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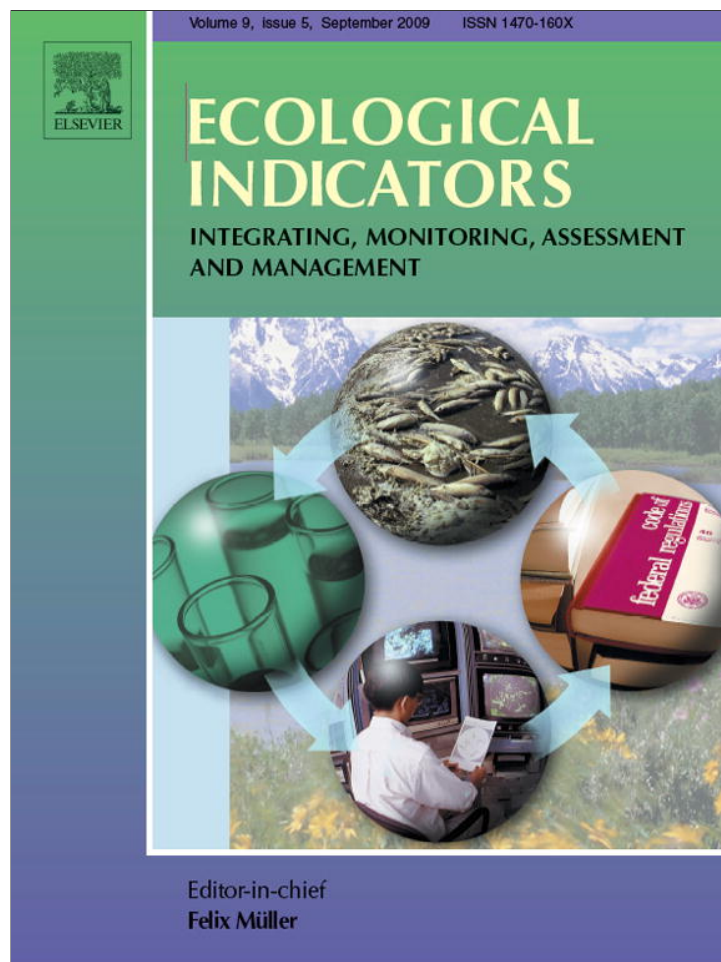


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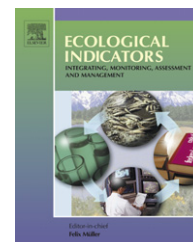


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Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests

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ABSTRACT

Forest age is one of the most simple but ecologically effective key values that may be controlled by forest management. Young and mature but managed forests differ significantly from old-growth forests in species composition, structure and socio-ecological function. Human land-use has already caused the loss or dramatic reduction in occurrence of some entire species assemblages, especially of logging-sensitive species, in Central European forests. These general statements also apply to beech forests, beech (*Fagus sylvatica*) being the naturally dominating tree species in Central Europe. Based on data for breeding birds (from 258 sampling plots in a sub-montane and 228 plots in a montane area), molluscs (36 plots in the sub-montane and 79 plots in the montane area) and lichens (84 plots in the montane forest), this paper aims at identifying significant forest age threshold ranges for the occurrence of these old-growth sensitive taxa. The sampling plots in the sub-montane zone (420–520 m a.s.l.) are in beech-oak forests, plots in the montane zone (650–1150 m a.s.l.) are in beech-spruce-fir forests. Stand ages in both areas range up to around 350–400 years. Threshold values for the total number of species related to stand age were calculated by recursive partitioning.

In all three taxonomic groups the number of species per plot significantly increases with forest age. The same analysis was run for red-listed lichen and mollusc species as well as hole-nesting bird species. The threshold values obtained are very similar to those for the whole species assemblages, except for molluscs where considerably lower threshold values are computed with red-listed species assemblages. Regarding the confidence intervals, the difference pattern between the whole species datasets and the more sensitive species subsets is inconsistent. Threshold values in sub-montane beech forests range from 100 to 170 years and in mixed montane forests from 160 to 220 years.

These threshold levels are clearly incompatible with economic interests that aim on reducing the rotation period in beech stands to less than 140 years to avoid formation of red heartwood. It would therefore seem to be essential to establish a network of trees and stands that are never logged and may thus act as areas for retreat and dispersion for logging-sensitive species.

