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Reappearance of Old-Growth Elements in Lowland Woodlands in Northern Belgium: Do the Associated Species Follow?

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The forest cover of the western European lowland plain has been very low for centuries. Remaining forests were intensively managed, and old-growth elements like veteran trees and coarse woody debris became virtually absent. Only over the last decades have these old-growth elements progressively redeveloped in parks, lanes and forests, and have now reached their highest level over the last 500–1000 years. Biodiversity associated with these old-growth elements makes up an important part of overall forest biodiversity. The ability of species to recolonise the newly available habitat is strongly determined by limitations in their dispersal and establishment. We analyse the current status and development of old-growth elements in Flanders (northern Belgium) and the process of recolonisation by means of specific cases, focussing on saproxylic fungi and saproxylic beetles. Our results show that 'hotspots' of secondary old growth, even isolated small patches, may have more potential for specialised biodiversity than expected, and may provide important new strongholds for recovery and recolonisation of an important share of old-growth related species.

Keywords colonisation, saproxylic species, dead wood, very large trees
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1 Introduction

1.1 A Long History of Low Forest Cover and Fragmentation

Flanders (northern Belgium) is a highly industrialised, densely populated area with over 450 people per km^2 (FPS Economy, SMEs, Self-employed and Energy 2009). Its countryside has been intensively used and altered by man over centuries. This is clearly reflected in the area and characteristics of forest cover. The present forest area is about 146 000 ha (i.e. 11% of the total area) and together with Ireland (10%), the Netherlands (11%) and the UK (12%), Flanders ranks among the least forested regions of Europe (MCPFE 2007). This low forest cover is not a recent phenomenon. As early as the first century BC, forest cover had gradually decreased to about 50% of the total land cover, followed by a slight recovery during the Dark Ages (4th–8th century AD) (Verhulst 1995). Especially during the Full Middle Ages (12th–13th century AD) a steep decline of forest cover took place: demographic pressure led to woodland clearance to create more farmland. Around 1250 less than 10% of forest cover was left (Verhulst 1995, Tack and Hermy 1998). Since that time, total forest cover has remained at a similar figure, with a slight increase in the 18th century to about 12%, and a minimum of about 9% halfway through the 19th century. Although total forest area remained relatively stable during the last centuries, the spatial distribution of the forests dramatically changed with deforestation on fertile silt loam soils (30–50% decrease) and new afforestation on former heathlands and alluvial meadows (De Keersmaeker et al. 2001, Vandekerkhove et al. 2005, Hermy et al. 2008). As a result, the current forest is severely fragmented both in space and time. Only a small fraction (15%) of the current forest cover is considered to be ancient woodland, which is defined as having remained continuously forested between the end of the 18th century and now (De Keersmaeker et al. 2001, Hermy and Verheyen 2007, Hermy et al. 2008). Most forests are 19th and 20th century afforestations, in particular even-aged poplar (*Populus* × *euramericana* and *Populus* × *interamericana)* and conifer plantations (primarily Scots pine, *Pinus sylvestris*). They contain trees of less than 80 years old and are now gradually being transformed into mixed stands (Afdeling Bos en Groen 2001b, Vandekerkhove et al. 2005).

Not only has the total forest cover been very low during past centuries, but the remaining forests were used very intensively in order to maximise the production of resources like firewood, utensils and construction wood (Tack et al. 1993, Tallier 2004). Until the 18th century, most forests were managed as coppice systems, and coppice with standards in the larger estates of nobelty and monasteries on richer soils in the south. High forest was exceptional (Tack et al. 1993, Tack and Hermy 1998, Tallier 2004).

This history of low forest cover, shifts through recent deforestations and afforestations, and continuous intensive use is comparable with other regions in the Northwest-European lowlands (the Netherlands, northwest Germany, southern England) (Buis 1985, Rackham 1986, Peterken 1993, Watts 2006).

1.2 Old-Growth Elements: Reappearance after Centuries of Absence

Large quantities of dead wood and a high density of very large trees are characteristic elements of the old-growth phase of natural forests (Harmon et al. 1986). They are often referred to as ‘typical’ elements for natural forests, that are absent or rare, even in forests under close-to-nature commercial management (e.g. Christensen and Emborg 1996, Korpel 1997, Bobiec 2002). An important share of forest biodiversity is strictly or primarily dependent on these elements for their survival (e.g. Harmon et al. 1986, Kirby and Drake 1993, Samuelsson et al. 1994, Økland et al. 1996, Esseen et al. 1997, Siitonen 2001, Heilmann-Clausen and Christensen 2003, Vandekerkhove et al. 2003, Ódor et al. 2006). For instance, Siitonen (2001) calculated that a decline of the total amount of coarse woody debris by 90–98%, may lead to the disappearance of at least 22–32%, and more probably over 50%, of all saproxylic species. If this habitat loss is combined with habitat fragmentation, this proportion is expected to be even larger.

The situation in Flanders (and other regions in the western European lowlands) has been even worse, with very fragmented forests and virtually no large trees and dead wood as a result of the traditional management regime. Except for some corner trees, marking the border between two properties, no standard trees were left to reach sizes over 60–80 cm DBH, as they would be too heavy to manipulate and have higher risks of defects. Even in the forest of Meerdaal, famous for its high quantity and quality of standard oak trees, only a few trees were selected to grow to sizes over 80 cm DBH: at the end of the 19th century, the forest only contained about 30 such trees on an area of over 1500 ha (Vandekerkhove et al. 2009b).

Century-old user rights involved the right to remove all dead and dying trees both in private and public forests (Tack et al. 1993, Tallier 2004). Decadent and dead trees and even dead branches on trees were promptly removed. Even the smallest branches were sought after. Older coppice stools that became less productive were entirely taken out, including the root bole. The same was done with the standard trees: they were not cut down, leaving dead stumps, but felled by digging and cutting over of the roots. The root bole was a too precious resource to be left in the forest (Tack et al. 1993, Vandekerkhove et al. 2009b).

In the 19th and 20th century, traditional management systems were replaced by high forest management and plantation forestry. These management systems also excluded dead wood and large trees (Branquart et al. 2004). Large tree dimensions were economically not desired (no specific market, difficult to transport, risk of hidden defects like discoloration and rotten core) and forest management was tailored to this. Dead wood was considered a potential source of disease outbreaks, waste of resource or an indication of negligence.

Only over the last 30 to 40 years has the ecological value of dead wood and veteran trees progressively gained attention in forest management. Over the last two decades, the conservation of a certain amount of dead wood and old trees has been fully integrated in principles and practices of sustainable forest management, together with smaller scale forest operations, longer rotations and transformation of plantations to more mixed stands (Ammer 1991, Burschel 1992, ONF 1993, Hodge and Peterken 1998, Afdeling Bos en Groen 2001a, Harmon 2001, Kappes and Topp 2004). This has lead to a gradual increase of the average stand age and structural diversity of forest stands, and a significant increase of dead wood and large trees.

Regional forest policies, including the Flemish policy, frequently have the explicit goal to further increase both quantity and quality of dead wood and conserve old and large trees, through a two-way approach. In multifunctional forests, the aim is to gradually improve both quality and quantity of dead wood by leaving some of the dead and dying trees during forest operations. For large trees, 5–10 trees per ha should be selected to be left uncut (Afdeling Bos en Groen 2001a). At the same time, a network of strict forest reserves (SFR) is being developed, covering up to 5% of the forest area. In these, a spontaneous build-up of dead wood and veteran trees to natural levels is taking place (so-called ‘secondary old growth’). Analyses of this process have shown for dead wood an average net accumulation of about 1,5 $m^3 ha^{-1} y^{-1}$ but there is wide variation around this mean (Vandekerkhove et al. 2009a). It is expected to take about one century, on average, to reach natural levels of dead wood estimated at 100–150 $m^3 ha^{-1} y^{-1}$ (Kraigher et al. 2002, Meyer et al. 2003, Muller-Using and Bartsch 2003, Christensen et al. 2005, von Oheimb et al. 2005, Vandekerkhove et al. 2009a). As most sites already contain mature and old forest stands, the same time horizon to reach natural densities of large trees (e.g. Nilsson et al. 2002) is expected.

It is believed that the combination of these two approaches is necessary and complementary to reach the overall goal of biodiversity conservation and restoration in forests (Parviainen et al. 2000, Frank et al. 2007).

1.3 Is Recolonisation by Old-Growth Associated Species Possible?

Due to the long history of absence of old-growth elements, species typically associated to them are likely to have disappeared completely, or may be restricted to rare relictual fragments of old-growth elements. Nowadays, the availability of redeveloped habitat offers important possibilities for recolonisation by old-growth associated species.

Colonisation is the joint result of successful dispersal and successful establishment (e.g. Jonsson et al. 2005). In Flanders, studies on colonisation and recolonisation have primarily been focused on dispersal and recruitment limitations for vascular plants (e.g. Butaye et al. 2001, Verheyen and Hermy 2001, 2004, Verheyen et al. 2003a, 2003b, Hermy and Verheyen 2007). These studies show wide ranges in dispersal and recruitment capacities, with particularly low dispersal and recruitment figures for so-called ancient woodland indicator species.

We analysed this potential for recolonisation by saproxylic fungi and beetles, two groups with a strong link to old-growth elements, covering a wide range of dispersal limitation and habitat requirements (Kallio 1970, Solbreck 1980, Nilsson 1984, Ranius and Hedin 2001, Edman et al. 2004a, 2004b). Their response was analysed both using nationwide distribution data (if available) and specific cases from sites with high potential for recolonisation: ancient semi-natural woodlands with large amounts of dead wood and very large trees in strict forest reserves. In the discussion, we also linked the development of oldgrowth characteristics to literature and published trends on cavity-nesting birds.

2 Materials and Methods

2.1 Quantification of the Amount of Dead Wood and Large Trees in Flemish forests

We summarised the actual status of dead wood quantity and quality in Flemish forests from data of the forest inventory of the Flemish Region. This inventory uses a systematic sample resulting in 2665 plots (Waterinckx and Haelvoet 1997). The first inventory of all plots was performed between 1997 and 2000. Since 2009 a second inventory has been conducted, switching to a continuous inventory in which every year about 1/10 of the plots is measured (Wouters et al. 2008).

Our calculations are based on the datasets of the first inventory (2665 plots) updated with preliminary results from a selection of plots from the second inventory.

Standing trees (both alive and dead) with DBH between 7 cm and 40 cm are sampled in circular plots with a radius of 9 meter; trees with DBH ≥ 40 cm are sampled in a larger circle ($R = 18$ m). Species, status (alive/dead), DBH and height are recorded. Volume calculations for living and intact standing dead trees use regional tariffs based on DBH and height measurements. Volumes of standing wood fragments (snags) were calculated using formulas of truncated cones. In the first forest inventory, no quantitative data for lying dead wood are available. In the second inventory, additional sampling of lying dead wood is performed using Line Intersect Sampling (Warren and Olsen 1964), with 3 lines of 15 m sampled in every plot in 3 fixed directions from the plot centre (Wouters et al. 2008, Govaere et al. 2010). This ‘fan-design’ is also used in other countries (e.g. Böhl and Brändli 2007). Volumes are calculated using the formula of van Wagner (1968).

An estimate of the density of large and very large trees (over 80 and 95 cm DBH respectively) was derived from the sample of the first forest inventory (total sampled area 271 ha). Because of the very low incidence of occurrence, the sampled population in the forest inventory was very small, allowing no further detailed analysis. Additional inventories were therefore performed in a selected set of ‘hotspot’ sites (Table 1). These are ancient woodlands that are known for their relatively high densities of very large trees. A full survey of these sites was done in parallel strips. Every tree surpassing the threshold diameter of 95 cm DBH was registered, and marked in the field (in order to avoid double counts). Tree species, DBH and health status were recorded. In total over 5000 ha of forest were surveyed in this way.

2.2 Saproxylic Fungi

Data on fungi are derived from the centralised database on fungal distribution in Belgium (FUNBEL, database of the Royal Flemish Mycological Society – KVMV, before Royal Antwerp Mycological Circle – KAMK). This database contains over 500 000 records on more than 5300 taxa. All records are also geographically positioned based on the national 4 km × 4 km floristic atlas grid.

Table 1. Overview of monumental trees in 12 selected ancient woodland sites, both in absolute numbers and densities (number of trees per ha) for different girth thresholds (in cm).

