input variable to split is based on the univariate *P*-values, avoiding a variable selection bias toward input variables with many possible thresholds.

Constructing such conditional inference trees enables the user to solve several statistical problems in one application: First, the threshold estimation and hypothesis testing procedure does not make any assumption regarding the distribution of the variables, which is often a problem in field research. Secondly, the model underlying the analysis is very simple and therefore facilitates the development of applicable guidelines. A further advantage of this approach in comparison with GLMs is the statistically better solution of the problem of multiple testing. The response variable can be presence/absence (see the example for the three-toed woodpecker in the Supplementary material), or count data (see the example for the red-listed species number in beech forests in the Supplementary material) and multivariate data, which makes this approach rather flexible, even with different types of dead-wood thresholds.

We demonstrate the use of both methods with an already analyzed (but only with logistic regression) and published data set of the three-toed woodpecker in Fennoscandia and Switzerland (Bütler et al. 2004) to illustrate the theoretical aspects with real results (Fig. 3) and provide an R script to alleviate calculation as shown in Fig. 3 (see also Supplementary material). For this methodological comparison, we initially used five predictors for each sample with a size of 1.0 km^2: basal area of snags (which was the final predictor for identifying the threshold), the occurrence of recent harvesting (% of occurrence by visual inspection), intensive harvesting (% of occurrence by visual inspection), the basal area of living trees (m^2 ha^{-1}), and road density (km km^{-2}). As the dependent variable, the presence/absence of the three-toed woodpeckers in each km^2 unit was chosen. To derive a threshold for snags, it first has to be shown that dead wood is the most important variable among different predictors. For the Fennoscandia data,

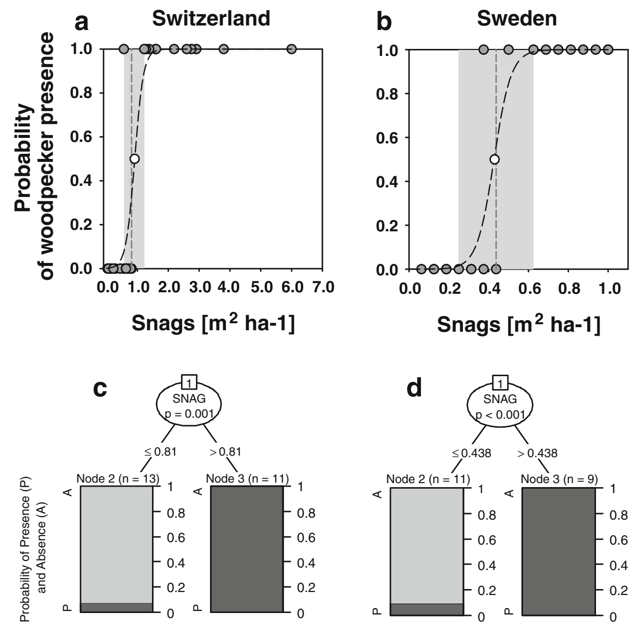

Fig. 3 Comparison of thresholds derived by conditional inference tree and logistic regression for the occurrence of the three-toed woodpecker in (**a**, **c**) Switzerland and (**b**, **d**) Sweden, related to the basal area of the snags threshold. The *dashed line* indicates the threshold value found by the conditional inference tree; *white dots* indicate the maximum value of the slope in the GLM curve. The *gray area* in the *scatter plot* indicates the 95% confidence interval for the thresholds based on 2000 replicates (Switzerland: 0.56–1.22; Sweden: 0.25–0.621). Note that the scale of the *x*-axes in the two plots differs and that the confidence bands overlap

almost identical results were obtained when a logistic regression with an expectation for the probability of woodpeckers of 0.5 and when the conditional inference tree were used. For the Switzerland data, in the first step, the conditional inference tree first selected the density of roads, which is negatively correlated with the amount of dead wood. Only after road density was eliminated were snags selected with a similar threshold for both methods. This already underlines the difficulty of an objective selection of the predictor variables, particularly with small data sets. Both applications underline the advantages and disadvantages of the two general threshold means of calculation. The GLM is more dependent on the a priori selection by the researcher, while the conditional inference tree selects the parameter which gives the best split. The choice depends on the aim of the threshold study.

The second new aspect on which we want to focus is the calculation of a threshold confidence band using bootstrapping in the *ctree* approach (gray band in Fig. 3). The "one" threshold approach has often been criticized and is probably rarely realized under environmental conditions even for a single species (Bütler et al. 2004; Ranius and Fahrig 2006). Instead of looking for a particular threshold value, it has been suggested that non-linear relationships should be viewed as having three intervals: unsustainable, meaning that the amount of the particular resource is well below the uncertainty interval; sustainable, meaning that the amount is well above this part of the gradient in the resource; and uncertain whether it is unsustainable or sustainable (Angelstam 2002). To statistically capture the latter uncertain range, two different general approaches are used. The first approach is to calculate with different data sets and different dependent variables for one ecosystem a range of thresholds (Fig. 2). The second approach is to use resampling methods in one data set, e.g., bootstrapping, to construct confidence bands for a threshold for a specific data set (Roff 2006). We applied such a bootstrap to the conditional inference tree using our three-toed woodpecker data sets (for R script, see Supplementary material). The results derived this way open a range including most parts of the steep curve of logistic regression (Fig. 3). This underlines that a discussion of the best value using the probability of the species in the logistic regression is less helpful if it falls in the full range of uncertainty of the data set.