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1. Introduction

Management guidelines require simple but ecologically effective key values. Among various forest parameters, age is one of the surrogates which can most easily be integrated in forest management. It is well known that old-growth forests differ significantly from young forests in their ecology, particularly with regard to species composition and structure. Old forests are characterized by higher proportions of large, old trees, multiple age-classes and high volumes of fallen and standing dead wood, as well as differences in function such as rate and routes of energy flow and cycling of nutrients and water (Franklin et al., 1981; Heliovaara and Vaeisaenen, 1984; Väisänen et al., 1993; Larsson, 2001; Humphrey, 2005; Liira et al., 2007). Intensive logging of old-growth forest reduces species diversity on the landscape scale by homogenization of forest structures, causing habitat loss and local extinctions of sensitive species (Heliovaara and Vaeisaenen, 1984; Niemela, 1997). In all taxonomic groups, the inhabitants of old forest that are most affected by anthropogenic disturbances are those which are sedentary (Opdam, 1990), have the poorest dispersal abilities (Primm et al., 1988; Bolger et al., 1991; Hermy et al., 1999; Floren and Linsenmair, 2001), have large area requirements (Wilcox, 1980), or are invertebrates associated with micro-habitats of natural old-growth forest, such as coarse woody debris or large broadleaved trees (Niemela, 1997). It is mostly in these groups that some entire species assemblages have already been lost or dramatically reduced in occurrence in Central Europe (Heliovaara and Vaeisaenen, 1984; Speight, 1989; Thomas et al., 1994; Larsson, 2001; Grove, 2002; Cameron and Pokryszko, 2004; Pykälä, 2004). Consequently, remaining old-growth forests have a very high significance for biodiversity conservation and as donor resources for developing mature forests.

In this context the factor of forest continuity has been extensively but controversially debated in biodiversity conservation, especially with regard to spatial and temporal scales at which continuity may influence populations and species (Sverdrup-Thygeson and Lindenmayer, 2003; Palto et al., 2007). Although species which indicate ecological continuity have been identified, e.g. for lichens (Selva, 1994; Kuusinen, 1996), this practice has been questioned because of the difficulty in defining continuity and separating it from other ecological factors (Nordén and Appelquist, 2001; Rolstad et al., 2002). However, the assumption that forest age is a good integrating parameter for habitat continuity is less disputed (Tibell, 1992; Kuusinen, 1996; Müller et al., 2005b). As stand age is generally readily available information for most forests, we use it as a surrogate factor for habitat continuity in the sense of continuity of habitat structures. It is not regarded as a surrogate for forest continuity. The distinction is important because the latter does not necessarily entail continuity of appropriate habitats, especially for species depending on structures typical of old growth. In this paper we use the term old forest for those forest stands in which old-growth forest structures have developed to such an extent that species are present which are known to depend on such structures.

In Central Europe, beech (*Fagus sylvatica*) would dominate forests under current climatic conditions (Tüxen, 1956; Ellenberg, 1996; Björse and Bradshaw, 1998; Bradshaw and

Holmqvist, 1999; Dierschke and Bohn, 2004). Taking Germany as an example, beech would potentially cover 74% of the forested area. However, at present beech forests in Germany, where only 30% of the total land area is still forested, make up 14.8% of the woodland area. Only 6.0% of these beeches are older than 160 years and less than 0.1% of the total German land area is covered by unmanaged beech forests (Schmitz et al., 2004). The situation of old-growth beech forests has accordingly been assessed as critical (Thomas et al., 1995). As Central Europe is the centre of the world distribution of beech-dominated forests, this forest type has attracted a lot of attention in conservation oriented discussions in recent years (Plachter, 1997; Heinrih, 2001; Berg et al., 2002). However, from an economic point of view rotation periods for beech stands are required to be kept short to avoid formation of red heartwood (Knoke, 2003).

Much of the shortfall in applying the results of ecological research in guidelines for land managers results from the highly complex relationships between species and their environment. Clear formulation of descriptive guidelines based on research may be extremely difficult. For this reason, statistically derived threshold values are increasingly recommended as a basis for forest management guidelines (Angelstam et al., 2003; Müller and Hothorn, 2004; Guenette and Villard, 2005; Lindenmayer and Luck, 2005; Ranius and Fahrig, 2006).

Due to the complexities involved, the predictive capacity of threshold values in nature conservation is always a critical theme. Several approaches, including pre-defined threshold values (e.g. Uliczka and Angelstam, 1999), have been attempted. In the present study we have chosen to identify, using recursive partitioning, the data segment along the age gradient that represents the most intense change in species number. The rationale for this method originates in abundant evidence of discontinuities and threshold effects arising as the consequence of human influence on forest systems (e.g. Kuusinen and Siitonen, 1998; Angelstam et al., 2003; Bütler et al., 2004). The large number of threatened species in forests is an indication that ecological age thresholds have already been crossed on a large scale (Scherzinger, 1985; Väisänen et al., 1993; Angelstam and Mikusinski, 1994; Berg et al., 1994, 2002; Fuller, 1995; Gustafsson et al., 2004). This paper aims to identify critical forest age threshold ranges for the two major altitudinal distribution zones of Central European beech forests, with respect to general species density of logging-sensitive taxa and subsets of these taxa which contain species which are presumably even more sensitive.

