SCIENTIFIC SUPPORT PLAN FOR A SUSTAINABLE DEVELOPMENT POLICY

SPSD II

A RESEARCH PROJECT TO STUDY PATTERNS, ROLES AND DETERMINANTS OF WOOD-DEPENDENT SPECIES DIVERSITY IN BELGIAN DECIDUOUS FORESTS (XYLOBIOS)

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ATMOSPHERE AND CLIMATE

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TERRESTRIAL ECOSYSTEMS AND BIODIVERSITY

NORTH SEA

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PART 2

GLOBAL CHANGE, ECOSYSTEMS AND BIODIVERSITY

SCIENTIFIC SUPPORT PLAN FOR A SUSTAINABLE DEVELOPMENT POLICY
(SPSD II)

Part 2:
Global change, Ecosystems and Biodiversity

FINAL REPORT

A RESEARCH PROJECT TO STUDY PATTERNS, ROLES AND DETERMINANTS OF WOOD-DEPENDENT SPECIES DIVERSITY IN BELGIAN DECIDUOUS FORESTS
(XYLOBIOS)

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ABSTRACT

Key-words: Belgium, biodiversity, dead wood, deciduous forest, saproxylic

Originating from the cautious recommendations by the European Council and the Bern Convention to retard the current erosion of biodiversity and link species loss with ecosystem functioning, this project aimed to clarify the ecological and functional values of dead wood habitats (including dead parts of living trees) in Belgian oak and beech forests. Among ecological benefits, we were interested to assess the relative importance of dead woody debris for representative species groups of forest biodiversity such as saproxylic insects, wood-decaying macrofungi, cavity-nesting birds and bats. At times when numerous beech trees were dying over a large part of southern Belgium, we wanted to see whether the development of large populations of damaging beetles in individual stands was causally related to a high dead wood supply, or if perhaps other factors would also come into picture. Among benefits for forest functioning, the possibility that a high supply of decaying wood on the forest floor could influence the geochemistry of the soil upper layer, with implications for plant growth and stand productivity, needed some clarification. From a management perspective, retaining overmature and dead trees for biodiversity implies some loss of production for the forest owner, which should be estimated when trying to optimise wood production at minimal costs.

We found the amount of dead wood to be highly beneficial for saproxylic insect, macrofungi and bird species diversity. Among insects, bark beetles, including the potentially damaging ambrosia beetles (*Trypodendron* spp.), were more numerous in stands classified as with dead wood (55 m^3 ha^{-1} on average) than stands without dead wood (12 m^3 ha^{-1} on average). However, they were not more numerous in those stands with a dead wood volume above 50 m^3 ha^{-1} compared to those with a lower dead wood supply. Besides a better understanding of key ecological factors for the different taxa, perhaps a major finding of our research was the confirmation of critical thresholds for those different factors below which risks of population depletion and species extinction are greatly increased. By providing threshold values for diverse habitat parameters shown to be important for numerous saproxylic species, this project calls for forest management procedures that also take into account their biological requirements in the management plans. Furthermore, the retention of those key habitats for biodiversity does not contradict with wood production for economical purposes, as shown for example by our estimates of soil fertility or bark beetle population size at the highest dead wood volume.

1. INTRODUCTION

Dead wood is a conspicuous and multifunctional component of dynamic forest ecosystems. Under natural conditions, its accumulation in a stand is determined by the balance between input and decay rates (Siitonen 2001). The input rate is related to the stand successional stage. As the stand develops, the amount of woody debris produced by annual mortality increases, first due to competition and self-thinning, and later because of older trees becoming more susceptible to disturbance factors such as wind, insects and disease (Harmon et al. 1986). Prevailing disturbance regime and site productivity affect the volume of dead wood as well (Sturtevant et al. 1997). The decay rate of woody debris, on the other hand, is a function of tree species, tree size, wood quality, and climate, which control the activity of decomposing organisms (Morrison & Raphael 1993, Siitonen 2001).

Recent inventories of naturally dynamic forests have revealed dead wood volumes between 40 to 200 m3 ha-1 (Vallauri et al. 2002), sometimes up to 570 m3ha-1 (Christensen et al. 2005), depending on the regions and dominant tree composition. The proportion of snags and logs of the dead wood volume vary considerably between vegetation types, with different tree species having different modes of death. In the natural forests of Northern Europe, snags are typically more numerous in Scots pine *Pinus sylvestris* dominated stands compared to spruce *Picea abies* dominated forests, due to a higher susceptibility of spruce trees to uprooting and stem breakage (Liu & Hytteborn 1991, Siitonen et al. 2000). Similarly, in temperate deciduous forests, old beech trees *Fagus sylvatica* become increasingly predisposed to break-up compared to oak *Quercus* spp, with implications for gap dynamics (Mountford 2004). On average, it is usual to find between 40 to 140 snags, 10-40 broken stems, and 10-20 (up to 60) cavity trees per hectare of broad-leaved old-growth forests (Vallauri et al. 2002). In the Bialowieza primeval forest, Poland, dead wood accounts on average for 5-30% of the standing wood volume (Falinski 1978).

During the last decades saproxylic organisms, those that depend upon wood substrates or upon the presence of other saproxylics for at least part of their life cycle (Speight 1989), have received increasing attention from ecologists, conservation biologists, and forest managers (Samuelsson et al. 1994, Grove 2002, Vallauri et al. 2002). Detailed species inventories showed their highly significant contribution to forest overall species diversity. In Finland for example, a conservative estimate of 4000 to 5000 species has been suggested to depend on dead wood habitats, which account for as much as 20-25% of all forest-dwelling species (Siitonen 2001). In Germany, about 1500 species of fungi and about 1350 species of beetles, major contributors to the earth biodiversity (Franklin 1993), are known to live exclusively on dead wood (Albrecht 1991). In Norway and in Sweden, approximately 1000 saproxylic beetles have been inventoried (Økland et al. 1996, Jonsell et al. 1998). Wood-dependent organisms are also functionally important to forest ecosystems. They play critical roles during the processes of woody debris decomposition and nutrient cycling through multitrophic interactions (Harmon et al. 1986, 1994, Edmonds & Eglitis 1989, Bengtsson et al. 1997). By contributing to natural tree mortality, they influence forest structure and composition (Kuuluvainen 2002). The availability of saproxylic insects affects forest bird communities, notably by limiting the populations of most woodpecker species, important cavity providers for secondary cavity-nesters (Martin & Eadie 1999, Bednarz et al. 2004).

Some saproxylic organisms have narrow micro-habitat requirements and poor dispersal capacities (Siitonen 2001, Grove 2002). This makes them a group of species particularly susceptible to habitat loss and fragmentation and, as a result, extinction-prone. Accordingly, Speight (1989) estimated some 40% of Europe’s saproxylic invertebrates to be already on the verge of extinction over much of their range while the majority of the remainder would be in decline. Due to their specificity for substrate and microclimatic conditions characterising mature timber habitat, saproxylic communities have been suggested as useful bio-indicators of forest quality, and as tools in the process of identifying important forests for nature conservation (Speight 1989, Good & Speight 1996). Ultimately, a major argument for maintaining dead wood habitats and preserving saproxylic assemblages is that losses of saproxylic species diversity may impair processes required for the long-term functioning of the forest ecosystems (Bengtsson et al. 2000), such as nutrient cycling.

An important reason why woody debris are systematically removed from forests originate from the specificity of a very few among saproxylic insects (less than 1% of all forest insect species (Nageleisen 2003)), mainly bark beetles (Coleoptera, Scolytidae), to reach under particular environmental conditions epidemic levels and kill apparently healthy trees in large numbers (Vité 1989). Fear of significant economical losses has even led authorities to establish in some countries regulations for forest protection from so-called insect pests (Ehnström 2001). Cautious management procedures stem mostly from widespread observations that stand hazard and windthrown trees act as major factors determining risk of beetle outbreak (e.g., Reynolds & Holsten 1994). On the other hand, contrarily to the common belief that forest management helps to limit bark beetle populations, studies comparing saproxylic assemblages between managed and natural forests have brought surprising results. Already in 1968, Nuorteva remarked that the thinning and clear-cutting of finnish forests lead to the increase of bark beetle population, presumably as a result of increased availability of breeding material and warmer temperature conditions. Still in Finland, looking at the trunk fauna of coniferous trees, Väisänen et al. (1993) found the proportion of bark beetles to be about 52% of the individual beetles collected in managed forests, but only 3% in natural old-growth forests. This was recently confirmed by Martikainen et al. (2000), who found the proportion of bark beetles out of all saproxylic beetles caught smaller in old-growth than in managed forests, despite roughly five to tenfold more decaying wood in the former habitat. In similar old-growth habitats, Fayt (2003a,b) found primary conifer bark beetles to account for only 1.14% of the total catch (25,000 bark beetles). The same pattern holds whether the insects were collected with standard window-flight traps or from bark samples. In German commercial forest where dying and dead trees have been retained for a decade, bark beetle species known as pest species contributed to less than 10% of the number of all beetle individuals captured (Kleinevoss et al. 1996). Inversely, bark-beetle predators and other enemies (parasitoids) have been found more abundant in unmanaged forests, probably as a result of the higher amount and diversity of recently dead wood (Martikainen et al. 1999). Those findings suggest a possible role for wood-living predators and associates in regulating partly bark beetle populations below epidemic levels, as long as enough decaying wood is available.

Although Europe covers a relatively small area of the globe, it is characterised by various kinds of forest landscapes, with management histories that are specific to a particular country (Mikusiński & Angelstam 1998). Spatial variation in composition and structural heterogeneity reflects the profound impacts that the past geopolitical location of the different countries has had on the amount of deforestation and intensity of landscape transformation. Already 2000 years ago, very few patches of secondary forests were left apart in the Mediterranean region (Speight 1989). In western Europe, roots of this phenomenon dates back in particular to the eighteenth and nineteenth centuries, when the start of the Industrial Revolution lead to dramatic economical developments in the United Kingdom before to spread towards other western European countries, with direct implications for forest uses. Simultaneously, large tracks of naturally dynamic forests remained little affected in the east or some parts of Fennoscandia and western Russia. As a result, the present-day European countries clearly differ in terms of the proportion of the forest land that has retained elements of the original forest cover, namely a high tree species diversity with a dominant deciduous component, a continuous supply of large overmature and dead trees, and on-going vegetation dynamics. Perhaps one of the most obvious consequence is a general impoverishment of the biological legacy of European forests from the east to the west, as shown for example for woodpecker species diversity (Mikusiński & Angelstam 1998).

With an area of 30,230 km2 and forests covering 22.2% of the land, Belgium is one of those western European countries that have undergone dramatic changes in forest cover, composition and structure during the last centuries. As a general observation, use and transformation of Belgian forest landscapes has been closely connected to the changing economical needs of developing human societies (Tallier 1998). From a saproxylic organism's point of view, living conditions have been profoundly deteriorated. In Wallonia, in the southern half of the country, Lecomte mentioned in 2006 an average dead wood volume of 6 (beech) and 7.5 (oak) m^3 ha^{-1}, based on the Walloon Permanent Forest Resource Inventory. This is particularly low if compared with volumes found under natural conditions (Vallauri et al. 2002), corresponding to a dead wood reduction over 95% (!). In addition to habitat loss, which is known to cause species extinction in a non-linear manner (Connor & McCoy 1979), the forest cover has been increasingly fragmented and relict saproxylic populations increasingly isolated, whether directly (e.g., agriculture, road network,…) or in a more subtle way (e.g., large-scale afforestation with non-native conifer trees). Depending on the region, populations of wood-dependant organisms are expected to have badly suffered from the loss of spatio-temporal continuity in suitable ecological conditions, with implications for species persistence (Nilsson & Baranowski 1997, Kehler & Bondrup-Nielsen 1999, Sippola & Renvall 1999, Nilsson et al. 2001).

In this report, we describe the objectives and the methods of the four-year research project named XYLOBIOS and we discuss its main results, mentioning implications for forest management. The project originates from the cautious recommendations of the European Council and the Bern Convention to retard the current dramatic erosion of biodiversity and link species loss with ecosystem functioning (Speight 1989, Good & Speight 1996). Its general aim is to address simultaneously and to link both major ecological and economical issues raised by the management of decaying woody debris in native mature deciduous forests (beech Fagus sylvatica and oak Quercus spp. dominated-) of central-southern Belgium. Notably, by providing new insights into key environmental factors for the distribution of saproxylic diversity, this project should help in the development of management guidelines favourable to biodiversity in temperate forests. Several Belgian research institutions took part in the project, among which two universities (FUSAGx, UCL), the Research Centre of Nature, Forests and Wood (DGRNE - Ministry of the Walloon region), and the Royal Belgian Institute of Natural Sciences (KBIN/IRSNB).

The report is subdivided into different work packages (WP), each with its own objectives, methods, results and possible implications for the research on saproxylic organisms in Belgium and their conservation in relation to diverse management scenarios. Basically, the project aimed to develop a national expertise in the study of distribution, diversity, ecology and roles of saproxylic organisms of deciduous forests.

2. SAMPLING SAPROXYLIC DIVERSITY (WP1)

2.1. Studying saproxylic organisms in Belgium: why, which and where?

Because of highly diverse and specialised requirements for woody substrates, limited dispersal abilities and their consequent sensitivity to habitat loss and fragmentation, part of saproxylic organisms have been suggested as potential useful bio-indicators of global forest quality (Speight 1989, Good & Speight 1996). One aspect covered by the project was to gain reliable and informative data on the current distribution of saproxylic organisms, aiding in the process of identifying important forests in Belgium for nature conservation. We were also particularly interested to clarify those environmental factors that best explained their local distribution, with emphasis on the effect of dead wood supply and quality on species diversity and abundance. Among practical implications, it was relevant to assess whether the accumulation of woody debris makes individual stands more susceptible to attacks by damaging beetles, with economical consequences, or not necessarily. Understanding species distribution, on the other hand, is a prerequisite in the process of correctly predicting priority habitats for forest biodiversity.

In this project, the selection of meaningful forest indicators followed Speight (1989)'s criteria, mainly that those species should (i) depend upon dead wood of dying and dead trees for their habitats, and (ii) be relatively easy to find and to determine. Information on their micro-habitat preferences and general life-history should also be available in ecological textbooks. We focused our research on four distinct taxonomic groups known for their preference for micro-habitats (woody debris, trunk cavities, rot-holes, …) and foraging grounds that typically develop in overmature stands, namely saproxylic insects, wood-decaying fungi, cavity-nesting birds, and bats. Among insects, we restricted the identification work to families for which we had taxonomic competence. We limited fungi monitoring to those species producing larger fruiting-bodies (macromycetes). Hole-nesting birds included both primary cavity nesters (i.e., excavators) and secondary cavity users (i.e., non-excavators), while non-cavity nesters were used as a control.

The selection of relevant study sites benefited from the help of the different forest districts, to whom we made enquiries about available forest statistics. Following field confirmation, a total of 22 sites (10 beech and 12 oak-dominated stands) were selected, distributed over four natural regions (Fig. 1). Dominant tree composition (oak/beech), forest age and availability of woody debris were the main criteria of selection.

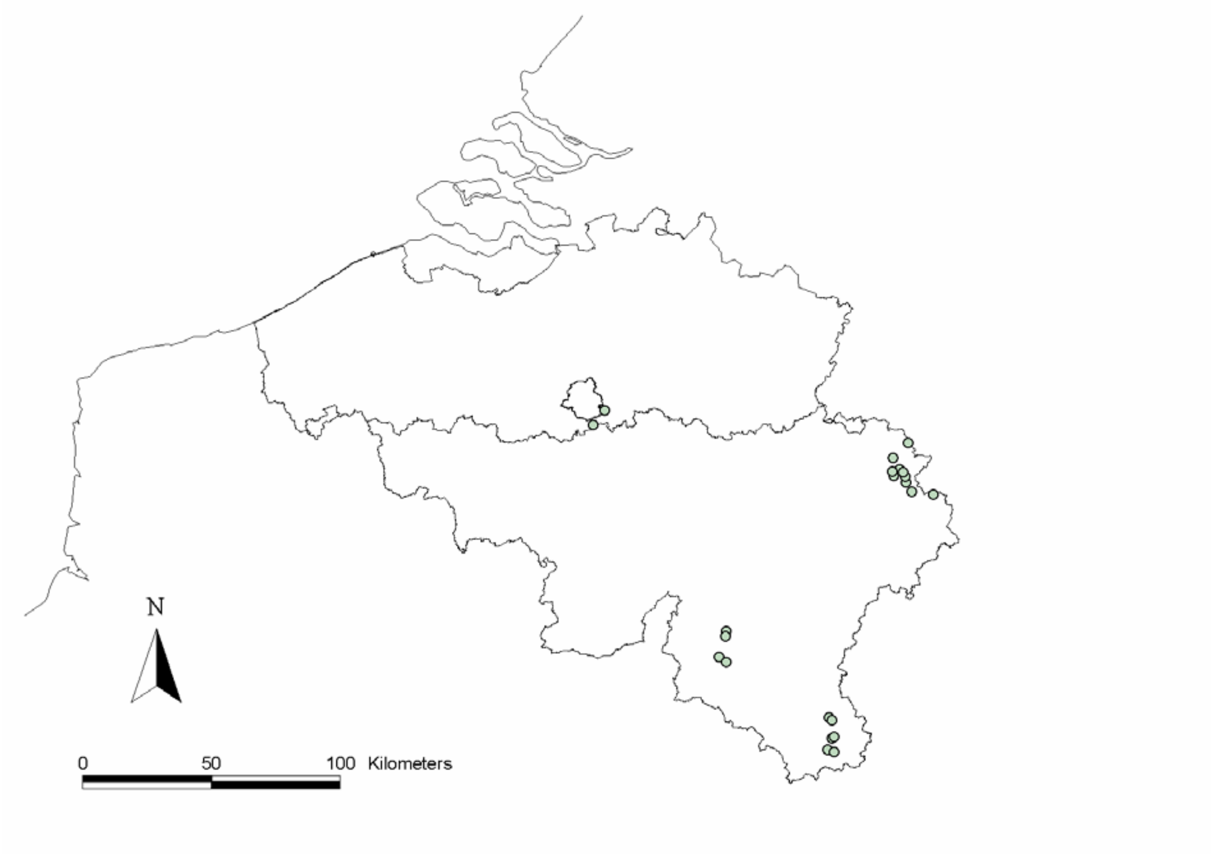

Figure 1. *Location of the study sites (circles).*

Sites were organised by pair (11 pairs), with pair stands showing similar plant composition, soil properties and abiotic factors (elevation) but differing visually in their overall amount of coarse woody debris. Accordingly, paired-stands were thereafter classified as having a high (or with dead wood) vs. low dead wood supply (or without dead wood) (Appendix 1). They were located 2-10 km apart from each other.

2.2. Sampling wood-dependent organisms: how?

2.2.1. Insects

We used various kinds of traps to study the insect composition of the different study sites, based on their trapping efficiency from the literature. Among available capture devices, flight-interception traps have been shown to capture a significant part of the flying beetle fauna (Muona 1999, Similä 2002), including saproxylic species (Siitonen 1994, Økland et al. 1996, Martikainen et al. 2000, McIntosh et al. 2001). Two main variants of this trap model exist, either placed independently of woody substrates (flight-window traps) or attached to tree trunks (trunk-window traps, Kaila 1993). Flight-window traps are suitable for comparing different forest environments, but are related to ecological conditions over wide areas (Økland 1996). This means that the position of the trap in relation to dead wood distribution does not greatly affect the number of species and individuals caught (Siitonen 1994). By contrast, trunk-window traps are more suitable for comparison of different substrates within the same forest environment than between forest stands (Kaila et al. 1994). This is because the substrate on which the trap is attached (typically trunks of dead trees, often close to the fruiting-bodies of polypores) serves as a bait, which has a strong effect on the composition of the species caught. Trunk-window traps are more effective in catching rare and threatened saproxylic species than freely-hanging flight-window traps (Martikainen 2000). Part of the insects (e.g., Diptera, Hymenoptera), however, have flying-abilities good enough to avoid obstacles, making them difficult to collect with conventional flight-interception traps. Instead, their propensity to avoid an obstacle by flying upwards towards the light makes them more susceptible to capture by Malaise traps (Malaise 1937). Finally, emergence traps allow the capture of insects when emerging from their breeding habitats, providing information on larval micro-habitat preferences (Owen 1989).

We sampled insects from March to October 2002-2003. The applied sampling protocol aimed to maximise sampling efficiency (i.e., collecting enough individual species to approach the true community value) of the target groups, while allowing comparison between sites (Fig. 2). In the 11 sites with a high amount of dead wood, insect traps were situated where woody debris were most abundant. In each stand, 8 flight-window traps (W) were placed and numbered along 2 x 100 m perpendicular transects crossing each other in their middle, with the traps number 1, 2, 3, 4 in the north-south direction, and the traps 5, 6, 7, 8 in the west-east direction. Traps 1-2, 3-4 and 5-6, 7-8 were suspended on a metal wire between trees 25 m apart, leaving the transect junction (between traps 2-3 and 6-7) free of window traps. Flight-window traps consisted of two perpendicular intercepting 40 x 60 cm transparent plastic panels, with a funnel leading to a container below the panels filled with water, salt and detergent. Traps were covered with a transparent 80 x 80 cm plastic roof to minimise funnel obstruction with plant debris and to divert rainfall. In those 11 stands with high dead wood volume, we added 8 roof-covered trunk-window traps of 2 x 40 x 60 cm (K); they were attached to randomly selected standing dead trees, with 2 traps per quarter of the sample plot. Contrarily to flight-window traps, funnels used for trunk-window traps were made flexible to facilitate a closer contact of the window against the trunk. To optimise the capture of insects that have contrasting flight behaviour and host preferences, we also used 2 Malaise (M) and 3 stump-emergence (E) traps. Malaise tents (with a second one only in 2003) were located apart near the centre of the plot in a sunny place, with ethylene-glycol in the container to preserve the insects. They were protected from wild boars *Sus scrofa* by a robust metal fence stretched on wooden posts. In 2003, together with the second

Malaise trap, we placed 1 intercept panel trap® (PS), made of black cardboard panels, where the sampling transects crossed.

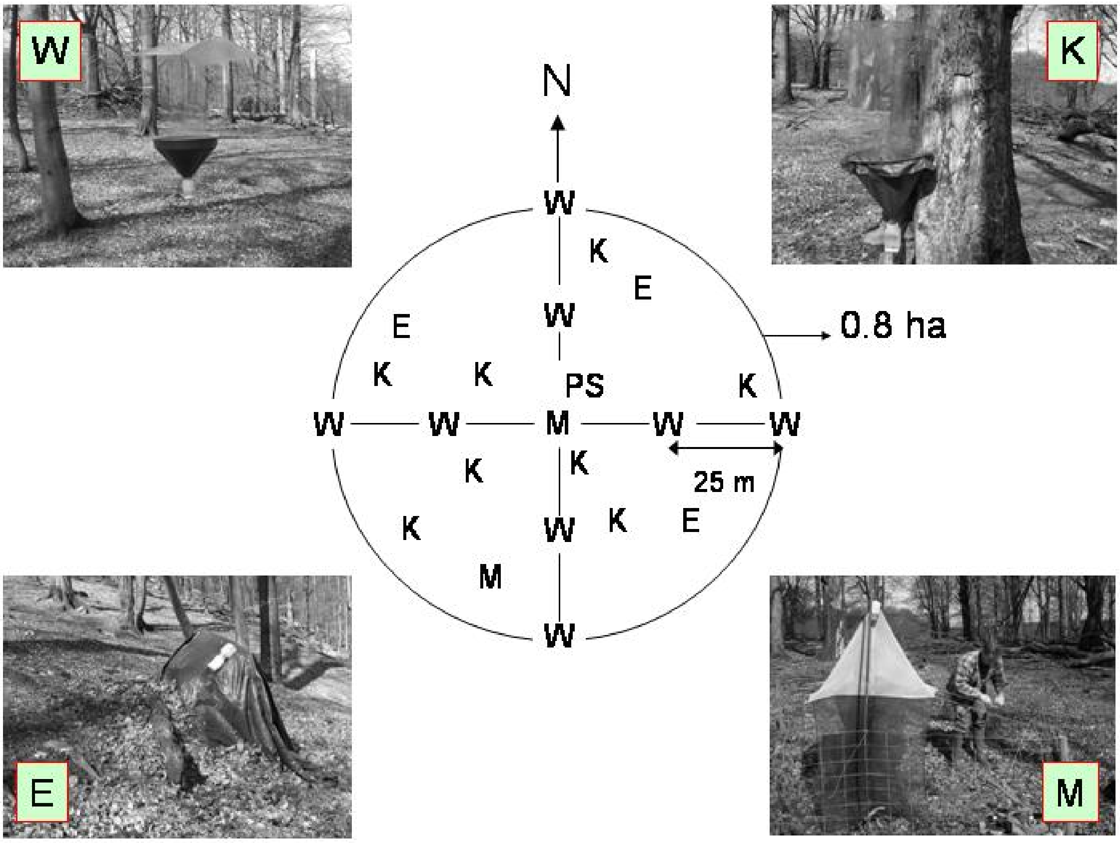

Figure 2. *Schematic view of a sampling unit designed to monitor local saproxylic insect diversity. Letters W, K, M, E refer to the different kinds of trap under use (see text for details).*

Traps were emptied once a month and regular visits were made in May-June to minimise the risks of trap funnel obstruction at times of maximum insect activity.

2.2.2. Wood-decaying fungi

Wood-inhabiting fungi account for a high proportion of known forest species. Only in Finland, they would represent up to 30-40% of the saproxylic species (Siitonen 2001). Key actors in the process of wood decomposition, fungi also influence the diversity of other organisms associated with dead wood, e.g. saproxylic insects (Jonsell & Nordlander 2002, Komonen 2003).

A survey of wood-inhabiting macrofungi was carried out by Ruben Walleyn (INBO) in 10 selected beech stands (5 pairs). Special attention was paid to strictly lignicolous macrofungi: agaricoid and boletoid fungi, gasteromycetes, hydnoid fungi, polypores, major corticioid fungi (Chondrostereum, Cristinia, Cystostereum, Laxitextum, Mycoacia, Phlebia, Peniophora, Steccherinum, Stereum), heterobasidiomycetes with fruitbodies larger then 1 cm, discomycetes with fruit bodies > 1 cm, and larger Pyrenomycetes: Camarops, Eutypa and Xylariaceae. The species inventory was based on the presence of fruiting bodies within a 4 ha sample plot, centred on the circular insect sample plot delimited by perpendicular transects. It took place in autumn-winter 2002-2004, each site being visited 2-5 times, depending on the amount of dead wood available (i.e., census effort) (Walleyn et al. 2004).

2.2.3. Forest birds

As a general pattern, cavity nesting bird density, diversity, and species richness are strongly positively influenced by increases in stand age and average tree dbh (diameter at breast height) (Ferry & Frochot 1970, Land et al. 1989, Newton 1994), as long as dead trees are not systematically removed. Among cavity users, primary cavity nesters (i.e., excavators such as woodpeckers) are keystone species in the forest environment, influencing the composition and abundance of obligate and facultative hole-nesting vertebrate communities (Martin & Eadie 1999; Bednarz et al. 2004, Martin et al. 2004). In Europe, about half of forest bird species use tree cavities for reproduction and maintenance activities.

In 2003, David Dufour (FUSAGx) estimated forest bird species and individual numbers among 16 of the 22 stands, located in eastern (Hertogenwald) and southernmost Belgium (Lorraine). Stands were organised by pairs (8), with half of them being classified as with a high volume of woody debris. Bird inventory was carried out from February-June 2003 in early morning (from dawn till 10 a.m.) under mild weather conditions (limited wind and no rainfall). Individual birds were censused by point counts, that is counts undertaken from a fixed location for a fixed time period (Gibbons et al. 1996). This method was preferred instead of other existing sampling alternatives such as territory mapping or presence/absence (EFP, Grimoldi 1976), providing estimates of the relative abundance of each species between habitats with limited effort (Muller 1987).

Except for woodpeckers, point count stations (the position from which the count was made) were laid out in a systematic manner within the study plots, with 3 point counts/site in homogeneous habitat conditions. To avoid counting the same individuals, count stations were selected to have a minimum distance of 300 m between each other. They were centred on the circular insect sample plot. The survey was splitted into two periods over the spring, to ensure the counting of early (mostly sedentary species) and late singers (i.e., migrants) and take into account seasonal variation in the detectability. The first survey was done from 25.03-25.04, and the second from 25.05-15.06. At each station, birds were counted for 20 minutes, a period of time suggested to be long enough for recording most individuals in forested environment (Blondel 1975, Grimoldi 1976, Bournaud & Corbillé 1979). All birds seen or heard were reported on field sheets using species codes, as well as their approximate positions according to cardinals. To convert numbers into densities, birds were recorded up to and beyond 50 m distance from the observer (Bibby et al. 1992), drawn on the field sheet as a concentric circle divided into four quarters.

In the case of woodpeckers however, with home-ranges typically covering distances over 300 m, we estimated their populations by enlarging the census area to a 113 ha circular plot (600 m radius from the centre of the insect plot). Within each plot, territorial woodpeckers, whether drumming or calling, were counted during 20 minutes at five point-count stations. Four of the stations were laid out according to cardinals, 500 m apart from a central station located at the centre of the insect plot (i.e., at the transect junction). We also counted individuals contacted over the whole sample plot, when moving from one station to the next. The census started from the central station, before being expanded to the rest of the 600 m-radius sample plot. Woodpeckers were counted over three successive periods (15.02-15.03, 25.03-25.04, 15.05-15.06). During the latter census period, nests were actively sought all over the sample plot, in addition to habitat mapping. They were located by nest-excavation noises, by fresh woodchips, by noisy vocalisations of offspring or by accident. Bird locations were reported on field sheets with the use of field codes, depending on whether the woodpeckers were flying, calling/drumming, fighting, alone/with a partner, or breeding. Back from the field, the different count data were translated into density estimates for the different species.