Site	Area (ha)	N > 300	N > 350	N > 400	N ha^{-1} > 300	N ha^{-1} > 350	N ha^{-1} > 400
Zoniënwoud	2475	7069	1867	288	2.86	0.75	0.12
Meerdaalwoud	1320	1230	270	35	0.93	0.20	0.03
Heverleebos	650	230	50	5	0.35	0.08	0.01
Veursbos	156	113	17	2	0.73	0.11	0.01
Neigembos	69	112	7	2	1.62	0.10	0.03
Kluisbos	57	109	19	3	1.91	0.33	0.05
Kolmont	18	95	38	12	5.28	2.11	0.67
Beiaardbos	17	93	15	1	5.45	0.88	0.06
Bellebargiebos	78	59	4	0	0.76	0.05	0.00
Wijnendale	65	53	14	3	0.82	0.22	0.05
Teuvenerberg	40	38	18	13	0.95	0.45	0.32
Bos Ter Rijst	29	35	10	2	1.22	0.35	0.07
Total	4974	9236	2329	366	1.86	0.47	0.07

Annual relative occurrences (this is the number of records of one species as a share of the total number of records for all species for that year in the database) were calculated for a selection of wood-decaying fungi: 4 currently widespread species (*Fomes fomentarius, Ganoderma lipsiense, Piptoporus betulinus* and *Trametes versicolor)* and a group of 21 highly selective and rare species that require a very specific substrate (wood mould in senescent trees and large dead wood) and high spatio-temporal continuity of this habitat (Christensen et al. 2005b). Trends of both groups were analysed by comparing average relative occurrences over the last 5 decades (Kruskal-Wallis rank sum test and paired comparisons with Wilcoxon rank-sum test). Trends in spatial distribution are derived from the comparison of number of occupied 4×4 km grid cells over the last 5 decades.

2.3 Saproxylic Beetles

Recent information on distribution and status of saproxylic beetles in Flanders is very limited. An analysis for the entire region based on existent centralised data is therefore not possible. This study compiles the existent recent information from a pilot study on saproxylic invertebrates (Versteirt et al. 2000, Heirbaut et al. 2001) together with a more thorough inventory of one specific site.

The pilot study involved a one-year sampling of 8 locations using a set of standardised sampling techniques: 3 pitfall traps, 3 colour traps, one stem-eclector, a large window-trap and a decoy-window-trap. All sites were ancient woodland sites with a moderate to high potential for saproxylic beetles, covering a wide range of dead wood volumes (8–140 m^3 ha^{-1}) and forest patch size (15–4500 ha). Dominant tree species were beech (*Fagus sylvatica*) or pedunculate oak (*Quercus robur*).

In 2008 and 2009 a detailed and elaborate inventory was made at one site from the previous set, Kolmont forest reserve (Köhler et al. 2011). This is an isolated forest patch of 17 ha containing an exceptionally high density and variability of habitat for saproxylic organisms, located in a countryside area with very low forest cover (<5%). In this sense it is a suitable site to study the potential for survival and recolonisation of saproxylic beetles in a landscape context that is representative for an important share of forest in Flanders. It is a very diverse and well structured mixed forest, on a hilly terrain, covering a wide range of soil conditions (from hydromorph rich alluvial soils to acid dry sandy loam). The forest is dominated by beech (*Fagus sylvatica*), with an important admixture of other tree species like oak (*Quercus robur*), ash (*Fraxinus excelsior*), birch (*Betula pendula*), gray poplar (*Populus canescens*), and sycamore maple (*Acer pseudoplatanus*). The site harbours a relatively high amount of dead wood in all forms and decay stages, and a high density of overmature trees: the amount of dead wood exceeds 40 $m^3 ha^{-1}$, including very large logs and snags, and a total of over 90 living trees with a DBH over 95 cm occur, almost all beech trees (density > 5 trees ha^{-1}). The sampling was spread over two years, and was done using window traps (3 normal traps and one decoy trap) 4 glue-rings, light traps and active catch by sifting of wood mould and hand catches on shrub vegetation and fungi. All coleoptera were identified to species level.

Recorded species were attributed to different substrate classes according to Köhler (2000), and their conservation status was assessed based on the Red Lists for Great-Britain, Germany and for Europe (Hyman and Parsons 1992,1994, Geiser 1998, Nieto and Alexander 2010), since no Red List for Coleoptera in Belgium exists (except for Carabid beetles; Desender et al. 2008). Indicator species for old-growth continuity were derived from the list developed by Müller et al. (2005) and the Saproxylic Quality Index (SQI) and Index of Ecological Continuity (IEC) developed for the UK for evaluation of the conservation value of sites for saproxylic beetles (Fowles et al. 1999, Alexander 2004) were calculated.

The results for Kolmont on total species number, number of red-listed species and share of different substrate classes were compared to a diverse set of beech-dominated strict forest reserves in Germany and Luxemburg that were sampled in an identical way (Köhler 2010a). Furthermore, Hurlbert's modified rarefaction curves (Hurlbert 1971, Simberloff 1972) were generated using BioDiversity-Pro software (McAleece 1997), on original datasets of Kolmont forest and 14 forest reserves in the west of Germany (Köhler, 1996, 2000, 2009) in order to provide a further comparison that is not affected by differences in sample size.

3 Results

3.1 Dead Wood and Large Trees in Flemish Forests

The average volume of dead wood (threshold diameter 7 cm) in Flemish forests derived from the first forest inventory was estimated at 7 $m^3 ha^{-1}$. As no concrete data were available for lying dead wood, this figure involved a very conservative estimate of the lying volume (about 3.5 $m^3 ha^{-1}$), based on the average volume of standing dead wood and the ratio of lying to total fractions derived from data in strict forest reserves. Preliminary results from the second inventory (on 221 plots) indicate that the total amount is now surpassing 13 $m^3 ha^{-1}$, with the lying fraction making up more than 70% of the volume. The estimate also indicates that trees with girth over 120 cm (= diameter of 38 cm) contribute for only 20% in this volume, while trees smaller than 60 cm (= diameter of 19 cm) make up half of the volume.

Based on the first forest inventory, the density of trees over 80 cm DBH is estimated at 0.656 trees per ha (95% confidence interval: 0.564–0.757). Extrapolated over the total forest surface (146 000 ha) this corresponds to approximately predicted 96 000 trees (82 000–110 000). The density of very large trees (DBH > 95 cm) is estimated at 0.132 trees per ha (95% confidence interval: 0.094–0.181) corresponding to 19 000 trees (13 700–26 300). About half of the registered trees (both at 80 and 95 cm DBH threshold) are beech trees, and one quarter are oaks (both *Quercus robur* and *Quercus petraea*). This is quite remarkable, as beech and oak stands only make up for about 5 and 15% of the total forest surface area respectively. The remaining quarter are mainly poplars and northern red oaks (*Quercus rubra*).

Detailed full surveys of selected sites showed that the very large trees are not equally distributed over the Flemish forest area but are mainly concentrated in 'hotspot' locations. On an area of less than 5000 ha (3% of the total forest area) we registered over 9000 trees over 95 cm DBH, corresponding with more than half of the total number of very large trees estimated in the forest inventory. An overview of trees over 95 cm DBH (300 cm girth) for the 12 selected locations is given in Table 1. This shows that the site 'Zoniënwoud' contains more than 1/3 of the estimated total number of very large trees (DBH > 95 cm) in Flanders. Densities are 20 times higher than the average. The forest complexes of Meerdaalwoud and Heverleebos also contain high amounts and densities of such trees. Over 500 of the recorded trees here are oaks, meaning that 10% of all monumental oaks are concentrated in these two ancient woodlands. Other investigated sites sometimes have very high densities of very large trees, but are all much smaller. This is in line with the findings of Götmark and Thorell (2003) for reserves in southern Sweden.

3.2 Saproxylic Fungi

The comparison of FUNBEL-records shows a clear increase in the registrations for saproxylic species. As shown in Fig. 1, the relative occurrence of common and widespread species like *Fomes fomentarius, Ganoderma lipsiense, Piptoporus betulinus* and *Trametes versicolor* have significantly increased over the last five decades (Kruskal-Wallis rank sum: $p<0.001$ for all species separately and the 4 species together), although the trend already starts to level out for several decades. *Fomes* shows a steady increase over time, while *Ganoderma* and *Piptoporus* appear to have stabilised over the last 40 years. A pairwise comparison over the periods 1970–89 and 1990–2009 for these two species and for all 4 species together show no further significant increase (Welch modified two sample t-test and one sided Wilcoxon rank-sum test: $p>0.05$). Still, comparing the last two decades, all 4 species again showed a renewed increase (one sided Wilcoxon rank-sum test: $p<0.05$).

The number of occupied grid cells also strongly expanded over time. Before 1970, these species were known from less than 3% of all 4 km × 4 km grid cells. They now occur in 15 to 30% of all grid cells. This means that they occur in the majority of grid cells containing forest, and can be considered widespread in all forests.

The trend for the group of species with high substrate requirements (21 species) is even more explicit (Fig. 2). Relative occurrence and average number of recorded species per year have significantly increased over time (Kruskal-Wallis rank-sum; $p<0.001$). The higher values for the first decade are entirely related to one species (*Inonotus cuticularis*), that was relatively often recorded in the 1960's. Pairwise comparisons over the last two decades and the periods 1970–89 and 1990–2009 show very strong increases both in number of recordings and yearly recorded number of species (one sided Wilcoxon rank-sum test: $p<0.001$).

Until the 1980's, species from this group occurred in less than 1% of all 4 km × 4 km grid cells, while in the last decade, over 7% of all grid cells contained at least one species, with several cells containing 4 species or more.

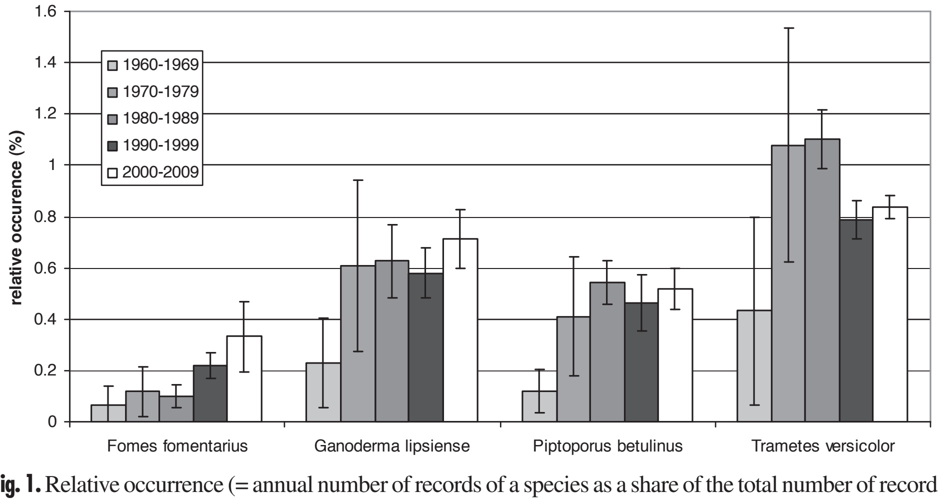

Fig. 1. Relative occurrence (= annual number of records of a species as a share of the total number of records that year) of four common and widespread saproxylic fungi in Flanders over the last 5 decades.

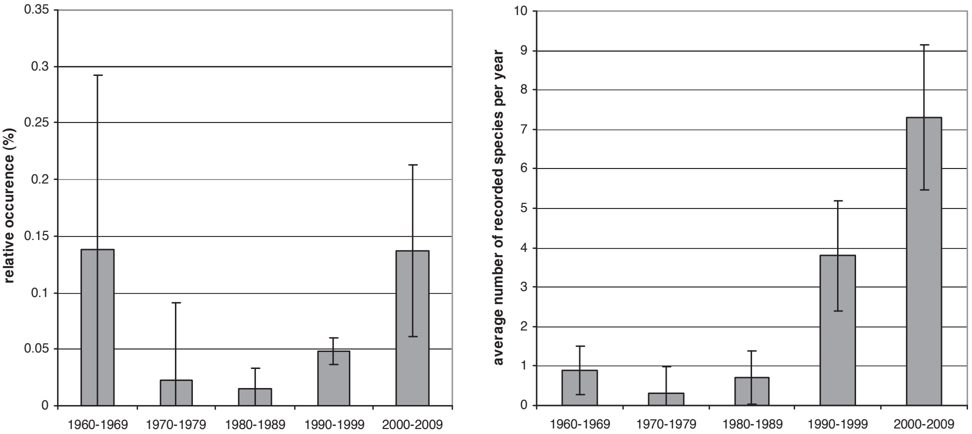

Fig. 2. Occurrence of European indicator species of saproxylic fungi with high substrate requirements (Christensen et al. 2005b) in Flanders over the last 5 decades. Left: relative occurrence of all 21 species combined; right: average number of recorded species per year.