2. Methods

2.1. Taxa studied

LICHENS are good model organisms for assessing the effects of human impact on ecosystems because of their sensitivity to various types of impact such as logging (Rose, 1992; Wirth, 1995; Uliczka and Angelstam, 1999; Hedenås and Ericson, 2003) or airborne emissions (e.g. sulphur; Garty et al., 1988; Richardson, 1998; Lippo et al., 1995; Ranta, 2001). Old-growth forests possess their own, distinctive lichen communities.

These forests usually contain many specific habitats suitable for the growth of different epiphytic lichens, such as large old trees, logs and snags (Peterson and McCune, 2001; Jürriado et al., 2003; Radies and Coxson, 2004). Numerous lichens, including many red-listed species, are thus observed more frequently on old than on young trees (Neitlich and McCune, 1997; Gustafsson et al., 2004). Furthermore, biomass of epiphytic lichens is strongly related to volume, dimensions and age of branches (Esseen et al., 1996; Fritz et al., 2008). Most of the threatened forest species, many of them being slow colonists (e.g. Sillet et al., 2000), are confined to specific substrates such as deciduous trees, dead wood and old trees (Berg et al., 1994; Esseen et al., 1997; Uliczka and Angelstam, 1999; Nascimbene et al., 2007). The limited amount of substrate available to lichens, and young age of branches which allows only a short time for lichen colonization and growth, are important factors limiting epiphytic lichen abundance in managed forests (Esseen et al., 1996; Kuusinen and Siitonen, 1998; Hilmo and Sâstad, 2001; Hilmo, 2002).

Many MOLLUSC species have powers of dispersal too low to enable them to overcome the effects of human-induced fragmentation, making breaks in habitat continuity in conjunction with their dependence on a stable microclimate particularly harmful (Wäreborn, 1979). Thus the snail fauna reacts very sensitively to logging in long undisturbed forest habitats (Tattersfield et al., 2001; Pilâte, 2003a). Although soil moisture and the closely linked soil pH have been pointed out as the strongest determinants of snail density and species richness at undisturbed woodland sites in Central Europe and beyond (Boag, 1985; Waldén et al., 1991; Hotopp, 2002; Martin and Sommer, 2004), the forest snail fauna depends on various forest attributes that are especially frequently encountered in Central European old forests. These include shadiness and humidity, a stable microclimate, adequate calcium content and sufficient amount of coarse woody debris, habitat continuity and richness of vegetation (Müller et al., 2005).

Although many BIRD species prefer a particular stage of growth, bird species richness tends to increase with stand age (Moss, 1978; Helle and Mönkkönen, 1990; Solonen, 1996; Laiolo, 2002). This may even be observed in the distribution of winter birds (Utschick, 2004). Birds are particularly good indicators for forest structures at the stand scale and may therefore function as a superior logging-sensitive indicator group (e.g. James and Wamer, 1982; Cody, 1985; Hagan and Meehan, 2002). For instance, most hole-nesters prefer mature trees (Fuller, 1995) and snags (Zarnowitz and Manuwal, 1985), but bird species which forage on branch surfaces, trunks and on the ground are also more abundant in mature stands (Bürger and Kloubec, 1994; Laiolo, 2002). Apart from the general decrease in bird species diversity in beech forests with increasing logging intensity (Müller et al., 2007), especially with respect to woodpeckers, a negative effect of logging on birds nesting secondarily in cavities and ground-gleaning birds has also been demonstrated (Helle and Jarvinen, 1986; Angelstam and Mikusinski, 1994; Lammertink, 2004; Augenfeld et al., 2008).

2.2. Study sites

The data originates from two study sites in Bavaria, south-eastern Germany. The “Northern Steigerwald” is a sub-

montane forest area of about 10,000 ha, located in northern Bavaria, dominated by beech and oak (mainly *Quercus petraea*). The altitudinal range extends from 420 to 520 m a.s.l., average daily temperatures range from 7 to 8 °C (Müller et al., 2005a). Some of the beech stands are regarded as among the oldest in Germany, being up to 350 years old (Müller et al., 2007). The selected stands grow on Triassic sandstones of various ages, thus the soils (mainly cambisols) are rather acid (pH 3.5–5.8). The proportion of coniferous trees in the investigated plots ranges from 0% to 25% and for oak from 0% to 40%. Average tree species number in the canopy layer per plot is 3.3 (range 1–7). Canopy cover varies between 20% and 100% (mean: 72%). Dead wood amounts vary between 3.5 and 500 m³/ha (mean: 58 m³/ha).

The Bavarian Forest National Park is situated within the south-western part of the Bohemian Massif, consisting of granite and gneiss. The soils are mainly podsollic cambisols derived from weathering of granite. Thus the soils are rather acidic (pH 2.3–4.8). The park covers approximately 24,000 ha, with an elevation range from 600 to 1430 m a.s.l. Mean annual temperature (1970–2003) varies between 3.8 and 5.8 °C (Bässler, 2004). The investigated area below 1150 m a.s.l. is montane mixed forest dominated by spruce (*Picea abies*), beech and fir (*Abies alba*). Average tree species number in the canopy layer per plot is two (range 0–5). Due to heavy infestation by bark beetles, mainly *Ips typographus*, canopy structure varies widely from open forests, dominated by dead wood, through patchy forest, to more or less dense, closed forest stands (canopy cover: 0–100%, mean: 48%). Dead wood amounts vary between 0 and 709 m³/ha.