Such resilient values independent from single observations seem helpful for the development of valid recommendations. If the aim is to guarantee improvement effects for the target species or community, one can choose the upper limit; if the aim is to arrive at an understanding of the minimum requirements for some improvement, one can use the lower range.

The choice of the dependent variable

As shown above, three levels of dependent variables were widely used in dead-wood threshold analysis: (1) the response of a single species, measured by its occurrence (presence/absence) or density (number of individuals), (2) the response of species numbers or the density of a community (e.g., threatened saproxylic species), and (3) the community composition (e.g., dissimilarity of plots along an ordination axis). The aim of a study decides which of these variables should be chosen. Especially in studies of focal species, there is a strong interest in understanding the extinction probability of a species dependent on an environmental factor (Angelstam 2004). However, the number of organisms affiliated with dead wood is too high to allow analyses of all single species (Villard 2009). Therefore, it can be of higher interest to identify the threshold of dead-wood volume for which a shift from low to high numbers of species is most significant (see Table 1).

A dependent variable that has been generally underrepresented in diversity studies (Basset et al. 2008) and particularly in threshold studies of dead wood (Table 1) is the species composition. It can be highly useful in identifying the level of dead wood at which the community composition changes, owing to, e.g., an alteration of weak to strong dead-wood colonizers (Andersen et al. 2008). This would allow management rules to be defined that aim at the conservation of an entire dead-wood community that is dependent on higher amounts of dead wood, even if single species are difficult to model because of their rarity. We demonstrated here one such application for wood-inhabiting fungi in beech–oak forests using the data from Müller et al. (2007b). In this study, wood-inhabiting fungi without corticoids were sampled on 69 sampling plots of 0.1 ha three times in 1 year together with an inventory of dead wood on the same plots. To quantify overall species turnover, we used de-trended correspondence analysis (DCA) with Hill's scaling on untransformed data (Fig. 4). The differences between the scores of any two sites on the first axis of the DCA represent a measure of species turnover between these two sites (ter Braak and Smilauer 1998; Basset et al. 2008). We then plotted these difference values against the log(dead-wood amount) (Fig. 4). The scatter clearly shows a non-linear shift with a threshold derived using a conditional inference tree of 81 m^3 ha^{-1} (95% confidence interval: 43–81 m^3 ha^{-1}). Such an application considers a broad community and is more stable against random occurrences or sampling efforts (Müller and Brandl 2009). Therefore, we highly suggest a broader application of these community shift approaches in dead-wood analyses.

Challenges for threshold approaches

Threshold range rather than threshold values

Basically, we have to expect an array of dead-wood threshold values for a range of single species and assemblages, and this

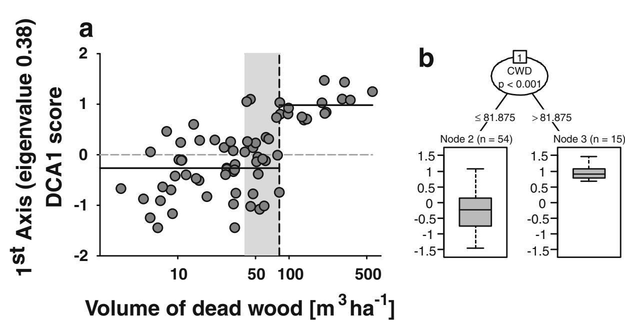

Fig. 4 **a** Threshold (*dashed line*) for wood-inhabiting fungi derived by maximally selected rank statistics (**b**) of a shift in communities of wood-inhabiting fungi, based on DCA scores of the composition (for details, see text) of fungi on 69 sampling plots in a beech–oak forest. The *gray area* shows the 95% confidence interval band of 1000 bootstraps of the threshold

hampers arriving at a clear value (Ranius and Fahrig 2006). Besides that, even within the same study of a single species in different regions (see the example of the three-toed woodpecker), different values for the same habitat factor can be derived. From the point of biodiversity conservation, we suggest that as many taxonomical groups as possible be addressed to avoid a mismatch of management recommendations and conservation success. On the other hand, our review showed similar peaks of thresholds for three rather different types of forests at 20–50 m^3 ha^{-1}, which definitely allows a recommendation for the minimum accumulation of dead wood required for conservation, even in managed forests.

Few reference forests and communities remain in central Europe

For all studies of our intensively managed forests in Central Europe, we have to be aware that we are dealing with reduced species communities, even if forest stands close to pristine forests are included (Speight 1989; Fowles et al. 1999; Brustel 2004; Müller et al. 2005a). Therefore, we can analyze only those species and communities that have been recorded in occurrences and densities that can be analyzed statistically. Areas with unreduced, i.e., natural, species communities have probably only survived in some postglacial eastern and northern European forest landscapes (Bussler et al. 2005). There is therefore the danger that derived thresholds are still too low for those species that have survived only in densities that make a statistical consideration impossible. If then the aim is to establish dead-wood habitats that allow all existing species to survive, an approach of species numbers could mask the higher requirements of single species. In this case, we highly recommend the additional analysis of single species.