3.3 Saproxylic Beetles

The pilot study revealed between 50 and 90 species per site, which is quite limited compared to other inventories (Köhler 1996, 1999, 2000). Still, between 20 and 30% of the recorded species at every site are considered rare or red-listed in Germany and the UK (Hyman and Parsons 1992,1994, Geiser 1998). Although these inventories probably did not reveal the complete species richness of the sites, they indicated that the species composition did not entirely consist of common fast colonisers, but also included more sensitive species that are susceptible to habitat decline (as shown by their Red List status). Some of the recorded species are known to require a high spatio-temporal continuity of dead wood (e.g. *Elater ferrugineus*, *Stictoleptura scuttellata*) and are included in the list of indicator species for sites of European importance for saproxylic invertebrates (Speight 1989).

The additional study of Kolmont forest in 2008–2009 was the first detailed inventory of saproxylic beetles in Flanders. It resulted in a much more complete picture of the total species richness with a total number of 824 species of Coleoptera identified (Köhler et al. 2011). Of these, 315 species are listed on the catalogue of xylobiontic beetles of Germany by Köhler (2000). At least 10 new species for Belgium were recorded. Results of the comparison with other beech forest reserves in Germany and Luxemburg that were surveyed in a similar way (Köhler 2010) are given in Table 2. The total species richness is quite high, placing Kolmont among the most species rich sites (average over 24 sites: 256 species).

This is also clearly illustrated in the rarefaction curves comparing Kolmont with 14 sites in the west of Germany (Fig. 3). The estimated species diversity and the steep inclination of the curve for Kolmont indicate a distinctively higher than average species richness.

The distribution of the recorded species over different substrate classes shows a well balanced saproxylic beetle community, including an important share of species living in wood mould, nests and saproxylic fungi, and is in line with the results from other sites in Germany and Luxemburg (Table 2).

Not only the quantity and composition of species surpassed expectations, the list also contains an important share of rare and endangered species (see Annex 1). Almost 30% of all registered saproxylic species in Kolmont (92) occur on the German Red List (average over 24 sites: 24.5%). Seven of these are listed as ‘critically endangered’, 24 as ‘endangered’ and 61 as ‘vulnerable’. More than 100 species are found on the British

Table 2. Saproxylic beetles: total species number, number of red-listed species and share of species in different substrate classes for the Belgian site of Kolmont compared to a diverse set of beech-dominated strict forest reserves in Germany and Luxemburg that were sampled in an identical way (Köhler 2010a). Sites are ranked in order of increasing species richness.

Reserve	Strict reserve since (year)	Elevation (m ASL)	Size (ha)	Average yearly temperature (°C)	Age-range of dominant trees	Estimated deadwood share (%)	Wood	Wood mould	Nests	Fungi	Bark	Exsudates	Total nr of saproxylic beetle species	German Red List 1998	Urwald relic species
Schönbuche	1988	410	27.9	7.8	120–160	4.0	37	30	2	35	63	1	168	23	0
Hohestein	1989	510	26.7	8.0	90–140	0.7	41	30	3	35	63	0	172	30	0
Gold- und Ziebachsrück	1988	330	31.3	8.0	120–160	0.5	36	32	1	40	64	2	175	22	0
Eischeid	1982	600	34.0	7.5	100–160	1.5	32	37	1	44	76	4	194	32	0
Niddahänge	1988	560	42.0	6.7	120–240	6.3	33	36	4	55	74	1	203	41	0
Schäferheld	1983	490	23.3	8.0	120–160	1.5	45	35	5	54	73	3	215	41	0
Etscheid	2001	490	40.0	7.9	100–160	1.0	54	34	4	49	74	5	220	33	0
Serrahner Berge	1998	120	73.3	8.0	>200	19.4	47	55	5	50	66	4	227	73	3
Geldenberg	1971	60	22.1	9.8	130–200	2.0	53	44	6	46	73	7	229	44	2
Dohlenwald	2000	50	45.1	8.3	80–120	5.0	61	40	7	56	61	6	231	61	2
Wiegelskammer	1983	410	13.9	8.0	80–120	2.0	54	37	2	54	79	5	231	31	0
Bohnrath	2003	60	34.2	8.2	200–240	5.8	59	58	9	57	75	4	262	79	5
Altwald Ville	1978	135	19.9	9.6	130–180	3.0	68	41	7	53	88	5	262	60	1
Himbeerberg	1991	540	42.0	7.4	140	40.0	60	44	2	52	102	5	265	39	0
Rotenberghang	1991	390	22.0	8.4	100–200	30.0	62	39	5	50	103	6	265	48	0
Stelzenbach	1995	370	74.0	8.6	120–160	3.0	62	51	3	59	86	5	266	41	0
Platte	1978	450	33.9	7.6	100–200	5.0	68	42	5	68	87	2	272	52	1
Heilige Hallen	1998	130	39.2	7.9	280–320	24.6	61	79	11	71	75	3	300	108	13
Laangmuer	2005	400	103.4	9.4	120–180	2.6	76	56	7	72	85	7	302	77	1
Conower Werder	2003	90	49.9	8.2	120–160	13.5	66	68	13	82	81	4	314	115	10
Useriner Horst	1998	60	37.4	8.1	>250	16.2	70	79	10	79	72	4	314	107	8
Kolmont	**1995**	**90**	**17.0**	**9.2**	**140–200**	**9**	**79**	**56**	**16**	**70**	**88**	**6**	**315**	**94**	**5**
Fauler Ort	1938	60	20.8	8.2	>350	27.8	85	93	16	76	80	7	357	149	17
Mummelskopf	1972	300	52.6	8.8	170	20.0	96	71	10	84	116	8	385	105	3
Average value for all 24 sites	1988	296	38.6	8.2	155	10.18	59	49	6	58	79	4	256	63	3

Red List, most of them in the 'notable' categories, but 10 are 'endangered'(RDB1), 6 'vulnerable' (RDB2) and 15 'rare' (RDB3).

Two species are listed on the new European Red List (Nieto and Alexander 2010): *Cerophytum elateroides* occurs in the category 'Vulnerable' and *Brachygonus megerlei* is on the additional list of 'Near Threatened' species. Another species in this category, *Elater ferrugineus* was also found in Kolmont, both in 2000 and in 2011, but not during the two year survey. This species, together with *Allecula rhenana, Abraeus parvulus, Micridium halidaii,* and *Batrisodes buqueti* are listed on the German indicator list of species that are considered to be associated with high spatio-temporal continuity of old-growth stand features (Müller et al. 2005). Hotspot sites for saproxylic beetles in Bavaria, Germany contain more than 10 of these species, whereas most investigated sites have two or less (Büssler 2010).

On the British indices (Fowles et al. 1999, Alexander 2004), Kolmont has a score of over 800 on the Saproxylic Quality Index (SQI) and 149 on the Index of Ecological Continuity (IEC).

Compared to over 150 sites from the UK, the SQI and IEC of Kolmont are only surpassed by

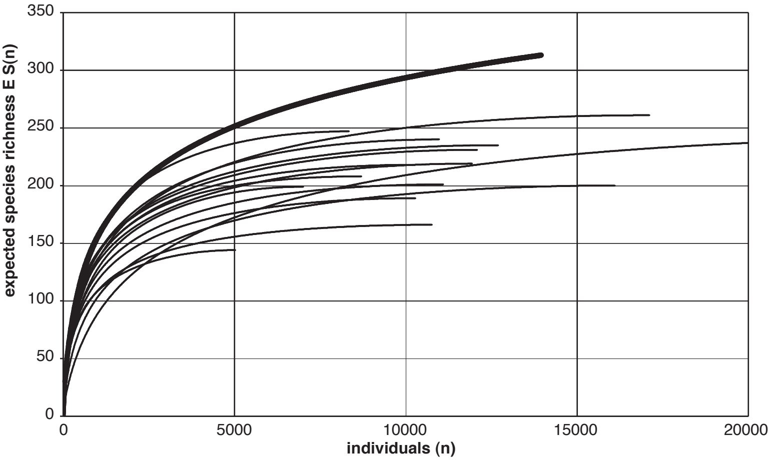

Fig. 3. Estimation of species richness using Hurlbert's modified rarefaction curves (Hurlbert 1971, Simberloff 1972) for Kolmont forest (bold line) compared to 14 forest reserves in the west of Germany

Windsor Great Park and New Forest (Alexander 2004, Saproxylic Quality Index… 2009). Sites in the UK with an IEC of over 80 are considered of international importance, deserving special conservation status and management (Alexander 2004).

4 Discussion

The average amount of dead wood in Flemish forests (over 13 m^3 ha^{-1}) is not exceptionally high but in line with other European countries: average figures per country in Europe vary from less than 1 to 23 m^3 ha^{-1} (MCPFE 2007). Nevertheless, we can clearly state that the amount of dead wood has not been as high as it is now over at least 500 years, and probably much longer.

The recorded figure, however, is still less than 10% of the amounts to be expected in natural forests in this part of Europe (Kraigher et al. 2002, Meyer et al. 2003, Muller-Using and Bartsch 2003, Christensen et al. 2005, von Oheimb et al. 2005, Vandekerkhove et al. 2009a). Considering that the climax vegetation in Flanders is forest for over 90% of its territory, the current amount of dead wood represents only 1% of the natural density, is very unevenly distributed, and consists mainly of small diameter material. The same conclusion can be drawn for very large trees: their average density is 10–50 times lower than in natural lowland forests (Nilsson et al. 2002, Bobiec 2002), and considering the low forest cover, the density of these trees in forest context is 100–500 times lower than in reference conditions. However, this calculation does not take into account the monumental trees in hedgerows, parks and tree rows that occur scattered in the open countryside and that may play an important part in the survival and recovery of old-growth associated species (see below).

Considering the estimates of species loss by Siitonen (2001) – estimated at a minimum of 22–32% and more likely over 50% of all saproxylic species in case of a decline of dead wood habitat by 90–98% – it is expected that forest biodiversity, especially saproxylic communities in Flanders have been decimated in the past and reduced to a small fraction of its original diversity. Due to the very recent increase in old-growth elements, a slow recovery could be assumed, through long distance recolonisation – or short distance in case relic populations are still present – of the newly available habitat.

4.1 Recolonisation: a Question of Dispersal Ability and Habitat Requirements

As shown in the historic account, old-growth elements have for centuries been completely absent from forests in Flanders. It is therefore assumed that most species that are strictly related to old-growth elements (dead wood and old trees) completely disappeared from these forests or only managed to survive in very scarce relics.

Over the last decades, conditions for these species have clearly improved in our forests to a level unprecedented over the last centuries, giving perspective for recovery (Ódor et al. 2006, Irmler et al. 2010). The level of recovery is strongly related to the ability of species to recolonise suitable habitat. This colonisation is the joint result of successful dispersal and successful establishment (e.g. Jonsson et al. 2005). The success is strongly dependent on the species-dependent dispersal and recruitment potential (e.g. for vascular plants: see Butaye et al. 2001, Verheyen et al. 2003b, 2004, Hermy and Verheyen 2007). When habitat disappears, species may manage to persist for a period of time – the so called ‘extinction debt’ – (e.g. Hanski 1999, 2000). For slow-colonising forest plants in Flemish forests for instance, it was determined that the loss of species due to land use shifts may still be ongoing (Vellend et al. 2006). Similarly, species recolonisation of newly established habitat might also be delayed because of lag phases in the dispersal and establishment of populations, the so-called colonisation or immigration credit (Hanski 2000, Jackson and Sax 2009, Baeten et al. 2010).

Forest birds are a well-studied group of evident good dispersers. Species from the ecological group of cavity-nesting birds, related to mature high forest with dead wood (according to Sierdsema 1995) are expected to react promptly on the improved condition of the forest habitat. Their response will depend on their reproductive potential and their requirements to the habitat. Woodpeckers (family Picidae), especially, have therefore been proposed as good indicators for forest biodiversity (Angelstam and Mikusiński 1994, Mikusiński et al. 2001). Requirements of the species are diverse with great spotted woodpecker (*Dendrocopos major*) and black woodpecker (*Dryocopus martius*) being less restrictive than others like middle spotted woodpecker (*Dendrocopos medius*) (Rolstad et al. 1998, 2000, Kosiński 2006, Bocca et al. 2007). Secondary cavity breeders like tits (family Paridae), European nuthatch (*Sitta europaea*), and tawny owl (*Strix aluco*) that are dependent on the old cavities provided by the former, are expected to quickly follow.