The age of all stands investigated was obtained from the permanent forest inventory data for both areas. Stand ages ranged from 50 to 350 years in the sub-montane area and from 0 to 400 years in the montane area. The age was determined by the age of the oldest tree within each inventory plot (0.05 ha).

2.3. Species sampling

Sampling campaigns were accomplished in the sub-montane zone in 2004 and in the montane zone in 2006 (molluscs)/2007 (birds and lichens). Breeding birds were sampled five times during the period March–June, using quantitative plot mapping of 1 ha plots as a standardized area count method on 258 plots in the sub-montane zone in 2004 and 222 plots in the montane zone in 2007. The plots were selected by stratifying them according to altitude, age and canopy cover along the elevation gradient. For details see Müller et al. (2007). Each plot was investigated for 10 min on each occasion. Only birds that were recorded within the plots were included in the analysis. Hole-nesting birds were classified following Bauer et al. (2005).

Molluscs were sampled in the sub-montane area on 37 plots, using 0.1 ha fixed-radius point counts. The minimum distance between the plots was 100 m. At each plot two standard time direct searches were conducted, once in April and once in June 2004. Additionally, litter humus and topsoil was collected from an area of 25 cm × 25 cm per plot. Fresh, empty shells were also counted. Old shells were generally scarce, because of rapid decay and re-use by other organisms. Shells were identified to the species level and individuals counted (for details see Müller et al., 2005a). Sampling

methods in the montane area were similar to those in the sub-montane zone, with the additional installation of one pitfall trap for 3 weeks in July 2006 in the centre of each of the 79 plots. Also, within an area of 0.1 ha around the centre of each sampling plot we collected for 30 min all individuals of living snails and slugs in September 2006. Dead wood structures and trees were primarily sampled, because low pH values cause the snail density to be very low in the litter. A detailed description is given in Müller et al. (in press). Red-listed species were classified following the Bavarian red list (Falkner et al., 2003).

Lichens were investigated in the montane area only. Each of the 84 plots was 8 m in diameter (0.02 ha). All objects carrying lichens in the plots were investigated in 2007. These included living trees, dead wood (standing, lying, snags, stumps, logs and branches) and soil and stones. Particular attention was paid to the main guilds represented. On most plots these were epiphytic lichens growing on living and dead wood. Those specimens that could not be determined in the field were later identified in the laboratory (Culbertson and Kristinsson, 1970; White and James, 1985; Huneck and Yoshimura, 1996). Red-listed lichens were classified following the Bavarian red list (Wirth et al., 1996).

2.4. Statistical analysis

We used the number of all registered species from all sampling campaigns per plot as the dependent variable. Threshold

values were calculated by recursive partitioning (Lausen and Schumacher, 1992; Hothorn and Lausen, 2003; Hothorn and Zeileis, 2008). This approach allows simultaneous identification of a threshold and assessment of its significance by means of a statistical test procedure, i.e. a decision whether or not there is a relationship between independent variable and the response. The thresholds are derived from estimates of break points by means of maximally selected two-sample statistics. Their validity is judged by multiple test procedures. The key results are those in which the difference between high and low values of the dependent variable, here number of species, is largest. After the data set is divided into two subsets by the threshold with highest explanatory power, the subsets are searched for additional thresholds. This method provides a decision tree with p-values for one or more critical thresholds (see example: Supplementary Fig. S1). Based on 5000 bootstrap samples a confidence interval (80%) was calculated for all thresholds. As the density plots of all bootstrapped thresholds show outstanding peaks, the thresholds are characterized by generally high significance levels (see example: Supplementary Fig. S2). In order to display confidence intervals that are meaningful in forest management, the 80% confidence intervals were chosen in preference to 90% intervals because the former are defining more tightly ranges. This methodology is a further development of some currently more popular implementations for 'recursive partitioning' or 'trees', such as 'CART' (Breiman, 1984) or 'C4.5' (Quinlan, 1993), which solves two fundamental statistical problems inherent to the earlier