2.2.4. Bats

Although a few bat species rely on human infrastructures for colony settlement, a majority of them are found depending on various properties of forest habitats to sustain their vital activities such as foraging, roosting, thermoregulation, and reproduction. Most commonly, bats use forest edges and canopy gaps as parts of their hunting grounds (Schober & Grimmberger 1991). However, part of them also use tree holes caused by rooting and/or woodpecker excavating and cracks behind the bark as roosting and reproduction sites. In Germany for example, the 20 known species have been shown to make use of forest habitats in some way, among which 8 species (40%) reproduce there on a regular basis while 4 species (20%) occasionally stay in natural tree holes or nest boxes (Meschede & Heller 2003). Thus, similarly to saproxylic insects, wood-living fungi and cavity-nesting birds, bats form a group of species highly susceptible to forest management and the consequent removal of old and dead trees.

In spring-summer 2005, Ben Van Der Wijden and Sven Verkem (A.B.Consultancy g.c.v.) carried out a bat inventory in 12 out of the 22 study sites (6 pairs with/without dead wood). Bats were investigated using time-expansion bat-detectors and a point-counts method to permit comparisons between plots (Van Der Wijden & Verkem 2005). A grid with 20 equidistant point-count stations (distance 50 m) was projected on the map of the forest plot and uploaded in a GPS. These stations were subsequently marked on the field. The transects were censused starting 30 minutes after sunset. All bat passes were noted and identified during a 3-minutes period, after which the observer moved on to the next station. All twenty point counts were completed within 3 hours. In addition to bat recordings at the stations, data were also collected while walking from one station to the next (outside point-count data). Transects in the pairs (dead wood / no dead wood) were inventoried simultaneously by the two observers. All plots were visited three times, i.e. in May-June, July and August to account for possible seasonal variation in habitat use by bats. After the transects were finished, the surroundings of the plot were further investigated. In May to July, the plot was cruised, starting 1.5 hours before sunrise to look for swarming bats.

The presence of seven species was further confirmed by capture (net, harp-trap, bag-trap) under licence of the Walloon region. The survey of one species (*Nyctalus leisleri*) by radio-tracking allowed the discovery of its first known breeding colony for Belgium. Practically, the bat was fitted with a Holohil emetor LB-2 (0.45 g) (Holohil Systems, Ontario, Canada), glued between the scapulars with Skin-Bond (Pfizer Hospital Products Group, Inc., Largo, Florida, U.S.A.). It was released a few minutes later at the capture site once the glue was hard enough to keep the emetor in the right position. Two days later, the bat was followed by “homing-in” technique (White & Garott 1990) with a receptor Stabo XR100, modified by GFT (Gesellschaft für Telemetriesysteme, Horst, Germany), and a Yagi antenna (3 pieces).

2.3. How efficient is the sampling? Saproxylic insects as an example

The sampling efficiency of insect communities in our study sites was assessed by drawing individual species accumulation curves in relation to the sampling effort applied over the study period (8 W (2002) + 8 W (2003), 8 K (2002) + 8 K (2003) and 1 M (2002) + 2 M (2003) traps). This procedure combines the average number of species per sampling unit, and variation in species composition among them, into the cumulative number of species. Importantly, the shape of the curve is a good indicator of the sampling efficiency, with the slope approaching the asymptote as the sample estimate becomes closer to the community true value. For each site, sampling efficicency was estimated by calculating the ratio a/N, where a is the number of species that were sampled only once, and N the number of sampling units (traps). This index expresses the slope of the curve when the whole community is inventoried, that is, the number of new species that, on average, would be expected to be gained if adding one more insect trap (Lauga & Joachim 1987). With a ratio a/N = 0.1 for example, we would need 10 more traps to gain a new species.

From 2002-2003, we collected altogether 115,468 insects of 77 families by using W, K, M, E and PS traps (see Fig. 2) (Appendix 2). We limited species identification to families known for their richness in saproxylic species and for which taxonomic competence was available. Altogether our sampling produced 393 insect species (beetles (Coleoptera) and hoverflies (Diptera)) from 38 families (Appendix 3). Looking at the saproxylic component of insect diversity, we collected 30,058 individuals (33 families) (Appendix 4) and identified 191 species (Appendices 5 & 6).

Overall, the number of saproxylic insect species collected with window (K, W) and Malaise (M) traps seemed approaching true community values, as suggested by species accumulation curves tending towards the asymptote (e.g., Fig. 3). Accordingly, the entirety of the study sites sampled for their most species-rich families with window traps had an average a/N value well below 1 (i.e., sites that would require more than one additional trap to collect a new species) (Table 1). Even more, 91% (10/11) and 77% (17/22) of the sites sampled with trunk- (K) and flight-window traps (W) would need more than two extra traps to collect an additional species (a/N < 0.5). Similarly, 3 Malaise traps (M) allowed an effective sampling of the local communities, since less than two new species, all the largest families combined, would be found if adding one trap in about 60% (13/22) of the sites (1 < a/N < 2), and less than three more species in 91% (20/22) of all cases (a/N < 3) (Table 1). These estimations clearly validate our insect sampling protocol applied throughout the project.

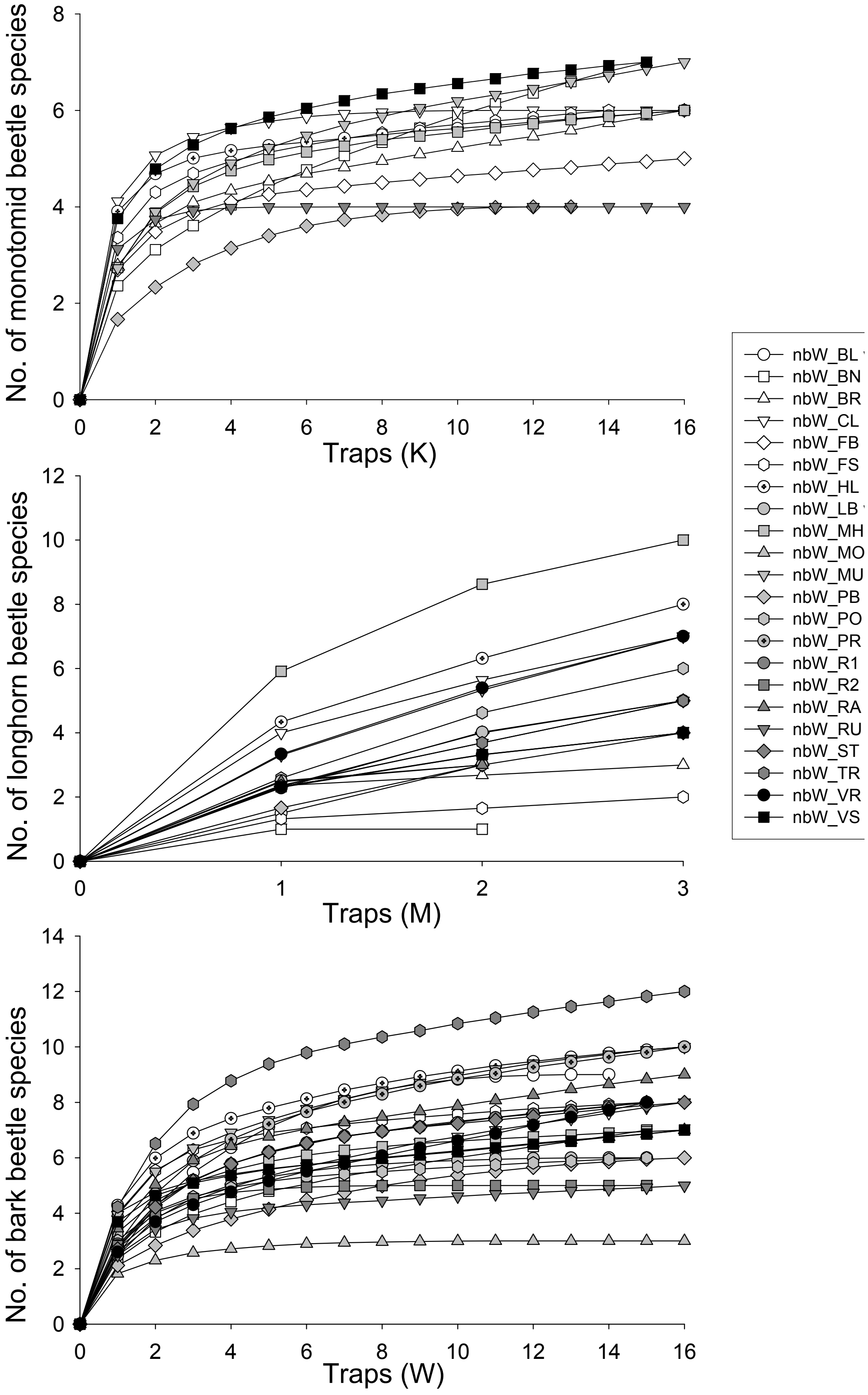

***Figure 3.** Cumulative number of various saproxylic insect species (here of monotomid, longhorn and bark beetles) in relation to trapping effort using different sampling devices (K, W and M traps), with data cumulated for 2002-2003.*

Table 1. *Level of sampling efficiency (a/N) for different trap models (K, M, W) in our study sites (2002-2003*). Only data for the most species-rich families (≥ 9 species) are reported, from sites with repeated captures. a/N gives the number of new species that, on average, would be expected to be gained with an additional trap. Trunk-window traps (K) were missing from the sites classified as with a low dead wood supply.*

												Site												
Family	**Trap**	**BL**	**BN**	**BR**	**CL**	**FB**	**FS**	**HL**	**LB**	**MH**	**MO**	**MU**	**PB**	**PO**	**PR**	**R1**	**R2**	**RA**	**RU**	**ST**	**TR**	**VR**	**VS**	**Mean**
Cerambycidae	K		0.30	0.29	0.17	1.67	0.20	0.5		0.42		0.25	0.33						0.25				0.43	**0.44**
	M	1.50	0.00	0.33	1.33	1.00	0.33	1.67	1.00	1.33		1.67	1.00	1.33	0.50	0.67	0.67	0.50	1.33		1.33	1.67	0.67	**0.99**
	W	0.25	0.33	0.56	1.00	0.67	0.08	0.67	0.31	0.40	0.40	0.20	0.31	0.20	0.14	0.78	0.25	0.14	0.87		0.40	1.50	0.42	**0.47**
Curculionidae*	K		1.37	0.29	0.62	1.40	1.00	0.37		0.87		0.86	0.50						0.33				0.12	**0.70**
	M																							
	W	0.12	0.50	0.25	1.12	1.43	0.50	0.50	0.87	0.62	0.62	0.75	0.37	0.71	0.75	0.50	0.37	0.50	0.12	1.43	0.75	0.25	0.25	**0.60**
Elateridae	K		0.12	0.19	0.31	0.21	0.19	0.19		0.20		0.19	0.44						0.13				0.25	**0.22**
	M	0.33	2.33	1.67	0.67	2.67	2.00	1.33	1.00	1.00	0.67	1.33	1.33	1.00	1.33	0.33	0.67	2.33	1.33	1.33	1.00	0.67	1.67	**1.27**
	W	0.19	0.20	0.12	0.25	0.40	0.19	0.25	0.12	0.31	0.19	0.12	0.19	0.31	0.06	0.31	0.00	0.06	0.19	0.19	0.25	0.25	0.31	**0.20**
Eucnemidae	K		0.08	0.00	0.33	0.29	0.07	0.09		0.11		0.09	0.17						0.12				0.14	**0.13**
	M			0.50		1.67	0.50	0.00	1.00	2.00		0.00	1.00	0.50	1.00		0.50	1.50	0.50	1.00	0.67	0.33		**0.79**
	W	0.25	0.50	0.40	0.50	0.37	1.33	0.33	1.00	1.67	0.00	0.33	0.09	0.43	0.00	0.00	0.17	1.00		0.60	0.33	1.00	0.22	**0.50**
Histeridae	K		1.00	0.60			0.25	0.42				0.33												**0.52**
	M																							
	W	0.33	0.12	0.00		1.00		1.00		1.00		0.14			0.33					1.33	0.50			**0.57**
Melandryidae	K		0.67		0.60	0.00	0.00	0.37		0.14		0.00	0.60											**0.30**
	M		0.00	0.00	0.00	0.00		0.00		0.33		0.50	1.00	0.50	0.33					0.00	1.00	1.5	1.5	**0.48**
	W	1.00	0.33	0.25	0.00	0.11	0.25	0.00	0.00	0.18	1.00	0.33	0.67	0.17	0.67	0.50	0.25			0.20	0.50	0.43	0.20	**0.35**
Monotomidae	K		0.20	0.12	0.00	0.06	0.07	0.06		0.06		0.12	0.00						0.00				0.07	**0.07**
	M		1.5									0.33						1.00		1.00	0.00	0.00	1.00	**0.69**
	W	0.00	0.07	0.19	0.27	0.00	0.00	0.07	0.00	0.12	0.00	0.12	0.15	0.09	0.18	0.06	0.00	0.11	0.00	0.15	0.00	0.06	0.07	**0.08**
Mycetophagidae	K		0.00	1.00			0.12	0.67		1.00		0.25												**0.51**
	M																							
	W			0.33				1.00				0.25	0.00				1.00				0.33			**0.48**
Scolytidae	K		0.07	0.13	0.20	0.12	0.19	0.07		0.07		0.12	0.00						0.07				0.13	**0.11**
	M				1.00	0.50														0.50	0.50	1.5		**0.80**
	W	0.00	0.20	0.12	0.19	0.13	0.07	0.12	0.00	0.06	0.00	0.12	0.06	0.07	0.19	0.13	0.00	0.19	0.06	0.12	0.19	0.27	0.12	**0.11**
Syrphidae	K		0.75	1.00		1.00	1.20	1.00		1.20		0.43	0.56						0.33				0.37	**0.78**
	M	2.50	5.50	8.00	6.00	7.67	5.00	5.33	6.33	15.00	3.67	9.67	4.33	3.33	4.00	3.50	2.00	5.33	9.33	7.67	3.67	11.50	3.67	**6.04**
	W	0.89	1.22	0.64	0.83	0.50	0.27	0.56	1.00	1.00	0.82	0.67	0.81	0.57	1.33	0.67	0.71	0.58	1.00	1.00	0.56	0.83	0.47	**0.77**
Mean	**K**		**0.46**	**0.40**	**0.32**	**0.59**	**0.33**	**0.37**		**0.45**		**0.26**	**0.33**						**0.18**				**0.22**	**0.36**
	M	**1.44**	**1.87**	**2.10**	**1.80**	**2.25**	**1.96**	**1.66**	**2.33**	**3.93**	**2.17**	**2.25**	**1.73**	**1.33**	**1.43**	**1.50**	**0.96**	**2.13**	**3.12**	**1.92**	**1.17**	**2.45**	**1.70**	**1.96**
	W	**0.34**	**0.39**	**0.29**	**0.52**	**0.51**	**0.34**	**0.45**	**0.41**	**0.60**	**0.38**	**0.30**	**0.29**	**0.32**	**0.41**	**0.37**	**0.31**	**0.37**	**0.37**	**0.63**	**0.38**	**0.57**	**0.26**	**0.40**

* except for the Curculionidae, identified at species-level only in 2002 (8 K, 1 M, 8 W).

3. UNDERSTANDING WOOD-DEPENDENT BIODIVERSITY (WP2)

3.1. Site characteristics

We were interested to relate insect, fungi, bird and bat data to factors assumed to have direct measurable effects on saproxylic species assemblages (vegetation structure and composition, floral resources, dead wood supply and quality, altitude). Patch occupancy was also studied in relation to the surrounding landscape composition, and in particular to the extent of exotic conifer plantations. This variable, a good indicator of the level of habitat continuity and connectivity over time (conifer plantations were still missing from Belgian forest landscapes in the 18th century (see Ferraris' historical maps)), was assumed to have long-lasting effects on the saproxylic population processes at landscape level and thereby population persistence in the deciduous forest remnants (Mazerolle & Villard 1999). Habitat description procedures followed pan-European recommendations for data collection in forest reserves (Hochbichler et al. 2000). Schematically, the sampling design was a collection of circular plots of different sizes and locations on a grid network of 50 x 50 m, according to the habitat features to be measured.

In each stand, we used 5 nested sample plots of 0.05 ha and 0.1 ha, with one located at the crossing of the insect sampling transects and the others 50 m apart in the cardinal directions, centred on the outsidemost flight-window traps (1, 4, 5, 8) (Fig. 4).

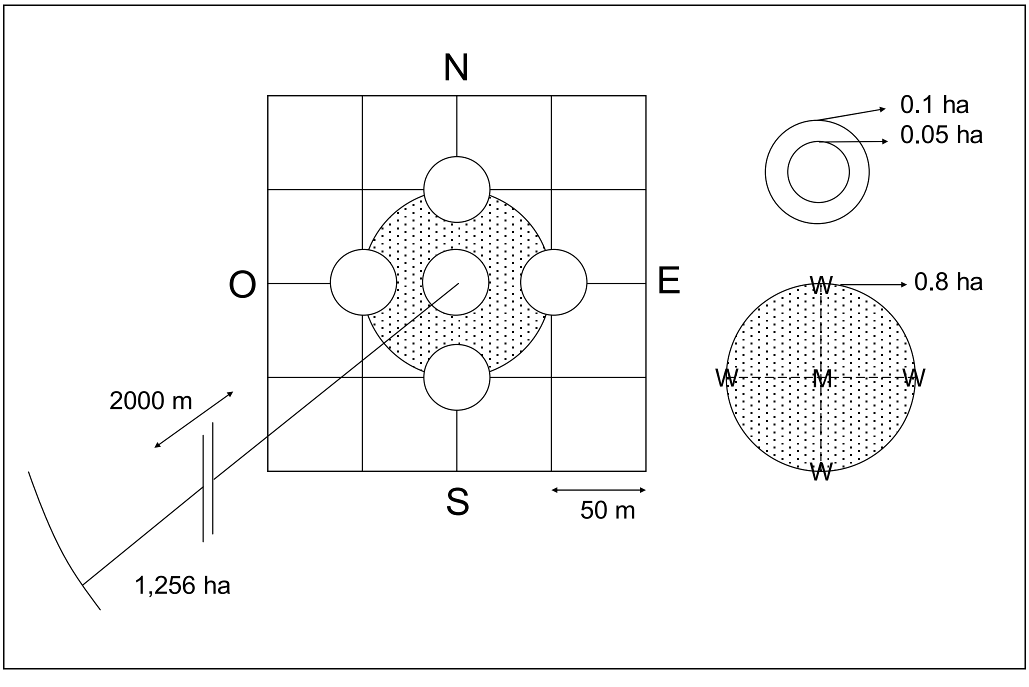

__Figure 4.__ Grid-based nested sample plots to characterise habitats.

In the 0.05 ha plots, we measured the volume of fallen branches with a diameter between 5 and 9 cm. We quantified the volume of standing living and dead trees with a girth at breast height between 16 and 125 cm. We also estimated the volume of logs showing a diameter at the smallest end between 10 and 40 cm. Larger living trees, snags, logs and fallen branches as well as stump volume and the number of tree species were measured in the 0.1 ha plots. The volume of living and recently dead trees was estimated from yield volume tables (Dagnelie et al. 1999), based on girth and height measurements. We applied the measurements guidelines developed by Harmon & Sexton (1996) to evaluate the volume of remaining woody debris. The volume of broken snags and stumps was calculated using a formula for a frustum of a cone: $V = H (A_b + (A_b A_t)^{0.5} + A_t)/3$, where H is the height, and A_b, A_t are the areas of the base and top. We used Newton's formula to evaluate log volume: $V = L (A_b + 4 A_m + A_t)/6$, where L is the length, and A_b, A_m, and A_t are the areas of the base, middle and end of the trunk. Fallen branch volume was derived from Huber's formula: $V = (\pi \times d^2/4) \times L$, where d is the middle diameter and L the length of the branch. Modified after Hunter (1990), four decay classes were used to describe the stage of wood decomposition of the different categories of woody debris. The first stage included snags, logs, branches and stumps with hard wood and intact bark cover and the second the substrates with bark partly loose. Wooden microhabitats in the third and fourth classes were both barkless, however with a friable wood texture in the last stage, leading to visible changes in their original shape.

We conducted a plant inventory and evaluated the bare soil, herb and tree layer covers in a 0.05 ha plot delimited from the centre of the 0.8 ha plot containing the insect traps (Appendix 7). An index of floral resources was built for each site by summing the respective cover of plants known to produce accessible amounts of pollen and nectar, among which *Crataegus laevigata* (Poir.) DC., *Crataegus monogyna* Jacq., *Frangula alnus* Mill., *Prunus avium* L., *Prunus spinosa* L., *Sorbus aucuparia* L., *Anemone nemorosa* L., *Angelica sylvestris* L., *Filipendula ulmaria* (L.) Maxim., *Hedera helix* L., *Hypericum pulchrum* L., *Potentilla reptans* sp., *Potentilla sterilis* (L.) Garcke, *Ranunculus ficaria* L., *Ranunculus repens* L., *Rubus idaeus* L., *Valeriana dioica* L., *Rosa* sp., *Rubus* sp., and *Taraxacum* sp.

We finally looked at landscape composition by calculating from satellite imaging and field mapping the amount of deciduous/coniferous/mixed forests and open fields (clear-cut, pasture, peatland, meadow) in a 1256 ha plot (2000 m radius) from the centre of the 0.8 ha insect sample plots (Fig. 4).

Overall, 37 variables were included as potential explanatory factors in the analyses (Table 2) (see Appendix 8 for the whole set of measured habitat variables). In those 16 stands where we surveyed the bird fauna, we also looked at the availability, characteristics and origin of tree cavities over 3 squared sample plots of 1 ha, centered on the bird point counts (300 m apart). The different measurements were carried out from 2002-2004.

Table 2. *List of measured explanatory variables, their description, mean values (± SE) and test values from paired-sample t-tests used to compare stands with high (n = 11) and low (n = 11) amount of coarse woody debris. Variables were transformed for normality (log + 1 for counts, arcsin-squareroot for percentages and proportions). Significant p-values in bold face, without Bonferroni correction. Minimum-Maximum values are given between arrows.*

Variable	Explanation	Unit	High cwd Mean ± SE	Low cwd Mean ± SE	t	*p*
Alt (115-600)	Altitude	m	408.08 ± 40.95	374.09± 37.01	2.645	**0.025**
Dec2000 (59.30-1042.60)	Amount of deciduous forests in 2000m-radius	ha	363.42 ± 91.72	304.84 ± 69.40	2.253	**0.048**
Con2000 (19.80-1025.20)	Amount of coniferous forests in 2000m-radius	ha	452.44 ± 90.09	494.43 ± 111.26	-0.374	0.716
Mix2000 (0.60-313.30)	Amount of mixed forests in 2000m-radius	ha	102.19 ± 35.99	60.06 ± 17.27	0.442	0.668
Ope2000 (16.20-758)	Amount of open land in 2000m-radius	ha	310.90 ± 50.17	341.21 ± 75.59	0.388	0.706
Cov_grd (0.5-5)	Bare soil cover	class^a	3.32 ± 0.48	2.32 ± 0.57	1.305	0.221
Cov_her (1-5)	Herbaceous plant cover	class^a	2.82 ± 0.40	3.18 ± 0.55	-0.231	0.822
Cov_flr (0-1.256)	Sum of flowering plant covers	%	0.28 ± 0.14	0.33 ± 0.14	-0.392	0.703
Cov_2 (0-3)	< 2m tree cover	class^a	0.96 ± 0.33	0.68 ± 0.19	0.599	0.563
Cov_2_8 (0-3)	2-8m tree cover	class^a	0.77 ± 0.25	0.77 ± 0.26	0.070	0.946
Cov_8_15 (0-4)	8-15m tree cover	class^a	1.59 ± 0.42	1.00 ± 0.22	1.109	0.293
Cov_15 (0.5-5)	> 15m tree cover	class^a	4.04 ± 0.43	4.09 ± 0.39	-0.400	0.698
Sp_herb (2-42)	No. of herbaceous plant species		13.09 ± 3.58	12.18 ± 3.41	0.567	0.583
Sp_tree (1-9)	No. of tree species		4.54 ± 0.58	4.82 ± 0.81	0.071	0.945
Bracan (0-774)	Amount of dead branches in canopy^b	no. ha^{-1}	235.64 ± 73.83	280.54 ± 87.52	-0.165	0.872
Cwd_sna (0-47.52)	Snag volume	m^3 ha^{-1}	28.40 ± 4.35	2.62 ± 0.87	5.597	**< 0.001**
Cwd_log (0-33.36)	Log volume	m^3 ha^{-1}	11.57 ± 4.00	0.98 ± 0.46	2.702	**0.022**
Cwd_lbr (0.72-73.40)	Volume of fallen large^c dead branches	m^3 ha^{-1}	10.40 ± 6.36	4.16 ± 1.67	1.898	0.087
Cwd_sbr (0.38-6.67)	Volume of fallen small^d dead branches	m^3 ha^{-1}	2.81 ± 0.46	1.75 ± 0.29	1.925	0.083
Cwd_grd (1.82-108.12)	Fallen dead wood volume^e	m^3 ha^{-1}	24.78 ± 9.12	6.89 ± 1.96	3.014	**0.013**
Cwd_stu (0.29-4.51)	Stump volume	m^3 ha^{-1}	2.14 ± 0.42	2.08 ± 0.18	-0.389	0.706
Cwd_tot (3.97-150.88)	Total dead wood volume^f	m^3 ha^{-1}	55.31 ± 10.35	11.60 ± 2.19	7.541	**< 0.001**
Cwd1_tot (0-25.31)	Dead wood volume in decay class 1^f	m^3 ha^{-1}	10.13 ± 3.13	0.89 ± 0.33	3.384	**0.007**
Cwd2_tot (0.65-76.36)	Dead wood volume in decay class 2^f	m^3 ha^{-1}	22.72 ± 6.39	5.63 ± 15.76	3.306	**0.008**
Cwd3_tot (0.79-45.50)	Dead wood volume in decay class 3^f	m^3 ha^{-1}	15.88 ± 4.29	3.05 ± 0.80	3.666	**0.004**
Cwd4_tot (0.57-24.27)	Dead wood volume in decay class 4^f	m^3 ha^{-1}	6.53 ± 1.93	2.08 ± 0.48	2.814	**0.018**

Tree_a40 (4-114)	Amount of living trees with dbh[g] ≥ 40cm	no. ha^{-1}	49.82 ± 8.72	53.27 ± 7.81	-0.121	0.906
Tree_b40 (36-1004)	Amount of living trees with 5cm ≤ dbh < 40cm	no. ha^{-1}	424.73 ± 89.06	309.82 ± 64.71	1.188	0.263
Tree40 (0.02-0.64)	Availability of living trees with dbh ≥ 40cm[h]		0.17 ± 0.06	0.20 ± 0.05	-0.503	0.626
Girt_a40 (136-267)	Mean girth of living trees with dbh ≥ 40cm[i]	cm	178.94 ± 10.84	173.36 ± 10.15	0.558	0.589
SG40 (1202-20358)	Summed girth of standing trees with dbh ≥ 40cm[i]	cm ha^{-1}	9005.00 ± 1630.52	10381.27 ± 1006.37	-1.377	0.199
SG60 (0-10494)	Summed girth of standing trees with dbh ≥ 60cm[i]	cm ha^{-1}	4268.73 ± 1144.52	4154.182 ± 1015.18	0.417	0.686
SG80 (0-6034)	Summed girth of standing trees with dbh ≥ 80cm[i]	cm ha^{-1}	1282.73 ± 545.18	1268.91 ± 396.77	-0.120	0.907
G (18.26-35.64)	Basal area of living trees	m^2 ha^{-1}	25.04 ± 1.45	25.90 ± 1.20	-0.423	0.681
G40 (1.46-29.76)	Basal area of living trees with dbh ≥ 40cm	m^2 ha^{-1}	13.88 ± 2.69	15.11 ± 1.72	-1.331	0.213
Gr_Fag (0-100)	Beech relative basal area	%	46.73 ± 12.40	48.47 ± 11.94	-0.865	0.407
Gr_Que (0-94.25)	Oak relative basal area	%	43.58 ± 10.88	44.21 ± 11.38	0.024	0.982

[a] 0 = 0%, 1 = 1-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, 5 = > 75%
[b] with a base diameter > 5 cm
[c] with a diameter ≥ 10 cm
[d] with 5 cm ≤ diameter < 10 cm
[e] Cwd_log + Cwd_lbr + Cwd_sbr
[f] Cwd_sna + Cwd_log + Cwd_lbr + Cwd_sbr + Cwd_stu
[g] diameter at breast height = 1.3m above ground level
[h] Tree_a40/(Tree_a40 + Tree_b40)
[i] measured at breast height

3.2. Sampling scheme

We conducted a validation test of our sampling scheme stratified by dead wood supply (high/low) using discriminant analyses. This allowed identifying the set of variables among the 37 included in the analyses that best explained the criteria applied when selecting the study sites. The importance of dead wood variables in separating sites classified as either with high or low amount of coarse woody debris was furthermore tested by comparing the mean values of the different variables between pair stands using paired-sample t-tests, followed by a sequential Bonferroni correction ($\alpha = 0.05$) to control for the error rate from multiple comparisons of means (Rice 1989) (Table 2).

On average, stands classified with a high and low amount of dead wood mostly differed in terms of their dead wood supply among the four decay classes, together with the altitude and the extent of native deciduous forests in the surrounding landscape (Table 2). After a Bonferroni correction, only the total amount of woody debris (Cwd_tot) and snag volume (Cwd_sna) were significant at the 0.05 level.

Table 3. *Results of Stepwise Discriminant Analysis showing the sets of environmental variables best explaining the criteria used for site selection. Significant effects (p < 0.05) are in bold-face print. See Table 2. for explanation of acronyms.*

Criteria	Value	Step no.	Variables entered	Variables removed	Partial R^{2a}	Model R^{2b}	*F*-value	*p*-value
Dead wood	High/Low	1	Cwd_tot		0.722	0.722	51.83	**< 0.001**
		2	Cwd_lbr		0.366	0.823	10.94	**0.004**
		3	Cov_2		0.114	0.844	2.32	0.145

[a] Proportion (%) of variance explained by the variables entered in the model.
[b] Total proportion (%) of variance explained by the model.