Trends for Flanders for the period 1990–2002 indeed indicate a significant increase of the breeding population of cavity-nesting birds (Dumortier et al. 2005). Tawny owl showed an increase between 20 and 50%, and European nuthatch, lesser spotted woodpecker (*Dendrocopos minor*) and black woodpecker populations increased by more than 50%. New assessments also confirm this trend for the next 5–6 year period (Van Daele et al. 2010). Comparing the recent population estimates with data covering the period 1973–1977 (Devillers et al. 1988), populations of lesser spotted and black woodpecker apparently have tripled, and those of great spotted woodpecker and European nuthatch quadrupled over the last 40 years. The most critical of this group of species is the middle spotted woodpecker, a species that is very strongly related to old broadleaved forests (Jöbges and König 2001, Angelstam et al. 2003, Pasinelli 2007, Müller et al. 2009). Until 1998 this species was not breeding in Flanders. In 1999 the first two breeding pairs were registered in the ancient woodland of Meerdaalwoud, where the population increased to 15 breeding pairs by 2003 (Moreau 2006). By that time breeding was also confirmed in other ancient woodlands in the southeast and southwest of Flanders (Vermeersch et al. 2004). The Flemish breeding population in 2005 was already estimated at over 50 breeding pairs and is still increasing and extending its breeding range (Vermeersch et al. 2006). More demanding species like middle spotted woodpecker apparently take much longer to react to the improved conditions, but are now also re-establishing and are strongly increasing. Similar trends are also seen for this species in the Netherlands and northwest Germany (Kamp 2008, van Dijk et al. 2010).

Like birds, fungi are in principle very good dispersers: they produce millions of spores, that can be spread over hundreds of kilometers (e.g. Risbeth 1959, Kallio 1970, Hallenberg and Kuffer 2001, Stenlid and Gustafsson 2001). However, only a very small fraction of the spores actually spreads over a longer distance (Kirk et al. 2008). Spore dispersal studies indicate that the vast majority of spores fall within a few meters of the fruiting body. The density of spores at 100 m distance is already 1000 times lower than at 1 m distance (Risbeth 1959, Kallio 1970). Ecologically effective spore spreading distances might be restricted to a few kilometres (Edman et al. 2004a, 2004b, 2004c). However, given the enormous number of spores, there is still a fair chance for some spores to travel over large distances. This small fraction is crucial to establish new populations in distant localities (Stenlid and Gustafsson 2001). Such long-distance dispersal events are considered to be crucial to range expansions (e.g. Pakeman 2001, Clark et al. 1998). In contrast to birds and insects, the spores cannot actively search for suitable substrate to germinate, thus depend entirely on coincidence. Moreover, even when a viable spore might reach a new substrate at long distance and be able to germinate, another compatible spore must reach the same substrate in order to mate and produce a dikaryotic mycelium that in its turn is able to produce fruit bodies and new spores (Stenlid and Gustafsson 2001). This process makes the development of a reproductive new mycelium at longer distance much more unlikely than expected from its reproductive and dispersal capacity. The mere occurrence of spores and presence of suitable substrate does not guarantee colonisation (Jonsson et al. 2005).

Historic descriptions on saproxylic fungi indicate how impoverished the mycoflora of saproxylic fungi in Flanders and the surrounding areas must have been after many centuries of absence of suitable habitat. Although already described for the area as early as the 17th century (Van Sterbeeck 1675), species like *Fomes fomentarius* that are now widespread were explicitly mentioned to be rare in 19th century reference works (Kickx 1835, 1867, Bommer and Rousseau 1879), and they still were halfway the 20th century. Van der Laan (1972) mentions only 10 known findings of this species for the Netherlands. In his description of the distribution of *Fomes fomentarius,* stretching over the whole temperate zone of the northern hemisphere, Jahn (1962) explicitly describes a 'hole' in the distribution covering northwest Germany, Belgium, The Netherlands and England. Species that live on small branches or stumps, like *Trametes versicolor*, were the only wood decaying fungi that were considered rather widespread in 19th century literature (Bommer and Rousseau 1879).

With the increased availability of habitat, fungal communities of dead and old trees are expected also to recover. Indeed, over the last decades, mycologists already reported an increase in both species richness and range of saproxylic fungi. Species like *Fomitopsis pinicola, Schizopora flavipora, Pholiota aurivella, Pluteus umbrosus, Ischnoderma benzoinum* and *Phleogena faginea* that used to be extremely rare, appeared to have gradually extended their range and were now found throughout the region (Walleyn 2003, 2004, 2006). Other species (e.g. *Mycena crocata, Plicaturopsis crispa, Hennigsomyces candidus, Hohenbuehelia auriscalpium, Cystoderma simulatum)* that were not recorded before the 1980's now have well established populations at several localities. The lack of records before that time could not simply be explained by a lack of knowledge or inventory, as also very conspicuous species abundantly producing fruitbodies every year (like *Mycena crocata*) were missed and the locations where they are now common were also visited regularly in the past (Walleyn 2003, 2004, 2006). Similar trends are also reported for the Netherlands (Arnolds and Van den Berg 2001, Veerkamp and Arnolds 2008).

In an attempt to quantify and statistically test these trends, we had to rely on the best available information: a centralised database compiled from mycological excursions, research projects, historical records in literature, herbarium collections, etc… These data are not based on standardised inventory protocols or sampling designs and data in the dataset are not equally distributed over time (the dataset contains more records in the last two decades than the decades before). Results were as far as possible standardised by using annual relative occurrences of species (as a weight factor for differences in record numbers) and identical time periods of 10 years. Only the last five decades that contained enough records for reliable analysis (> 10 000 records per decade) were taken into account. Over this period of 50 years the specific group of macrofungi related to dead wood has always been well studied and was indeed included in all inventories, although there might have been eras with more or less attention to certain groups of fungi causing some bias to the data. In this sense, the recorded trends are not 'absolute', but indicative. However, the trends are so distinctive and significant, that we are confident that they represent real trends.

Our results show that for species that are not too selective in their substrate requirements, the current density of available habitat appears sufficient to allow the steady development of new viable populations and expansion of their range. Some, like *Trametes versicolor* and *Piptoporus betulinus*, are now widespread in all forests, and appear to have reached a point of saturation. Species like *Fomes fomentarius* and *Ganoderma lipsiense*, that are both related to the more uncommon habitat of larger snags and logs, are still increasing. Similar trends are also observed in the Netherlands (Arnolds and Van den Berg 2001, Veerkamp and Arnolds 2008). Still, all four species appear to have further increased over the last two decades, which may be related to the further increase of available habitat.

A number of highly selective species though, like the indicators for habitat continuity of Christensen et al. (2005b) are still very rare or absent. They are often related to very specific rare and transient substrates like wounds or rotholes of old trees, or specific stages of decay of large size logs and snags. On the rare occasions that suitable habitat is available, these species may easily fail to arrive in time, especially if source populations are distant (Christensen et al. 2005b). Only 14 out of 21 species have up to now been recorded in Flanders and most of them are very rare with less than 30 records registered. Individual hotspot sites in France, UK, Denmark and Czech Republic may contain up to 16 species (Christensen et al. 2005b). This indicates the impoverished status of Flanders for these selective species.

This conclusion was also drawn in a comparative study of selected sites with high densities of dead wood in Hungary, Slovenia, Denmark, The Netherlands and Belgium (Ódor et al. 2006). Overall species richness per log or snag in the Belgian site was comparable to other countries, but country level species richness was lower only in the Netherlands. In both Belgium and the Netherlands the proportion of frequent species was higher than in the other countries. Focusing on more demanding species, the differences were even more distinct. The authors developed a list of 99 'species of special interest (SSI)'. The total number of SSI's recorded in the Netherlands (27) and Belgium (24) was much lower than in Hungary (51), Slovenia (43) and Denmark (41). Also the number of records and the proportion of these species were the lowest in the Netherlands and Belgium. For the highly selective species like the SSI-species of Ódor et al. (2006) and the indicator species of Christensen et al. (2005b), the required threshold of temporal and spatial continuity and density of suitable substrate necessary to build up viable populations appears to not yet have been reached. With suitable habitat widely distributed, but occurring at very low density and relatively ephemeral over time, their colonisation is strongly determined by stochasticity (Gu et al. 2002).

Still, also on this group of highly selective species, our analysis shows a distinct increase, both in number of species and records. Unlike the less selective species, the expansion does not appear to slow down over the last 20 years, but appears to become even more explicit. Over the last 20 years, 7 of the 21 indicator species of Christensen et al. (2005b) apparently have newly established in Flanders, of which 5 over the last 10 years.

These new establishments of species presumably had to rely on long distance inflow of spores. Sites with a high occurrence and density of suitable substrate not only increase the probability of these spores reaching suitable habitat and thus the chances of successful establishment, but also allow further development of larger local populations, with a lower risk for local extinction (Nordén and Appelquist 2001, Stenlid and Gustafsson 2001, Edman et al 2004a, 2004b, Jonsson et al. 2005, Christensen et al. 2005b). In order to persist as local populations species indeed must be able to colonise new suitable host trees at the same average rate as the old host trees become unsuitable. This requires sufficient suitable trees within dispersal range, thus high densities of potential habitat (Rukke 2000, Siitonen 2001). Not surprisingly, the observations of highly demanding species of fungi in Flanders are often concentrated in the rare localities with a high density of their specific habitat, like strict forest reserves, old park areas and landscapes with high densities of old tree rows. These new satellites may in the future develop to become new sources for further expansion (Siitonen 2001, Stenlid and Gustafsson 2001, Edman et al. 2004a, 2004b, Jonsson et al. 2005).

For saproxylic beetles, similar aspects of habitat requirements and availability are influencing possibilities for recolonisation as for birds and saproxylic fungi (Schiegg 2000, Jonsson et al. 2005), but the process is complicated by the extremely diverse dispersal potential of the different species (Jonsell et al. 1999). Some species, often linked with highly ephemeral habitats (like bark beetles) have a high dispersal capacity, while species inhabiting stable dead wood microhabitats (like species in wood mould) have low dispersal rates (Nilsson and Baranowski 1997, Jonsell et al. 1999, Köhler 2000). This dispersal ability may be a key characteristic for the survival and recovery potential of species (Ranius 2006). Brunet and Isacsson (2009) found that common species were not affected by isolation from old-growth forest, but for rare and red-listed species there was a significant effect after a few hundred meters, and some species appeared not to be able to cross a section of two km of unfavourable habitat. In a study on saproxylic beetles on beech trees by Weiss and Köhler (2005) the level of isolation of the tree also proved to be a significant factor in the colonisation rate of the trees.

Ips typographus and *Hylobius abietis* are known to be able to travel over distances of 10 km and even up to 80 km and can actively search and detect suitable habitat from long distance (Solbreck 1980, Nilssen 1984). They also have high reproduction capacities. These species are very quick colonisers and react promptly to the new availability of suitable habitat. However, many species are limited in their dispersal, rarely spreading over distances more than a few 100 meters. Jonsell et al. (1999) concluded that the fungi-inhabiting species they studied could colonise suitable substrate within 1 km of their point of origin, but noted a reduced colonisation over a distance of only 150 meters. Irmler et al (2010) found an asymptotic decrease of species richness of saproxylic beetles with distances of more than 80 meters from source populations.

For some species, dispersal over distances of as little as 200 m is even unlikely (Speight 1989, Nilsson and Baranowski 1997). Moreover some of these non-mobile species are very selective in their habitat. They are dependent on sites with high spatio-temporal continuity of habitat related to natural forests, and are therefore often used as indicator species for habitat continuity (Alexander 2004, Müller et al. 2005). As a consequence they are often rare or Red Listed in most countries where natural forests are rare or in decline.

Given the highly fragmented forest landscape and its management history in Flanders with the absence of suitable habitat for these species during centuries, it is highly unlikely to find any of these demanding species. What was expected was an impoverished fauna, containing the good dispersers with limited substrate requirements, but lacking the more demanding species, especially the dispersal limited species.

No extensive datasets are available in Flanders to underpin this hypothesis, but existing fragmentary information appears to confirm it. A comparison of the present-day carabid beetle fauna occurring in woods of Flanders with a unique data-set of archaeological carabid remains from a Late and Post-Roman forest at Velzeke (Eastern Flanders), showed a significant loss of stenotopic woodland species, with some of them considered extinct in Flanders (Desender et al. 1999). A study on saproxylic beetles and hoverflies in the south of Belgium (Fayt et al. 2006, Dufrêne et al. 2008) indicated an impoverished fauna with less than half of the expected species number found, and a large part of the species with residual and highly localised populations.