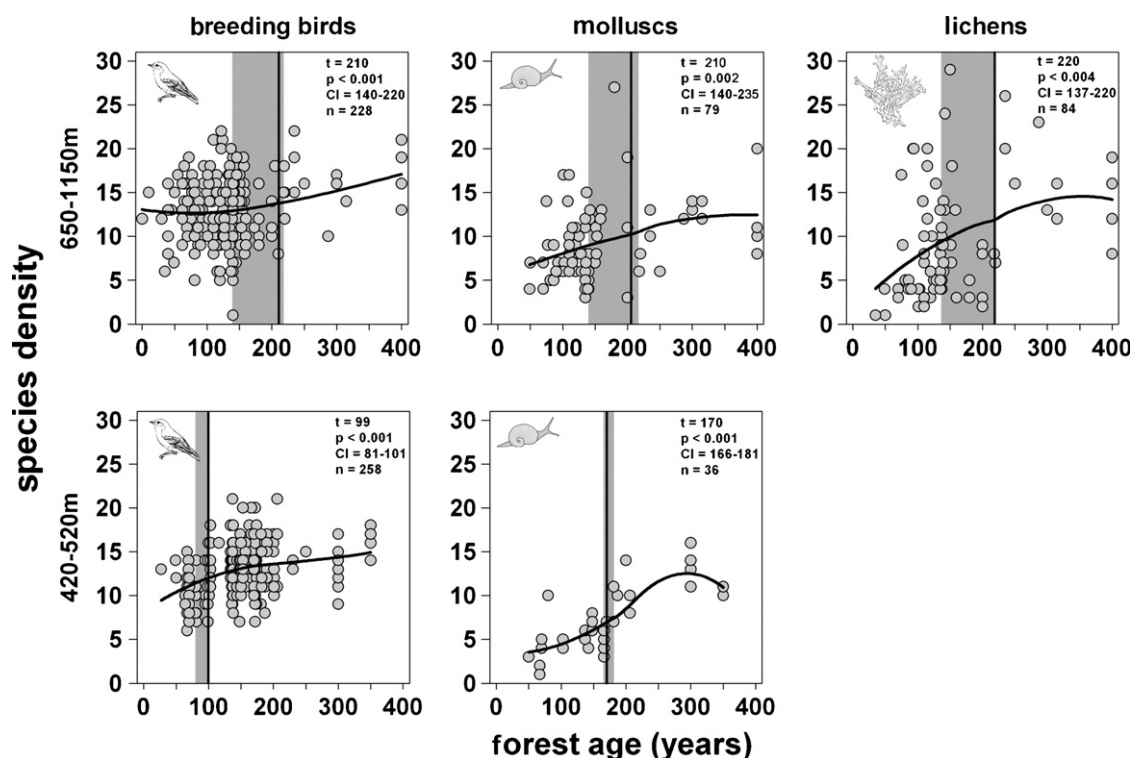


Fig. 1 – Data distribution (scatterplot graphs) for forest age (X-axis) and species density (Y-axis) of breeding birds (1.0 ha plots), molluscs (0.1 ha plots) and lichens (0.02 ha plots) per plot in the zone between 650 and 1150 m a.s.l. of the Bavarian Forest National Park and the zone between 420 and 520 m a.s.l. of the Steigerwald Area, with the appropriate Loess curves (local polynomial regression fitting). The grey boxes indicate the range of the 80% confidence intervals of the threshold values (black vertical lines) calculated by means of recursive partitioning. t = threshold value, CI = 80% confidence interval of the threshold, and n = number of plots.