Accordingly, discriminant analyses revealed that, among the different environmental variables, the total volume of coarse woody debris (Cwd_tot) best separated the two stand categories ($p < 0.001$) (Table 3). On average, some 55 m^3 ha^{-1} of dead wood were present in those stands classified as those with a high dead wood supply, against 12 m^3 ha^{-1} in habitats with woody debris available in low amounts.

3.3. Factors explaining species number and abundance

3.3.1. Insects

Insects were subdivided into ecologically meaningful groups to facilitate further analyses. Besides a traditional grouping of species into families, they were categorised either according to their micro-habitats and diet preferences following Köhler (2000) or their conservation status from German Red-Lists (Tables 4, 5 & 6). Among saproxylic beetles, species were classified according to their propensity to live on polypores (polyporicole), inside the wood (lignicole), in or beneath the bark layer (corticole), and inside well-decomposed woody-debris (xylodetricticole). Species guilds based on dietary preferences included fungi-eaters (mycetophageous), wood-eaters (xylophageous), and predators (zoophageous).

The effect of dead wood supply on insect distribution was first tested by comparing species number and abundance between pair stands (11), whether with high or low amount of dead wood (1,2), with year as a confounding factor (1,2). Analysis of variance was performed according to a split-split plot design, with deadwood as a main plot factor and year as a subplot factor. Deadwood and year were considered as fixed effects, while pair and deadwood x pair effects were included as random factors in the model. Insects were yearly collected over the 22 study sites with 3 stump-emergence, 1 Malaise and 8 flight-window traps.

Table 4. Results of mixed-model ANOVA assessing differences in species richness (S) and abundance (A) among selected (most species-rich) insect families between stands (11 pairs) with high and low amount of coarse woody debris (cwd) (2002-2003).

Variable	Explanation	*n*	High cwd Mean ± SE	Low cwd Mean ± SE	Source of variation	Error df	*F*	*p*
Number of species								
S_Cer	Longhorn beetles (Cerambycidae)	29	10.45 ± 0.80	8.45 ± 0.97	Deadwood	12.889	4.358	0.057
					Year	29.173	0.032	0.859
					Deadwood * Year	29.173	0.515	0.479
S_Ela_s	Saproxylic click beetles (Elateridae)	16	6.18 ± 0.40	5.82 ± 0.54	Deadwood	30.143	0.689	0.413
					Year	33.904	5.755	**0.022**
					Deadwood * Year	33.904	0.284	0.597
S_Ela_ns	Non-saproxylic click beetles	21	8.91 ± 0.63	7.82 ± 0.32	Deadwood	0.489	0.507	0.684
					Year	38.074	7.576	**0.009**
					Deadwood * Year	38.074	1.700	0.200
S_Euc	Eucnemid beetles (Eucnemidae)	10	3.91 ± 0.42	3.73 ± 0.38	Deadwood	6.580	0.004	0.949
					Year	13.128	30.605	**< 0.001**
					Deadwood * Year	13.128	3.854	0.071
S_Mel	Melandryid beetles (Melandryidae)	10	3.00 ± 0.50	3.36 ± 0.45	Deadwood	12.609	0.053	0.822
					Year	53.041	0.929	0.339
					Deadwood * Year	53.041	0.50	0.824
S_Mon	Monotomid beetles (Monotomidae)	9	5.00 ± 0.49	4.64 ± 0.31	Deadwood	77.257	2.934	0.091
					Year	26.080	15.412	**0.001**
					Deadwood * Year	26.080	8.021	**0.009**
S_Sco	Bark beetles (Scolytidae)[a]	16	7.64 ± 0.47	7.82 ± 0.78	Deadwood	1.423	0.291	0.662
					Year	21.441	0.147	0.705
					Deadwood * Year	21.441	0.409	0.529
S_Syr_s	Saproxylic hoverflies (Syrphidae)[b]	27	8.64 ± 1.13	6.27 ± 0.83	Deadwood	45.366	2.447	0.125
					Year	51.032	10.363	**0.002**
					Deadwood * Year	51.032	1.703	0.198
S_Syr_ns	Non-saproxylic hoverflies	79	27.36 ± 2.79	18.54 ± 1.58	Deadwood	0.866	13.140	0.201
					Year	7.838	18.265	**0.003**
					Deadwood * Year	7.838	0.650	0.444
Number of individuals								
A_Cer	Longhorn beetles	1545	88.36 ± 28.30	52.09 ± 19.62	Deadwood	17.461	3.208	0.091
					Year	7.994	1.938	0.201
					Deadwood * Year	7.994	0.143	0.715
A_Ela_s	Saproxylic click beetles	1326	67.55 ± 12.72	53.00 ± 11.65	Deadwood	8.559	1.519	0.250
					Year	18.845	2.406	0.137
					Deadwood * Year	18.845	0.244	0.627
A_Ela_ns	Non-saproxylic click beetles	11167	490.46 ± 89.95	524.73 ± 111.83	Deadwood	14.082	0.001	0.979
					Year	2.223	0.167	0.719
					Deadwood * Year	2.223	0.439	0.570

A_Euc	Eucnemid beetles	262	11.91 ± 2.71	11.91 ± 2.70	Deadwood	31.655	0.168	0.684
					Year	39.766	49.519	**< 0.001**
					Deadwood * Year	39.766	1.004	0.322
A_Mel	Melandryid beetles	201	10.36 ± 2.45	7.91 ± 1.45	Deadwood	12.591	1.028	0.330
					Year	49.311	3.932	0.053
					Deadwood * Year	49.311	0.215	0.645
A_Mon	Monotomid beetles	2496	123.55 ± 28.11	103.36 ± 18.14	Deadwood	36.215	2.161	0.150
					Year	28.285	97.746	**< 0.001**
					Deadwood * Year	28.285	12.797	**0.001**
A_Sco	Bark beetles[a]	7022	374.27 ± 58.39	264.09 ± 95.42	Deadwood	14.502	5.067	**0.040**
					Year	50.921	3.431	0.070
					Deadwood * Year	50.921	1.396	0.243
A_Syr_s	Saproxylic hoverflies[b]	747	35.09 ± 7.67	32.82 ± 13.59	Deadwood	25.589	0.925	0.345
					Year	30.781	9.682	**0.004**
					Deadwood * Year	30.781	0.912	0.347
A_Syr_ns	Non-saproxylic hoverflies	2273	142.64 ± 30.67	64.00 ± 12.53	Deadwood	32.625	10.044	**0.003**
					Year	12.717	30.594	**< 0.001**
					Deadwood * Year	12.717	4.673	0.050

[a] only species living on broad-leaved trees, [b] includes species with larvae living in trunk cavities, rot-holes, insect workings, sap runs, under loose bark and on snags, logs, stumps and rotting tree roots.

Deadwood, year and their interaction were entered into the model as fixed effects and pair and deadwood x pair as random effects. Variables were log-transformed +1 for normality, if necessary. Sample sizes (n) and mean values (± SE) are added, with significant effects ($p < 0.05$) in bold-face print. Insects were yearly collected with 3 stump-emergence, 1 Malaise and 8 flight-window traps.

When comparing insect data among most-species-rich families between stand pairs, dead wood was found to have a close to or significant positive impact on the species richness of longhorn and monotomid beetles and on the abundance of longhorn and bark beetles and non-saproxylic hoverflies (Table 4). Moreover, difference in dead wood explained variation in the number of monotomid species and individuals, depending on the year (a significant year x deadwood interaction). For most families, significant variation in species richness and abundance was apparent between years, independently of the dead wood supply.

If the beetle data were analysed as a function of the species habitat and diet profiles, we found dead wood to have a close to or significant positive impact on the abundance of saproxylic beetles, including the number of wood-living, mycetophageous and xylophageous beetles (Table 5). A positive effect was also found for bark-living and predatory species, depending on the year. On the other hand, dead wood did not have any effect on the beetle species richness, whether saproxylic or not.

Also, neither the number of threatened species nor individuals varied significantly with the dead wood supply, despite most of the species (91%) being saproxylic (Table 6).

Another option to analyse the data in a way to disentangle dead wood from year effects was to carry on a GLM repeated measures ANOVA limited to those 11 stands rich in dead wood and use the extra information provided by trunk-window traps (a sampling device more efficient in catching rare and threatened saproxylic beetles than normal freely-hanging flight-window traps, Martikainen 2000). Among major findings, and as shown in our mixed models, we found that dead wood increased bark beetle abundance and more generally on the abundance of saproxylic beetles among which wood-living and mycetophageous beetles, although depending on the year (Appendices 12 & 13). From a species number point of view, only xylodetriticolous beetles showed a positive response, depending also on the year. But like in the mixed ANOVA procedure, we found that dead wood did not explain significant variation in the number of threatened insect species and individuals (Appendix 14).

Because of high between-year variation in insect captures, one way to improve the statistical power of our analyses was to sum up the number of species and individuals collected over the two sampling years (2002 + 2003). Using paired-sample t-tests to compare insect numbers between stand pairs, the number of saproxylic click beetles and of bark beetles was higher in stands classified as rich in

Table 5. Results of mixed-model ANOVA assessing differences in species richness (S) and abundance (A) of beetles[a] between stands (11 pairs) with high and low amount of coarse woody debris (cwd) (2002-2003). Saproxylic species are categorised either according to their micro-habitats or diet preferences following Köhler (2000).

Variable	Explanation	*n*	High cwd Mean ± SE	Low cwd Mean ± SE	Source of variation	Error df	*F*	*p*
Number of species								
S_be_s	Saproxylic beetles[b]	142	50.18 ± 2.53	47.64 ± 3.03	Deadwood	37.684	1.858	0.181
					Year	19.450	0.241	0.629
					Deadwood * Year	19.450	0.010	0.923
S_be_ns	Non-saproxylic beetles	41	12.36 ± 0.72	11.00 ± 0.63	Deadwood	85.820	0.443	0.508
					Year	41.513	0.053	0.820
					Deadwood * Year	41.513	1.317	0.258
S_Poly	Beetles living on polypores[b]	16	3.55 ± 0.73	2.82 ± 0.40	Deadwood	22.517	1.254	0.275
					Year	57.016	0.288	0.593
					Deadwood * Year	57.016	0.177	0.676
S_Lign	Wood-living beetles	56	22.36 ± 1.43	20.27 ± 1.11	Deadwood	2.896	3.014	0.184
					Year	26.881	7.152	**0.013**
					Deadwood * Year	26.881	1.947	0.174
S_Cort	Bark-living beetles	46	16.82 ± 1.21	17.09 ± 1.43	Deadwood	0.423	0.215	0.785
					Year	17.803	0.488	0.494
					Deadwood * Year	17.803	3.919	0.063
S_Xdet	Xylodetriticolous beetles	21	6.27 ± 0.52	6.18 ± 0.78	Deadwood	32.201	0.472	0.497
					Year	20.809	3.907	0.061
					Deadwood * Year	20.809	0.124	0.728
S_Mage	Mycetophageous beetles[b] (fungi-eaters)	53	19.91 ± 1.27	19.45 ± 0.95	Deadwood	9.760	1.262	0.288
					Year	35.542	21.666	**< 0.001**
					Deadwood * Year	35.542	2.279	0.140
S_Xage	Xylophageous beetles (wood-eaters)	86	32.55 ± 1.81	31.00 ± 2.01	Deadwood	24.663	1.602	0.217
					Year	25.261	5.553	**0.027**
					Deadwood * Year	25.261	0.033	0.858
S_Zage	Zoophageous beetles (predators)	37	12.55 ± 1.08	12.36 ± 1.09	Deadwood	18.988	0.761	0.394
					Year	16.891	26.216	**< 0.001**
					Deadwood * Year	16.891	2.130	0.163
Number of individuals								
A_be_s	Saproxylic beetles[c]	16772	891.82 ± 143.05	632.91 ± 109.07	Deadwood	32.245	3.629	0.066
					Year	50.123	0.250	0.619
					Deadwood * Year	50.123	0.329	0.569
A_be_ns	Non-saproxylic beetles	11424	535.64 ± 110.80	502.91 ± 91.63	Deadwood	19.326	0.000	0.996
					Year	3.408	0.377	0.578
					Deadwood * Year	3.408	0.285	0.626
A_Poly	Beetles living on polypores[c]	369	19.09 ± 4.13	14.45 ± 2.27	Deadwood	33.014	0.858	0.361

					Year	56.754	2.994	0.089
					Deadwood * Year	56.754	0.375	0.543
A_Lign	Wood-living beetles	8393	446.73 ± 74.91	316.27 ± 111.26	Deadwood	20.519	9.930	**0.005**
					Year	35.959	3.755	0.061
					Deadwood * Year	35.959	2.393	0.131
A_Cort	Bark-living beetles	6527	356.09 ± 107.26	237.27 ± 23.36	Deadwood	3.140	1.156	0.358
					Year	58.238	2.398	0.127
					Deadwood * Year	58.238	5.735	**0.020**
A_Xdet	Xylodetriticolous beetles	1335	67.55 ± 12.99	53.82 ± 10.79	Deadwood	6.819	1.418	0.274
					Year	17.122	0.006	0.940
					Deadwood * Year	17.122	0.183	0.674
A_Mage	Mycetophageous beetles[c]	10112	546.46 ± 98.65	372.82 ± 90.23	Deadwood	29.050	3.297	0.080
					Year	82.084	13.288	**< 0.001**
					Deadwood * Year	82.084	1.207	0.275
A_Xage	Xylophageous beetles	7508	419.55 ± 99.17	263.00 ± 39.62	Deadwood	9.909	4.984	0.050
					Year	33.326	7.124	**0.012**
					Deadwood * Year	33.326	0.775	0.385
A_Zage	Zoophageous beetles	3652	179.27 ± 26.79	152.73 ± 17.50	Deadwood	29.293	1.397	0.247
					Year	29.636	73.092	**< 0.001**
					Deadwood * Year	29.636	7.322	**0.011**

[a]without Curculionidae, identified at species-level only in 2002, [b] without Cisidae, not identified at species-level, [c] with Cisidae

Deadwood, year and their interaction were entered into the model as fixed effects and pair and deadwood x pair as random effects. Variables were log-transformed +1 for normality, if necessary. Sample sizes (*n*) and mean values (± SE) are added, with significant effects ($p < 0.05$) in bold-face print. Insects were yearly collected with 3 stump-emergence, 1 Malaise and 8 flight-window traps.

Table 6. Results of mixed-model ANOVA assessing differences in species richness (S) and abundance (A) of threatened insects (beetles[a] + hoverflies from German Red-Lists) between stands (11 pairs) with high and low amount of coarse woody debris (cwd) (2002-2003).

Variable	Explanation	*n*	High cwd Mean ± SE	Low cwd Mean ± SE	Source of variation	Error df	*F*	*p*
Number of species								
S_rl	Red-listed species	43	9.27 ± 0.95	8.00 ± 1.00	Deadwood	3.938	1.299	0.319
					Year	34.126	0.505	0.482
					Deadwood * Year	34.126	1.246	0.272
S_rl_s	Red-listed saproxylic species	39	8.55 ± 1.03	8.00 ± 1.00	Deadwood	16.078	0.036	0.851
					Year	15.434	0.045	0.834
					Deadwood * Year	15.434	0.896	0.358
Number of individuals								
A_rl	Red-listed individuals	577	27.46 ± 5.76	25.00 ± 5.71	Deadwood	25.857	0.209	0.651
					Year	20.549	0.508	0.484
					Deadwood * Year	20.549	0.093	0.764
A_rl_s	Red-listed saproxylic individuals	568	26.64 ± 5.83	25.00 ± 5.71	Deadwood	36.323	0.038	0.847
					Year	23.315	0.593	0.449
					Deadwood * Year	23.315	0.060	0.809

[a] without Curculionidae, identified at species-level only in 2002.

Deadwood, year and their interaction were entered into the model as fixed effects and pair and deadwood x pair as random effects. Variables were log-transformed +1 for normality, if necessary. Sample sizes (*n*) and mean values (± SE) are added. Insects were yearly collected with 3 stump-emergence, 1 Malaise and 8 flight-window traps.

dead wood (Appendix 15), and so were the abundance of xylodetriticolous beetles (97% of saproxylic click beetles) and wood-living beetles (71% of bark beetles) (Appendix 16). In particular, among the bark beetles, the abundance of the potentially most damaging ambrosia beetle *Trypodendron domesticum* was significantly higher in stands with dead wood (t = 2.731, p = 0.021). Of the selected families, only non-saproxylic syrphid assemblages were more species-diversified in the presence of dead wood. Most probably, those stands contained also unmeasured habitat resources and conditions that are important for the non-saproxylic community, such as abundant aphid populations or aquatic microhabitats (Dusek & Laska 1986, Speight et al. 2004). And again, there was no effect of the dead wood supply on the species richness and abundance of threatened insects (Appendix 17).

If focusing solely on those stands rich in dead wood (+ trunk-window traps), and if we compared average numbers of species and individuals between stands with a dead wood volume above and below 50 m^3 ha^{-1}, there were no clear trends among selected families (Appendix 18). At the very most, saproxylic click beetles and eucnemid beetles were close to significantly more numerous above 50 m^3 ha^{-1}. Interestingly, neither the abundance of bark beetles nor the quantity of other saproxylic beetles, whether they were fungi-, bark- or wood-living and -foraging organisms, differed between site categories (Appendices 18 & 19). The same pattern hold for the ambrosia bark beetles like *T. domesticum* (ANOVA, $F_{1,9}$ = 0.713, p = 0.420). A lack of responses from threatened insects supported earlier results (Appendix 20).

Another way to achieve higher statistical power was to consider each year as a replicate, allowing us to double our site sample size (44 instead of 22). By doing this and comparing again insect numbers between stand pairs (22 pairs), we found that sites classified with a high dead wood supply hosted more species of longhorn beetles and more individuals of saproxylic beetles such as longhorn, click, monotomid and bark beetles (Appendix 21). Among functional groups, species richness in saproxylic beetles and in particular wood-living beetles was close to or significantly higher in stands with dead wood, respectively (Appendix 22). Moreover, the abundance of saproxylic beetles was markedly (significantly or close to) higher in the presence of dead wood, whether they were living on polypores, inside the wood and in well-decomposed woody debris, or feeding on fungi, wood or animal resources (Appendix 22). By contrast, the lack of eventual relationships between the number of threatened insect species and individuals and dead wood supply remained, including saproxylic species (Appendix 23).

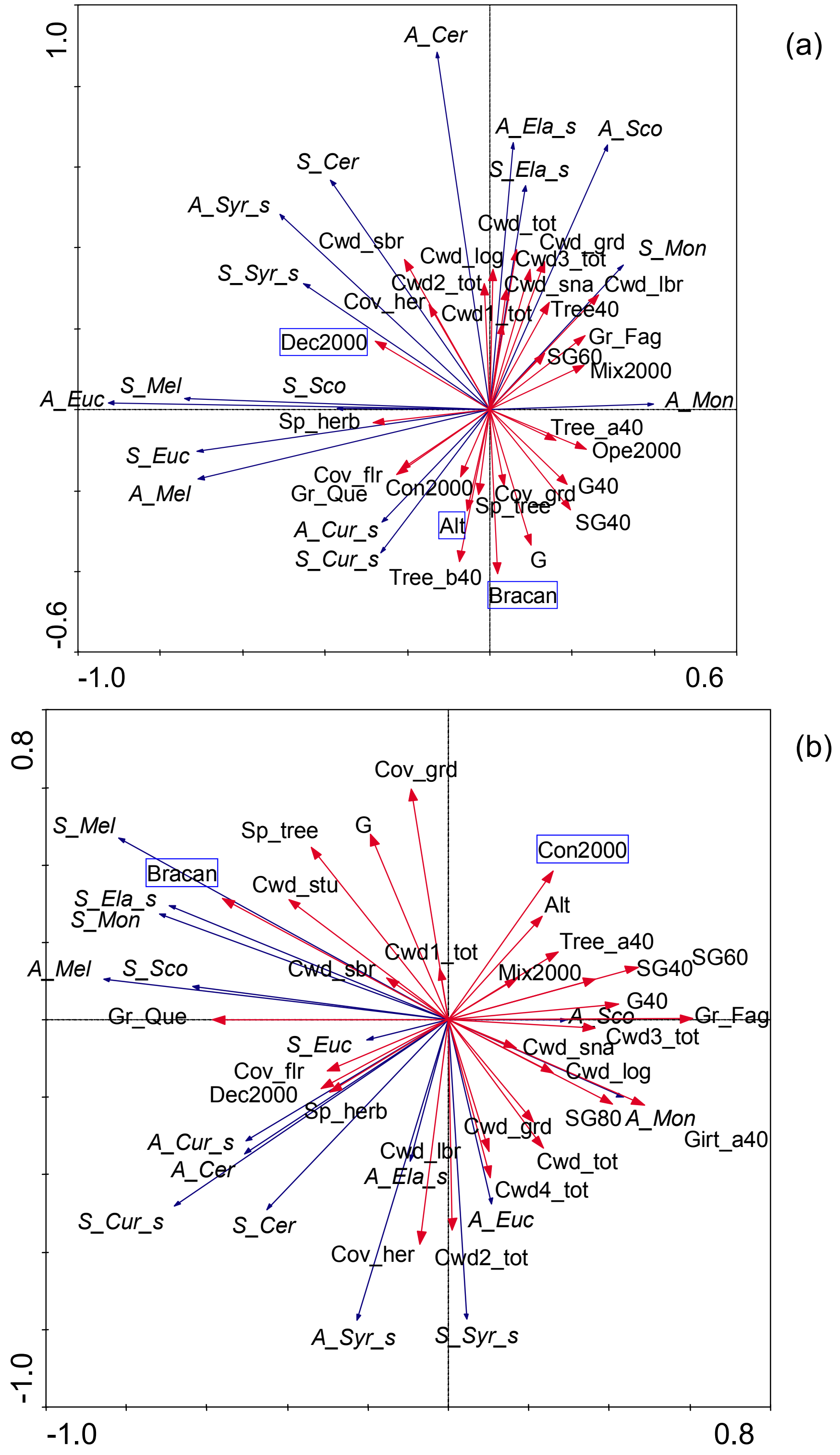

Figure 5. *pRDA-ordination of saproxylic insect family (Cerambycidae, Curculionidae, Elateridae, Eucnemidae, Melandryidae, Monotomidae, Scolytidae, Syrphidae) and environmental descriptors plotted in the plane determined by the first two principal axes. The dependent variables, measured (a) over all the study sites or (b) only in sites rich in dead wood, are shown in italic; the significant explanatory variables identified by forward selection after controlling for regional effect are framed. See Tables 2 and 4 for explanation of acronyms. Variance partitioning is given in Appendix 32.*

Comparing insects numbers (species and individuals) between stands rich in dead wood (+ trunk-window traps, year as a replicate), to see whether they may differ between stands with high (> 50 m^3 ha^{-1}) vs. moderate (< 50 m^3 ha^{-1}) amount of dead wood, only the number of eucnemid and monotomid beetle species changed significantly, although being higher below 50 m^3 ha^{-1} (Appendix 24). Looking at the number of individuals, only saproxylic click beetles increased in numbers at higher dead wood volume (Appendix 24). Accordingly, among saproxylic guilds, only the beetles classified as xylodetriticolous (including 95% of saproxylic click beetles) were more numerous in those stands with the higher dead wood supply (Appendix 25). The number of threatened species and individuals did not change between stand categories (Appendix 26).

We then performed stepwise multiple regression analyses to identify which among those 37 environmental variables we measured (Table 2) may also contribute to explain significant variation in local species richness and abundance, such as the altitude, local vegetation structure and composition, landscape quality and the availability of critical resources (nectar and pollen, dead wood, large trees). Separate analyses were carried out for all the 22 study sites and for those 11 sites classified as rich in dead wood, after pooling together the insect data collected over the two study years (Appendices 27-31). This approach was complemented by direct gradient analysis techniques (partial Redundancy Analyses) in order to clarify relationships between variables and calculate the proportion of variation of our biological data set (species richness and abundance) that is explained by a set of independent environmental variables once the effect of spatial structure (here the region) taken into account. Explanatory variables were expected to differ from one family to another, or from one guild to another, due to large variation in species-specific habitat requirements and life-histories (see Fig. 5).

Looking at longhorn beetles and saproxylic hoverflies for example, we found the two species groups to respond to different sets of local environmental conditions, despite a similar interest in wooden substrates for reproduction. While stands dominated by oaks with a high dead wood volume (log, snag) were highly favoured by longhorn beetles, saproxylic and threatened syrphids were limited to open-stands with large trees and a well-developed and species rich herb layer providing the floral resources required for their reproduction (Fayt et al. 2006).

Among families, multiple regressions revealed for instance a positive impact of large-diameter tree (SG80) and dead wood availability on local bark beetle abundance (Appendix 28). This was confirmed by ordination analyses (Fig. 6a). However, if only considering the stands with dead wood (half of the sites), the bark beetle population size benefited rather from the presence of large trees (Fig. 6b).

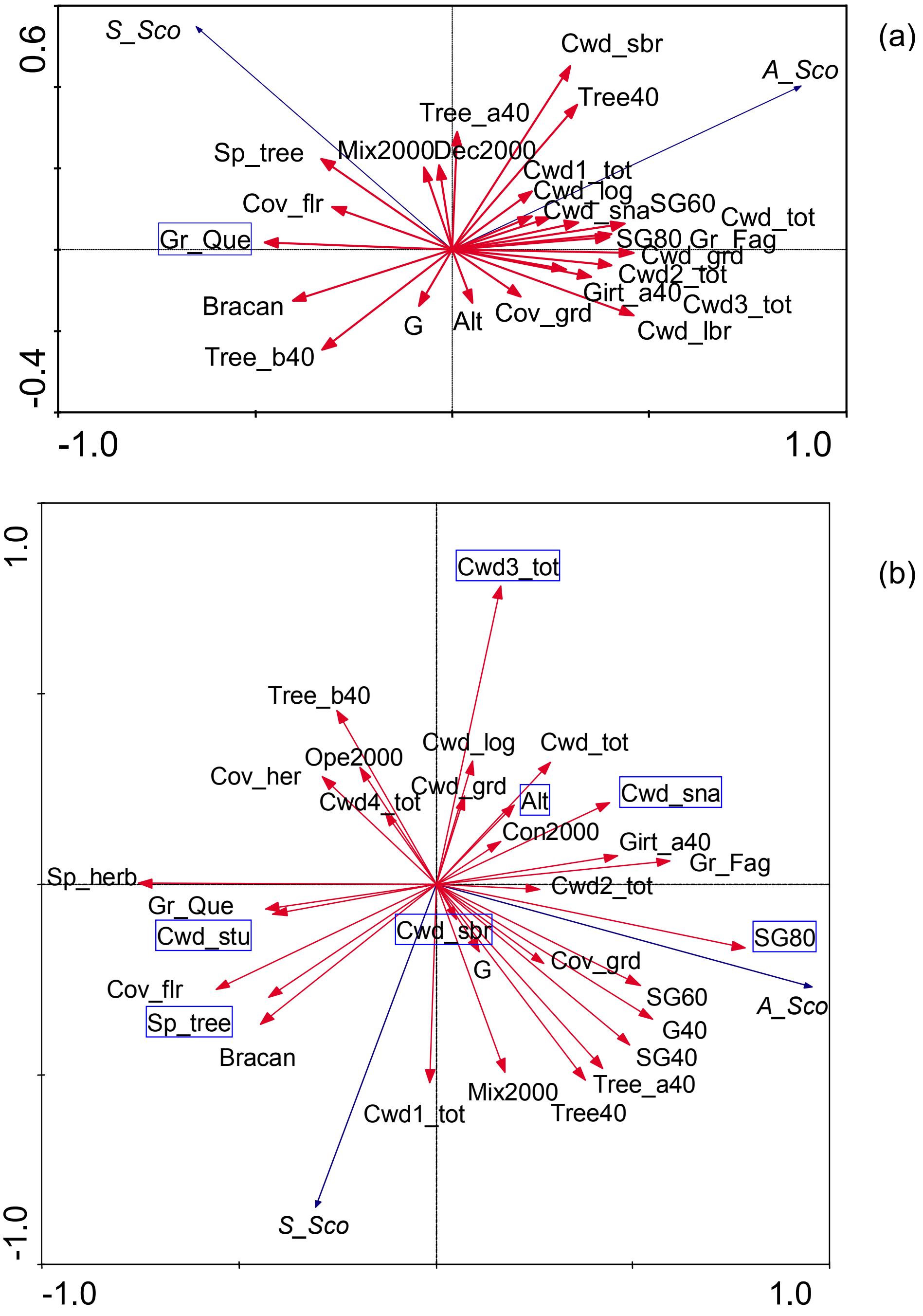

Figure 6. *pRDA-ordination of bark beetle and environmental descriptors plotted in the plane determined by the first two principal axes. The dependent variables, measured (a) over all the study sites or (b) only in sites rich in dead wood, are shown in italic; the significant explanatory variables identified by forward selection after controlling for regional effect are framed. See Tables 2 and 4 for explanation of acronyms.*

From a tree composition point of view, on the other hand, beech-dominated stands, with fewer tree species and the largest trees available, were more susceptible to host large numbers of bark beetles. So, perhaps the insects were more abundant in the monospecific beech stands due to a concentration of resources rather than a tree size effect per se. But this study was carried out at the end of a massive outbreak of *T. domesticum*, which could also explain high population levels in beech forests. Inversely, the number of bark beetle species was especially high in oak-dominated stands with numerous tree species and plenty of large dead branches in the canopy (Fig. 5 & 6) (Appendix 27).

Overall, the number of saproxylic beetle species and individuals was positively influenced by the dominant tree species (oak), tree size, various dead wood supply estimates, the number of tree species, or stand openness (herb cover), depending on functional groups (Appendices 29 & 30). In general, saproxylic species richness benefited more from the presence of numerous trees species dominated by oaks and stand openness (i.e., with a well-developed and species rich herb layer providing abundant floral resources), while beetle abundance was rather a function of beech dominance (and in turn tree size) and dead wood supply (total and fallen) (Fig. 7).