Signs of recovery are also fragmentary but indicate a similar long lag phase as for saproxylic fungi. A species like *Bolitophagus reticulatus* living in fruit bodies of *Fomes fomentarius* only managed to recolonise in the last decade, although suitable substrate was already available for some time. The first recordings of the species in Flanders were made in 2002–2003 (Troukens 2004, Dufrêne et al. 2008) and by now it has been recorded in several locations all over the territory. In the Netherlands a first specimen was found in 1984 (de Goffau 1984), but only in 2005 populations were found in several locations (Moraal et al. 2007). Studies on this species have shown that it is normally a short distance disperser, moving only up to 100 m (Sverdrup-Thygeson and Midtgaard 1998, Rukke and Midtgaard 1998), but with the capacity for incidental long distance dispersal (Jonsell et al. 2003). Like for fungi, sites with high amounts of suitable habitat are considered of high importance both to increase incidence and continuity of suitable resources and possibilities to establish viable populations (Rukke 2000, Jonsson et al. 2005).

Species depending on even more specific habitat (like old trees with rotholes) with very limited dispersal abilities like *Lucanus cervus* and *Osmoderma eremita* (Ranius and Hedin 2001, Rink and Sinsch 2007, Thomaes et al. 2008b) had probably already been lost from most, if not all, forests by the middle ages. They are considered close to extinction or extinct in Flanders (e.g. *Osmoderma*: Ranius et al. 2005) or restricted to a few small relics (e.g. *Lucanus*: Thomaes et al. 2008a).

4.2 Relic Sites: Essential for Dispersal Limited, Selective Species

The inventory in Kolmont revealed an unexpected quantity and quality of species richness in saproxylic beetles. The share of German red-listed species is quite remarkable, even taking into consideration the fact that this list contains a few species with a more Atlantic distribution that are considered widespread in Flanders. Both total species richness and number of red listed species are comparable with sites like ‘Heilige Hallen’ or ‘Fauler Ort’. These are reserves that are renowned for their exceptionally old beech stands with high amounts of dead wood in all decay stages, and can be considered as reference sites for beech forest biodiversity in western Europe. Moreover, most of the reserves in Table 2 and Fig. 3 are embedded in extensive woodland areas, thus much less isolated than Kolmont and therefore expected to be richer in species.

Also, the high scores on SQI and IEC (Fowles et al. 1999, Alexander 2004) indicate this very small site to be of high importance, although it should be acknowledged that the saproxylic fauna of the British Isles is somewhat poorer than on the European continent, and a few widespread species on the continent are endangered in the UK.

Several explanations for this exceptional result may be given. First of all, although very small, the site contains a large variety of abiotic and biotic conditions, with a high density of very large trees and an amount of dead wood (>40 $m^3 ha^{-1}$) that surpasses the threshold value of 20–30 $m^3 ha^{-1}$ that might be required to safeguard the complete spectrum of species that rely on dead wood (Angelstam et al. 2003, Humphrey et al. 2004, Müller and Büssler 2008). The admixture of other tree species like pedunculate oak, ash and sycamore may also be higher than in some of the German sites. Also, good conditions for thermophilous species may also be more abundant in south-exposed slopes, gaps and along the forest edge in Kolmont.

Moreover, and contrary to what was expected, the site contains some highy selective, dispersal limited species that are indicative for a high spatio-temporal continuity of their specific habitat like wood mould in tree cavities at the site or its immediate surroundings (Alexander 2004, Müller et al. 2005, Nieto and Alexander 2010).

Indeed, the site may have known an exceptional history of continuity in old-growth characteristics, clearly atypical to the Flemish situation. From the 12th to 15th century, the site supported a castle of high strategic importance, its vicinity covered with protective woodland. Also, in later times, the site never had high economic value to its owner, and was incorporated in a ‘romantic’ park landscape in which old and decaying trees were considered of ornamental value. At least over the last two decades no interventions were made in the forest, allowing the dead wood amount and density of old and decaying trees to further increase.

Moreover, this small forest island (merely 17 ha) used to be surrounded by a traditional landscape with extensive old fruit orchards and hedges with pollarded trees. For old-growth related species this landscape provided very valuable alternative habitat. Speight (1989), Alexander (2004, 2008) and Dubois et al. (2009) already pointed out the importance of these alternative habitats for saproxylic species, especially dispersal limited species of wood mould in hollow trees. In this sense, the site was not as isolated as it appears at first sight. We come to the conclusion that this site had an atypical continuity of old-growth characteristics in the forest and probably also in the surrounding countryside. Indeed, the matrix context may clearly influence and enhance the functionality of the reserve area (Franklin and Lindenmayer 2002).

The results for the investigated sites of the pilot study were too fragmentary to make similar conclusions, but suggest that some of these sites may also contain species that are indicative of relic habitat and populations. These sites were indeed not randomly selected but involve sites that actually bear good quantities of suitable habitat. Some of them may have known a less intensive management in the past than the average forest, allowing relic populations to survive. Future and ongoing inventories at these and other sites should reveal more relic populations that may prove to be essential for the survival of dispersal-limited species.

In many parts of Flanders, the traditional countryside landscape with old pollard trees and traditional fruit orchards may have played an essential role in extending the survival for many slow colonising species, especially saproxylic beetles living in wood mould. These very slow colonisers (limited dispersal and specific substrate requirements) may therefore been able to uphold better than expected. This is also the case in other countries, where strongholds of old-growth species are primarily found in ancient wood pastures, royal hunting grounds and deer parks and traditional orchards and pollards in the countryside (e.g. Speight 1989, Alexander, 2004, 2008, Dubois et al. 2009). In Flanders, similar wood pastures and deer parks were absent, but orchards and pollards frequently occurred in the countryside, providing alternative and relic habitat for at least a specific part of the old-growth related biodiversity. However, these alternative habitats in their turn have been lost during the second half of the 20th century: most of the trees were cut (Deckers et al. 2005), and the few old orchards that were spared were often treated with pesticides. Thus, despite the relative stability in forest area and improvement of saproxylic habitat within, fragmentation and loss of habitat severely increased both on a regional and a local scale, because forest habitats are surrounded by an increasingly hostile environment, where the survival of forest species becomes highly unlikely (Bailey 2007, Hermy et al. 2008).

This may have been the final blow to many species. Exemplary for this situation is *Gnorimus nobilis*, a typical species of rotholes, that was uncommon but widespread in Belgium until the 1950's surviving mainly in fruit orchards (Janssens 1960). Most of these orchards have since then been cut down or treated with pesticides. As a consequence *Gnorimus nobilis* disappeared from all but one of its localities: it is now at the brink of extinction, restricted to one known locality in Flanders (the extensive forest of Zoniënwoud).

4.3 Conclusion and Future Prospects

In Flanders, 'old-growth elements' have been virtually absent from the intensively used, fragmented forests for centuries. They are now slowly but gradually reappearing in our forests, with higher concentrations in non-intervention sites ('secondary old growth'). Species related to old-growth elements are responding to this improved situation depending on their (re-)colonisation capacities. Species with good dispersal potential and moderate habitat requirements often show a remarkably quick and strong response, that is widespread over the whole forest area, wherever suitable habitat is available. Examples are cavity nesting birds related to mature and senescent forest developmental stages, and moderate to low selective saproxylic fungi and beetles. Although no long-term standardised inventories are available in northern Belgium for saproxylic beetles and fungi to underpin this statement, we believe that the trends and results we compiled are so explicit we can assume that they indeed reflect a genuine positive trend for these less selective species.

Species with higher substrate requirements but with the capability of long-distance dispersal (some of the rare saproxylic fungi and beetles, middle spotted woodpecker) also appear to increase, although there appears to be an important lag phase in the establishment of their populations. Some species are still missing although suitable habitat is available, representing an important immigration credit (Hanski 2000, Jackson and Sax 2009, Baeten et al. 2010). Stochasticity may play an important role in determining whether these species are able to establish and persist. In this sense, locations with high concentrations of old-growth related habitat (like parks and forest reserves) can play a very important role increasing the chance of establishment of permanent populations, that in their turn can act as new sources for dispersal. Repeated studies in three strict forest reserves in Rhineland (Germany) indeed indicated a clear increase in species richness of saproxylic beetles over the last 20 years. The positive trend is related to both increase in dead wood supply and changed climatic conditions (Köhler 2010b).

Species with high restrictions both in dispersal and substrate requirements are very unlikely to recolonise over longer distances and appear to be restricted to and relying on relic sites. These can be old orchards, parks and pollard landscapes that have escaped from destruction and pesticide influence over the last 50 years, or forest patches like Kolmont that retained or redeveloped suitable habitat before the loss of the alternative habitat took place. An active search for such relic sites, based on historic information and old distribution maps of indicative species, and subsequent inventory of these sites for these species could be of great interest for species conservation. Protection, restoration management of these sites, and extension of small relics are crucial to guarantee the survival and recovery to viable populations of their valuable saproxylic communities.

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References

Afdeling Bos en Groen. 2001a. Beheervisie voor openbare bossen. Ministry of the Flemish Community, Brussels. 98 p.

— 2001b. De bosinventaris van het Vlaamse Gewest. Resultaten van de eerste inventarisatie 1997–2000. Ministry of the Flemish Community, Brussels. 486 p.

Alexander, K.N.A. 2004. Revision of the Index of Ecological Continuity as used for saproxylic beetles. English Nature Research Reports 574. English Nature, Peterborough. 60 p.

— 2008. The special importance of traditional orchards for invertebrate conservation, with a case study of the BAP priority species the Noble Chafer Gnorimus nobilis. Landscape Archaeology and Ecology 7: 12–17.

Ammer, U. 1991. Konsequenzen aus den Ergebnissen der Totholzforschung für die forstliche Praxis. Forstwissenschaftliches Centralblatt 110: 149–157.

Angelstam, P. & Mikusiński, G. 1994. Woodpecker assemblages in natural and managed boreal and hemiboreal forest – a review. Annales Zoologici Fennici 31: 157–172.

— , Bütler, R., Lazdinis, M., Mikusiński, G. & Roberge, J.-M. 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation – dead wood as an example. Annales Zoologici Fennici 40: 473–482.

Arnolds, E. & van den Berg, A. 2001. Trends in de paddestoelenflora op basis van karteringsgegevens. Coolia 44: 139–152.

Baeten, L., Hermy, M., Van Daele, S. & Verheyen, K. 2010. Unexpected understorey community development after 30 years in ancient and post-agricultural forests. Journal of Ecology 98: 1447–1453.

Bailey, S. 2007. Increasing connectivity in fragmented landscapes: an investigation of evidence for biodiversity gain in woodlands. Forest Ecology and Management 238: 7–23.

Bobiec, A. 2002. Living stands and dead wood in the Białowieża Forest: suggestions for restoration management. Forest Ecology and Management 165: 125–140.

Bocca, M., Carisio, L. & Rolando, A. 2007. Habitat use, home ranges and census techniques in the Black Woodpecker Dryocopus martius in the Alps. Ardea 95: 17–29.

Böhl, J. & Brändli, U.-B. 2007. Deadwood volume assessment in the third Swiss National Forest Inventory: methods and first results. European Journal of Forest Research 126: 449–457.

Bommer, E. & Rousseau, M. 1879. Catalogue des champignons observés aux environs de Bruxelles. Bulletin de la Société royale de botanique de Belgique 18: 61–219.

Branquart, E., Vandekerkhove, K., Bourland, N. & Lecomte, H. 2004. Les arbres sur-âgés et le bois mort dans les forêts de Flandre, de Wallonie et du Grand-Duché de Luxembourg. In: Vallauri, D., André, J., Dodelin, B., Eynard-Machet, R. & Rambaud, D. (eds.). Bois morts et à cavités – une clé pour des forêts vivantes. Lavoisier, Paris. p. 19–28.

Brunet, J. & Isacsson, G. 2009. Restoration of beech forest for saproxylic beetles – effects of habitat fragmentation and substrate density on species diversity and distribution. Biodiversity and Conservation 18: 2387–2404.

Buis, J. 1985. Historia forestis: Nederlandse bosgeschiedenis. Studia Historica XIV. HES, Utrecht. 1058 p.

Burschel, P. 1992. Totholz und Forstwirtschaft. Allgemeine Forst Zeitschrift 21: 1143–1146.

Büssler, H. 2010. Hotspot-Gebiete xylobionter Urwaldreliktarten aus dem Reich der Käfer. LWF Aktuell 76: 10–12.