A second problem can be identified using only commercial forests in threshold analyses, which in most cases do not span the possible dead-wood amount and range and the composition of related forest species. For example, in the analysis of dead-wood thresholds for beech forests, first only commercial forests were considered, and then strictly protected sites with volumes comparable to those of pristine forests were considered. The values derived in the latter case were significantly higher (Müller and Bussler 2008). Therefore, we have to keep in mind that if the focus is on species richness or species composition as dependent variables; the aim of such an analysis should be to consider the dead-wood amounts of the entire possible gradient of a landscape. This can be reached in most cases by including the few strict forest reserves remaining in most landscapes.

Extinction debt: species may become extinct above the threshold

Even if our results seem to allow derivation of dead-wood thresholds that can be recommended for an ecologically sustainable forestry, we found single values that lie far above the general ranges. One example is the rare boreal beetle *Pytho kolwensis,* which occurs only in natural forest sites without any logging and with dead-wood volumes >70 m^3 ha^{-1} (Siitonen and Saaristo 2000). Another example is the parasitic fungus *Antrodiella citrinella,* which can be found even on spruce dead wood, on sporocarps of the common fungus *Fomitopis pinicola*. Despite this, at a first glance widely distributed habitat feature, we found the species only in stands with >120 m^3 ha^{-1} dead wood (Bässler and Müller 2010). Similar to the beetle *Pytho kolwensis,* this fungus also is not able to survive in areas with logging management, which yields habitat features that reduce the population to the extinction level. Both examples show that even if we derive a threshold range for a larger set of species and assemblages, some may still become extinct.

In addition, we have to be aware that species can become extinct even after dead-wood volumes lie above the critical threshold. According to Tilman et al. (1994), a metapopulation decline in response to habitat destruction occurs with a time delay, called the “extinction debt”. This means that many species may remain as “living dead” for a long time in a landscape that has already lost its capacity to support them in the long run. This could be the case for the three-toed woodpecker, whose population in Fennoscandia is declining (Bütler et al. 2004). Both aspects clearly show the limitation of such simple guidelines based on general dead-wood thresholds. We therefore urgently need more studies that also consider the landscape scale and connectivity of the metapopulation in threshold analyses. Only a few studies have begun to consider also these different scales, and our knowledge about the dispersal ability of saproxylics is still rather low (Okland et al. 1996; Ranius 2006; Ranius and Fahrig 2006).

Future directions

As our review shows, studies dealing with dead-wood thresholds are restricted to some single species or the species richness of single taxonomical groups. To derive valuable guidelines for whole communities and their sustainable conservation, we suggest using more community composition for analyzing dead-wood thresholds. This could be a bridge between the rarity of some species and a consideration of broad group compositions living in dead wood. A second problem in threshold studies is their restriction to a single spatial scale (Lindenmayer and Luck 2005), as sampling plots, forest stands, or local forest regions. One reason may be that the quantity, composition, and distribution of dead-wood features across the landscape are often poorly known (Ekbom et al. 2006), because the quantification of dead wood using field approaches is time-consuming. Especially for species that act on a large scale, such as bird populations, the distribution of dead wood on the landscape scale is highly important but difficult to sample (Roberge et al. 2008). This is probably true as well for saproxylic organisms (Ranius 2006; Müller and Goßner 2010). We can assume that several extinct species disappeared because of the reduction in dead wood. For example, the beetle *Rhysodes sulcatus* was once distributed throughout Europe but became extinct, even though the species was able to live in the dead wood of various tree species, such as oak, poplar, beech, and fir (Speight 1989). Habitat thresholds exist at different spatial scales, from the stand to the landscape scale (Angelstam et al. 2003). If stand-specific dead-wood thresholds supply some information about the local presence of a species or species group, landscape-level dead-wood thresholds would be necessary when considerations about the viability of metapopulations are required. Much work still needs to be done in this field.

Conclusions

Thresholds vary among studies with different species, and in different regions and habitats, and the most-demanding species require amounts of dead wood that are virtually impossible to reach in managed forests (Ranius and Fahrig 2006). Yet we demonstrated that a similar peak of threshold values can be found for the three main types of Central European forests (lowland beech–oak forests, mixed-montane forests, and alpine-boreal montane forests) at 20–50 m^3 ha^{-1}, ranging from 20 to 70 m^3 ha^{-1} when most values are included. This range is, however, much higher than the general amount of dead wood found in commercial forests. We therefore conclude that it is necessary to establish several forest stands with dead-wood amounts >20–50 m^3 ha^{-1} in a network of forest landscapes rather than to aim on a lower mean in all stands. How large and connected an area of such stands is needed is still unknown, even though some information indicates that the surroundings also play an important role (Okland et al. 1996). To develop a more comprehensive picture of these benchmarks, we urge researchers to use inferential statistics to analyze their forest ecological data with the aim of further identification of thresholds, especially in mixed-montane forests, where the data base is still small.

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