But eventually one of the most important findings of our research was that, besides insect responses to local stand-level habitat characteristics, the composition of the surrounding landscape had a major influence on the saproxylic species assemblages of our studied deciduous forest remnants (Appendices 27-30). Low numbers of saproxylic species and individuals were associated with stands embedded in conifer-dominated forest landscapes (high Con2000) (Fig. 7), even though woody debris or large trees were present. Conversely, the extent of deciduous tree cover in the surrounding (Dec2000) had a substantial positive impact on local species number and abundance, whether they were bark-, wood-, and polypore-visitors, or relying upon fungi, wood, or other insects for food (Fig. 7). Accordingly, we found that the amount of deciduous or coniferous forest in the surrounding matrix explained most of the saproxylic species variance, with either Dec2000 or Con2000 being the first variable to be selected in our explanatory models by a manual forward selection procedure (Appendix 32). Even more, our two descriptors of landscape composition were the only variables to account for variation in the number and abundance of threatened species (Appendix 31); they explained most of the variation in our threatened insect data set (Appendix 32) (Fig. 8).

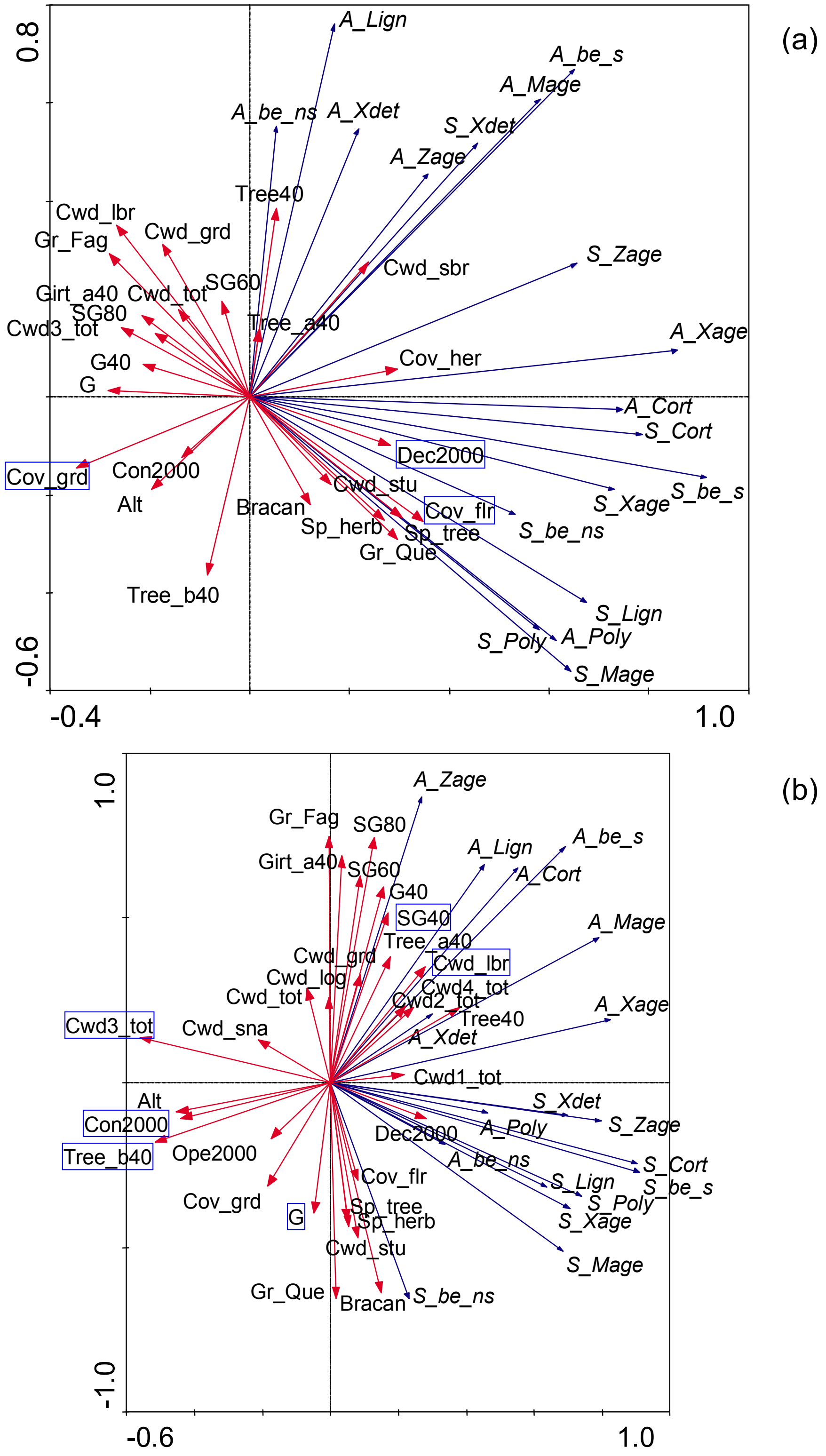

Figure 7. *pRDA-ordination of beetle and environmental descriptors plotted in the plane determined by the first two principal axes. The dependent variables, measured (a) over all the study sites or (b) only in sites rich in dead wood, are shown in italic; the significant explanatory variables identified by forward selection after controlling for regional effect are framed. See Tables 2 and 5 for explanation of acronyms. Variance partitioning is in given Appendix 32.*

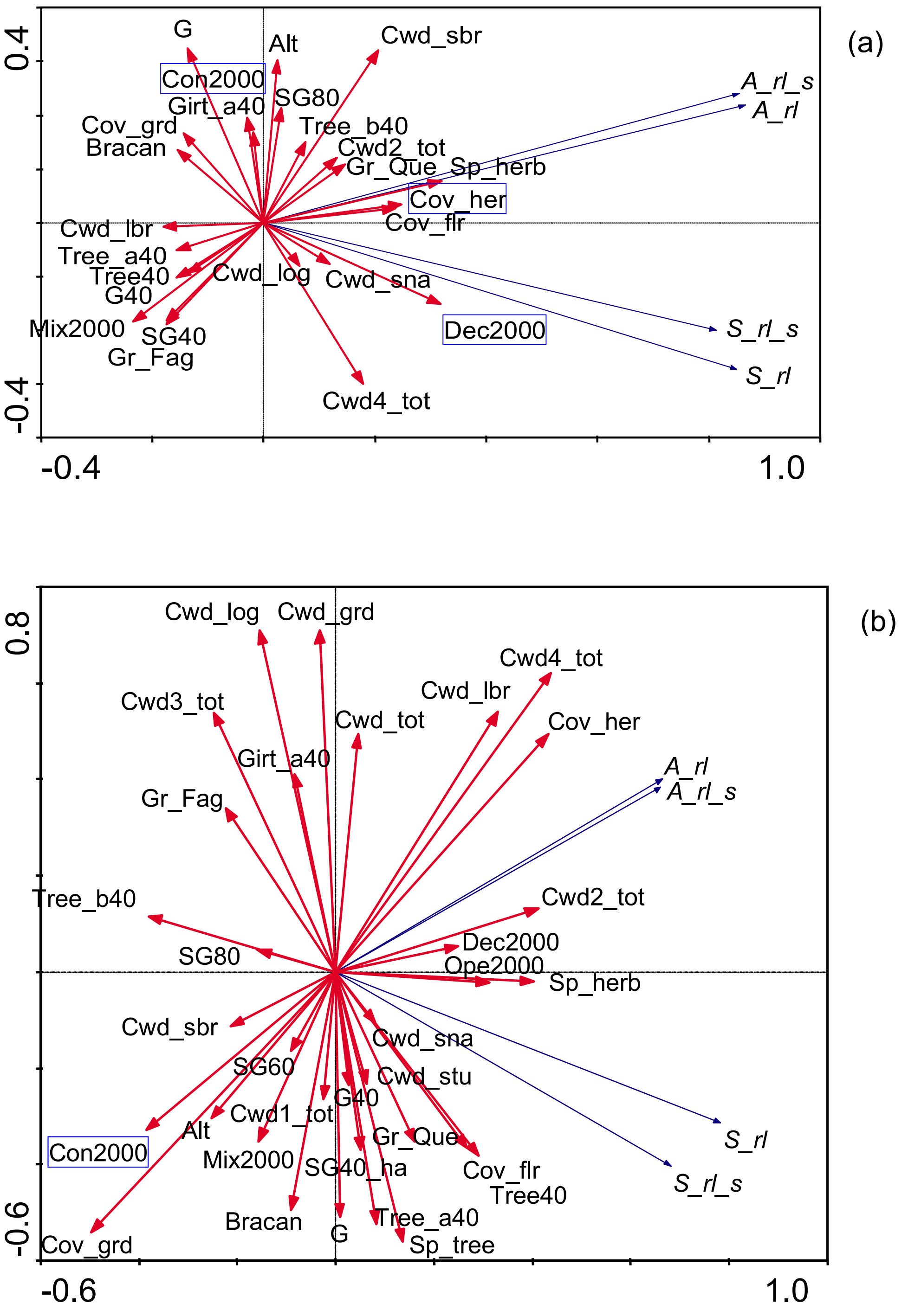

Figure 8. *pRDA-ordination of threatened insect and environmental descriptors plotted in the plane determined by the first two principal axes. The dependent variables, measured (a) over all the study sites or (b) only in sites rich in dead wood, are shown in italic; the significant explanatory variables identified by forward selection after controlling for regional effect are framed. See Tables 2 and 6 for explanation of acronyms. Variance partitioning is given in Appendix 32.*

3.3.2. Wood-decaying fungi

A total of 174 wood-living fungi were inventoried in our 10 beech study plots, among which 147 in a systematic way (Appendix 9). They included 39 species of polypores and 8 species known to indicate high level of forest naturalness for the BENELUX (Walleyn et al. 2004, Walleyn & Veerkamp 2005).

Stands were organised by pair, with half of them being well provided with dead wood. Paired-sample t-tests indicated a significantly higher number of species, including polypores and indicator species, in stands classified as rich in dead wood (Table 7).

***Table 7.** Number of wood-living fungi species (S) between paired-beech stands with high and low amount of coarse woody debris (cwd), including polypores (pol) and species with high indicator value for forest biodiversity in BENELUX (BNL). See Appendix 9 for species details.*

Variable	Explanation	High cwd (5 stands) Mean ± SE	Low cwd (5 stands) Mean ± SE	t	*df*	*p*
S_all	All species	68.40 ± 8.87	24.60 ± 4.17	6.072	4	**0.004**
S_pol	Polypores	17.20 ± 1.32	7.40 ± 1.33	7.897	4	**0.001**
S_BNL	Indicator species BENELUX	3.80 ± 1.07	1.20 ± 0.37	3.079	4	**0.037**

Variables were log-transformed +1 for normality, if necessary. Sample sizes (*n*) and mean values (± SE) are added, with significant effects ($p < 0.05$) from paired-sample t-tests in bold-face print.

The importance of dead wood in explaining diverse saproxylic fungi communities was confirmed by multiple regressions, with the total volume of dead wood (Cwd_tot) being the first variable to enter the models (Table 8).

***Table 8.** Results of stepwise multiple regression analyses showing the sets of environmental variables that explain significant variation in the number of wood-living fungi species in beech forests, including polypores and species with high indicator value for forest biodiversity in BENELUX. See Table 2 for explanation of acronyms.*

Step	Variables entered	Partial R^{2a}	Model R^{2b}	*F*	*p*	Effect
All species						
1	Cwd_tot	0.889	0.889	64.18	< 0.001	+
2	Alt	0.065	0.954	10.06	0.016	-
Polypores						
1	Cwd_tot	0.847	0.847	44.15	< 0.001	+
2	Bracan	0.085	0.932	8.81	0.021	-
Indicator species BENELUX						
1	Cwd_tot	0.628	0.628	13.51	0.006	+
2	Gr_Fag	0.304	0.932	31.15	< 0.001	+
3	Cwd4_tot	0.037	0.969	7.20	0.036	+

[a] Proportion (%) of variance explained by the variables entered in the model, [b] Total proportion (%) of variance explained by the model.

Variables were transformed for normality (log + 1 for counts, arcsin-squareroot for percentages and proportions).

Accordingly, partial RDA analyses revealed that the total explained variance of the biological data was 86.4% (!), of which 85.3% was explained by (in order of selection) the total volume of dead wood (Cwd_tot) and the number of large dead branches in the canopy (Bracan) (Fig. 9). Spatial structuring of the data not attributable to the environmental variables accounted for only 1% of the total variance, indicating no fundamental spatial structuring process has been missed. The remaining 0.1% was explained by the interaction between the biological data, the environment and spatial structuring (regional effect).

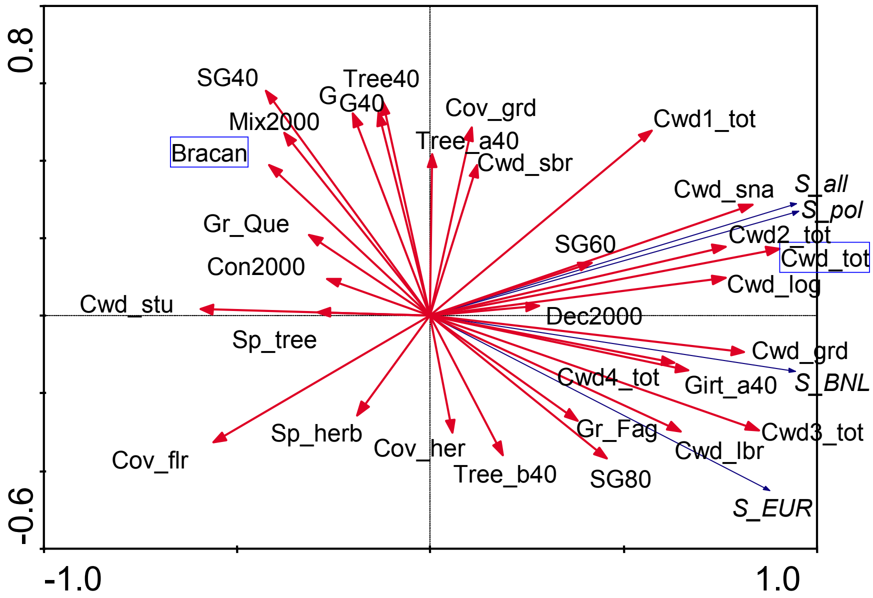

Figure 9. *pRDA-ordination plot, with fungi diversity descriptors shown in italic and the significant explanatory variables (identified by forward selection after controlling for regional effect) within a frame. See Tables 2 and 7 for explanation of acronyms.*

Among the fungi, indicator species favoured stands with a large amount of well-decomposed woody debris (Cw3_tot, Cwd4_tot) (Table 8, Fig. 9), supporting their high indicator value for habitat continuity.

3.3.3. Forest birds

Overall 46 bird species were contacted over the two natural regions inventoried (Hertogenwald and Lorraine). The hole-nesting species were classified into different guilds according to their mode of cavity acquisition, whether they excavate their own nest (primary cavity nesters) or not (secondary cavity nesters). They included 6 woodpecker and 14 secondary cavity-nesting species (Appendix 10). In addition to “traditional” habitat measurements (Table 2), we also related bird counts to the availability of woodpecker-made cavities (Woodpcav) vs. tree cavities created by stem decay (Fungicav), as well as to estimates of food abundance – no. of individual beetles (A_col) – and diversity – no. of beetle species (S_col) and families (F_col). Because of its influence on prey availability, we splitted the number of tree species into native (Sp_treen) and exotic tree species (Sp_treee), and into deciduous (Sp_treed) and coniferous tree species (Sp_treec). The 16 study sites were oganised by pair, with half of them being classified as rich in dead wood.

Table 9. *Bird species number (S) and density (D) between paired-stands with high and low amount of coarse woody debris (cwd). See Appendix 10 for species details.*

Variable	Explanation	High cwd (8 stands) Mean ± SE	Low cwd (8 stands) Mean ± SE	t	*df*	*p*
Species richness						
S_pcn	Primary[a] cavity-nesters	3.50 ± 0.50	2.75 ± 0.37	1.655	7	0.142
S_scn	Secondary[b] cavity-nesters	9.25 ± 0.31	7.37 ± 0.42	2.813	7	**0.026**
S_ncn	Non-cavity nesters	14.50 ± 0.57	13.75 ± 0.75	0.887	7	0.405
S_tot	Total bird community	27.25 ± 0.70	23.87 ± 1.22	2.388	7	**0.048**
Density (pairs/ha)						
D_pcn	Primary[a] cavity-nesters	0.06 ± 0.01	0.04 ± 0.01	2.503	7	**0.041**
D_scn	Secondary[b] cavity-nesters	8.24 ± 0.54	5.61 ± 1.00	3.639	7	**0.008**
D_ncn	Non-cavity nesters	9.22 ± 0.40	7.65 ± 0.49	4.366	7	**0.003**
D_tot	Total bird community	17.51 ± 0.82	13.31 ± 1.41	4.312	7	**0.004**

[a] cavity excavators (woodpeckers), [b] non-excavating hole-nesting species.

Variables were log-transformed +1 for normality, if necessary. Sample sizes (*n*) and mean values (± SE) are added, with significant effects ($p < 0.05$) from paired-sample t-tests in bold-face print.

Looking at species richness, we found the total number of bird species higher in stands with dead wood (Table 9). Among cavity-nesting birds, only secondary species were significantly more numerous in the presence of dead wood. Bird densities, on the other hand, clearly benefited from the dead wood supply (Table 9).

The only variables that were correlated with the number of woodpecker species (S_pcn) once controlling for the spatial structure (region) of the data (partial correlative tests, $p < 0.05$) were the number of (native) tree species (Sp_tree, Sp_treen) and beetle families (F_col) (Fayt et al. 2005) (Appendix 33, Fig. 10). Importantly, the number of beetle families was, in turn, correlated with the number of native deciduous tree species, but was not with the number of exotic trees (Sp_treee), including conifers (Sp_treec) (Fig. 10). High woodpecker abundance (D_pcn) was associated with high snag and total dead wood volume (Cwd_sna, Cwd_tot), and in particular the availability of woody substrates with bark partly loose (Cwd2_tot).

Species richness in secondary cavity-nesting birds (S_scn) was (positively) correlated with snag volume, the total volume of dead wood in an advanced stage of decay (Cwd4_tot), and the availability of woodpecker-made cavities (Woodpcav) (Fig. 10). Similarly, their density (D_scn) was a function of snag volume, woodpecker cavities and total dead wood volume (Appendix 33).

The number of non-cavity nesting species increased with the different estimates of food supply (F_col, S_col, A_col), their density with the availability of woodpecker cavities (Fig. 10).

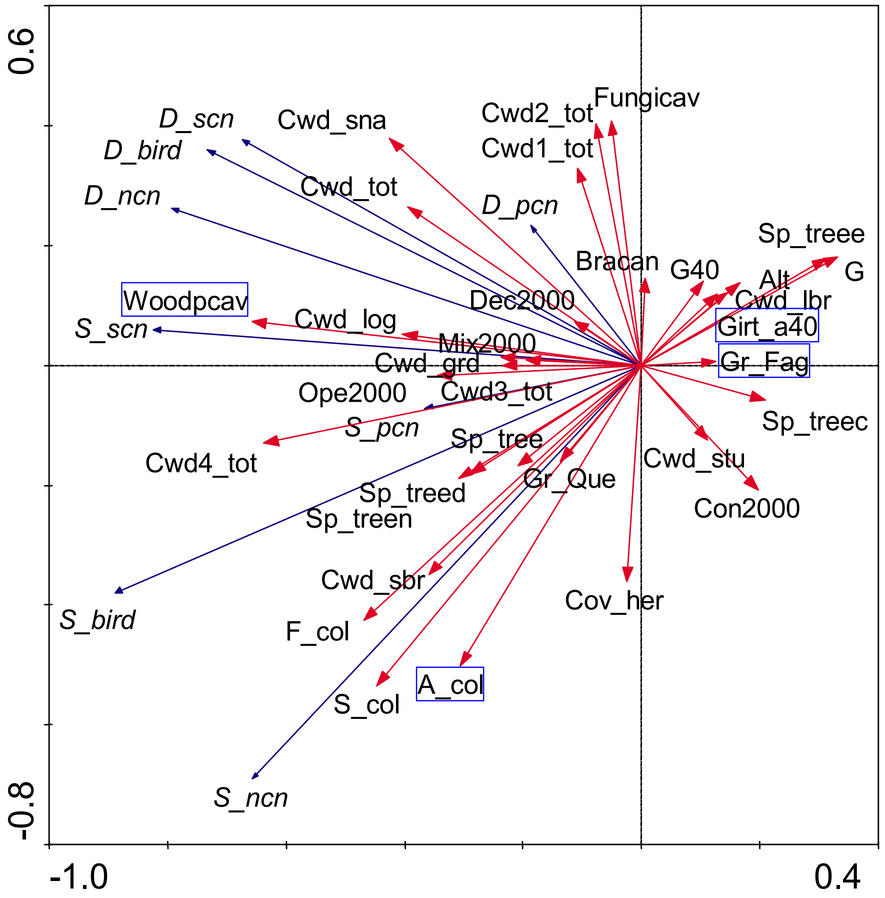

Figure 10. *pRDA-ordination plot, with forest bird descriptors shown in italic and the significant explanatory variables (identified by forward selection after controlling for regional effect) within a frame. See Tables 2, 9 and text for explanation of acronyms.*

Overall, high bird species richness was noticed in stands with numerous native tree species, a high supply of well-decomposed woody debris, diverse and abundant beetle families and species, and plenty of woodpecker cavities (Fig. 10). Forest bird density benefited from a high snag volume and supply of woodpecker cavities.

Some 49.2% of the total explained variance of the bird data (73.9%) was solely explained by (in order of selection) the availability of woodpecker cavities, the beech relative basal area (Gr_Fag) , beetle abundance, and the mean girth of large living trees (dbh $\geq$ 40 cm) (Girt_a40) (Fig. 10). Spatial structuring of the data not attributable to the environmental variables accounted for 5.3% of the total variance, and 19.4% was explained by the interaction between the biological data, the environment and spatial structuring.

3.3.4. Bats

A total of 14 different bat species were counted at 12 forest sites, of which 12 were observed in or near the Xylobios study plots (Van Der Wijden & Verkem 2005) (Appendix 11). The presence of 7 species was further confirmed by capture under licence of the Walloon region. Eight new bat roosts were localized, of which the first tree roost of Bechstein's bat (*Myotis bechsteinii*) and Leisler's bat (*Nyctalus leisleri*) known in Belgium. A majority of them used tree cavity and cracks behind bark as roosting sites (Meschede & Heller 2003) (Appendix 11). Due to night sampling uncertainty, the number of bat species was estimated by averaging the minimum and maximum number of bats potentially present in the habitat (Appendix 8), both at point counts (local species richness) and outside (regional species richness). The 12 study sites were oganised by pair, with half of them being classified as rich in dead wood. Besides vegetation and landscape characteristics (Table 2), we also related bat counts to estimates of prey availability – the number of insect (hoverflies + beetles) families (F_ins), species (S_ins) and individuals (A_ins).

The number of bat species did not differ between paired-stands (Table 10), which put into question the importance of dead wood in explaining bat diversity hotspots. On the other hand, partial correlations (controlling for regional variation) revealed positive significant associations between stand-level bat species diversity (S_loc) and indicators of overmature tree availability (Tree_a40, SG40), in addition to the amount of mixed stands in the surrounding landscape (Mix2000) (Appendix 34) (Fig. 11).

Table 10. *Number of bat species (S) between paired-stands with high and low amount of coarse woody debris (cwd), among which a majority uses tree cavity and cracks behind bark as roosting sites. See Appendix 11 for species details.*

Variable	Explanation	High cwd (6 stands) Mean ± SE	Low cwd (6 stands) Mean ± SE	t	*df*	*p*
S_loc	Local sampling[a]	3.92 ± 0.73	4.17 ± 0.79	-0.193	5	0.855
S_reg	Regional sampling[b]	6.75 ± 1.36	6.75 ± 1.05	-0.114	5	0.913

[a] at point count stations, [b] outside point count stations.

Variables were log-transformed +1 for normality, if necessary. Sample sizes (*n*) and mean values (± SE) are added.

The regional bat species richness (S_reg) was positively significantly correlated with the propotion of mixed stands in the landscape, and close to significantly related to oak dominance and the presence of large-diameter trees (Tree_a40, SG40) (Fig. 11).

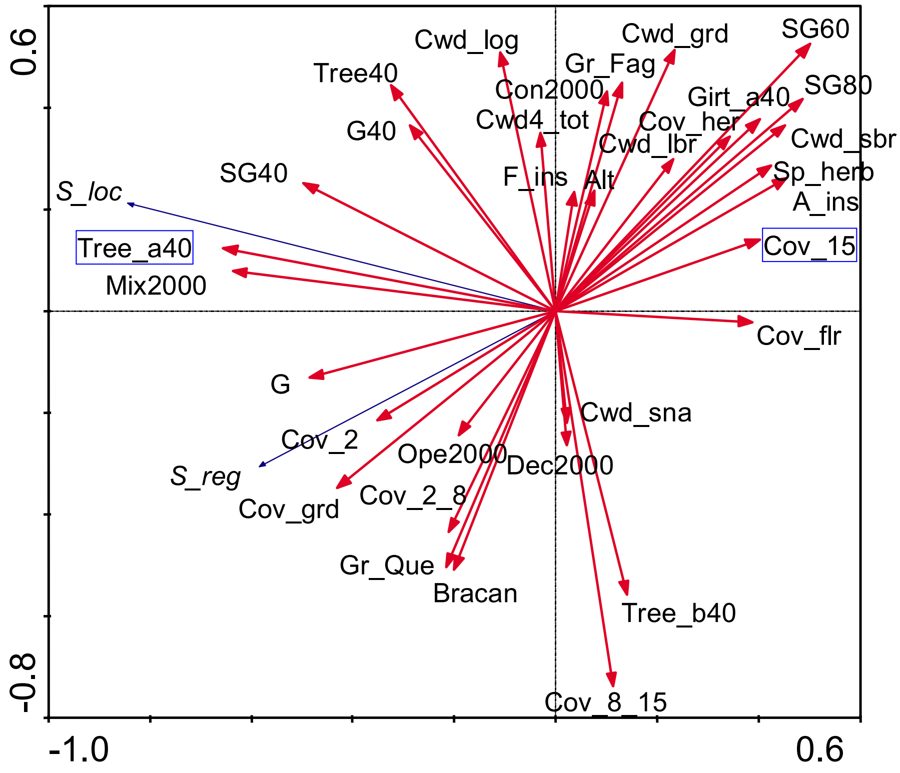

Figure 11. *pRDA-ordination plot, with forest bat descriptors shown in italic and the significant explanatory variables (identified by forward selection after controlling for regional effect) within a frame. See Tables 2, 10 and text for explanation of acronyms.*

4. WOODY DEBRIS, NUTRIENT CYCLING AND SOIL FERTILITY (WP3)

Woody debris play a critical role in promoting the differentiation of the humus layer of forest soils and tree regeneration (Harmon et al. 1986). At first, wood decomposition and nutrient release is speeded up by the activity of wood-boring insects (Edmonds & Eglitis 1989). Decaying logs and stumps store nutrients and water, and affect their flows through the litter. They serve as substrate for nitrogen fixing bacteria and wood-living fungi and sustain ectomycorrhizal formation and activity, providing shelter and ecological conditions ideal for seedling establishment (Harvey et al. 1979, Jurgensen et al. 1987, Kuuluvainen & Juntunen 1998). By facilitating tree regeneration, decaying stumps and logs contribute to successional changes in the vegetation (Lee & Sturgess 2002). An important feature of woody debris is that, although in lower amount, stored nutrients are released at slower rates during the decomposition process than from the nutrients recycled from the annual leaf fall. As a result, nutrients are retained in the ecosystem and available for tree growth for prolonged periods (Harmon & Chen 1991). Dead woody roots, for example, may release nitrogen that matches the demand of a rapidly regenerating forest (Chen et al. 2001).

In practice, forest soils rich in humus and remnants of decayed wood, and especially in long-lasting lignin molecules, have a high water potential, increased cation-exchange capability and reduced soil acidity (Harvey et al. 1979, Lindgren 2001). Following sustained log removal, nitrogen may become limiting in forest soils, leading to chain effects on the capacity of fungi to decay wood, which is dependent on the concentration of nitrogen in the surrounding litter (Johnston & Crossley 2002). The alteration of soil chemical properties may also progressively lower the rate of breakdown of forest litter by soil invertebrates and impair nutrient cycling (Cárcamo et al. 2001). And Holub et al. (2001) to conclude that the removal of woody debris could potentially reduce the nutrient capital of forest habitats, eventually leading to a decline in site productivity. However, so far, empirical data supporting this possibility are few and controversy still exists about the relative importance of dead wood to forest productivity (Harmon et al. 1986, Spies et al. 1988, Prescott & Laiho 2002).

In this third part, we were interested to assess whether forest soil fertility, estimated from diverse indexes, may vary as a function of the amount and quality of decaying wood available. Our approach was multi-scale, first comparing the soil properties of our 11 pair stands, differing in their overall dead wood supply, and then looking at soil parameters within one stand (with the highest amount of well-decayed wood) in relation to decaying log proximity.

4.1. Influence of overall dead wood supply on stand soil fertility

4.1.1. Material and methods

Soil samples (20 cm-deep) were collected by Agnès Guerin (FUSAGx) over the 22 study sites from September-April 2002-2003, with 3 samples per site (total of 66 samples). Sampling points were located 50 m apart from each other, centered on the insect sample plot, following the slope. While digging the soil, care was taken to exclude the upper organic layer (leaves, seeds, ...) from the samples. In the lab, samples were dried out before being analysed. In this study, we focused on three main groups of variables known to contribute to variation in soil fertility, namely the level of soil acidity (pH H_2O, pH KCL, [Al], exchangeable acidity), the relative amount of organic material (C, N, C/N, OM), and nutrient availability ([Ca], [Mg], [K], [P], [Mn], cation exchange capacity, base saturation).

4.1.2. Results

On average, stands classified with a high and low amount of dead wood did not differ in terms of their soil chemical properties (Table 11).