Butaye, J., Jacquemyn, H., Honnay, O. & Hermy, M. 2001. The species pool concept applied to forests in a fragmented landscape: dispersal limitation versus habitat limitation. Journal of Vegetation Science 13: 27–34.

Christensen, M. & Emborg, J. 1996. Biodiversity in natural versus managed forest in Denmark. Forest Ecology and Management 85: 47–51.

— , Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, P., Meyer, P., Winter, S. & Vrska, T. 2005a. Dead wood in European beech (Fagus sylvatica) forest reserves. Forest Ecology and Management 210: 267–282.

— , Heilmann-Clausen, J., Walleyn, R. & Adamčik, S. 2005b. Wood-inhabiting fungi as indicators of nature value in European beech forests. In: Marchetti, M. (ed.). Monitoring and indicators of forest biodiversity in Europe—from ideas to operationality. EFI Proceedings 51: 229–237.

Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G., Lewis, M., Lynch, J., Pacala, S., Prentice I. C., Schupp, E. W. Webb III, T. & Wyckoff, P. 1998. Reid's Paradox of rapid plant migration. BioScience 48: 13–24.

de Goffau, L.J.W. 1984. Bolitophagus reticulatus (Linné, 1767) een nieuwe soort voor Nederland (Coleoptera: Tenebrionidae). Entomologische Berichten 44: 56.

De Keersmaeker, L., Rogiers, N., Lauriks, R. & De Vos, B. 2001. Ecosysteemvisie bos Vlaanderen, ruimtelijke uitwerking van de natuurlijke bostypes op basis van bodemgroeperingseenheden en historische boskaarten. Report VLINA C97/06, AMINAL, Brussels. 109 p.

Deckers, B., Kerselaers, E., Gulinck, H., Muys, B. & Hermy, M. 2005. Long-term spatio-temporal dynamics of a hedgerow network landscape in Flanders, Belgium. Environmental Conservation 32: 20–29.

Desender, K., Ervynck, A. & Tack, G. 1999. Beetle diversity and historical ecology of woodlands in Flanders. Belgian Journal of Zoology 129: 139–156.

— , Dekoninck, W., Maes, D., Crevecoeur, L., Dufrêne, M., Jacobs, M., Lambrechts, J., Pollet, M., Stassen, E. & Thys, N. 2008. Een nieuwe verspreidingsatlas van de loopkevers en zandloopkevers (Carabidae) in België. INBO Report R.2008.13. Instituut voor Natuur- en Bosonderzoek, Brussels. 184 p.

Devillers, P., Roggeman, W., Tricot, J., del Marmol, P., Kerwijn, C., Jacob, J.P. & Anselin, A. 1988. Atlas van de Belgische broedvogels. KBIN, Brussels.

Dubois, G., Vignon, V., Delettre, Y.R., Rantier, Y., Vernon, P. & Burel, F. 2009. Factors affecting the occurrence of the endangered saproxylic beetle Osmoderma eremita (Scopoli, 1763) (Coleoptera: Cetoniidae) in an agricultural landscape. Landscape and Urban Planning 91: 152–159.

Dufrêne, M., Grootaert, P., Lebrun, P. & Rondeux, J. 2008. A research project to study patterns, roles and determinants of wood-dependent species diversity in Belgian deciduous forests (XYLOBIOS): final report. Belgian Science Policy, Brussels.

Dumortier, M., De Bruyn, L., Wils, C., Paelinckx, D., Vander Mijnsbrugge, K., Cox, K., Sioen, G., Roskams, P., Vandekerkhove, K. & Hens, M. 2005. Bossen en struwelen. In: Dumortier, M. (Ed.). Natuurrapport 2005 – toestand van de natuur in vlaanderen: cijfers voor het beleid. Mededeling van het Instituut voor Natuurbehoud 24. p. 115–128.

Edman, M., Gustafsson, M., Stenlid, J. & Ericson, L. 2004a. Abundance and viability of fungal spores along a forestry gradient – responses to habitat loss and isolation? Oikos 104: 35–42.

— , Kruys, N. & Jonsson, B.G. 2004b. Local dispersal sources strongly affect colonisation patterns of wood-decaying fungi on experimental logs. Ecological Applications 14: 893–901.

— , Kruys, N., Gustafsson, M., Stenlid, J., Jonsson, B.G. & Ericson, L. 2004c. Spore deposition of wood-decaying fungi: importance of landscape composition. Ecography 27: 103–111.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997. Boreal forests. Ecological Bulletins 46: 16–47.

Fayt, P., Dufrêne, M., Branquart, E., Hastir, P., Pontégnie, C., Henin, J.-M. & Versteirt, V. 2006. Contrasting responses of saproxylic insects to focal habitat resources: the example of longhorn beetles and hoverflies in Belgian deciduous forests. Journal of Insect Conservation 10: 129–150.

Fowles, A.P., Alexander, K.N.A. & Key, R.S. 1999. The Saproxylic Quality Index: evaluating wooded habitats for the conservation of dead-wood Coleoptera. The Coleopterist 8: 121–141.

FPS Economy, SMEs, Self-employed and Energy. 2009. Key figures 2009 – Belgium and the European Union. Brussels. 133 p.

Frank, G., Parviainen, J.,Vandekerkhove, K., Latham, J., Schuck, A. & Little, D. (eds.). 2007. COST Action E27 Protected Forest Areas in Europe – analysis and harmonisation (Profor): results, conclusions and recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW).Vienna, Austria. 211 p.

Geiser, R. 1998. Rote liste der Käfer (Coleoptera). In: Bundesanstalt für Naturschutz (ed.). Rote Liste gefärdeter Tiere Deutschlands. BfN, Bonn-Bad Godesberg. p. 168–230.

Götmark, F. & Thorell, M. 2003. Size of nature reserves: densities of large trees and dead wood indicate high value of small conservation forests in southern Sweden. Biodiversity and Conservation 12: 1271–1285.

Govaere, L., Roelandt, B. & Waterinckx, M. 2010. Handleiding tweede bosinventarisatie. Versie 2010.1. Agentschap voor Natuur en Bos, Brussels.

Gu, W., Heikkilä, R. & Hanski, I. 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landscape Ecology 17: 699–710.

Hallenberg, N. & Kuffer, N. 2001. Long-distance spore dispersal in wood-inhabiting basidiomycetes. Nordic Journal of Botany 21: 431–436.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press. 313 p.

— 2000. Extinction debt and species credit in boreal forests: modeling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37: 271–280.

Harmon, M.E. 2001. Carbon sequestration in forests: addressing the scale question. Journal of Forestry 99: 24–29.

— , Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. & Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Heilmann-Clausen, J. & Christensen, M. 2003. Fungal diversity on decaying beech logs-implications for sustainable forestry. Biodiversity and Conservation 12: 953–973.

Heirbaut, W., Desender, K., Debakker, D., Versteirt, V. & Grootaert, P. 2001. Inventarisatie en determinatie van ongewervelden als ecologische indicatoren in Vlaamse integrale bosreservaten. Inventarisatie en determinatie van xylobionte arthropoden in integrale bosreservaten. Rapport ENT.2001.04. Royal Institute for Natural Sciences, Brussels.

Hermy, M. & Verheyen, K. 2007. Legacies of the past in the present day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecological Restoration 22: 361–371.

— , Van Der Veken, S., Van Calster, H. & Plue, J. 2008. Forest ecosystem assessment, changes in biodiversity and climate change in a densely populated region (Flanders, Belgium). Plant biosystems 142: 623–629.

Hodge, S.J. & Peterken, G.F. 1998. Dead wood in British forests: priorities and a strategy. Forestry 71: 99–112.

Humphrey, J., Sippola, A.-L., Lempériere, G., Dodelin, B., Alexander, K.N.A. & Butler, J. 2004. Deadwood as an indicator of biodiversity in European forests: from theory to operational guidance. In: Marchetti, M. (ed.). Monitoring and indicators of forest biodiversity in Europe – from ideas to operationality. EFI Proceedings 51: 193–206.

Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology

52: 577–586.

Hyman, P.S. & Parsons, M.S. 1992. A review of the scarce and threatened Coleoptera of Great Britain. Part 1. UK Nature Conservation 3. Joint Nature Conservation Committee, Peterborough. 484 p.

— & Parsons, M.S. 1994. A review of the scarce and threatened Coleoptera of Great Britain. Part 2. UK Nature Conservation 12. Joint Nature Conservation Committee, Peterborough. 248 p.

Irmler, U., Arp, H. & Nötzold R. 2010. Species richness of saproxylic beetles in woodlands is affected by dispersion ability of species, age and stand size. Journal of Insect Conservation 14: 227–235.

Jackson, S.T. & Sax, D.F. 2009. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends in Ecology & Evolution 25: 153–160.

Jahn, H. 1963. Mitteleuropäische Porlinge. Westfälische Pilzbriefe 4: 1–143.

Janssens, A. 1960. Faune de Belgique. Insectes Coléoptères Lamellicornes. Institut Royal des Sciences Naturelles de Belgique, Brussels. 411 p.

Jöbges, M. & König, H. 2001. Urwaldspecht im Eichenwald. LÖBF-Mitteilungen 2: 12–27.

Jonsell, M., Norlander, G. & Jonsson, M. 1999. Colonization patterns of insects breeding in wood-decaying fungi. Journal of Insect Conservation 3: 145–161.

— , Schroeder, M. & Larsson, T. 2003. The saproxylic beetle Bolitophagus reticulatus: its frequency in managed forests, attraction to volatiles and flight period. Ecography 26: 421–428.

Jonsson, B.G., Kruys, N. & Ranius, T. 2005. Ecology of species living on dead wood – lessons for dead wood management. Silva Fennica 39: 289–309.

Kallio, T. 1970. Aerial distribution of thr root rot fungus Fomes annosus in Finland. Acta Forestalia Fennica 107. 55 p.

Kamp, J. 2008. Bestandszunahme und Ausbreitung des Mittelspechts Dendrocopus medius in NW-Deutschland. Vogelwarte 46: 280.

Kappes, H. & Topp, P. 2004. Emergence of Coleoptera from deadwood in a managed broadleaved forest in central Europe. Biodiversity and Conservation 13: 1905–1924.

Kickx, J. 1835. Flore cryptogamique des environs de Louvain, ou description des plantes cryptogames et agames qui croissent dans le Brabant et dans une partie de la province d'Anvers. Bruxelles, Vandooren.

Kickx, J.J. 1867. Flore cryptogamique des Flandres. Oeuvre posthume de Jean Kickx. Tome I & II. Gand, Librairie Générale de H. Hoste.

Kirby, K.J. & Drake, C.M. 1993. Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. English Nature, Peterborough.

Kirk, P.M., Cannon, P.F., Minter, D.W. & Stalpers, J.A. 2008. Dictionary of the Fungi. 10th edition. CABI, U.K. 784 p.

Köhler, F. 1996. Käferfauna in Naturwaldzellen und Wirtschaftswald. Vergleichende Untersuchungen im Waldreservat Kermeter in der Nordeifel. Schriftenreihe LÖBF/LAfAO NRW 6. Recklinghausen. 283 p.

— 1999. Die Totholzkäferfauna (Coleoptera) der Naturwaldreservate "Möderhäufel" und "Stuttpferch" im Bienwald in der nördlichen Oberrheinebene. Mainzer naturwissenschaftliches Archiv 37: 213–280.

— 2000. Totholzkäfer in Naturwaldzellen des Nördlichen Rheinlandes. Vergleichende Studien zur Totholzkäferfauna Deutschlands und Deutschen Naturwaldforschung. Schriftenreihe LÖBF/LAfAO NRW 18. Recklinghausen. 351 p.

— 2009. Die Totholzkäfer (Coleoptera) des Naturwaldreservates Laangmuer. Naturwaldreservate in Luxemburg 5: 48–115.

— 2010a. Die Käfer (Coleoptera) des Naturwaldreservats Goldbachs- und Ziebachsrück (Hessen). Untersuchungszeitraum 1994–1996. In: Dorow, W. H. O., Blick, T. & Kopelke, J.-P. (eds.). Naturwaldreservate in Hessen. Band 11/2.2. Goldbachs- und Ziebachsrück. Zoologische Untersuchungen 1994–1996, Teil 2. Mitteilungen der Hessischen Landesforstverwaltung 46: 7–98.

— 2010b. Die klimabedingte Veränderung der Totholzkäferfauna (Coleoptera) des nördlichen Rheinlandes. Analysen zur Gesamtfauna und am Beispiel von Wiederholungsuntersuchungen in ausgewählten Naturwaldzellen. Report for Ministerium für Umwelt und Naturschutz Landwirtschaft und Verbraucherschutz des Landes Nordrhein-Westfalen. Koleopterologisches Forschungsbüro, Bornheim, 184 p.