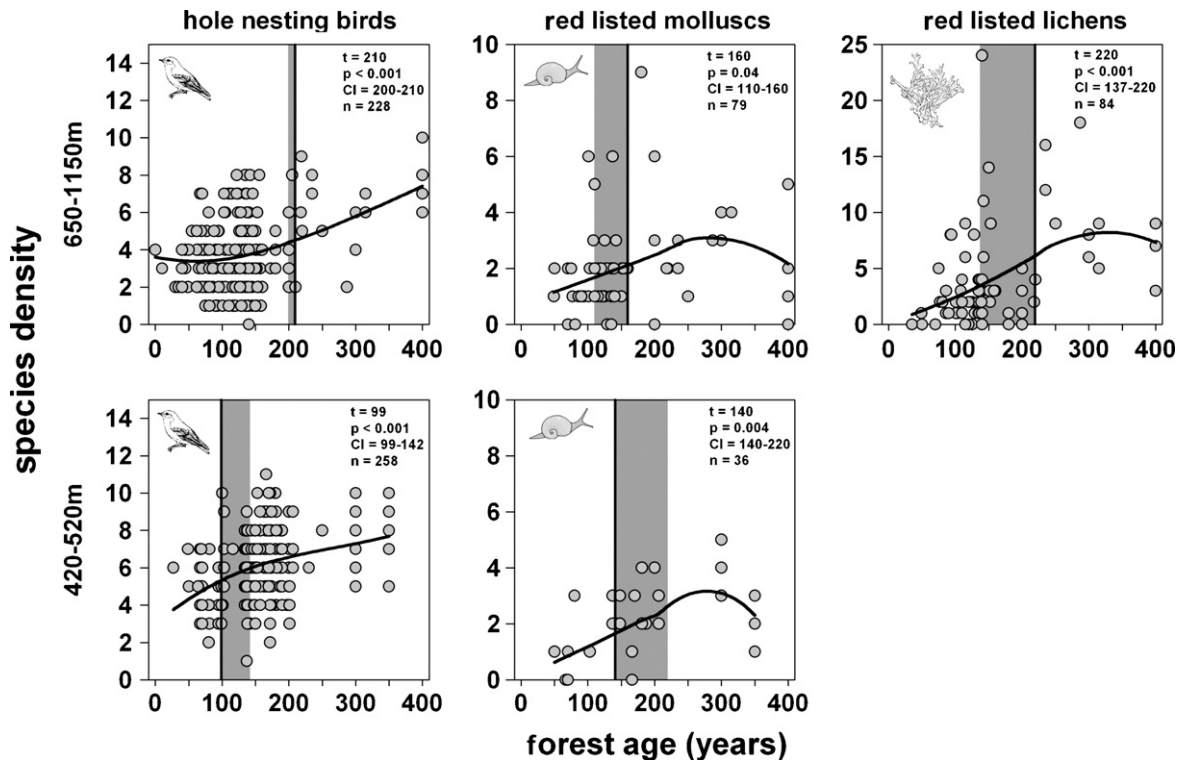


Fig. 2 – Data distribution (scatterplot graphs) for forest age (X-axis) and species density (Y-axis) of hole-nesting birds (1.0 ha plots), red-listed molluscs (0.1 ha plots) and red-listed lichens (0.02 ha plots) per plot in the zone between 650 and 1150 m a.s.l. of the Bavarian Forest National Park and the zone between 420 and 520 m a.s.l. of the Steigerwald area with the appropriate Loess curves (local polynomial regression fitting). The grey boxes indicate the range of the 80% confidence intervals of the threshold values (black vertical lines) calculated by means of recursive partitioning. t = threshold value, CI = 80% confidence interval of the threshold, and n = number of plots.

approaches: overfitting and a selection bias towards covariates with many possible splits or missing values. The method and a comprehensive model comparison are described in Hothorn et al. (2006a).

The calculations were performed using the statistical software R 2.4.1 (RDevelopmentCoreTeam 2006) with the add-on package ‘party’ (Hothorn et al., 2006b). For details of R-script see Supplementary material S1.

Data distribution was visualized by construction of scatterplot graphs. In order to enhance the visual information on the scatterplots, smoothed points were computed and plotted as loess curves (Figs. 1 and 2). Locally weighted scatterplot smoothing (LOESS) is a method for smoothing a scatterplot, achieved by fitting simple models to localized subsets of the data to build up a function that describes the deterministic part of the variation in the data, point by point. Each smoothed value is expressed as a weighted quadratic least square regression over the span of values of the scatterplot y-axis criterion variable (Cleveland, 1979; Cleveland et al., 1992).

3. Results

In all three taxonomic groups the number of species per plot increases significantly with forest age (Fig. 1). The threshold values in the montane zone for species density of all groups as

well as the confidence intervals of the thresholds all fall within the same range, which indicates that forest age reflects similar effects acting on all taxonomic groups in comparable ways (Fig. 1). This does not apply to the sub-montane forest area, where the threshold for birds is at 99 years while that of molluscs is at 170 years. Comparing the results for the sub-montane forest with those for the montane forest, it can be seen that a significantly higher species density level in breeding birds is reached much earlier in the sub-montane than in the montane zone (Fig. 1).

We also tested the number of red-listed lichen and mollusc species as well as hole-nesting bird species per plot for threshold values with respect to forest age (Fig. 2). Nevertheless, the results for threshold values are basically the same as for the whole species assemblages (compare Fig. 1 with Fig. 2), except with molluscs, where abundance of red-listed species reveals threshold values being considerably lower than for all species together. Regarding the confidence intervals, the patterns of difference between the datasets for all species and the subsets for more sensitive species are inconsistent.

4. Discussion

Among the chosen taxonomic groups there are many which would presumably represent good indicators for old-growth

forest structures. Saproxyllic beetles are a fine example of a group sensitive to presence of such structures. Managed and secondary forests generally support fewer individuals, fewer species and different assemblages to old-growth forests (Grove, 2002). However, this group depends mainly on a single forest attribute (dead wood) and thus its species density is not suitable as a prime indicator of forest age (Müller et al., 2007). Similar results have been obtained for polypores (Penttilä et al., 2004) and amphibians. The latter are represented only by a few species in Central European forests and mainly depend on the occurrence of wetlands, but have been shown to be sensitive to logging of old forest, e.g. in California (Bury, 1983) or tropical forests (Ernst and Rödel, 2005). Hence we selected three taxonomic groups that are known to depend on old-growth structures in multiple ways.