Table 11. *List of measured soil variables, their description, mean values (± SE) and test values from paired-sample t-tests between stands with high (n = 11, 55.31 ± 10.35 m^3 ha^{-1}) and low (n = 11, 11.60 ± 2.19 m^3 ha^{-1}) amount of coarse woody debris. Variables were transformed for normality (log + 1 for counts, arcsin-squareroot for percentages and proportions).*
Minimum-Maximum values are given between arrows.

Variable	Explanation	Unit	High cwd Mean ± SE	Low cwd Mean ± SE	t	*p*
pH H_2O (3.97-5.67)	pH		4.41 ± 0.14	4.35 ± 0.10	0.787	0.450
pH KCL (3.17-4.37)	pH		3.59 ± 0.11	3.51 ± 0.08	0.934	0.372
ExAc (0.90-13.07)	Exchangeable Acidity	me/100g	6.11 ± 0.94	7.04 ± 0.70	-1.667	0.127
Al (0.30-9.30)	Amount of aluminium	me/100g	3.76 ± 0.72	4.51 ± 0.61	-1.840	0.096
C (1.67-8.70)	Proportion of carbon	%	4.16 ± 0.64	4.47 ± 0.76	-0.436	0.672
N (0.11-0.51)	Proportion of nitrogen	%	0.25 ± 0.03	0.30 ± 0.04	-1.457	0.176
C/N (9.93-29.93)	Ratio carbon/nitrogen		16.50 ± 1.48	14.75 ± 0.74	1.568	0.148
OM (3.30-17.37)	Estimated proportion of organic material	%	8.31 ± 1.52	8.92 ± 1.52	-0.432	0.675
K (0.06-0.23)	Amount of potassium	me/100g	0.14 ± 0.01	0.15 ± 0.02	-0.653	0.529
Ca (0.13-3.44)	Amount of calcium	me/100g	0.53 ± 0.29	0.44 ± 0.15	-0.010	0.992
Mg (0.07-2.94)	Amount of magnesium	me/100g	0.39 ± 0.25	0.22 ± 0.05	0.545	0.598
CEC (3.70-13.60)	Cation Exchange Capacity	me/100g	7.15 ± 0.79	7.85 ± 0.68	-1.395	0.193
V (4.21-45.76)	Base saturation	%	11.04 ± 3.54	10.75 ± 2.77	0.046	0.964
P_2O_5 (2.60-17.13)	Amount of available phosphorus	mg/100g	7.97 ± 1.22	8.26 ± 1.11	-0.310	0.763
Mn (3.45-83.23)	Amount of manganese	mg/kg	42.60 ± 5.71	39.08 ± 5.95	0.703	0.498

When limiting the comparison to sites of Ardennes and Hertogenwald, to overcome problems linked to regional variation in altitude and its effects on soil chemistry, only the amount of manganese was found higher in stands with dead wood (46.60 ± 6.24 $m^3 ha^{-1}$) (Table 12).

Table 12. *List of measured soil variables, their description, mean values (± SE) and test values from paired-sample t-tests between stands of Ardennes and Hertogenwald with high (n = 7, 46.60 ± 6.24 m^3 ha^{-1}) and low (n = 7, 13.22 ± 3.35 m^3 ha^{-1}) amount of coarse woody debris. Variables were transformed for normality (log + 1 for counts, arcsin-squareroot for percentages and proportions). Minimum-Maximum values are given between arrows.*

Variable	Explanation	Unit	High cwd Mean ± SE	Low cwd Mean ± SE	t	*p*
pH H_2O (3.97-4.53)	pH		4.25 ± 0.06	4.22 ± 0.09	0.511	0.628
pH KCL (3.17-3.97)	pH		3.49 ± 0.09	3.47 ± 0.11	0.229	0.827
ExAc (5.83-13.07)	Exchangeable Acidity	me/100g	7.61 ± 0.98	8.33 ± 0.69	-1.091	0.317
Al (3.10-9.30)	Amount of aluminium	me/100g	4.89 ± 0.81	5.59 ± 0.65	-1.310	0.238
C (2.93-8.70)	Proportion of carbon	%	5.35 ± 0.64	5.98 ± 0.69	-0.725	0.495
N (0.17-0.51)	Proportion of nitrogen	%	0.30 ± 0.02	0.38 ± 0.04	-1.882	0.109
C/N (12.83-29.93)	Ratio carbon/nitrogen		18.24 ± 2.05	16.00 ± 0.62	1.161	0.290
OM (5.87-17.37)	Estimated proportion of organic material	%	10.68 ± 1.27	11.92 ± 1.38	-0.716	0.501
K (0.09-0.20)	Amount of potassium	me/100g	0.14 ± 0.01	0.15 ± 0.01	-0.581	0.583
Ca (0.13-0.36)	Amount of calcium	me/100g	0.22 ± 0.02	0.25 ± 0.03	-0.653	0.538
Mg (0.11-0.30)	Amount of magnesium	me/100g	0.15 ± 0.01	0.18 ± 0.02	-0.818	0.445
CEC (6.33-13.60)	Cation Exchange Capacity	me/100g	8.10 ± 0.99	8.91 ± 0.71	-1.102	0.313
V (4.21-9.99)	Base saturation	%	6.59 ± 0.61	6.65 ± 0.72	-0.052	0.960
P_2O_5 (4.40-14.33)	Amount of available phosphorus	mg/100g	8.24 ± 0.91	8.66 ± 1.53	-0.192	0.854
Mn (3.45-83.23)	Amount of manganese	mg/kg	49.05 ± 7.11	35.28 ± 8.56	2.441	0.050

After controlling for the regional effect, the study of associations between dead wood and soil variables over the 22 study sites revealed a positive correlation between the amount of phosporus available for plant growth and the total volume of dead wood on the forest floor (logs + branches) ($r = 0.506$, $n = 19$, $p = 0.019$).

This finding was supported by the results of a partial RDA ordination analysis, where we looked at the proportion of variation of our soil variables that was explained by a set of three meaningful dead wood variables (the total dead wood volume (Cwd_tot), including the log volume (Cwd_log) and the total fallen dead wood volume (logs + branches) (Cwd_grd)) once the effect of spatial structure (here the region) taken into account (Fig. 12). Only the soil variables P, $pH_{H2O/KCL}$, Al, and ExAc were included in the analysis (i.e., with a variance explained cumulatively by the first two axes > 20%).

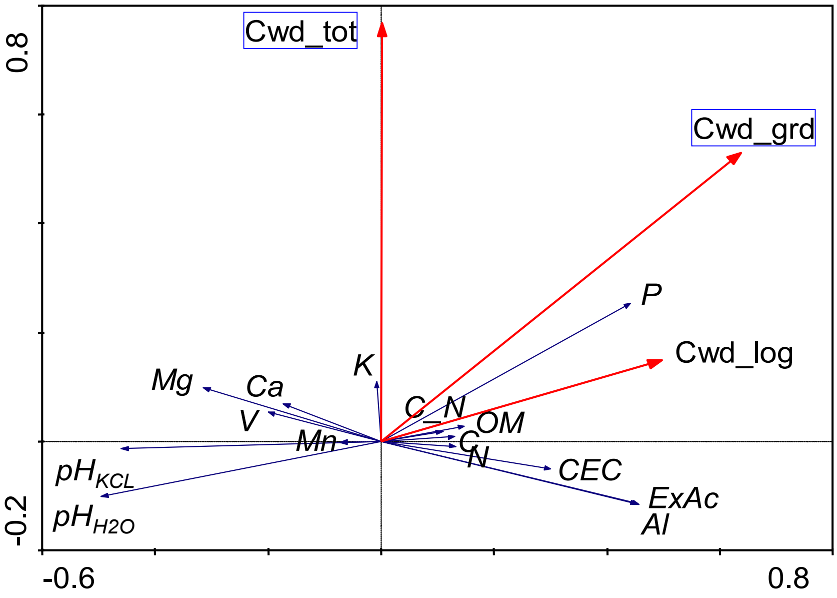

Figure 12. *RDA-ordination of the soil and dead wood descriptors plotted in the plane determined by the first two principal axes. The dependent variables are shown in italic; the significant explanatory variables identified by pRDA (forward selection subroutine) after controlling spatial structuring of the data (Region) are framed. See Tables 2 and 11 for explanation of acronyms.*

The direct gradient analysis revealed that the total explained variance of the soil data (P, $pH_{H2O/KCL}$, Al, ExAc) was 61.8%. Of this, 22.5% was explained by a linear combination of two dead wood variables, namely, in order of selection, the total fallen dead wood volume (Cwd_grd) and the total dead wood volume (Cwd_tot). Spatial structuring of the data not attributable to the dead wood variables accounted for 6.50% of the total variance. The remaining 9.2% was explained by the interaction between the soil data, the environment (dead wood) and spatial structuring (regional effect). The model was significant ($p < 0.05$, Monte Carlo permutation tests (999 permutations under full model)).

We found that stands with a large amount of dead wood, and in particular of trunks and branches fallen on the forest floor, had a higher availability of phosporus in their upper soil layer (first 20 cm) and less acidic soil conditions.

4.2. Influence of decaying log proximity and history on soil fertility

4.2.1. Material and methods

Another approach to study the potential impact of wood decay on forest soils was to relate small-scale variation in soil parameters within a stand to decaying log proximity. Here we chose the strict forest reserve of Kerselaerspleyn, in the Sonian forest, being the forest with the largest amount of wood on the forest floor (108 $m^3 ha^{-1}$) among our study sites, including 24 $m^3 ha^{-1}$ of woody debris in the most advanced stage of decay (i.e., with bark loose or absent and the wood structure soft and friable). The study was limited to 6 large beech logs (length: 36.65 ± 1.21 m, dbh: 89.17 ± 3.96 cm) in advanced decay (class 3-4), with trees that fell after major storms in 1983 (3 trees) and 1990 (3 trees). To reduce the influence of external factors on nutrient dynamics, the logs shared similar microhabitats (shady, moist patches in the understorey) and were not located near other decaying logs. For each log, 12 soil samples (20 cm-deep) were taken in September 2005 in cooperation with the INBO (Bart Christiaens and Peter Van de Kerckhove), with 6 samples beside the trunk (0.1 m distance, 3 on each side) and 6 samples at 5 m distance perpendicular to the trunk (3 on each side) (Fig. 13). We excluded the upper organic layer which was filled with vegetation debris from the samples.

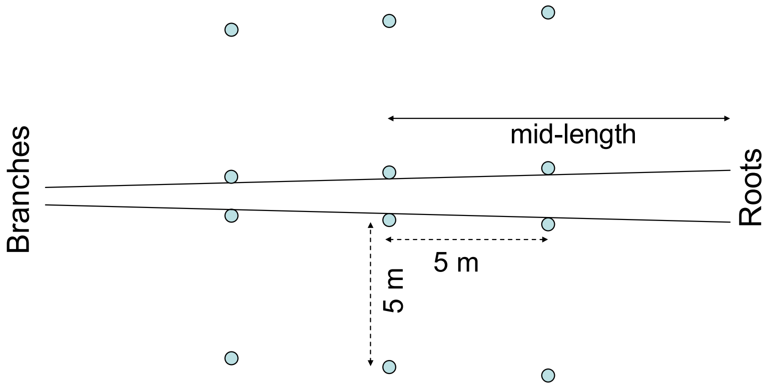

Figure 13. *Sampling protocol to study the effect of log decomposition on soil chemistry. Circles are the sampling positions.*

Detailed analyses in laboratory allowed then to measure their acidity (pH H2O, pH KCL, [Al]), nutrient ([Ca], [Mg], [K], [P], [Mn]) and organic (C, N, C/N, OM) contents.

4.2.2. Results

When pooling the samples (trees from 1983 and 1990), we found significantly higher amounts of K, P, Ca, Mn, and Mg near by the trunks (0.1 m distance) compared to

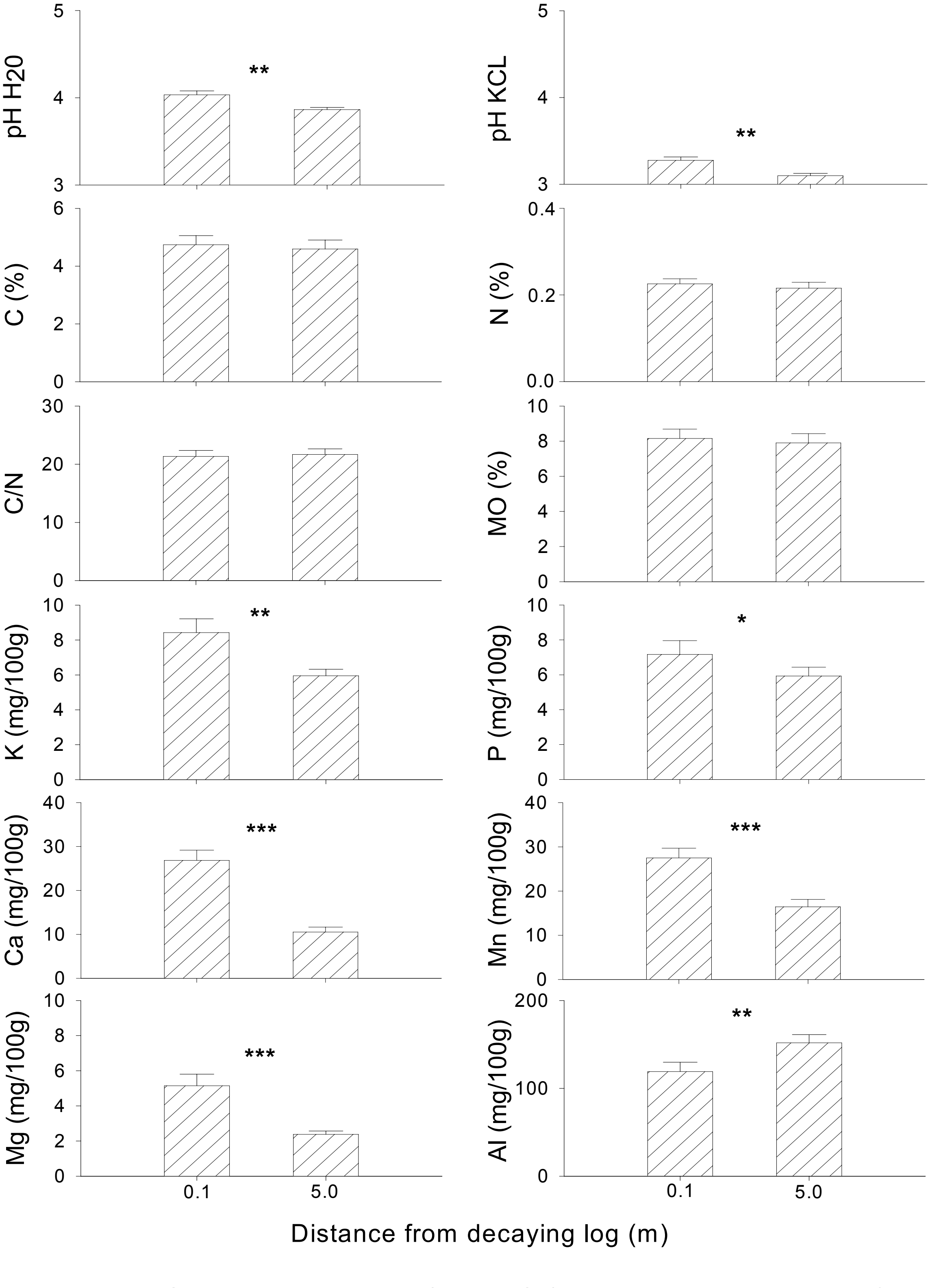

***Figure 14.** Soil chemical properties (mean ± SE) measured at 0.1 m vs. 5.0 m from decomposing beech logs (n = 6), Kerselaerspleyn strict forest reserve. Asterisks denote significant changes (paired-sample t-tests, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Variables were transformed for normality.*

levels 5 m away from the trunks (Fig. 14). We also found less acidic soil conditions beside the trunks, as revaled by the lower pH values and higher amount of Al with increasing distance from the logs (Fig. 14).

If analysing the logs that were 22 year old (1983) and 15 year old (1990) separately (i.e., taking into account their different decay history), it is interesting to notice that part of the differences that were found significant in 1990 (pH, K, P, Al) levelled off for trees that fell 7 years earlier (Table 13). Although non-conclusive due to the limited tree sample size, those results suggest relatively rapid changes (about 20 years) in the contribution of decaying beech logs to the forest soil local biogeochemistry.

Table 13. *Summary of test values from paired-sample t-tests of soil chemical properties measured at 0.1 m vs. 5.0 m from beech logs after 15 (n = 3) and 22 (n = 3) years of decay, Kerselaerspleyn strict forest reserve (Sonian forest). Variables were checked for normality. Significant p-values in bold face. See Table 11 for explanation of acronyms.*

Variable	15 years old (1990)			22 years old (1983)		
	t	df	*p*	t	df	*p*
pH H_2O	3.174	17	**0.006**	1.806	17	0.089
pH KCL	3.142	17	**0.006**	1.981	17	0.064
Al	-2.754	17	**0.014**	-1.641	17	0.123
C	-1.473	17	0.159	1.613	17	0.125
N	-0.965	17	0.348	1.525	17	0.146
C/N	-0.426	17	0.676	-0.014	17	0.989
OM	-1.474	17	0.159	1.612	17	0.125
K	3.021	17	**0.008**	1.934	17	0.070
Ca	4.091	17	**0.001**	5.488	17	**< 0.001**
Mg	2.883	17	**0.010**	3.645	17	**0.002**
P_2O_5	1.908	17	0.073	0.985	17	0.338
Mn	3.433	17	**0.003**	2.615	17	**0.018**

5. UNDERSTANDING TREE MORTALITY: THE CASE OF THE "WALLOON BEECH DISEASE" (WP5)

Within the framework of what the forest world has called the "beech disease", nearly 2 000 000 m³ of beech wood (*Fagus sylvatica* L.) have been damaged in Wallonia from 1999 to 2003. Often occurring together on a tree, several agents where involved in the damage: frost, Scolytid (mainly *Trypodendron domesticum*) and Lymexylonid (*Hylecoetus dermestoides*) Coleoptera, as well as several lignivorous fungi species.

It is difficult to evaluate precisely the global financial loss due to this exceptional event. The depreciation of around 2 000 000 m³ of damaged beech wood probably constitutes the greatest part of the economic loss; moreover, over half of the damaged trees has a girth at breast height comprised between 120 and 240 cm (i.e. trees that present the greatest possibilities of use and the highest financial potential). Thus, arriving on a market already saturated by the windthrows blown down by the Lothar hurricane – which in December 1999 ruined large forest areas in Eastern and Northern France – the "diseased beech trees" were sold at very low prices. However, in addition to the devaluation of the m³ of wood, lots of other costs or losses must also be taken into account[1]. Without being exhaustive, we can cite for instance:

- the losses due to the damage to "non-diseased" trees (i.e. trees not frozen or attacked by beetles or fungi): sunburn to shade-tolerant tree species being brought brutally to the light, crown or trunk injuries due to the fall of diseased trees, soil compaction and damage linked to sanitary felling and log harvesting, etc;
- the anticipated exploitation (loss on the present value of future cashflows);
- the cost of the reforestation's operations carried out in order to avoid too long-lasting lack of financial incomes;
- the economical and environmental costs of the several techniques used to try to control the insect populations (of which 20 000 attractant traps at the cost of about € 25 each, and about 16,000 trap trees sprayed with poorly selective pesticides), as well as the cost of the manpower to set and keep them up;
- the weak confidence that wood market will have in the next years regarding the products originating from the "diseased regions", and consequently the low prices offered for them (as the wood of many trees with a healthy appearance is more or less severely discoloured and/or damaged).

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[1] Although not dedicated to a catastrophe of biotic origin, an brief analysis of the "side-effects" of a large scale and sudden natural disaster in temperate forests is given in Peyron (2002), who discuss the economic consequences of the 1999 hurricanes on the French wood chain.

Although insignificant in comparison with the total economic impact of the disease, the nearly 4,800,000 € paid by the “Fonds des Calamités” to indemnify forest owners attest the importance of the phenomenon (Mazay & de Wouters 2005). From a strictly economic point of view, this event was therefore catastrophic, in particular for the numerous Ardenne districts of which a significant part of the budget is directly linked to the exploitation of wood products. We can thus quite easily understand the need to analyse accurately the mechanisms underlying the past crisis in order to prevent (as much as possible) the repetition of it, or to optimise its management if such an event recurs.

In 2000 and at the beginning of 2001, during the elaboration of the XYLOBIOS program, numerous points remained hazy concerning the understanding of the disease. Five departments or units within four universities or research institutions (FUSAGx, CRAW, ULB and UCL) therefore contributed to the comprehension of this extraordinary event *maybe*[2] unprecedented in the history of the broad-leaved forests of Wallonia.

We must however point out that despite the fact that various expertise were brought together, it has been impossible to give without any doubt a complete understanding of the phenomenon, because of interactions dealing with climate, soils, sylviculture, previous storm damages, etc.. Nevertheless, as the understanding of the epidemiology of the disease grew, it appeared that certain questions asked or experimentations initially planned as part of the WP5 were not or were no longer completely opportune. This document therefore presents the results of our researches and our thoughts that are adapted to the changing character of the knowledge of this disease.

In particular, we present hereafter :

- the development of the crisis, as well as the role of xylophagous insects and lignivorous fungi which revealed the problem ;
- the importance of different elements supposed to have sensitise trees to the disease ;
- the role of the pre-disease dead wood stock and of saproxylic organisms (*stricto sensu*) ;
- the measures that should be taken in order to optimise the future management of such natural catastrophes.

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[2] « *maybe* » since Prieels (1954) and Poncelet (1965) report important Scolytid attacks and damages in the beech stands of the Ardenne, as a consequence of the severe winter 1941-1942. During several years following this winter, *T. domesticum* outbreaks were observed in those woodlands. Unfortunately (but obviously, regarding the period concerned by this event), there isn’t any estimate of the total volume of damaged wood, nor of the area concerned by those unusual attacks.

5.1. Development of the "beech disease": short summary

During autumn 1999, the first worrying symptoms of the beech disease were observed. Beetle attacks and fruiting bodies of lignivorous fungi appeared on numerous beech trees in the Ardenne and in Lorraine (contiguous natural regions of Southern Belgium). In 2000, the beetles and fungi attacks grew considerably. In spring 2001, whereas scientists and foresters expected a stagnation or even a reduction in the intensity of attacks (at least concerning the entomological ones), the latter grew with an acuteness never reached before. Trees that presented a healthy aspect were attacked despite not having been in 1999 or 2000. The distribution of the damaged beech stands and the local acuteness of the disease have been assessed at the beginning of the summer 2001. The results are represented on Fig. 15 (a more detailed version of the figure is presented in Henin et al., 2003b; see also footnote 3).

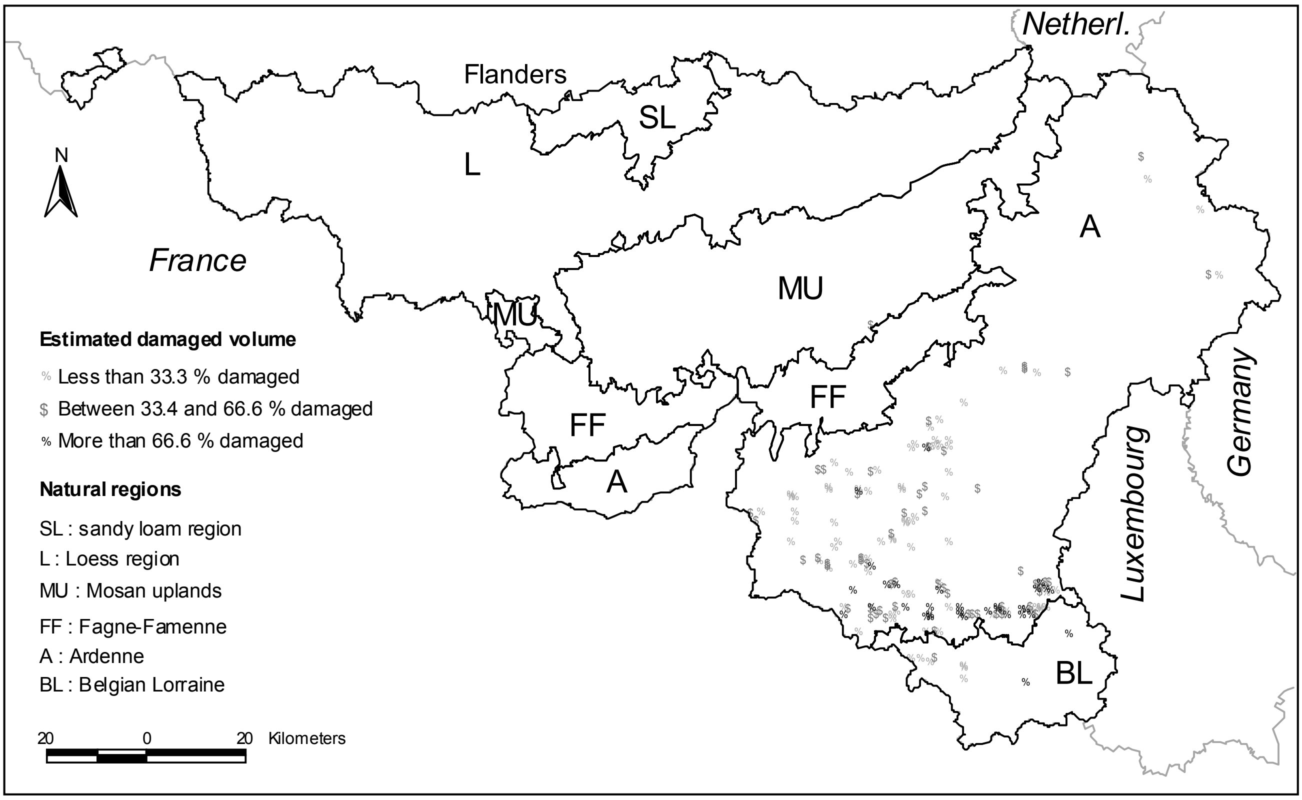

Figure 15. Distribution of damaged stands and local damage level, according to a survey carried out in 2001.

The attacks on standing trees continued in 2002 and 2003, but they never happened on trees that remained healthy until 2001 included (all the trees attacked in 2002 and 2003 were therefore attacked for the first time at the latest in 2001). In a 2 ha "untreated" area located in a "heavily diseased beech stand" (State forest of Sainte-Cécile, near Florenville), the state of the trees was compared three years after the first scolytid/fungi attack they undergone:

- only 7% of those attacked in 1999 still looked healthy in 2002 (sample of 27 trees). Virtually all of them were broken in 2005;
- 50% of those attacked in 2001 apparently "recovered" and seem today sound, exhibiting no polypore on the trunk or loss of bark (based on a sample of 72 trees).

This obvious difference in the fate of the trees, depending on the period of the first attack, suggests that two phenomena are probably involved and two steps have to be distinguished in the disease.

5.2. Epidemiology of the disease: hypotheses and explanations[3]

5.2.1. Attacks of 1999 and 2000

Due to the thinness of its bark and the absence of real rhytidome, beech is particularly sensitive to large and sudden variations in temperature. Its resistance to frost depends on several complex physiological mechanisms which, step by step, gradually decrease the sensitiveness of bark to cold temperatures (Huart & Nageleisen 2003, pers. comm.). However, if the drop of temperature (a) is too fast and too important, and/or (b) occurs too early during the autumn, the different processes are not completely achieved and cortical and/or sub-cortical[4] tissues may be killed.

In mid-November 1998, an abnormally early and heavy frost occurred in Wallonia. Because of the nearly univocal relationship that, in Belgium, links several climatic parameters (of which temperature) to altitude (Dufrêne & Legendre 1991), the intensity of the frost was of course maximum at the highest altitudes, i.e. in the Ardenne and Belgian Lorraine. Throughout these regions, minimal daily temperature (T_{min}) in average dropped 14°C from November 15th to 23rd (data recorded in 8 sites). Whereas on November 14th, 15th and 16th T_{min} was positive in all but one of 43 Belgian meteorological stations, temperatures of -16°C were locally reached one week later (average T_{min} of -13°C in the 8 Ardenne/Lorraine meteorological stations, on Nov. 23rd). Lots of trees, which were still physiologically active (sap flows not stopped yet), were therefore damaged due to these adverse climatic conditions.

The very cold temperatures observed at that time were the consequence of the presence of an anticyclone on Russia, which blew continental winds westwards (IRMB, 1999). This probably explains why north-eastern France, western Germany

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[3] This chapter has been greatly inspired by Huart & Rondeux (2001), Rondeux et al. (2002), Huart et al. (2003) and Henin et al. (2003), of which it constitutes a kind of synthesis (with regard to the phytosanitary aspects of the disease). For more information on this phenomenon (notably the distribution of the damaged volumes per natural region, topographical situation, administrative territories, …), please consult the three first papers.

and Luxembourg were also concerned, to a lesser extent however, by the disease (for damage distribution in the 4 countries, see Nageleisen & Huart 2005).

Although other elements could have affected the sturdiness of the beech stands (see §5.3.), the climatic stress of November 1998 very likely triggered off the disease. It caused (sub-)cortical lesions and necrosis to a great number of beech trees. A very similar event was observed on Plane trees in the UK, about 55 years ago (Crandall 1943). The activity of the micro-organisms which developed in the trees presenting these symptoms resulted in the emission of certain volatiles. Among these substances, ethanol naturally attracted organisms adapted to the colonisation of substrates that release these informative signals (i.e. weakened plants), that means e.g. Scolytids and the Lymexylonid *Hylecoetus dermestoides* (Moek 1970, Kerk 1972, Klimetzek et al. 1986, Byers 1992). This way, the populations of *Trypodendron domesticum*, of *T. signatum* and of *H. dermestoides* took advantage of an important and sudden availability of suitable resources.