— , Crevecoeur, L. & Vandekerkhove, K. 2011. Saproxylic beetles of the Forest Reserve Kolmontbos. Results and analysis of a two-year survey. Report INBO.IR.2011.21. Instituut voor Natuur- en Bosonderzoek, Brussels. 49 p.

Korpel, S. 1997. Totholz in Naturwäldern und Konsequenzen für Naturschutz und Forstwirtschaft. Forst und Holz 52: 619–643.

Kosiński, Z. 2006. Factors affecting the occurrence of middle spotted and great spotted woodpeckers in deciduous forests a case study from Poland. Annales Zoologici Fennici 43: 198–210.

Kraigher, H., Jurc, D., Kalan, P., Kutnar, L., Levanic, T., Rupel, M. & Smolej, I. 2002. Beech coarse woody debris characteristics in two virgin forest reserves in southern Slovenia. Zbornik Gozdarstva in Lesarstva 69: 91–134.

Lindenmayer, D.B. & Franklin, J.F. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington DC. 351 p.

McAleece, N. 1997. BioDiversity 1997 NHM & SAMS. Available at: http://www.sams.ac.uk/research/software/.

MCPFE. 2007. State of Europe's forests 2007. The MCPFE report on sustainable forest management in Europe. Jointly prepared by the MCPFE Liaison Unit Warsaw, UNECE and FAO. MCPFE Liaison Unit Warsaw, Poland.

Meyer, P., Tabaku, V. & von Lupke, B. 2003. Die Struktur Albanischer Rotbuchen-Urwälder – Ableitungen fur eine naturnähe Buchenwirtschaft. Forstwissentschaftliches Centralblatt 122: 47–58.

Mikusiński, G., Gromadzki, M. & Chylarecki, P. 2001. Woodpeckers as indicators of forest bird diversity. Conservation Biology 15: 208–217.

Moraal, L., Veerkamp, M., Jagers op Akkerhuis, G., Cuppen, J. & Heijerman, T. 2007. Echte tonderzwam geeft bijzondere kever volop kansen. Vakblad Natuur Bos Landschap 4: 20–21.

Moreau, K. 2006. De Middelste Bonte Specht (Dendrocopus medius) in Meerdaalwoud. Natuur.oriolus 72: 4–13.

Muller-Using, S. & Bartsch, N. 2003. Totholzdynamik eines Buchenbestandes (Fagus sylvatica L.) im Solling. Nachlieferung, Ursache, und Zersetzung von Totholz. Allgemeine Forst und Jagdzeitung 174: 122–130.

Müller, J. & Büssler, H. 2008. Key factors and critical thresholds at stand scale for saproxylic beetles in a beech dominated forest, southern Germany. Revue d'Écologie (la Terre et la Vie) 63: 73–82.

— , Büssler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmidl, J. & Zabransky, P. 2005. Urwald relict species – saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie Online 2: 106–113. [Online journal]. Available at: http://www.afsv.de/docs/literatur/waldoekologie-online_heft2.html. [Cited 30 Oct 2010].

— , Pöllath, J., Moshammer, R. & Schröder, B. 2009. Predicting the occurrence of Middle Spotted Woodpecker Dendrocopos medius on a regional scale, using forest inventory data Forest Ecology and Management 257: 502–509.

Nieto, A. & Alexander, K.N.A. 2010. European red list of saproxylic beetles. Publications Office of the European Union, Luxembourg. 48 p.

Nilssen, A.C. 1984. Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. Annales Entomologici Fennici 50: 37–42.

Nilsson, S.G. & Baranowski, R. 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography 20: 491–498.

— , Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusiński, G. & Ranius, T. 2002. Densities of large and dead trees in old-growth temperate and boreal forests. Forest Ecology and Management 161: 189–204.

Nordén, B. & Appelqvist, T. 2001. Conceptual problems of ecological continuity and its bioindicators. Biodiversity and Conservation 10: 779–791.

Ódor, P., Heilmann-Clausen, J., Christensen, M., Aude, E., van Dort, K.W., Piltaver, A., Siller, I., Veerkamp, M.T., Walleyn, R. & Standovar, T. 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological Conservation 131: 58–71.

Økland, B., Bakke, A., Hågvar, S. & Kvamme, T. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation 5: 75–100.

ONF. 1993. Instruction et guide sur la prise en compte de la diversité biologique dans l'aménagement et gestion forestière. ONF, Paris.

Pakeman, R.J. 2001. Plant migration rates and seed dispersal mechanisms. Journal of Biogeography 28: 795–800.

Parviainen, J., Bücking, W., Vandekerkhove, K., Päivinen, R. & Schuck, A. 2000. Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-action E4). Forestry 73: 107–118.

Pasinelli, G. 2007. Nest site selection in middle and great spotted woodpeckers Dendrocopos medius & D. major: implications for forest management and conservation. Biodiversity and Conservation 16: 1283–1298.

Peterken, G.F. 1993. Woodland conservation and management. 2nd edition. Chapman and Hall, London.

Rackham, O. 1986. The history of the countryside. J.M. Dent, London.

Ranius, T. 2006. Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. Population Ecology 48: 177–188.

— & Hedin, J. 2001. The dispersal rate of a beetle, Osmoderma eremita, living in tree hollows. Oecologia 126: 363–370.

— , Aguado, L.O., Antonsson, K., Audisio, P., Ballerio, A., Carpaneto, G.M., Chobot, K., Gjurašin, B., Hanssen, O., Huijbregts, H., Lakatos, F., Martin, O., Neculiseanu, Z., Nikitsky, N.B., Paill, W., Pirnat, A., Rizun, V., Ruicănescu, A., Stegner, J., Süda, I., Szwałko, P., Tamutis, V., Telnov, D., Tsinkevich, V., Versteirt, V., Vignon, V., Vögeli, M. & Zach, P. 2005. Osmoderma eremita (Coleoptera, Scarabaeidae, Cetoniinae) in Europe. Animal Biodiversity and Conservation 28: 1–44.

Rink, M & Sinsch, U. 2007. Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. Journal of Zoology 272: 235–243.

Risbeth, J. 1959. Dispersal of Fomes annosus and Peniophora gigantea. Transactions of the British Mycological Society 42: 243–260.

Rolstad, J., Majewski, P. & Rolstad, E. 1998. Black woodpecker use of habitats and feeding substrates in a managed Scandinavian forest. Journal of Wildlife Management 62: 11–23.

— , Rolstad, E. & Sæteren Ø. 2000. Black woodpecker nest sites: characteristics, selection, and reproductive success. Journal of Wildlife Management 64: 1053–1066.

Rukke, B.A. 2000. Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. Ecography 23: 492–502.

— & Midtgaard, F. 1998. The importance of scale and spatial variables for the fungivorous beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae) in a fragmented forest landscape. Ecography 21: 561–572.

Samuelsson, J., Gustafsson, L. & Ingelog, T. 1994. Dying and dead trees – a review of their importance for biodiversity. Swedish Threatened Species Unit, Swedish University of Agricultural Sciences, Uppsala.

Saproxylic Quality Index: evaluated sites ranked by SQI. 2009. [Internet site]. Available at http://yrefail.net/Coleoptera/sqi.htm. [Cited 30 Oct 2010].

Schiegg, K. 2000. Effects of dead wood volume and connectivity on saproxylic insect species diversity. Ecoscience 7, 290–298.

Sierdsema, H. 1995. Broedvogels en beheer. Het gebruik van broedvogelgegevens in het beheer van bos- en natuurterreinen. SBB-rapport 1995-1, SOVON-onderzoeksrapport 1995/04. SBB/SOVON, Driebergen/Beek-Ubbergen. 99 p.

Simberloff, D. 1972. Properties of the rarefaction diversity measurement. The American Naturalist 106: 414–418.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41.

Solbreck, C. 1980. Dispersal distances of migrating pine weevils, Hylobius abietis, Coleoptera, Curculionidae. Entomologia Experimentalis et Applicata 28: 123–131.

Speight, M. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series 42. Council of Europe, Strasbourg.

Stenlid, J. & Gustafsson, M. 2001. Are rare wood fungi threatened by inability to spread? Ecological Bulletins 49: 85–91.

Sverdrup-Thygeson, A. & Midtgaard, F. 1998. Fungus infected trees as islands in boreal forests: Spatial distribution on the fungivorous beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae). Écoscience 5: 486–493.

Tack, G. & Hermy, M. 1998. Historical ecology of woodlands in Flanders. In: Kirby K., Watkins C. (eds.). The ecological history of European forests. CAB International, New York, USA. p. 283–292.

— , van den Bremt, P.& Hermy, M. 1993. Bossen van Vlaanderen. Een historische ecologie. Davidsfonds, Leuven, Belgium.

Tallier, P.-A. 2004. Forêts et propriétaires forestiers en Belgique de la fin du XVIIIe siècle à 1914. Histoire de l'évolution de la superficie forestière, des peuplements, des techniques sylvicoles et des débouchés offerts aux produits ligneux. Académie Royale de Belgique, Brussels.

Thomaes, A., Kervyn, T. & Maes, D. 2008a. Applying species distribution modelling for the conservation of the threatened saproxylic Stag Beetle (Lucanus cervus). Biological Conservation 141: 1400–1410.

— , Kervyn, T., Beck O. & Cammaerts, R. 2008b. Distribution of Lucanus cervus in Belgium: surviving in a changing landscape (Coleoptera: Lucanidae). Revue d'Ecologie (Terre & Vie) 63: 139–144.

Troukens, W. 2004. Bolitophagus reticulatus aan de westrand van Brussel (Coleoptera: Tenebrionidae). Phegea 32: 151–152.

Van Daele, T., Van Reeth, W., Dumortier, M. & Peymen, J. 2010. Natuurindicatoren 2010. Toestand van de natuur in Vlaanderen: cijfers voor het beleid. Mededeling van het Instituut voor Natuur- en Bosonderzoek, INBO.M.2010.2, Brussels.

Van der Laan, H.F. 1972. Is Fomes fomentarius minder zeldzaam aan het worden? Coolia 15: 156–158.

van Dijk, A., Hustings, F., Boele, A., Koffijberg, K., Zoetebier, D. & Plate, C. 2010. Kolonievogels en zeldzame broedvogels in Nederland in 2006 en 2007. Limosa 83: 1–20.

Van Sterbeeck, F. 1675. Theatrum fungorum oft het tooneel der Campernoelien. Antwerpen, Ioseph Iacobs. 396 p.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. Forest Science 14: 20–26.

Vandekerkhove, K., van Dort, K., Baeté, H. & Walleyn, R. 2003. Species richness of mosses, fungi and vascular plants on coarse woody debris of beech in the Flemish forest reserve 'Kersselaerspleyn' (Zoniënwoud). Scripta Botanica Belgica 24: 83–91.

— , De Keersmaeker, L., Baeté, H., Walleyn, R. 2005. Spontaneous re-establishment of natural structures and related diversity in a previously managed beech forest in Belgium after 20 years of non intervention. Forest Snow & Landscape Research 79: 145–156.

— , De Keersmaeker, L., Menke, N., Meyer, P. & Verschelde P. 2009a. When nature takes over from man: dead wood accumulation in previously managed oak and beech woodlands in North-West- and Central Europe. Forest Ecology and Management 258: 425–435.

— , Van der Aa, B., Baeté, H. & Meuleman, B. 2009b. Bakermat van duurzaam bosbeheer. « Pour le plus grand profit de son excellence ». In: Baeté, H., De Bie, M., Hermy, M. & Van den Bremt, P. (eds.). Miradal – Erfgoed in het Meerdaalwoud en het Heverleebos. Davidsfonds, Leuven. p. 139–171.

Veerkamp, M. & Arnolds, E. 2008. Ecological monitoring network newsletter 9. Coolia 51: 97–108.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., van Calster, H., Peterken, G.F. & Hermy, M. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87: 542–548.

Verheyen, K. & Hermy, M. 2001. An integrated analysis of the spatio-temporal colonization patterns of forest plant species. Journal of Vegetation Science 12(4): 567–578.

— & Hermy, M. 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. Journal of vegetation science, 15(1): 125–134.

— , Guntenspergen, G., Biesbrouck, B. & Hermy, M. 2003a. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. Journal of Ecology 91: 731–742.

— , Honnay, O., Motzkin, G., Hermy, M. & Foster, D. 2003b. Response of forest plant species to land-use change: a life-history trait-based approach. Journal of Ecology 91: 563–577.