It is well known that in forests the number of logging-sensitive species is higher in the subset of red-listed mollusc and lichen species as well as the subset of hole-nesting birds than in the respective, entire species assemblages (Smith et al., 1985; Thor, 1998; Gustafsson et al., 2004). One would thus expect that the logging-sensitive species subsets display even higher age threshold intervals when compared to the whole species sets (e.g. Uliczka and Angelstam, 1999). However looking at all groups as a whole this trend could not be observed (Figs. 1 and 2). Generally both, generalists as well as the more specialized red-listed lichens/molluscs and hole-nesting birds contribute significantly to the species increase along the age gradient, as demonstrated by highly significant correlations between non-threatened and red-listed species of lichens and molluscs (Supplementary Figs. 3 and 4) and between non-hole nesting and hole-nesting birds (Supplementary Fig. 5, except sub-montane area). This implies that high numbers of generalist species are generally accompanied by high numbers of specialized species. In molluscs the proportion of red-listed species remains the same along the age gradient (Supplementary Fig. 3), while in birds and lichens the proportion of hole-nesting and red-listed species increases with forest age (Supplementary Figs. 4 and 5).

Our results therefore only offer slight support for recommending the use of species diversity of red-listed molluscs/lichens and hole-nesting birds for the identification of ecologically critical forest ages in preference to species numbers of all species. On the other hand, to detect effects of forest age on these taxonomic groups, sampling of only the subsets of logging-sensitive species makes sense, because of the greatly reduced field work effort required.

In nearly every group, instances occur where high numbers of (red listed) species are present below the threshold values. This reflects the high variance level in the datasets, caused by diversity of structure where comparatively small plots are situated within very varied stands. However, comparing larger forest areas with each other would not be a valid alternative, because larger plots vary internally in history and contain areas with widely different numbers of age dependent structures and would thus yield increasingly meaningless averages. Furthermore, it would be methodologically impracticable to obtain standardized mollusc and lichen data from large forest areas. Structures that support typical old-growth forest species may also occur regularly in younger stands (e.g. caused by wind throw, or tree damage resulting in nesting

holes). This underlines that in detail and on a short time scale, species diversity is only loosely correlated with forest age. However, in old stands above the threshold values, low species diversity becomes increasingly rare. Although the higher species numbers obtained in very old stands are based on rather few plots, because availability of old forest in the study areas is limited, the positive relation between forest age and species diversity is apparent in every taxonomic group investigated and is valid for the whole altitudinal gradient (Figs. 1 and 2).

The species density increase along the age gradient in the investigated taxonomic groups has been well documented by various previous research projects. Forest structures that are typical for old-growth stands such as rough bark, large amounts of dead wood, nesting cavities and large trees seem to account for the bird species increase in old forests (Moss, 1978; Helle and Mönkkönen, 1990; Solonen, 1996; Laiolo, 2002). Studies suggest that bird community composition and diversity increase as the complexity and variability of forest vertical structures increases (Terborgh, 1977; Rice et al., 1984; MacArthur et al., 1966), an effect which was also demonstrated for pristine beech forests (Kornan, 2000). Although selective logging and clear-cutting in temperate forests in the United States had specific effects only on certain guilds and species, these operations resulted in a marked decrease of total bird abundances and species richness (Thompson and Fritzell, 1990; Probst et al., 1992; Thiollay, 1997; Yahner, 1997). The amplified structural complexity in old-growth stands generally provides a wider diversity of foraging sites and microhabitats upon which birds can specialize, eventually increasing the bird species diversity (Urban and Smith, 1989; Karr, 1990; Cueto and de Casenave, 1999; Kornan, 2000). Dead wood quantities increase in old-growth stands, which thus support a huge invertebrate community that in turn represents a rich food resource for many birds such as woodpeckers (Nilsson, 1979). Additionally, other authors were able to detect a strong influence on bird communities of tree volume, a factor that is positively correlated with stand age (Jokimäki and Huhta, 1996). Especially hole-nester abundance increases significantly with stand age, because these species are often confined to the oldest stands with greater availability of holes and crevices in mature trees (Smith et al., 1985).

Bird populations vary from year to year. However, the increase in species number along the age gradient is apparent in both datasets, although they were obtained in different years. Thus we consider the link between forest age and bird species diversity to be generally valid.

A significantly higher bird diversity level is reached much earlier in the sub-montane forest than in the montane forest. This applies to the whole species set as well as to hole-nesting birds (Figs. 1 and 2). In the mixed montane forest area the diversity level remains rather unchanged for the first 150 years, while in the sub-montane area it increases quickly with a threshold value confidence interval resulting already at 81–101 years for all species and at 99–142 years for hole-nesting birds (Figs. 1 and 2). The development of old-growth structures is highly site-dependent and especially elevation-dependent (Dittmar et al., 2003). Thus the critical old-growth forest structures for birds such as cavities increased dead wood amounts and diverse stratification may develop much more

quickly in the area of the sub-montane zone at lower elevations.