Regarding the attacks of 1999 and 2000, the pertinence of accrediting the “frost episode” of November 1998 as a determining cause is great. As this has already been discussed in several publications and reports of the Forest and Nature Management Unit of the Gembloux agricultural University (cf. footnote 3), we only refer three major evidences. Firstly, according to the observations carried out in 2000 on over 120 randomly chosen beech trees, the presence of a large (sub)-cortical lesion situated on the north, the east or the north-east side of the trees was a necessary and sufficient condition to trigger off the beetle attacks in 1999 and 2000. Secondly, considering on the one hand that only the regions situated above 350 m in altitude were affected by this disease, and on the other hand that the seriousness of the damage increased with altitude (i.e. the damage gradient fits with the temperature gradient). Finally, we must point out that attacks of *Trypodendron* spp. have, in the regions affected by the beech disease, also been observed on sycamore trees. The thinness of the bark of this species is likely a reason, as for the beech, of the sensitivity of its cortical tissues to frost. That these two species predisposed to frost damage are concomitantly, and in the same wide regions, the target of attacks of weakness pests may be considered as extra proof for the climatic origin of the crisis.

5.2.2. Trypodendron spp. population dynamics

Introduction

Initially at endemic levels, both “broad-leaved *Trypodendron* species” and *H. dermestoides* therefore benefited, as from spring 1999, from conditions that

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[4] Written “(sub-)cortical” in the rest of the chapter.

caused the outbreak of their populations. Since little information exist on the *Trypodendron* spp. population dynamics (particularly the biological factors regulating their populations), we attempted to contribute to improve the understanding of this topic. In the context of the beech crisis, such information was important in order to enable forest managers to react as efficiently as possible by taking into account the potential effect of *Trypodendron* spp. antagonists (natural enemies and competitors). Hence, we planned to focus our observations A. on the identification of the main antagonists of *T. domesticum* and *T. signatum*, as well as B. on their potential role in decreasing the abundance of the beetles. Unfortunately, several problems mentioned hereafter made the results particularly unreliable. The latter have thus to be considered with extreme carefulness. In particular, between stand comparison (according to the amount of dead wood) is not possible. Nevertheless, as the topic is very poorly documented in the literature, we decided to present the data collected as well as a brief discussion about *Trypodendron* spp. population dynamics.

Material and method

A network which initially comprised over 200 traps**[5]** (see Fig. 16) in the Sonian Forest (FS and RA sites) and in Northern Ardenne (BR, R2, RU and MO) made it possible to gather biological data on *Trypodendron* spp., as well as information on the organisms that are associated with. Those *individual emergence traps* (I.E.T.) are set up as follow: 1. a circular piece of bark, centred on a *Trypodendron* gallery orifice, was removed; 2. a central plastic tube, perfectly fitting in the debarked area, was firmly applied against the sapwood; 3. a few nails were fixed around the tube and adhesive tape strengthened the system; 4. a collector plastic vial was finally fitted into the central plastic tube. The I.E.T. were installed on a dozen of beech trees (ca 125 cm girth at breast height) which were cut for the purpose of this study, in December 2001 (Soignes, BR and R2) and February 2002 (RU and MO). Because colonisation was insignificant in 2002, the traps were set up in June 2003 and were followed up to the end of summer 2004. Unfortunately, some uncertainty remains as for the possibility that some individuals (particularly flat insects as *Rhizophagus* spp.) could have penetrated into the traps through the tiny interstice sometimes existing between the wood and the central plastic tube, and therefore may not have emerged from the beetle galleries. This severely affects the reliability of our observation.

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[5] But their number gradually decreased because of destruction due to wind, game and vandalism.

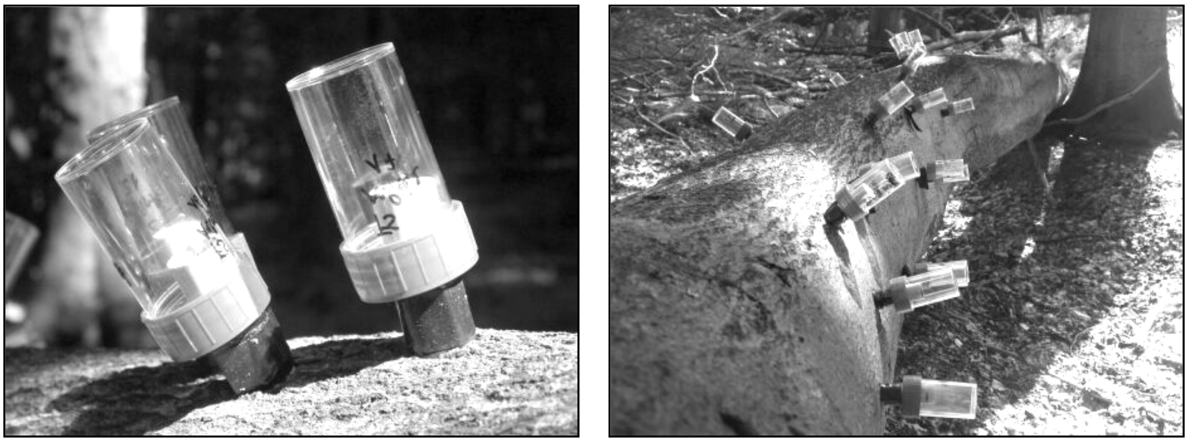

Figure 16. *Individual emergence traps used to gather biological data on Trypodendron spp. and on their natural enemies.*

<u>Results and discussion</u> (see Appendix 35)

Taking into account only the I.E.T. in which offspring was collected[6], one couple of *T. domesticum* engenders an average of 21.2 (STD=16.4) "emergent adults" (n=82). We call "emergent adults" the descendants which will take part in the "aerial phase", that means the dispersion from and possibly the aggregation on a host tree (see Fig. 17). Some couples however have over 60 descendants! Regarding *T. signatum*, although some couples have an offspring exceeding 40 individuals, the average number of emergent adults is only 10.1 (STD=11.1 and n=30). This last result is similar to those obtained by Grégoire & De Proft (2002).

Several researchers (Borden & Grégoire 2001, pers. comm., De Proft 2002, pers. comm.) initially considered, on the basis of *Trypodendron* spp. gallery analyses carried out in 2001 or earlier, that the rate of mortality due to the Arthropoda predators, parasites or parasitoïds was practically null during the "woody phase" (i.e. inside the host tree). The fact that *Trypodendron* spp. brood represent a relatively limited food source, not easily accessible because of the permanent presence of both parents in the gallery (which constitute a considerable physical obstacle), was supposed to virtually prevent these beetles from pre-imaginal parasitism and predation. Surprisingly however, numerous entomophagous insects and a few parasitoïd-looking wasps apparently emerged from the I.E.T.. Amongst those species, we can list:

- more than 300 Monotomid beetles (formerly Rhizophagidae), of which 94% Rhizophagus dispar, 5% R. nitidulus and 1% R. bipustulatus. Some Rhizophagus spp. are known to be important predators of Scolytids (Kenis et al. 2004).

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[6] The traps of which no adult Scolytids emerged were not taken into account in the calculation of the average, because those observations were considered as abnormal.

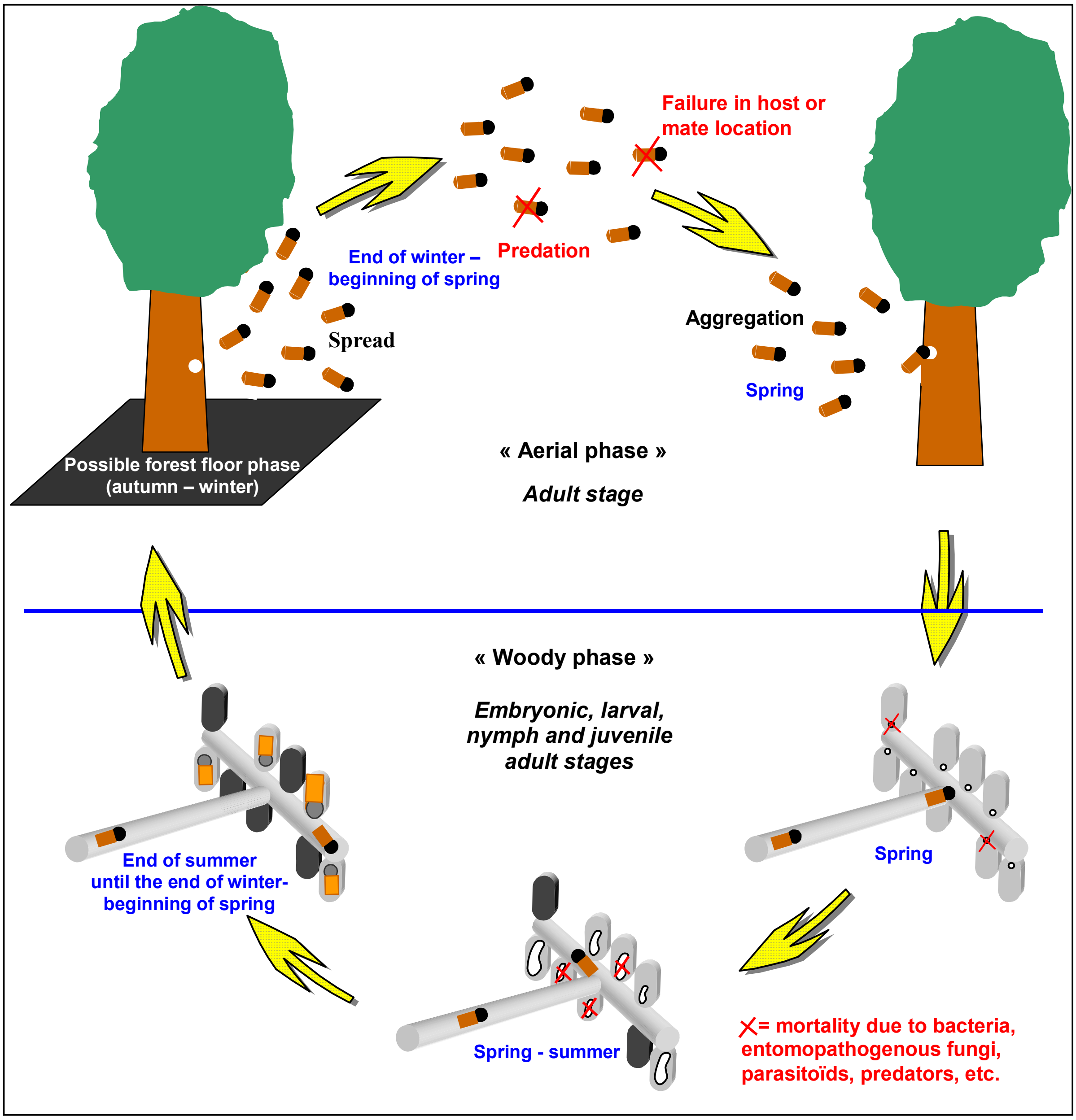

Figure 17. *Scheme of Trypodendron spp. lifecycle.*

- According to Magema et al. (1981), R. bipustulatus (as well as R. depressus, which has not been captured in our study) also occurs in the galleries of Trypodendron lineatum (Olivier 1795);

- a few Staphylinids (species not identified). Kappes & Topp (2004) suspect more than 40 species of this family (only among the ones they caught) to predate upon Scolytid bark beetles;

- Rhinosimus ruficollis (Coleoptera, Salpingidae), which is considered as a predator of T. domesticum and T. signatum (Haase et al. 1998, Bader 2004). Magema et al. (1981) also consider this species, as well as Rhinosimus planirostris, as T.

lineatum predators. According to the latest authors however, predation of Rhinosimus spp. do not occur in the ambrosia beetles' galleries, as the former are too large;

- tiny parasitoïds (Hymenoptera) belonging notably to the families Braconidae and Pteromalidae, which are known to count important Scolytid enemies (Kenis et al. 2004). Unfortunately, it has not been possible to identify the insects to the species level.

With the help of I.E.T. identical to the ones we used, De Proft (2004, pers. com.) also gathered lots of supposed "associated insects" (besides Trypodendron spp.). Those observations suggest that some possible or confirmed antagonists succeed in penetrating in ambrosia beetle[7] galleries.

Regarding some of these species, particularly the predators, it is however very difficult to assess the impact they have on Scolytid populations. Some non-obligatory predators may indeed behave (at least partly) as commensals (Kenis et al. 2004). For instance, several species of the genus Rhizophagus have a mixed diet, combining mycetophagy and entomophagy (Grégoire 2004, pers. com.). Some Staphylinidae only occasionally prey upon beetle eggs and larvae (Kappes & Topp 2004, Kenis et al. 2004), and are therefore likely to affect the potential prey populations. Hence, because of the uncertainty regarding the proportion of entomophagy in the diet of those insects, assessment of the extent of the impact of partially entomophagous taxa on Trypodendron spp. populations should be based on experimentation rather than on observation (Grégoire 2004, pers. com.). It is also worthwhile to note that, by preying on or parasitizing other Scolytid antagonists, many Scolytid parasitoïds and predators reduce the total impact that natural enemies could have on Scolytoïd populations if such mutual interference (see Begon et al. 1996 for more details) among consumers did not exist (Kenis et al. 2004). The global impact of the natural enemies collected in the I.E.T. on the beetles populations is thus unfortunately impossible to estimate.

The importance of different factors susceptible to influence the dynamics of those insect populations remain thus unknown. Those points mainly concern: A. the causes and rates of mortality during the embryonic, larval and pupal stages, B. the rate of mortality of the hibernating population (winter mortality rate, W.M.R.) and C. the

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[7] *Ambrosia beetles*, like *Trypodendron* spp., feed upon symbiotic "ambrosia" fungi which grow on the walls of the larval "room". The spores of the ambrosia fungus are transported by the females, in a particular organ called mycangium. Ambrosia beetles differ from *bark beetles* (living in or underneath the bark) in that way that the adults of the former excavate radial galleries which penetrate (sometimes deeply) in the wood. Their larvae feed upon the fungus and do not dig galleries. Conversely, bark beetle larvae stay in the bark or in the cambium where they actively dig in and feed on tree tissues (Balachowsky, 1949).

proportion of emergent adults that succeed in colonising a tree, finding a mate and generating descendants (hereunder named Gene Transmitters Ratio, GTR). Regarding T. domesticum, which most generally overwinters in the host tree (Gaubicher et al. 2003; pers. obs.), the results acquired with the I.E.T. integrate A. and B.; these results unfortunately do not enable to dissociate both mortality rates. Regarding T. signatum, which preferentially emerged before the winter (Gaubicher et al. 2003; pers. obs.), the I.E.T. results only take into account A.

For information purposes, Figures 18 a&b illustrate the scale to which T. domesticum populations, i.e. the most problematic among the species involved in the beech disease, may have increase after November 1998. To draw up those graphs, the following values were used:

- average number of emergent adults produced per couple: 21.2;
- Female-ratio (FR) of adult populations: 0.29, i.e. 2.5♂:1♀ (according to Paiva, 1982[8]) in Fig. 18a; to have a better idea of the possible range of the populations increases, FR of 0.33 and 0.50 (i.e. 2♂:1♀ and 1♂:1♀, respectively) were used in Fig. 18b;
- Gene Transmitters Ratio (GTR) when resource availability is "unlimited": three GTR, namely 0.50, 0.75 and 0.90, were associated to each FR tested.

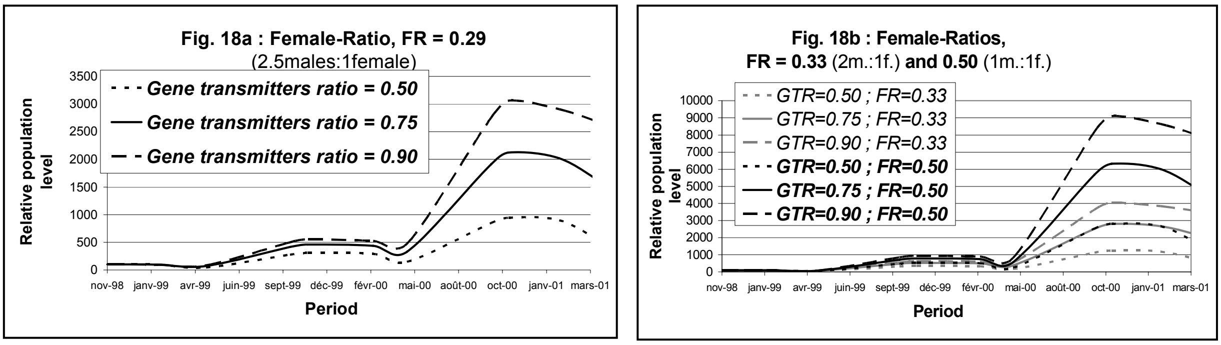

Figure 18 a (left) & b (right). *Possible evolution of T. domesticum population levels according to different Female-ratios and Gene Transmitters Ratios. Population level of November 1998 = 100 %.*

As shown on Fig. 18a, the populations of the Scolytid greatly increased once the availability of breeding material temporarily ceased to be a limiting factor. It seems reasonable to consider that, fixing an hypothetical FR of 0.29, *T. domesticum* population levels may have been, at the end of the winter 1999-2000, the 3-, 4- or even more then the 5-fold (GTR of 0.5, 0.75 and 0.9, respectively) than what they

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[8] Although the use of attractive compounds to sample beetle populations may have biased the sex-ratio observed in this study. According to De Proft (2005, pers. comm.), the sex-ratio within *Trypodendron* spp. populations should be around 0.5.

were one year before. Benefiting from the still suitable 1998-frozen trees, *T. domesticum* populations pursued their multiplication during the growing season of 2000. At the end of this year, they could have reach the 10-, 20- or even 30-fold of the level they had two years ago (GTR= 0.5, 0.75 and 0.9, respectively). Depending on the actual GTR and FR, *T. domesticum* population growth may even have exceeded those values (Fig. 18b).

To conclude this paragraph, we would like to mention the American studies of Knight (1958), Otvos (1965) and Moore (1972), for instance, which highlighted the notable action that woodpeckers (Picidae) may exert on Scolytid populations. Nevertheless, those studies concerned bark and not ambrosia beetles (see footnote 9). As Picidae predation occurs during the "woody phase" (Otvos (1965) virtually only found Scolytid larvae in woodpeckers stomachs), and since *Trypodendron* spp. brood represents a very poor resource located several centimetres inside the wood, the impact of woodpeckers on *Trypodendron* spp. pre-imaginal stages is undoubtedly null. Regarding avian predation, the more vulnerable phase during an ambrosia beetles' life is probably when the insects aggregate on a host. At this moment, increased food density probably enhances the predator's answer, as the birds are likely to exhibit a "*type 2 or 3 functional response*" and since prey profitability is constant (as discussed in Begon et al. 1996). To the best of our knowledge however, no data exists on the hypothetical bird-induced beetle mortality during the aggregation phase of *Trypodendron* spp. or of any other ambrosia beetle.

5.2.3. Attacks of 2001

Although the populations of *Trypodendron* spp. were extremely high in autumn 2000, it is probable that, without any change in the regional phyto-sanitary context, the availability of the resources usually used by these species (that means wounded or very weakened trees) would have been problematic in 2001 and the majority of the until-then non-attacked trees would have remained sound.

Nonetheless, at the beginning of 2001, new climatic hazards changed the situation. Exceptional rainfalls occurred in March and April of that year. In several regions of the country, March and/or April rainfalls were 3 times higher than normally. Considering both months together, the rainfalls were the heaviest ever recorded for this period since the beginning of the observations of the "Royal meteorological Institute of Belgium". It should also be noted that the rainfall excess (i.e. difference with average value) was higher in the Ardenne and Belgian Lorraine than in the other Belgian regions.

Hypoxic conditions (like root anoxia caused by the flooding of the soil) can induce the metabolic production of ethanol in stressed trees (MacDonald & Kimmerer 1991). It is therefore reasonable to think that the highly extraordinary climatic conditions of March-April 2001 contributed to weaken and make attractive numerous trees which, up to the beginning of the 2000-2001 winter, had been saved from the entomological and fungi attacks.

In this context, the very large beetle populations found alternative substrates in these temporarily weakened and attractive trees and caused the heavy attacks of spring and summer 2001. It is probable that lots of these trees (that were attacked for the first time in 2001 and that did not had large injury due to the frost of 1998) would not have been attacked with the force of summer and spring 2001 if the beetles populations had not been so large at that time. Indeed, although the exceptional rainfalls of 2001 concerned the entire Walloon Region, only the Ardenne and Belgian Lorraine, where the levels of beetles populations were very high at the end of winter 2000-2001, were subject to an increase in attacks. This observation aims to show that, regarding the trees attacked for the first time in 2001, a *sine qua non* condition seems to be that they had to be situated in an environment where the beetles populations were extremely high (otherwise beech stands growing on poorly drained soils outside the Ardenne and Belgian Lorraine, as in some parts of the Sonian forest for instance, would also have been attacked). Unfortunately, it has not been possible to verify “scientifically” (i.e. experimentally) this hypothesis regarding 2001 attacks, which is mainly based on theoretical arguments. In this context, it should also be reminded that, apart from the heavy spring rains, 2001 attacks could also have been enhanced by “long term” effects of the 1998 frost episode (different from the immediate (sub)-cortical necrosis).

The above-mentioned theoretical hypothesis is easily understood considering, as L.-M. Nageleisen pointed out (2004, pers. comm.), that when secondary pests pullulate, the individuals remain secondary but the population may tend to primarity[9]. Due to the limitation of usual resources, the insects, which normally only colonise very weak plants, then attack moderately or slightly weakened trees and sometimes succeed, thanks to their abundance, to overcome the defences of the plants. Such examples of switching resources due to the lack of them are frequent in insects, mainly in case of pest outbreaks. In that way, temporary resource switching may consist in (both cases are not exclusive):

- increased virulence of secondary pests, which decrease their dependence on host sturdiness. Typically, many Scolytid species benefit from high population densities regarding their ability to colonise trees. In Europe, the most emblematic

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[9] A *secondary pest* or *pathogen* is dependant on the physiological state of its host: it can only colonise weakened plants. On the opposite, a *primary pest* or *pathogen* can establish itself on perfectly healthy and sturdy hosts (Dajoz, 1998).

example of such a “density-dependent population aggressiveness” is the spruce bark beetle *Ips typographus*;

- expended range of consumed plant species. This behaviour is quite common in generalist herbivore species with irruptive population dynamics (Rossiter, 1987). In Portugal for instance, the pine processionary moth *Thaumetopoea pityocampa* (Lepidoptera, Notodontidae) can, when its populations are extremely high, colonise *Acacia* spp. (M.R. Paiva 2000, pers. comm.)!

Despite the extent of the damage observed in the Walloon beech stands, the beetles involved in the beech disease have therefore remained secondary pests, revealing underlying phyto-sanitary problems: their biology did not changed at all.

5.2.4. The role of fungi

Whatever the status of the insect pests involved in the beech disease may be, the countless galleries that they dug, as well as the frost-induced bark necrosis, permitted wood-living fungi to enter (mainly Basidiomycetes), such as the tinder polypore *Fomes fomentarius.* This is fungi of which some have a considerable wood-digesting ability which is the main cause of the weakening and the breaking of the diseased beech trees. We must however point out that the offending polypores are secondary pathogens that, according to Battisti (2004, pers. comm.) and Nageleisen (2004, pers. comm.), can only establish themselves on weakened trees or, regarding non stressed trees, on individuals presenting relatively important bark lesions. We understand in this way that the trees attacked for the first time in 2001, on which the only gateways for the fungi spores were the tiny orifices of the beetles galleries, could only have been colonised by fungi due to their loss of sturdiness. Once these trees recovered, a lot of them managed to heal the wounds caused by the beetles and the development of fruiting bodies was prevented or stopped (in 2004, no polypore visible on ca 50% of those trees; cf. §5.2.1.). These elements show the strictly secondary character of the pathogens involved in the beech disease. Another conclusive element of the “non-primarity” of the beech associated fungi is the fact that the percentage of trees attacked by these organisms in the stands adjacent to forest reserves (in the Sonian forest for example) or to primary forests (in Central or Eastern Europe) is no higher than in stands that are situated far from such forests (which harbour high levels of fungi populations). If fungi such as *Fomes fomentarius* were primary pathogens that had to be systematically destroyed in our forests, and taking into account the astronomical quantities of spores produced by this species for example, the inevitable wounds present on most trees (wounds linked to other trees or branches falling, to human activities, to game, etc.) should provoke the attack of a high percentage of the latter by these polypores (which *a priori* is not the case).

We will end this paragraph by pointing out that the symbiotic fungi that the *Trypodendron* spp. feed on is an Ascomycetes belonging to the *Ophiostoma* genus. The *Ophiostoma* species taken in beetle galleries in the Ardenne is different from the currently known species and strains of this fungus (Maraite & Carlier 2004). This new species, *Ophiostoma arduennense*, will be described in a future paper (Carlier et al., accepted). According to Maraite and Carlier (in Huart et al. 2003), a considerable aggressiveness should characterise this strain. These researchers even put forward the hypothesis that *O. arduennense* could have had the effect of “preparing the ground” for the lignivorous fungi by weakening the colonised beech trees. It is difficult to verify this hypothesis and, if we could, to know to what extent *O. arduennense* contributed to reinforce the stress evoked previously (frost and root anoxia). In France however, the INRA (National Institute for Agronomic Research) carried out tests with some strains apparently very similar to the species found in Belgian beech stands (Huart 2003, pers. comm.) : it seems these strains have little (if any) effect on the trees vigorousness. Furthermore, the healing phenomenon observed on numerous trees attacked for the first time in 2001 (healing by the trees after they recovered their sturdiness) tends to show that the hypothetical role played by *O. arduennense* inoculated by the beetles is less important than the one played by the climatic stresses of 1998 and 2001.

5.3. Aggravating elements

As mentioned earlier, independently of the climatic stresses of 1998 (frost and cold winds) and of 2001 (heavy rainfalls), certain elements probably contributed towards the weakening of the beech stands[10]. Within these factors, there are:

- the storms of the 90’s that unsettled certain trees and damaged their root system;
- repeated shortages in water supply during several summers preceding the crisis, sometimes combined with unusually high temperatures (as shown in Bréda et al. 2004 for Northern France). Many authors (e.g. Peterken & Mountford 1996, Stribley & Ashmore 2002) documented the conspicuous and long-lasting effects that drought may have on beech sturdiness. Concerning this type of stress, poorly drained acidic soils still worsen its consequences (Power et al. 1995);
- acidic soils, which have been shown to sensitize beech trees to atmospheric pollutant (Ling et al. 1993); acidic soils represent the prevailing edaphic conditions of the Ardenne;

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[10] For a brief analysis of the impacts of climatic stresses (wind, drought, frost, high temperatures, …) on forest tree sturdiness and physiology, see Aussenac & Guehl (1994).

- soil compaction problems linked to logging. Several studies carried out in Belgian beech stands shown that mechanised harvesting lead to significant changes in both physical and mechanical soil properties (Rohand et al. 2003), as well as to "rapid soil degradation through active hydromorphic processes" (Herbauts et al. 1996). Polomski & Kuhn (2001) even consider that "diseases caused by soil compaction, harvesting or other human-induced injuries are far more important causes of damage to the stability of roots and root systems than damage caused by soil acidification or environmental pollution". A brief review of soil compaction effects is presented in de Paul & Bailly (2005).

Regarding environmental pollution, it is worth to note that in highly industrialised countries as those of Western Europe, the atmospheric deposits of nitrogen reach high levels for many years, as a consequence of human activities. On the one hand, some studies showed that soil-nitrogen imbalance can sensitise beech trees to frost (Jonsson 2000a,b). The considerable atmospheric nitrogen deposits recorded in west European forests could thus have, to an extent that it is not possible to estimate, predisposed the beech stands to frost damage. On the other hand, Fluckiger & Braun (1998 & 1999) also revealed that excessive N deposits may, notably through complex mechanisms leading to changes in the ratio between N and other nutrients in the plant tissues, sensitize trees to attacks of some pests and pathogens. Regarding beech trees, these authors mention sensitization to fungi and Aphids attacks.

Among the factors supposed to have weakened the trees, decaying mosses are also suspected to have reinforced the effect of the frost (since a strong correlation was found between the presence of decaying mosses and Scolytid attacks). Indeed, dense moss present on many beech trees contained important quantities of water which, once frozen, may have had a cold-mass effect (reinforced by the wind). It is also plausible that, beyond this effect, these stressed and decaying mosses (they were most of the time discoloured) also increased the attractivity of the trees, by releasing semiochemicals of which some could have enhanced the response of the beetles (ethanol for instance). Unfortunately it has not been possible to verify this hypothesis.

Finally, (sub-)cortical tissue discoloration have been observed on many beetle-attacked beech trees. The origin and nature of these necrosis, as well as their role in the beech disease, are unfortunately unknown. Nonetheless, Zwolinski et al. (1995), studying completely different ecosystems, evidenced the facilitating role of fungi-induced cambium necrosis in bark beetles colonisation of stressed pines. A similar phenomenon maybe worsened the condition of the Belgian beech trees.

Nevertheless, because they do not only concern *F. sylvatica* but also all the other forest tree species, it is probable that the role played by most of these "aggravating factors" in the starting of the attacks is secondary (if not other pests would probably have manifested themselves on other tree species).

5.4. Role of dead wood and saproxylic organisms in the beech disease

Although mentalities are slowly evolving, numerous foresters are still very wary, or even hostile regarding dead wood, because of the risks of pests outbreaks wrongly associated with the presence of this habitat. It has however been proven that wood that has been dead for 3 to 4 years never constitutes a danger for wood production nor a reservoir for potentially noxious xylophagous pests (Nicolai 1997, Nageleisen 2003, Kappes & Topp 2004). Indeed, the status of pest implies physiological and ethological adaptations that saproxylic insects *sticto sensu* do not have. Therefore, only decaying trees or recently dead wood can be problematic and encourage (at least temporarily) organisms that could potentially affect the timber production function of the forest. Regarding the impact of the pre-existing stock of dead wood in the development and acuteness of the beech disease, it is noticeable that in the Ardenne and Jurassic region the mean stock of dead wood was below 10 m^3ha^{-1}. This very low quantity of dead wood did not prevent the outbreaks of beetles. On the other hand, in a forest reserve of ca 18 ha situated in the Sonian forest, where the total stock of dead wood reaches 150 m^3ha^{-1} for many years, no attack on healthy-looking standing trees was so far observed. Similar observation can be done in primary forests in Eastern Europe where, despite stocks of dead wood equal to several tens, even hundreds of m^3ha^{-1} (Schnitzler-Lenoble 2002, Christensen & Hahn 2005), no proliferation of xylophagous insects or fungi has apparently been observed within living memory (Battisti 2004, pers. comm.).