Verhulst, A. 1995. Landschap en landbouw in middeleeuws Vlaanderen. Gemeentekrediet, Brussels. 191 p.

Vermeersch, G., Anselin, A., Devos, K., Herremans, M., Stevens, J., Gabriëls, J. & Van Der Krieken, B. 2004. Atlas van de Vlaamse broedvogels 2000–2002. Mededelingen van het Instituut voor Natuurbehoud 23, Brussels. 495 p.

— , Anselin, A. & Devos, K. 2006. Bijzondere broedvogels in Vlaanderen in de periode 1994–2005: populatietrends en recente status van zeldzame, kolonievormende en exotische broedvogels in Vlaanderen. Mededelingen van het Instituut voor Natuur- en Bosonderzoek 2006(2). Instituut voor Natuur- en Bosonderzoek, Brussels. 64 p.

Versteirt, V., Desender, K., Geudens, G. & Grootaert, P. 2000. Determinatie en bioindicatie van bosgebonden ongewervelden. Verkennend onderzoek naar de potentiële waarde van integrale bosreservaten voor het behoud van xylobionte arthropoden. Rapport ENT.2000.04. Royal Institute for Natural Sciences, Brussels.

von Oheimb, G., Westphal, C., Tempel, H. & Härdtle, W. 2005. Structural pattern of a near-natural beech forest (Fagus sylvatica)(Serrahn, North-east Germany). Forest Ecology and Management 212:

253–263.

Walleyn, R. 2003. Quelques récoltes intéressantes en Forêt de Soignes (2). Revue du Cercle de Mycologie de Bruxelles 3: 3–10.

— 2004. Verspreiding en ecologie in Vlaanderen van enkele houtzwammen met voorkeur voor beukenhout. Mededelingen Antwerpse mycologische Kring 2004: 16–22.

— 2006. Verspreiding en ecologie in Vlaanderen van enkele houtzwammen met voorkeur voor Beuk (2de reeks). Mededelingen Antwerpse mycologische Kring 2006: 37–43.

Warren, W.G. & Olsen, P.R. 1964. A line intersect technique for assessing logging waste. Forest Science 10: 267–276.

Waterinckx, M. & Haelvoet, P. 1997. Operationaliseren en begeleiden van de uitvoeringsfase van de bosinventarisatie van het Vlaamse Gewest. Eindverslag. Afdeling Bosbeheer en Ruimtelijke Informatietechnieken. University of Ghent. 117 p.

Watts, K. 2006. British forest landscapes the legacy of woodland fragmentation. Quarterly Journal of Forestry 100: 273–279.

Weiss, J. & Köhler, F. 2005. Erfolgskontrolle von Maßnahmen des Totholzschutzes im Wald. Einzelbaumschutz oder Baumgruppenerhaltung? LÖBF-Mitteilungen 3: 26–29.

Wouters, J., Quataert, P., Onkelinx, T. & Bauwens, D. 2008. Ontwerp en handleiding voor de tweede regionale bosinventarisatie van het Vlaamse Gewest. Report INBO.R.2008.17, Instituut voor Natuur- en Bosonderzoek, Brussels.

Total of 161 references

Annex 1. Overview of all Red-listed species (with number of individuals caught) in the Kolmont Strict Forest Reserve. German Red list categories (Geiser 1998): 1 = critically endangered, 2 = endangered, 3 = vulnerable; Red list for Great Britain (Hyman & Parsons 1992,1994): 1 = endangered, 2 = vulnerable, 3 = rare; European red list (Nieto and Alexander 2010): NT = near threatened; VU = vulnerable; RELIC = list of European indicator species for old-growth continuity (Urwald relict species, Müller et al. 2005).

Family	Species	Number	German RL	GB-RL	EUR-RL	RELIC
Histeridae	Plegaderus dissectus (ER., 1839)	271	3			
Histeridae	Abraeus granulum (ER., 1839)	51	3			
Histeridae	Abraeus parvulus (AUBE, 1842)	4	2			×
Histeridae	Aeletes atomarius (AUBE, 1842)	421	1	3		
Histeridae	Paromalus flavicornis (HBST., 1792)	378		1		
Cholevidae	Nemadus colonoides (KR., 1851)	1	3			
Leiodidae	Liodopria serricornis (GYLL., 1813)	1	3			
Scydmaenidae	Stenichnus godarti (LATR.,)	26		3		
Scydmaenidae	Micoscydmus minimus (CHAUD., 1845)	20	3			
Scydmaenidae	Scydmaenus rufus (MULL.KUNZE, 1822)	30		2		
Scydmaenidae	Scydmaenus perrisii (RTT., 1881)	41	2			
Ptiliidae	Nossidium pilosellum (MARSH., 1802)	124	3			
Ptiliidae	Ptenidium gressneri (ER., 1845)	2	3			
Ptiliidae	Micridium halidaii (MATTH., 1868)	1	3			×
Ptiliidae	Ptinella limbata (HEER, 1841)	38		K		
Ptiliidae	Ptinella denticollis (FAIRM., 1857)	1	1			
Staphylinidae	Siagonium quadricorne (KIRBY, 1815)	6	3			
Staphylinidae	Phyllodrepa nigra (GRAV., 1806)	1	3	I		
Staphylinidae	Phloeonomus minimus (ER., 1839)	1	2			
Staphylinidae	Xylodromus testaceus (ER., 1840)	4		1		
Staphylinidae	Phyllodrepoidea crenata (GRAV., 1802)	30	3			
Staphylinidae	Hypnogyra glabra (NORDM., 1837)	38	3			
Staphylinidae	Veilleius dilatatus (F., 1787)	5	3	1		
Staphylinidae	Quedius brevicornis (THOMS., 1860)	1	3			
Staphylinidae	Holobus apicatus (ER., 1837)	18	3			
Staphylinidae	Gyrophaena munsteri (STRAND, 1935)	4		K		
Staphylinidae	Gyrophaena polita (GRAV., 1802)	10	3			
Staphylinidae	Agaricochara latissima (STEPH., 1832)	50	3			
Staphylinidae	Autalia impressa (OL., 1795)	3		3		
Staphylinidae	Thamiaraea cinnamomea (GRAV., 1802)	93	3			
Staphylinidae	Thamiaraea hospita (MARK., 1844)	2	2			
Pselaphidae	Plectophloeus nitidus (FAIRM., 1857)	2		2		
Pselaphidae	Trichonyx sulcicollis (REICHB., 1816)	6	3	2		
Pselaphidae	Batrisodes delaporti (AUBE, 1833)	6		1		
Pselaphidae	Batrisodes buqueti (AUBE, 1833)	1	2	1		×
Pselaphidae	Batrisodes unisexualis (BES., 1988)	3	3			
Pselaphidae	Batrisodes oculatus (AUBE, 1833)	2	1			
Cleridae	Tillus elongatus (L., 1758)	78	3			
Trogositidae	Nemosoma elongatum (L., 1761)	5		3		
Elateridae	Ampedus sanguineus (L., 1758)	1		E		
Elateridae	Ampedus nigroflavus (GOEZE, 1777)	1	3			
Elateridae	Brachygonus megerlei (LACORD., 1835)	1	2		NT	
Elateridae	Procraeus tibialis (LACORD., 1835)	10	2	3		
Elateridae	Elater ferrugineus (L., 1758)	1	2	1	NT	×
Elateridae	Stenagostus rhombeus (OL., 1790)	28	3			
Cerophytidae	Cerophytum elateroides (LATR., 1804)	2	2		VU	
Eucnemidae	Eucnemis capucina (AHR., 1812)	2	3			
Eucnemidae	Dromaeolus barnabita (VILLA, 1838)	2	2			
Eucnemidae	Dirhagus pygmaeus (F., 1792)	1	3			

Family	Species	Number	German RL	GB-RL	EUR-RL	RELIC
Eucnemidae	Dirhagus lepidus (ROSH., 1847)	3	3			
Eucnemidae	Hylis olexai (PALM,1955)	26	3			
Lissomidae	Drapetes cinctus (PANZ., 1796)	1	3			
Dermestidae	Trinodes hirtus (F., 1781)	1		3		
Nitidulidae	Epuraea neglecta (HEER, 1841)	4		I		
Silvanidae	Silvanoprus fagi (GUER., 1844)	12		1		
Erotylidae	Triplax rufipes (F., 1775)	282	1			
Erotylidae	Dacne rufifrons (F., 1775)	42	2			
Biphyllidae	Biphyllus lunatus (F., 1792)	1	1			
Cryptophagidae	Cryptophagus labilis (ER., 1846)	2	2			
Cryptophagidae	Atomaria elongatula (ER., 1846)	3	3			
Latridiidae	Latridius hirtus (GYLL., 1827)	11	3			
Latridiidae	Enicmus brevicornis (MANNH., 1844)	8	3			
Latridiidae	Enicmus testaceus (STEPH., 1830)	116	2			
Latridiidae	Stephostethus pandellei (BRIS, 1863)	1	3			
Latridiidae	Corticaria alleni (JOHNS., 1974)	5	2			
Latridiidae	Corticaria longicollis (ZETT., 1838)	1		K		
Mycetophagidae	Triphyllus bicolor (F., 1792)	19	3			
Mycetophagidae	Mycetophagus piceus (F., 1792)	34	3			
Mycetophagidae	Mycetophagus populi (F., 1798)	1	3			
Colydiidae	Cicones variegatus (HELLW., 1792)	1	3			
Colydiidae	Cicones undatus (GUER, 1844)	1	3			
Colydiidae	Colydium elongatum (F., 1787)	6	3	3		
Corylophidae	Orthoperus nigrescens (STEPH., 1829)	108	2			
Endomychidae	Symbiotes gibberosus (LUC., 1849)	4	2			
Cisidae	Ropalodontus perforatus (GYLL., 1813)	2	3	3		
Cisidae	Orthocis pygmaeus (MARSH., 1802)	17	3			
Anobiidae	Grynobius planus (F., 1787)	1	3			
Anobiidae	Ochina ptinoides (MARSH., 1802)	51	3			
Anobiidae	Gastrallus laevigatus (OL., 1790)	1	2			
Anobiidae	Anobium denticolle (CREUTZER, 1796)	5	3			
Anobiidae	Mesocoelopus niger (MULL., 1821)	2	3			
Anobiidae	Dorcatoma chrysomelina (STRM.)	19	3			
Anobiidae	Dorcatoma dresdensis (HERBST, 1792)	6	3			
Anobiidae	Dorcatoma robusta (STRAND, 1938°	64	2			
Scraptiidae	Scraptia fuscula (MULL., 1821)	28	3	1		
Scraptiidae	Anaspis lurida (STEPH., 1832)	2	3			
Scraptiidae	Anaspis garneysi (FOWL., 1889)	2	1			
Aderidae	Euglenes oculatus (PAYKULL)	10	2			
Melandryidae	Phloiotrya rufipes (GYLL., 1810)	1	3			
Melandryidae	Melandrya caraboides (L., 1761)	24	3			
Tetratomidae	Tetratoma desmarestii (LATR., 1807)	2	1			
Tetratomidae	Tetratoma ancora (F., 1790)	11	3			
Alleculidae	Allecula morio (F., 1787)	4	3			
Alleculidae	Alleculla rhenana (BACH, 1856	31	2			×
Alleculidae	Prionychus ater (F., 1775)	5	3			
Alleculidae	Pseudocistela ceramboides (L., 1761)	8	2			
Tenebrionidae	Bolitophagus reticulatus (L., 1767)	42	3	3		
Tenebrionidae	Diaperis boleti (L., 1758)	21		2		
Tenebrionidae	Platydema violaceum (F., 1790)	1	3	1		
Tenebrionidae	Pentaphyllus testaceus (HELLW., 1792)	23	3	U		
Tenebrionidae	Corticeus unicolor (PILL. Mitt., 1783)	32		3		
Tenebrionidae	Corticeus bicolor (OL., 1790)	5	3			
Scarabaeidae	Trichius zonatus (GERM., 1794)	1	3			
Cerambycidae	Leptura aurulenta (F., 1792)	3	2			

Family	Species	Number	German RL	GB-RL	EUR-RL	RELIC
Cerambycidae	Obrium cantharinum (L., 1767)	1	2	E		
Cerambycidae	Pyrrhidium sanguineum (L., 1758)	2		2		
Cerambycidae	Plagionotus detritus (L., 1758)	1	2			
Cerambycidae	Exocentrus adspersus (MULS., 1846)	2	3			
Anthribidae	Choragus sheppardi (KIRBY, 1818)	5	3			
Scolytidae	Kissophagus hederae (SCHMITT., 1843)	6	3			