Even if donor sites are available to contribute to the colonization of heavily disturbed forest areas (e.g. affected by clear-felling), the snail fauna is only fully restored after decades when large tracts are affected and correspondingly large distances are involved (Reinink, 1979; Suško, 1997; Watters et al., 2005). Colonization may occur considerably more rapidly if only small patches are affected and (micro) refugia remain close by (Shikov, 1984; Strayer et al., 1986). Although precise guidelines still have to be developed for the optimal distribution of snail donor sites in managed beech-dominated forest landscapes, we may conclude from our results that these donor sites should exceed the age range of 180–230 years.

Patterns of forest-age dependent mollusc diversity are little known and far from being consistent. For example, a decrease in average species abundance was found at boreal riparian clear-cutting patches in southern Sweden 2.5 years after harvesting. From 40 to 60 years later, these patches showed higher abundances of individuals and species than the 150-year-old forest stands. However, higher abundances and species richness are in young riparian forests mainly associated with the higher litter pH (Ström, 2004), which does not apply to non-riparian woodlands such as beech-dominated forests. Although there is a slight trend towards a species decrease in very old forests in our data, these were however only obtained from very few plots (Figs. 1 and 2).

Comparing the overall mollusc species increase with age in the montane with that of the sub-montane forest, it becomes apparent that the species increase of the whole species dataset (Fig. 1) in the sub-montane area is steeper, resulting in a much narrower confidence interval. As for birds, the homogeneity of tree species composition might be one reason for this. The confidence intervals of the threshold values for the whole species datasets as well as for the red-listed species datasets are showing overlapping ranges in both areas. In contrast to the birds, mollusc species seem to depend on forest attributes and structures that form in about the same period of time in both areas. These may include shadiness and humidity, a stable microclimate, adequate calcium content and amount of coarse woody debris, habitat continuity and richness of vegetation (Müller et al., 2005). As both areas are essentially semi-natural, populations of old-growth forest snails acting as sources for the colonization of old forests are always close by, which leads to the assumption that the similar threshold intervals reflect the period of time that is generally needed by snails for the immigration of the full species assemblage. If this is so, habitat continuity would have to be regarded as the main driving factor of snail diversity levels in beech forests under the precognition that adjacent populations for the colonization of newly arising habitats are available.

Although no lichen data from the sub-montane beech forests are available, it becomes evident that high lichen diversity levels (all species and red-listed species) are only attained at habitats that are older than 220 years in mixed montane forests (Figs. 1 and 2). This value results for mixed montane forest stands taken as a whole. However, major differences in the lichen species composition and speed of

lichen colonization exist between the dominating trees species (Uliczka and Angelstam, 1999). These differences are concealed in our presentation. Although the increase of lichen diversity with increasing age in boreal forests is well documented even for single tree species (e.g. Uliczka and Angelstam, 1999), comparably little is known about forest age dependent thresholds in lichen diversity. For example, species increases were found in stand ages up to 120 years in boreal forests (Kuusinen and Siitonen, 1998; Price and Hochachka, 2001). Uliczka and Angelstam (1999) detected rates of occurrence frequency >20% in lichen species sensitive to habitat change in tree age-classes ranging from 21–40 to 141–160 years in pine and spruce and from 21–40 to 61–80 years in aspen and birch. In beech forests of southern Sweden, lichens associated with very late succession stages were lacking in stands younger than 160 years, while stands older than 350 years had significantly higher lichen species numbers and also contained old-growth species (Fritz et al., 2008).

4.1. Management implications

In considering all the scientific discussion about thresholds, one has to keep in mind that only simple threshold values for important surrogates that mirror biodiversity patterns allow the implementation of scientific insights in forest management practices, not least because the use of thresholds has gained wide acceptance (Angelstam et al., 2003; Müller and Hothorn, 2004; Guenette and Villard, 2005; Lindenmayer and Luck, 2005; Ranius and Fahrig, 2006).

Taking Central European beech-dominated sub-montane and montane forests as a whole, a basic guideline for forest management is that these first acquire significantly higher densities of total species as well as of specialized species from the age of about 200 years.

Most of the age threshold values for different taxonomic groups given above exceed by far the economically reasonable maximum rotation age, which is around 120–140 years in beech (Knoke, 2003). Unlike boreal spruce stands (Kuusinen and Siitonen, 1998), the recommendation of prolonged rotation of the stands is feasible for these taxonomic groups only to a limited extent. Apart from the recommendation of the integration of old trees in commercial stands, there is a need to establish a denser network of strict forest reserves than exists today, which can act as refuge and dispersion areas for logging-sensitive taxonomic groups. The effectiveness of such a network has been proven in temperate forests, e.g. for lichens (Sillet et al., 2000; Peterson and McCune, 2001; Rolstad et al., 2001; Pilate, 2003a; Löhmus and Löhmus, 2007). Occasional high diversity levels in younger stands show that it is also possible to enhance their biodiversity. A better understanding of the factors which determine this would possibly permit improved realization of nature protection targets in forests managed primarily for economic production.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.ecolind.2008.11.002](https://doi.org/10.1016/j.ecolind.2008.11.002).

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