The beech disease is a good example of this acknowledgement : it is because of the plethora of weakened trees that certain beetles have proliferated in the Ardenne and the Belgian Lorraine. Fig. 15 shows that the damage is limited to these two natural regions, although it has been shown that both *Trypodendron* species involved in the beech disease are present in the six natural regions of Wallonia (see Fig. 19) and that their *presence rates* in the different regions are very similar[11] (Henin et al. 2003a).

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[11] These *presence rates* correspond to the number of traps in which a species was captured, in a given natural region, expressed as a proportion of the total number of traps set up in the same natural region (in the framework of the Scolytids survey described in Henin et al., 2003a,b). Note that the presence of both species in the sandy loam region was evidenced in another context than the survey described in Henin et al., 2003a,b.

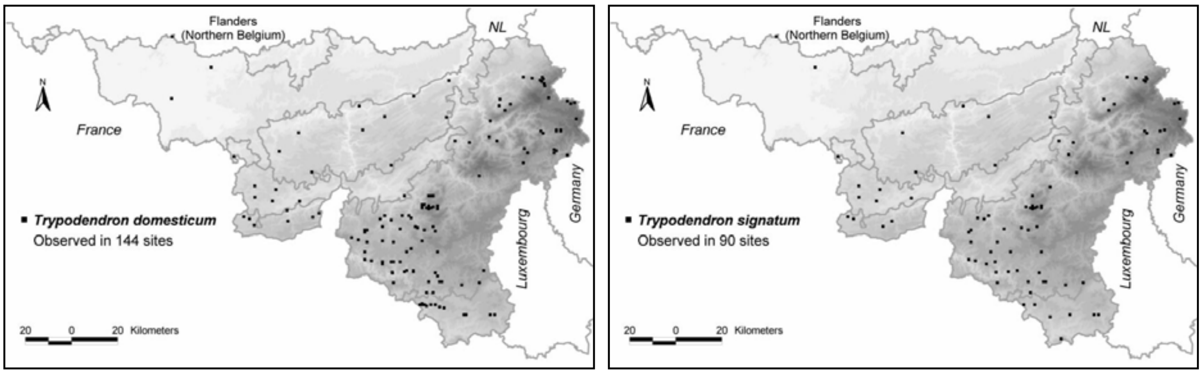

Figure 19. *Observations of the Trypodendron spp. involved in the beech disease, according to a survey carried out in 2001 (from Belgian J. Zool.: see Henin et al. 2003b).*

Moreover, the sampling carried out in the Xylobios paired-stands (2.1.) showed that the levels of *T. domesticum* populations were not significantly higher in stands with high levels of dead wood than in those with small amounts of this substrate (Henin et al., 2004). Nevertheless, regarding this last point, the way a *Trypodendron* spp. population disperses itself from a host or a stand is relatively unknown. Some researchers report for *T. domesticum* flight distances of ca 1 km (Huart et al., 2003). However, it is not clear if this corresponds to an average or to a “nearly maximum” flight distance, covered by only a few individuals. Studying *T. lineatum*, Dyer (1961) estimates that this species “may in some circumstances fly several miles to attack logs”. The percentage of the population that covers those miles, and the circumstances that set off such far scattering are however hazy. In this context, it is not known what proportion of the dispersing beetle population “remains” when moving away from the source tree or stand. Does it fit with a normal distribution, or with a leptokurtic distribution? As these points remains vague, it is difficult to know if, for certain pairs of “Xylobios stands”, stands affected by the beech disease have not constituted sources of *T. domesticum* that homogenised the levels of the populations of this species between the “rich” and “poor stands” (regarding dead wood).

Anyway, while the ecological function of the forest is increasingly highlighted in Western Europe (initiatives such as Natura 2000, the creation of forest reserves or green tree retention, for instance, testify this), the acknowledgement of the secondary character of the pests and pathogens of beech trees is reassuring and confirms that nature conservation and economy are not antagonistic in temperate beech stands (at least for phytosanitary reasons).

5.5. Conclusions and perspectives

We can without any doubt draw up the conclusion that the stocks of dead wood present before the beech disease as well as the saproxylic organisms *stricto sensu* have absolutely not encouraged the apparition nor worsened the acuteness of the beech disease. Regarding the pathogens and xylophagous insects involved in the disease, the numerous researches carried out and the information collected attest their secondary character. The proliferation of these insects and fungi was not "abnormal"; they only revealed under-lying problems (which constitutes the nature of these organisms). The extent of the attacks observed after the climatic accident of 1998 (and probably of 2001, according to the hypothesis described in 5.3) was the result of exceptional circumstances. Outside such periods, the fungi and entomological species involved in the beech disease cannot jeopardize wood productivity in sturdy stands. Therefore it would be useless and illusory to want to eradicate them.

These organisms only becoming problematic when the availability of suitable resources increases heavily, and to a certain extent suddenly, it would be preferable to focus the management policy of their populations on the early detection of the risks of outbreak. Not adopting this policy and waiting for signs of proliferation of pest and pathogen populations to react, as was the case for the beech disease, forces the forest managers into a "fireman" position. On the other hand, the adoption of a strategy aiming to "nip the problem in the bud" could make it possible to minimise the damage as well as the use of treatments. Regardless of financial considerations, such treatments (e.g. mass-trapping thanks to semiochemicals, use of pesticides, etc.) have a negative impact on non-target organisms, because their selectivity is never perfect (Rauhut et al. 1993, Zach 1997, Martikainen 2001, Martikainen et al. 2001, Grégoire & De Proft 2002). In some circumstances, this negative impact is supposed to surpass the benefit resulting from the treatment (from the viewpoint of pest populations dynamics). For instance, two studies dedicated to the pertinence of pheromone-based trapping campaigns of the spruce bark beetle *Pityogenes chalcographus* (L.) pointed out that, in tune with their average prey consumption, the number of *Nemosoma elongatum* (L.) (an important bark beetle predator) caught in the traps would have destroyed several times more bark beetles than were caught in the same traps (Wigger 1993, Baier 1994). Similarly, comparing the effectiveness of different types of pheromone-lures on Scolytids and associated species, Nicolai et al. (1992) report that "*it seems possible that all predators caught in the traps would have had a greater impact on the population of the bark beetles in the field, if not caught*". Without assessing the effect they could have had if left "free", Zumr (1983) also reports the capture of high numbers of bark beetles predators with Pheroprax, a widely used bark beetle lure. Other examples demonstrated, now from an economical point of view, that the expenses realised to control pest populations sometimes exceeded the value of loss reduction. This is the conclusion reached by König (1992) who assessed the opportunity of a pheromone-based mass trapping campaign of *Trypodendron lineatum* Ol. led in Germany. The same author suggests that, concerning non-aggressive pests like *Trypodendron* spp., low efficacy and unfavourable economic balance can make pheromone-based mass trapping unsuitable! Without taking into account the economic aspects of such undertakings, Dimitri et al. (1992) also conclude that "*the population density* [of *T. lineatum*] *could not be substantially influenced by a massive and continuous mass trapping with pheromone baited traps*" (during outbreaks). Besides, this is the acknowledgement generally accepted when considering outbreaking populations (e.g. Payne et al. 1985). In that context, it should have been very useful to leave some forest areas "uncontrolled" (in order to enable a better assessment of the pertinence and efficiency of the measures taken to reduce the consequences of the disease). Use of pheromone-baited traps, of trap trees, sanitary cuttings, rapid removal of infested woody material, etc: which of these measures were the most efficient? Were some of these unnecessary (cost unbalanced by loss reduction)? As all known control techniques have been used together, their individual and global impact is unfortunately difficult to assess. More attention should have been paid to the need to understand as comprehensively as possible this exceptional event and to enable a feedback of what have been done. Some State-owned forests could have been devoted to these Research needs (which in turn could have had positive economical applications in the future). Far from this "integrated" (long term conceived) approach of the problem, the whole panel of control techniques has been set up everywhere it was possible, the only objective being a short term decrease of the economical consequences of the disease. Consequently, when such an event will recur, the future forest managers unfortunately will have to face the same dilemma: what should we do? Do control measure expenses counterbalance loss reduction?

In a more preventive approach, following what already exists in many countries and was suggested by Henin et al. (2003b), it should be judicious to set up in Wallonia an organisation similar to the French "Forest Health Department" (F.H.D.). Such a structure could be devoted to the monitoring of certain pests and pathogens as well as to the collection of some information (climatic for example) which could make possible the early detection of problematic situations. A F.H.D. would enable forest managers to optimise the management of crises such as the one that happened in the Walloon beech stands, and maybe to reduce their impact. In this perspective, we must point out that Wallonia has already got a network of forest sample plots covering the whole of the Region. Essentially aimed at evaluating and characterising the stock of wood material present in the forests of Wallonia, the Walloon Permanent Forest Resources Inventory (W.P.F.R.I.) presents a considerable potential for the follow-up of the sanitary state of these biotopes. With a total of ca 11 000 permanent plots (whose installation will be achieved in a near future), it is a representative sample of the Walloon forest that is therefore regularly checked by the technical staff of the W.P.F.R.I. team. Each plot of this network being accurately characterised at topographical, phytosociological, silvicultural, pedological and biological levels (dead wood…), the W.P.F.R.I. would be a relevant tool for putting in relation the characteristics of stands with their sanitary state and to evaluate their sensitiveness to certain problems, permitting therefore to better understand the determinism of the latter. The beech disease has given the opportunity to use the W.P.F.R.I. for the first time with an objective of following the health of the stands and evaluating the damage. In this context, the set up of a F.H.D. should include some expertise in inventories methodology.

6. MODELLING DEAD WOOD AND LEGACY TREE RETENTION IN RELATION TO VARIOUS FOREST MANAGEMENT PLANS, WITH IMPLICATIONS FOR FOREST PRODUCTION LOSS (WP6)

The WP6 initially planned the development of a model that could simulate coarse wood debris (CWD) accumulation according to different management scenarios of hardwood stands.

In the literature concerning biodiversity, CWD management is however often considered in parallel with the retention of green or legacy trees[12] (LT). Indeed, among other important roles, CWD and LT have been shown to support tremendous number of species and therefore highly enhance the diversity of many taxonomic groups such as birds, invertebrates, lichens, etc. (Harmon et al. 1986, Speight 1989, Branquart et al. 2004). It has thus been decided to integrate both types of habitat in the proposed model.

This model can be used in the framework of multifunctional management plans as it enables to assess the proportion that retained CWD and LT volumes represent versus wood production[13]. These proportions can be considered as economical indicators of the "sacrifice" that CWD and LT retention represent. Since these economical indicators also depend on other factors (site productivity, wood quality, wood trade market …), it will be assessed on a relative basis.

Because of the short duration of the project (in comparison with the studied phenomenon), the model is relatively simple and is mainly based upon data gathered in the literature. This model is presented in § 6.1., whereas the relationship between the model and the economic indicators is developed in § 6.2. An application of the model is presented and discussed in § 6.3. This example concerns an oak stand and includes an estimate of productivity loss as a function of CWD and LT volumes. We conclude with some recommendations (§ 6.4).

6.1. Simulation of CWD and LT retention

6.1.1. Introduction

The model comprises three parts. The first one estimates the growth of living stems. The second one handles the designation of LT and the application of a tree mortality

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[12] We call *legacy trees* the trees which will not be harvested but will be maintained in site for ecological purposes, becoming over mature trees and finally dead wood.

[13] In this chapter, the commercial and economic consequences of not harvesting a part of the trees for ecological purposes (CWD and LT) will be called *loss of* (*stand – wood*) *production*, *production loss* or *productivity loss.*

rate (in order to assess CWD input rate). Finally, the third part describes the decay process of CWD. The model is designed to run on the basis of the silvicultural cycles (corresponding to the periodicity of selective cuttings).

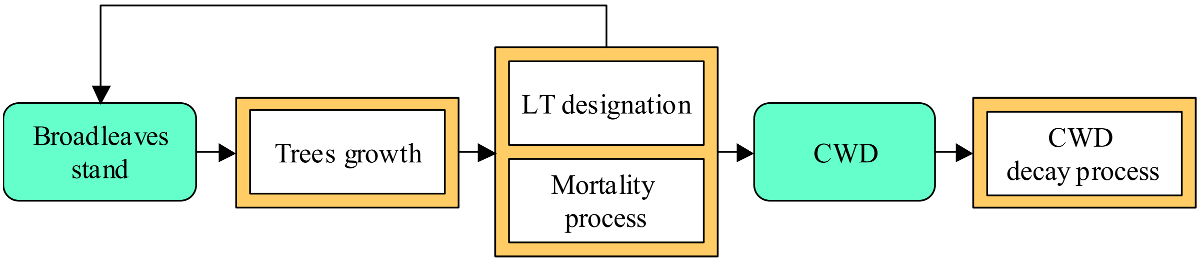

Figure 20. *Relationship between the different parts of the model.*

Most of the CWD models described in the literature are designed to run on a long period of time (from one to several centuries), so as to take into account the progressive effect of different management regimes (Mellen & Ager 2002, Ranius et al. 2003). Considering the available data and the irregular structure of the stands, we have estimated that this approach was not feasible, namely because of the difficulty to forecast the natural regeneration installation in these stands (Lejeune 1994). The model application will thus be restricted to a short period of time (8-12 years), and the impact of CWD and LT retention on wood production will be estimated at the same scale of time.

Even if this model is applicable to different types of broadleaved stands, the availability of data has constrained us to focus its calibration on oak stands. Nevertheless, we also mention some bibliographical data on CWD decay process for beech wood.

6.1.2. Growth model

The growth model has a very simple form since it considers that girth growth only depends on the tree species and on the site productivity of the stand. Growth is thus considered independent of tree size or stand density. This simplification do not compromises the accuracy of the model since correlations between girth increment and stand or tree variables are very low in the case of uneven-aged hardwood stands like the ones we have considered (Lejeune 1994).

6.1.3. Mortality of trees and designation of legacy trees

As the designation of legacy trees directly depends on the forester, this part of the process has been included into the model parameters. It can thus be fixed by the user.

It is very difficult to estimate the average rate of tree mortality in managed stands without an inventory whose duration exceeds the one of the project (Ranius et al. 2003). Hence, to have a rough estimate of the quantity of standing dead trees in oak stands, we used data derived from management inventories. We have therefore considered that the observed dead trees died during the period going from the last selective cutting to the date of the inventory (10 years). This approximation is relatively rough as some dead trees probably have been harvested during intermediate sanitation cuttings (no data recorded for this operation). Moreover, our estimate doesn't include natural disasters (storms, diseases, pest outbreaks …), which are known to account for an important part of the global tree mortality over long time scales (Attiwil, 1994). Table 14 presents the mortality model for oak stands. The inventory on which this model is based is described in appendix 36.

Table 14. *Estimate of annual mortality rate (% of number of trees) in oak stands, according to girth class.*

gbh[14] (cm)	Annual mortality rate (%)
40 - 150	0.08
150 - 240	0.25
≥ 240	1.00

6.1.4. Decay process of CWD

Most models describing the decay process of CWD consider different decay classes and the mean residence time of the stems in each class (Kruys et al. 2002). Most documents we found on beech and oak CWD decay process only provide global decay durations and do not differentiate decay classes (Table 15). Comparing these different estimates, we finally considered, in a first approach, a total decay duration of 30 and 80 years, for beech and oak respectively.

6.1.5. Presentation of the model

The model of simulation is developed in an Excel worksheet. This worksheet gathers the different sub-models, the input data (forest inventory) and the model parameters (growth rate, cutting pattern, cutting interval, wood decay time …). The period of the simulation corresponds to the cutting interval, which typically ranges from 8 to 12 years in the studied stands. Fig. 21. gives an overview of the simulation model structur

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[14] gbh: girth at breast height.

Table 15. *Estimates of the duration of the decay process for beech and oak stems.*

Species	Diameter	Decay duration	Reference
Oak	> 30 cm	> 50 years	KOOP et al. (1990, in VAN HEES & CLERKX 1999)
	10, 20, 30 and 40 cm (stems)	≈ 35, 45, 60 et 90 years respectively	VAN HEES & CLERKX (1999)
Beech	10 to 60 cm (logs)	20 - 35 years (≈ 3 more years by 10 cm of diameter increment)	VAN HEES & CLERKX (1999)
	> 30 cm	30-40 years	KOOP et al. (1990, in VAN HEES & CLERKX 1999)
	« large trunks »	≈ 30 years	KOOP & HILGEN (1987)
	Not mentioned	≈ 40 years	MÜLLER-USING & BARTSCH (2003)
	Not mentioned	40-45 years	ÓDOR & STANDOVÁR (2003)
	Not mentioned	≈ 50 years	CHRISTENSEN & VESTERDAL (2003), KRAIGHER et al. (2003)

6.2. Impact of CWD and LT retention on productivity loss

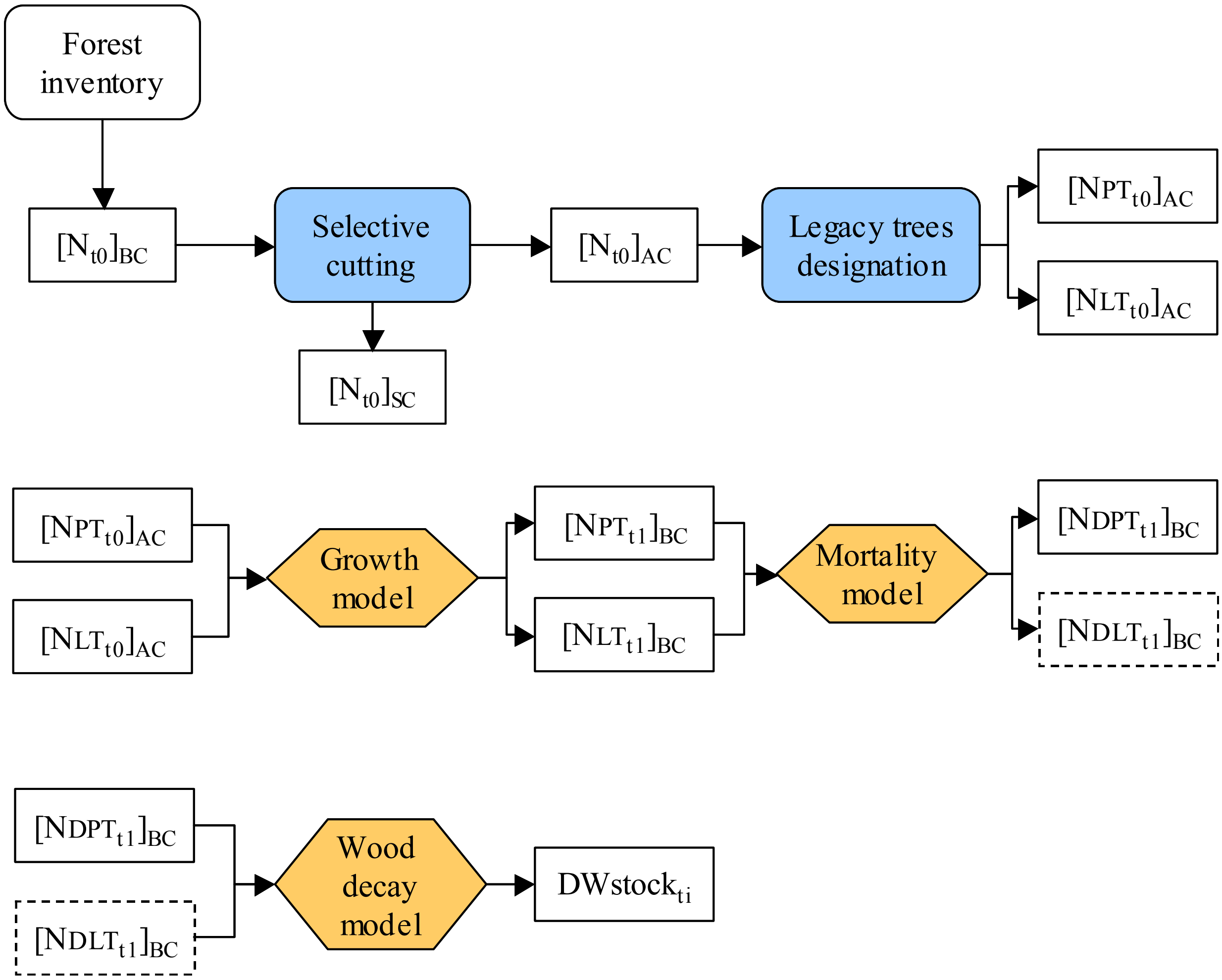
One of the main concern of forest managers regarding CWD and LT retention is the financial impact of these measures. Consequently, a module that enables assessment of wood production and production loss has been added to the simulation model. The wood production model estimates the merchantable volume (VMERCH), which corresponds to the amount of wood that is considered saleable (≈ stem or limb with smaller girth ≥ 80 cm). This merchantable volume can be differentiated in two categories, since the end-product of trees with gbh < 120 cm will be essentially used as fuel or pulp wood. Production loss has thus been also assessed for merchantable volume of trees with gbh ≥ 120 cm (VMERCH120+).

The table 16 presents the formulas used to compute the wood production and productivity loss from the raw data delivered by the simulation model.

6.3. Application of the simulation model

6.3.1. Introduction

To illustrate the use of the model, the impact of LT retention (1, 2, 3 or 4 trees/ha) and of CWD accumulation (1, 2, 3 or 4 trees/ha) was simulated in an oak stand.



Legend:

Symbol between brackets represent vectors of numbers of trees par girth class (/ha)

$[N_{t0}]_{BC}$: number of trees in t0 before cutting

$[N_{t0}]_{AC}$: number of trees in t0 after cutting

$[N_{t0}]_{SC}$: number of trees removed in t0 by selective cutting

$[NPT_{t0}]_{AC}$: number of productive trees in t0 after cutting

$[NLT_{t0}]_{AC}$: number of legacy trees in t0 after cutting

$[NPT_{t1}]_{BC}$: number of productive trees in t1 before cutting

$[NLT_{t1}]_{BC}$: number of legacy trees in t1 before cutting

$[NPDT_{t1}]_{BC}$: number of productive trees dead in t1 before cutting

$[NDLT_{t1}]_{BC}$: number of legacy trees dead in t1 before cutting

$DWstock_{ti}$: volume of dead wood stock (m³/ha) in ti

Figure 21. *Schematic representation of the simulation model.*

Table 16. *Equations used to derive increment, wood production and production loss from data produced by the simulation model.*

$$\mathrm{INCR}_{tot} = \frac{V_{t1BC} - V_{t0BC} - V_{IGt01}}{t1 - t0} \qquad \textbf{[eq 6.1]}$$

$$\mathrm{PROD}_{tot} = \mathrm{INCR}_{tot} + \frac{V_{IGt01}}{t1 - t0} \qquad \textbf{[eq 6.2]}$$

$$\mathrm{PROD}_{net} = \mathrm{PROD}_{tot} - LV_{LT} - LV_{DT} \qquad \textbf{[eq 6.3]}$$

$$LV_{LT} = \frac{V_{LTt0}}{\overline{LD}_{LT}} + \left(V_{LTt1} - V_{LTt0}\right) \qquad \textbf{[eq 6.4]}$$

$$LV_{DT} = \frac{V_{DPTt1}}{WDD} \cdot \left(1 - DT_{rec}\right) \qquad \textbf{[eq 6.5]}$$

$$V = \sum_{j=1}^{m} n_j . v_j \qquad \textbf{[eq 6.6]}$$

Legend :

INCR_{tot} : **Total volume increment (m³/ha/year) of trees with gbh > 40 cm**

V_{t0BC} , V_{t1BC} : **Stand volume before cutting at time = t0 or t1 (m³/ha)**

t1 – t0: simulation model time interval (equal to cutting interval)

PROD_{tot} : **Total wood production (m³/ha/year)**

V_{IGt01} : **Volume corresponding to ingrowth during t0-t1 period (m³/ha)**

PROD_{net} : **Net volume production (m³/ha/year)**

LV_{LT} : **Production loss due to legacy trees retention during period t0-t1 (m³/ha)**

LV_{DT} : **Production loss due to CWD accumulation during period t0-t1 (m³/ha)**

V_{LTt0} : **Volume of legacy trees in t0 (m³/ha)**

V_{LTt1} : **Volume of legacy trees in t1 (m³/ha)**

$\overline{LD}_{LT}$: **Mean life span of legacy trees (years)**

V_{DPTt1} : **Volume of dead productive trees in t1 (m³/ha)**

WDD : **Wood decay duration (years)**

DT_{rec}: Dead trees recovery rate [0,1]

V: generic representation of volumes calculated at the stand level

m: number of girth classes considered in the trees distributions

n_j: number of trees in class j of a trees distribution

v_j: individual volume of a tree whose girth corresponds to the central value of class j

6.3.2. Initial stand and model parameters

The data characterizing the initial stand are derived form the inventory described in appendix 36. The parameters used in the model are described in table 17. The growth parameters, the ingrowth and the cutting intensity are based upon information delivered by the local forest manager.

Table 17. *Model parameters used in the example.*

Growth model :

- **girth increment (oak) : 1.1 cm/year**
- **girth increment (other) : 1.5 cm/year**
- **ingrowth : 5 trees/ha/year**

Selection cutting intensity :

- **18 % (of total volume)**

Mortality model (annual morality rate according to gbh class) :

- **40-150 cm : 0.1 %**
- **150-240 cm : 0.25 %**
- **≥240 cm : 1 %**

CWD decay process

- **decay duration : 80 years**

LT retention pattern

- **150 cm : 40 %**
- **170 cm : 25 %**
- **190 cm : 15 %**
- **210 cm : 12.5 %**
- **230 cm : 5 %**
- **250 cm : 2.5 %**

LT life span

- **150 years**

6.3.3. Results

Tables 18 and 19 present the main results of the simulation. Four levels have been computed for the amount of LT and dead trees: from 1 to 4 trees per ha. It is important to notice that the relative loss of production is by far more important if we consider trees that have a real economical value (VREC120+).

In the case of dead trees, the recovery rate explains the proportion of dead trees that are nevertheless harvested and thus do not participate in CWD accumulation.

Table 18. *Impact if LT retention (LT in stems/ha) on production for an oak stand: total volume of living LT (VOL in m³/ha), loss of production (in %) for total merchantable volume production (VREC) and for merchantable volume production of trees with gbh > 120 cm (VREC120+).*

LT (trees/ha)	VOL (m³/ha)	Loss of production (%)	
		VREC	VREC120+
1	2.2	1.08	2.53
2	4.5	2.16	5.07
3	6.7	3.23	7.60
4	8.9	4.31	10.14

Table 19. *Impact of CWD accumulation (CWD in trees/ha) on production for an oak stand: total volume of CWD (VOL in m³/ha), recovery rate (in %), loss of production (in %) for total merchantable volume production (VREC) and for merchantable volume production of trees with gbh > 120cm (VREC120+).*

CWD trees/ha	VOL (m³/ha)	Recovery rate (%)	Loss of production (%)	
			VREC	VREC120+
1	3.6	78	1.16	2.13
2	7.1	56	2.32	4.27
3	10.7	33	4.48	6.40
4	14.3	11	4.65	8.53

6.3.4. Analysis of the sensitivity of the model

Dead trees decay duration and LT life span are important parameters in the model. Because of the numerous biotic and abiotic factors that influence both of them, it is very difficult to have an accurate estimate of their average duration. Hence, the sensitivity of the model has been assessed through a measure of the impact of a variation of these parameters on the simulation results. Fig. 22 presents the relationship between the production loss and these parameters (dead trees decay duration and LT life span) in the case of a simulation considering 2 LT /ha and 2 dead trees /ha. We can see on this figure that the production indicator is more sensitive to the variation of dead trees decay duration than to the variation of LT life span.

6.4. Conclusion and recommendation

A simple simulation model has been developed to evaluate the impact of LT and dead trees (DT) retention on wood production.

An application of this model to oak stand in the Famenne region shows that the relative loss of production ranges from 2.2 % to 9.0 % when both stocks of LT and DT vary from 1 to 4 per ha respectively. If we consider the production loss within the most valuable trees (gbh > 120 cm), it ranges from 4.7 % to 18.7 % for the same range of LT and DT. The difference is obvious if we consider the fact that LT retention only concerns trees with gbh > 120 cm. A sensitivity analysis of the model emphasize the fact that estimated DT decay duration and LT life span play an important role in the accuracy of the production loss assessment.

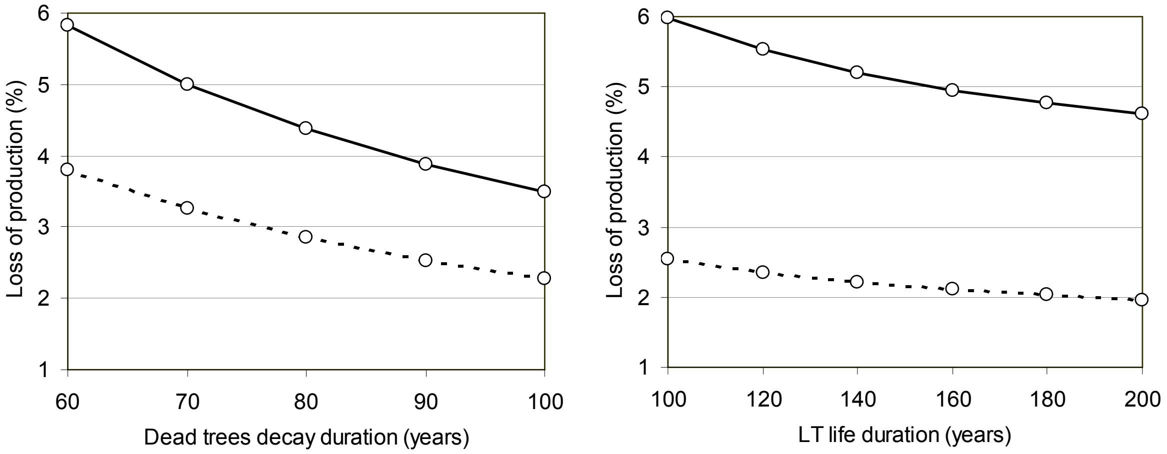


Figure 22. *Relationship between the loss of production and (i) mean decay duration of dead trees and (ii) mean LT life span. These results correspond to a simulation with 2 LT /ha and 2 dead trees /ha. (—○— : VREC120+; ····○····: VREC).*

To pursue the quantitative evaluation of *the* impact of DT and LT retention on wood production in Belgian deciduous forests, it is necessary to settle relevant inventories in order to refine the simulation model. As a result, DT decay duration and LT life span must be more accurately determined.

7. GENERAL DISCUSSION

7.1. The context of the research

Over the past few decades, world-wide efforts directed towards forest species inventories have emphasised the importance of coarse woody debris and microhabitats found on overmature trees for forest biodiversity. In Europe, basic knowledge on wood-dependent species taxonomy, distribution and ecology have improved considerably, allowing overall species numbers to be better estimated. In Finland for example, after a great deal of in-depth investigation across available information, Siitonen (2001) came to the conclusion that saproxylic organisms, those that depend upon wood substrates or upon the presence of other saproxylics for at least part of their life cycle (Speight 1989), would account for as much as 20-25% of all forest species inventoried. Most species-rich groups were macromycetes (1500 species) and insects (1880-2880 species). Nevertheless, a better knowledge of the species abundance and distribution over longer periods of time also revealed the scale of their population decline. Looking at invertebrates, Speight (1989) estimated some 40% of Europe's saproxylic species to be already on the verge of extinction over much of their range while the majority of the remainder would be in decline. In Germany, about 60% of the saproxylic beetle species and 25% of macromycetes are now classified as threatened (Albrecht 1991, Geiser 1986, Schmid 1986). In Finland, 65% of the epixylic bryophyte species are under threat (Laaka 1992). In Belgium, so far, reliable pieces of information on species distribution and population trends have been hardly available for most saproxylic organisms, leaving the basic question "how many species do we have left?" open. Understanding species distribution, on the other hand, is a prerequisite in the process of correctly predicting priority habitats for forest biodiversity.

Meanwhile, the importance of woody debris in promoting the differentiation of the humus layer of forest soils and tree regeneration has been increasingly acknowledged (Harvey et al. 1979, Harmon et al. 1986, Jurgensen et al. 1987, Kuuluvainen & Juntunen 1998). Among factors influencing wood decay, early colonisers like wood-boring beetles and associated fungi have been shown to be especially important in speeding up wood decomposition through their enzymatic and foraging activities (Edmonds & Eglitis 1989). Overall, wood-living organisms, whether they are invertebrates, macromycetes or nitrogen-fixing tiny bacteria, contribute greatly to the recycling of large amount of nutrients through multitrophic interactions (Harmon et al. 1986). This led several researchers like Holub and co-authors (2001) to suggest that the removal of woody debris could potentially reduce the nutrient capital of forest habitats, eventually leading to a decline in site productivity. However, so far, empirical data supporting this possibility are few (and so the unmanaged forests) and controversy still exists about the relative importance of dead wood to forest productivity (Harmon et al. 1986, Spies et al. 1988, Prescott & Laiho 2002).

But for most people, leaving dead wood in the forest is more often seen as a sign of negligence from the forest manager, being thought to promote the development of large populations of herbivorous insects able to cause widespread tree mortality (Vité 1989). This attitude stems mainly from observations, typically from managed forests impoverished in their original tree composition and dead wood supply, that stand hazard and windthrown trees act as major factors determining risk of bark beetle outbreak (e.g., Reynolds & Holsten 1994). However, it does not take into account most recent advances in ecological research, showing how actually fewer of those so-called “pest” insects, like bark beetles, can be found under natural old-growth conditions compared to managed forests, despite several times more decaying wood in the former habitat (Väisänen et al. 1993, Kleinevoss et al. 1996, Martikainen et al. 2000). It also neglects recent conclusions from forest entomologists, that less than 1% of all forest insect species could incur significant economical losses, depending on stand and dead tree characteristics (Nageleisen 2003). From 1999 to 2003, a major outbreak of ambrosia bark beetles (mainly *Trypodendron domesticum*), together with lymexylonids (*Hylecoetus dermestoides*) and lignivorous fungi, spread over most mature beech stands of south-southeast Belgium, causing about 2,000,000 m^3 of beech wood to become depreciated. Although particularly dramatic for local economies, such a spectacular event provides also researchers and forest managers an opportunity to better understand ecological conditions that triggered the beetle population increase and thereby tree mortality. Among practical implications, it is relevant to assess whether the accumulation of woody debris makes individual stands more susceptible to attacks by damaging beetles, with economical consequences, or not necessarily.

Originating from the cautious recommendations of the European Council and the Bern Convention to retard the on-going erosion of biodiversity and link species loss with ecosystem functioning, this project aimed to clarify the ecological and functional values of dead wood habitats (including dead parts of living trees) in Belgian oak and beech forests. Among ecological benefits, we were interested to assess the relative importance of dead woody debris for representative species groups of forest biodiversity such as saproxylic insects, wood-decaying fungi, cavity-nesting birds and bats. At times when numerous beech trees were dying over a large part of Wallonia, we wanted to see whether the development of large populations of damaging beetles in individual stands was causally related to a high dead wood supply, or if perhaps other factors would as well come into picture. Among benefits for forest functioning, the possibility that a high supply of decaying wood on the forest floor could affect the geochemistry of the soil upper layer, with implications for plant growth and stand productivity, needed some clarification. From a management perspective, retaining overmature and dead trees for biodiversity implies some loss of production for the forest owner, which should be taken into account when trying to optimise wood production at minimal costs.

7.2. Ecological and functional benefits of dead wood: a brief summary

Focusing on 22 forest stands organised by pairs that were best separated by their overall dead wood supply (high or with: 55 m^3 ha^{-1} vs. low or without: 12 m^3 ha^{-1} on average), we found the amount of dead wood to be highly beneficial for saproxylic insect, wood-inhabiting fungi and forest bird species diversity. Among insects, species richness in saproxylic beetles and in particular wood-living beetles were close to or significantly higher in stands with dead wood, respectively. The abundance of saproxylic beetles was markedly (significantly or close to) higher in the presence of dead wood, whether they were living on polypores, inside the wood or in well-decomposed woody debris, feeding on fungi, wood or animal resources. At family level, sites classified with a high dead wood supply hosted for example more species of longhorn beetles and more saproxylic individuals such as longhorn, click, and monotomid beetles. By contrast, the number of non-saproxylic beetle species and individuals did not differ between stand categories. The number of fungi species, including polypores and species with a high indicator value of beech forest naturalness in BENELUX, was much higher in beech stands with a high dead wood supply. Finally, the bird fauna was more diverse and abundant in the presence of dead wood. Only bat species richness did not change in relation to the dead wood availability, but this may be an outcome of the limited sampling effort, besides the inherent difficulties of doing night survey. Still, in those stands that we classified as with a low dead wood supply, the average dead wood value (12 m^3 ha^{-1}) was relatively higher than what is usually found in Belgian forests (e.g., for beech and oak, about 6 m^3 ha^{-1} and 7.5 m^3 ha^{-1} on average in Wallonia, IPRFW, 2006).

The total amount of bark beetles was found significantly ($p = 0.041$, with year as a replicate) different between pair stands (with vs. without dead wood), being higher in the presence of dead wood (although the level of difference was rather small). Among bark beetles, the population level of the potentially most damaging bark beetle *Trypodendron domesticum* (see WP5) was significantly higher in stands with dead wood. However, when comparing their populations among stands with dead wood, bark beetles, and especially ambrosia beetles such as *T. domesticum* were not more numerous in stands with a dead wood volume above 50 m^3 ha^{-1} in comparison to those with less woody debris. Among the most species-rich families we studied, only saproxylic click beetles were more abundant above 50 $m^3 ha^{-1}$ of dead wood. Results from multivariate analyses suggested that, among stands classified as with dead wood, those with numerous large trees (high SG40, SG60, SG80) supported more bark beetles. On the other hand, stands with large trees were also typically dominated by beech trees, and so with few other tree species, raising the possibility whether bark beetle abundance may have resulted from a concentration of resources rather than a tree size effect per se. High population levels of bark beetles in those stands with numerous large-diameter beech trees may also be a partial outcome of population changes operating on larger scale, since the study was being carried out at the end of a massive outbreak of *T. domesticum* over southern Belgium.

We found less acidic conditions and a higher availability of nutrients (phosporus) in the upper soil layer of stands with dead wood. However, this relationship did not hold anymore when excluding from the analyses the forest of Kerselaerspleyn (the study site with the largest amount of fallen dead wood – 108 m^3 ha^{-1}, including 24 m^3 ha^{-1} in the most advanced stage of decay). At the other sites, the estimated average amount of fallen dead wood was 11 m^3 ha^{-1} (1.8-42.3), with only 1.4 m^3 ha^{-1} (0.1-4.4) in friable decay conditions. Thus, perhaps the importance of nutrient dynamics at the wood-soil interface is more likely to be emphasised in habitats where the amount of well-decomposed woody debris (i.e., with bark loose or absent and the wood structure soft and friable) on the forest floor is large enough to allow any measurable effects. In the strict forest reserve of Kerselaerspleyn for example, the amounts of K, P, Ca, Mn, and Mg were significantly higher and soil acidity lower near large decaying beech logs (0.1 m distance) compared to levels 5 m away from the trunks. Interestingly, we found that the level of variation for some of our soil fertility estimates (pH, K, P, Al) that was significant along 15 year old logs levelled off for 22 year old trees. Inversely, differences in the amounts of Ca and Mg with the distance from the logs were even steeper after 22 years of decay.

7.3. Implications of the results for biodiversity and forest management

Several management guidelines can be drawn from our results, aiming to conciliate the sustainable use of temperate forests with the restoration of its original biodiversity. It is however relevant to remember that, in our study plots, most of the dead woody debris available was there since only recently, originating from storm events in the early 90s, and that old trees with large diameter trunks such as oaks were particularly few or missing. Loss of the microhabitat continuity can be especially serious for those saproxylic organisms with limited dispersal capabilities, such as those associated with the stable microhabitats of overmature trees, or species that depend on temporary conditions of wood decay. It is thus likely that the present-day communities we sampled, especially insects and wood-decaying fungi, were historically impoverished, with just a few relict populations having survived in a handful of localities over the landscape (Fayt et al. 2006). A consequence of this could be a progressive mismatch between dead wood and old tree variables and species distribution.

At stand level, the number of saproxylic insect species and individuals was positively influenced by the dominant tree species (oak), tree average diameter, various dead wood estimates, the number of tree species, or stand openness (herb cover), depending on the species dietary and habitat preferences. In general, saproxylic beetle species richness benefited more from the presence of numerous trees species dominated by oaks and stand openness (i.e., with a well-developed and species rich herb layer providing abundant floral resources), while beetle abundance was rather a function of beech dominance (and in turn tree size) and dead wood supply.

Nevertheless one of the major findings of our study was that stand variation in saproxylic insect composition was additionally much affected by the composition of the surrounding landscape. Low numbers of saproxylic species and individuals were associated with stands embedded in conifer-dominated forest landscapes, even though woody debris or large trees were present. Conversely, the extent of deciduous tree cover in the surrounding had a major positive impact on local species richness and abundance, whether they were bark-, wood-, and polypore-visitors, or relying upon fungi, wood, or other insects for food. Caution is however needed when considering the apparent negative impact of surrounding coniferous forests on local saproxylic assemblages. Indeed, most spruce forests, when planted in the early 20th century, did not actually replace deciduous forests but covered mainly open areas (heaths, peatbogs,…). Hence, the percentage of coniferous stands in the surrounding may rather be used as an indirect indicator of the actual proportion of deciduous forests (and thereby of the likely level of habitat spatial continuity) that has been available in a landscape since a few hundred years, without having a detrimental influence in itself. However, our results may also suggest that recent conifer plantations do not improve connectivity between populations, as shown for European hoverflies (Speight 2000).

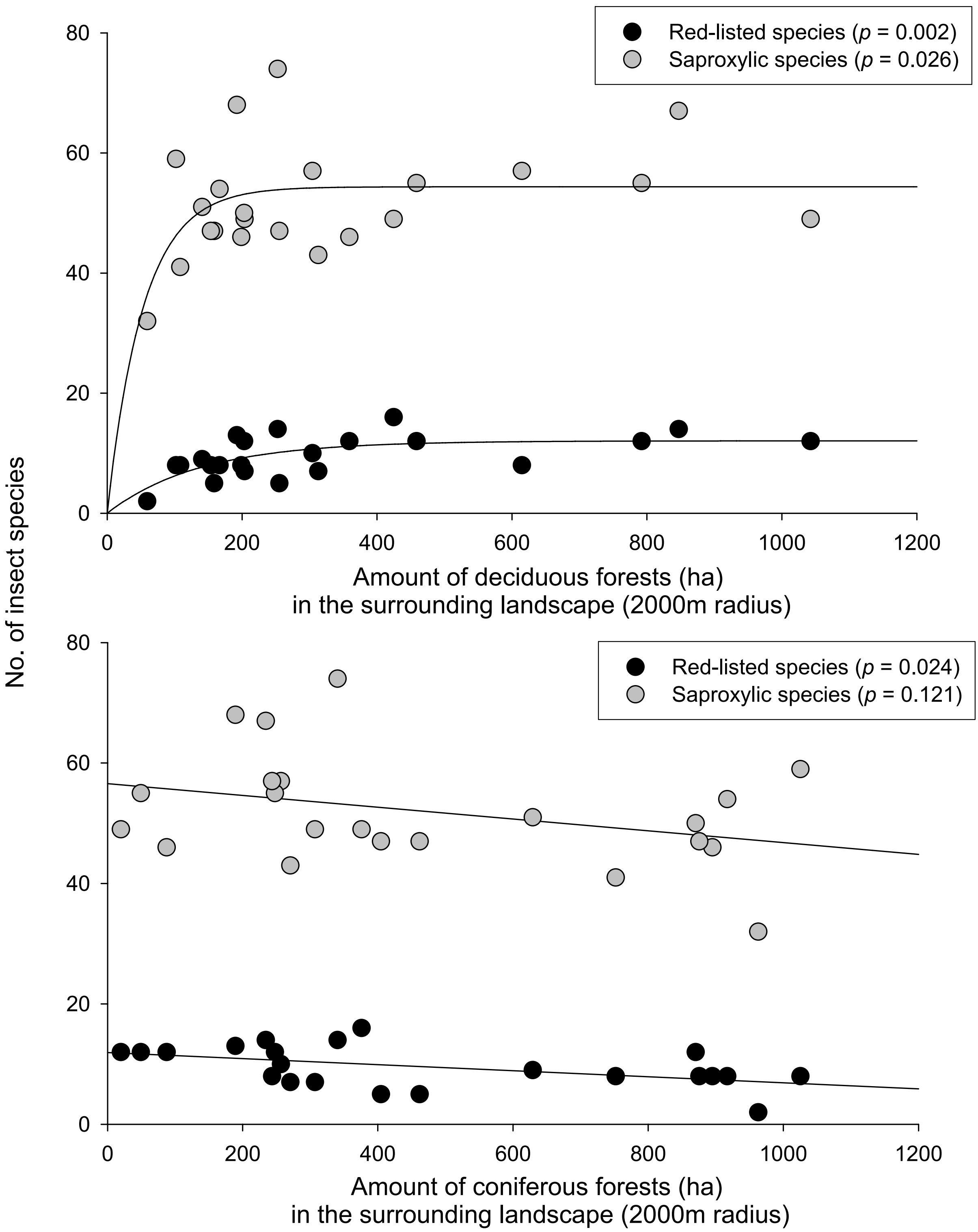


***Figure 23.** Relationship between the number of saproxylic and threatened insect species (beetles + hoverflies) in deciduous stands and the dominant tree composition of the surrounding forest landscape (native deciduous vs. exotic coniferous trees).*

Considering local saproxylic insect populations as open dynamic systems in space and time, we suggest that the level of landscape original composition and connectivity could be especially crucial for the species distribution and local population persistence (Didham et al. 1996, 1998, Mazerolle and Villard 1999), presumably by influencing dispersal success and propensity of individuals over the landscape (Speight 2000). The importance of landscape composition for local population persistence is supported by the finding that our two descriptors of landscape composition were the only variables to account for variation in the number and abundance of threatened insect species. The fact that 95% of the threatened species were saproxylic remind us however that Belgium is one of those Western European countries that underwent dramatic reduction in their availability of overmature and dead trees over the past centuries (Lemaire 2001, Branquart et al. 2005), reinforcing the potential and long-lasting effects of landscape transformation and fragmentation on local community composition. Results from regression analyses suggest that maintaining a minimum of 300-400 ha of deciduous forests in the immediate surrounding of focal deciduous habitats (here in a 2000m radius circular sample plot) is highly favourable to local saproxylic insect diversity, and in particular to threatened species diversity (Fig. 23). Inversely, the higher is the amount of conifers in the surrounding, the less diverse deciduous remnants become in saproxylic insect species, including threatened ones. Accordingly, we argue that the composition of the surrounding should also be taken into account in the process of identifying stands with a high conservation value for saproxylic insects.

We found dead wood supply to be especially important for wood-decaying fungi species diversity. In beech stands, the more dead wood there was, the more species there were, including polypores and species whose occurrence indicates beech habitats that are important for biodiversity in the BENELUX (Fig. 24). The highest number of species was recorded in the strict forest reserve of Kerselaerspleyn, with 105 species for a dead wood volume of 151 m^3 ha^{-1}. Conversely, as few as 14 species were found below 10 m^3 ha^{-1}. Especially, macrofungi communities benefited from the presence of different indicators of habitat resource continuity, such as woody debris in all stages of decay and overmature trees.

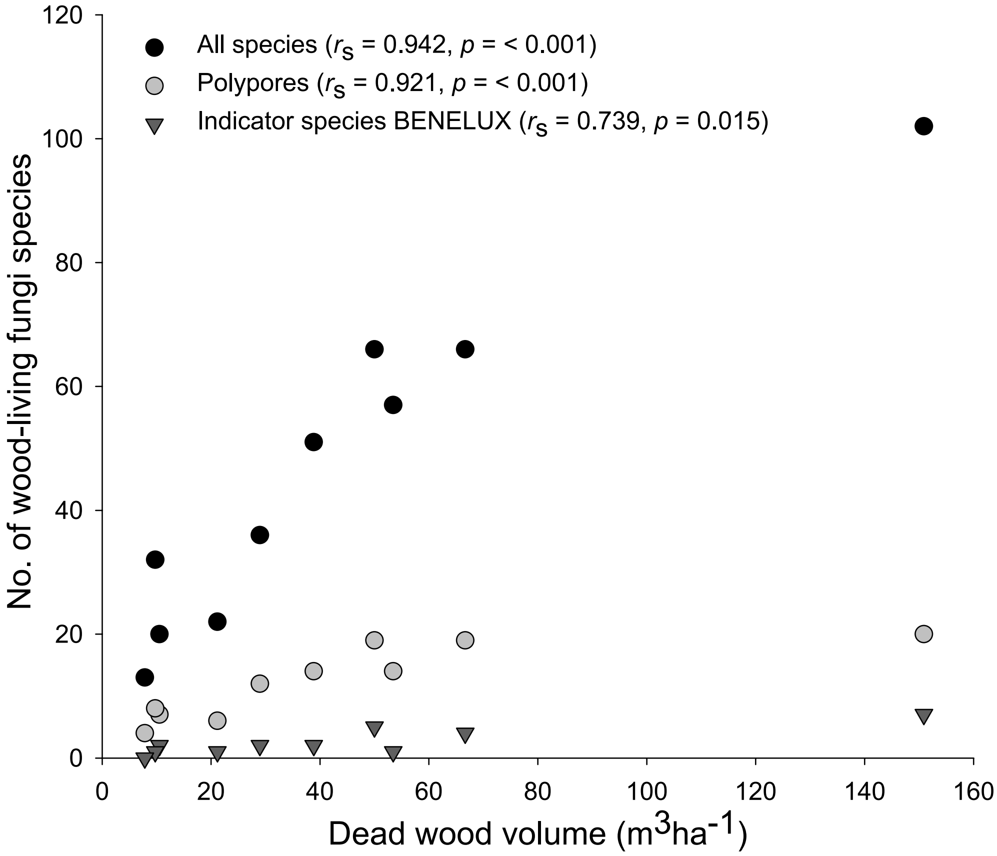


Figure 24. *Relationships between the volume of decaying wood and the number of wood-dependent fungi species in beech stands.*

Interestingly, stands with the highest dead wood values (> 50 m^3 ha^{-1}) did not host more damaging bark beetles than habitats with a lower dead wood supply, demonstrating a lack of conflict of interest between dead wood retention and wood production. In a broader context, the observed Scolytid ambrosia beetles involved in the beech disease were all so-called secondary species (colonising weakened trees) that only took benefits from the particular ecological conditions which followed unusual climatic events. As such, the bark beetles and associated species did not act as the initiators of subsequent tree mortality, but rather as simple consumers of resources (weakened trees) made suddenly available by some external events (temperature stress followed by heavy rainfalls). As mentioned previously, the past mass mortality of beech trees over south-southeast Belgium was an economic catastrophe. From the perspective of the forest biodiversity, on the other hand, this event has provided an opportunity for many specialised species (e.g., light-demanding plants) to take advantage of the newly created but temporary habitat conditions, leading to expected changes in stand tree species composition and structure (Attiwil 1994). Thus, as a matter of fact, the beech crisis may also have given the unfortunate forest owners a possibility to re-orientate their restoration efforts towards stand diversification. Due to strong tree host-specificity among the beetles, it is likely that the presence of various native tree species in forested habitats shall help to alleviate future risks of bark beetle outbreak following extreme weather circumstances, in addition to major benefits for most components of forest biodiversity.

Among vertebrates, cavity-nesting birds form a group of species that is structured by keystone interactions and processes (Bednarz et al. 2004), meaning that forest management strategies taking into consideration the maintenance of species diversity must recognize and retain these complex multispecies processes.

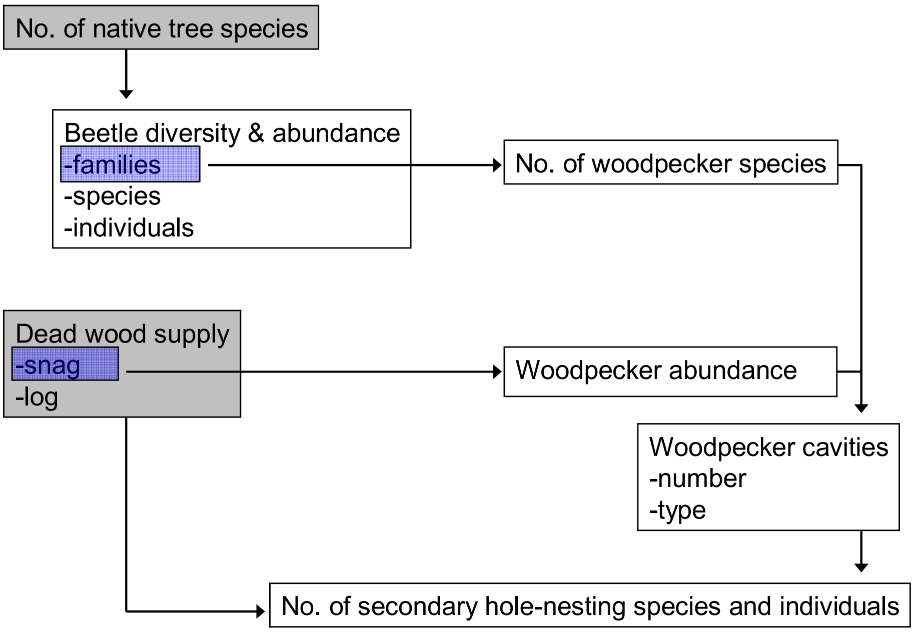


Figure 25. *Diagram showing how the number and abundance of hole-nesting bird species is closely dependent on compositional and structural habitat properties that are typical for old-growth deciduous forests.*

We found the availability of woodpecker cavities to explain most of the variance in forest bird diversity. Typically, stands with numerous bird species (hole-nesters and others) had many native tree species, a high supply of well-decomposed woody debris, diverse and abundant beetle families and species, and plenty of woodpecker cavities. High bird density was associated with a high snag volume and supply of woodpecker cavities. As shown on Figure 25, the availability of woodpecker cavities was in turn a function of the number of native tree species and the snag supply, by influencing the number and kind of excavators present in the habitat. A high snag volume and the presence of numerous woodpecker cavities differing in size and condition were especially important for the non-excavating hole-nesting birds, both in terms of number of species and individuals (Fig. 26).

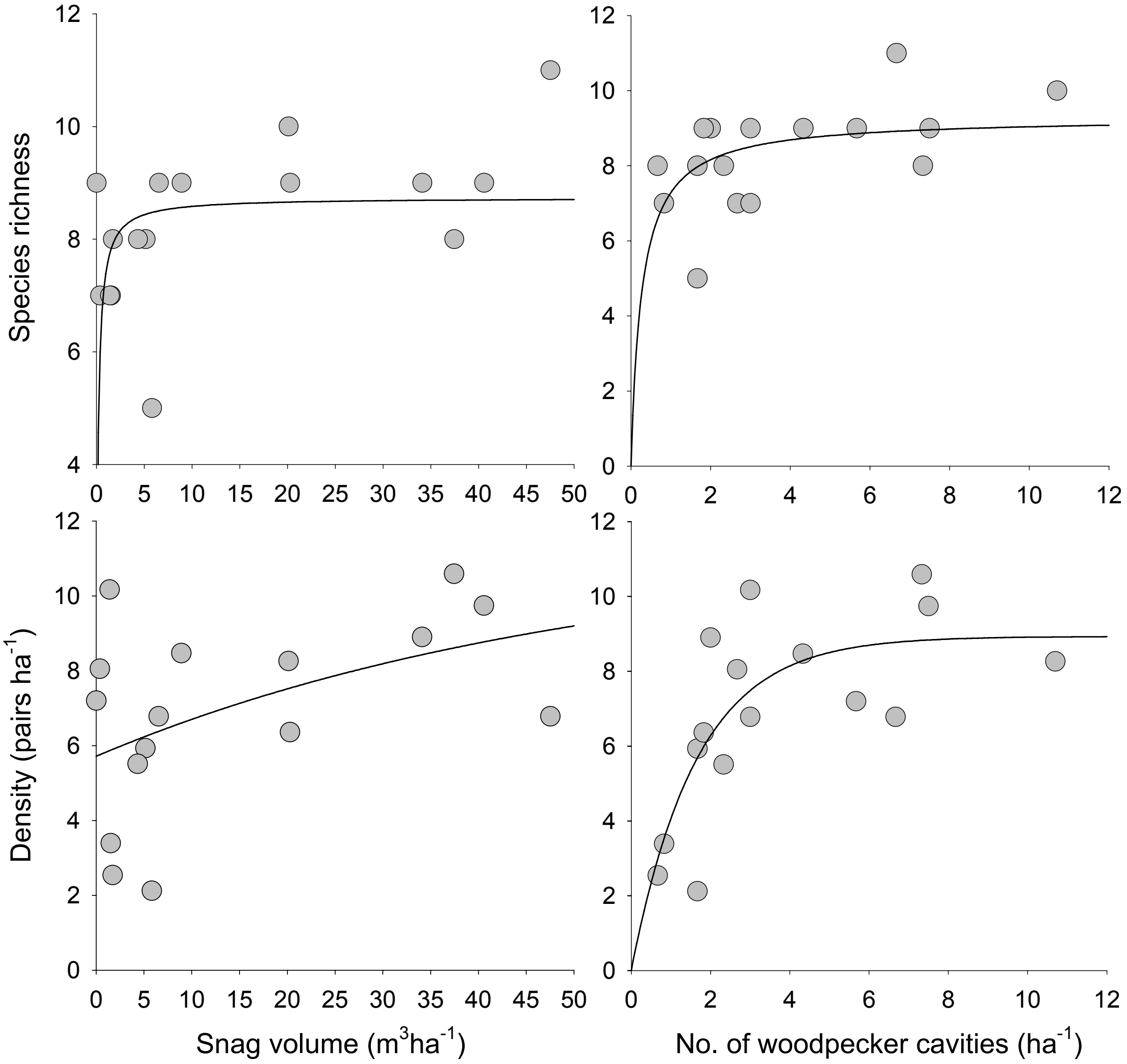


Figure 26. *Number and abundance of secondary hole-nesting bird species in relation to snag and woodpecker cavity supplies.*

Practically, retaining a snag volume between 10-20 m^3 per ha and trees with woodpecker cavities between 4-6 per ha would help to maintain diverse cavity-nesting bird communities in Belgian deciduous forests (Fig. 26).

Thinking of their high mobility, it is without surprise that we found bat diversity to be sensitive to the composition of the forest landscape, with more species in mixed (deciduous/coniferous) forest environments. Among the most likely explanations, mixed forests could offer a larger supply of different kinds of prey than in less heterogeneous habitats. It remains now to be seen what proportions of deciduous and coniferous forests should be in the landscape to maximise local and regional bat species diversity. At stand level, the number of bat species increased with overmature tree availability, most probably because of a higher availability of potential roosting sites (tree cavities and cracks behind bark) in various size and condition with increasing trunk diameter (Dufour 2003, Meschede & Heller 2003).

From the ecosystem functioning point of view, a particularly high volume of well decomposed woody debris on the forest floor (>20 m^3 ha^{-1}) allowed us to find significant changes in the soil upper chemical profile. In one of our study site, it was interesting to see that decaying logs had a positive impact on soil parameters known to limit plant growth, although limited to the immediate vicinity of the trunk. Also, changes in soil chemistry beneath decaying logs seemed to occur relatively rapidly over time, with noteworthy differences between trees that fell down 15 and 22 years ago. Accordingly, even though non-conclusive due to the limited tree sample size, our results suggest that decaying wood on the forest floor should be available in a sufficient amount, distributed all over and accumulate on a regular basis to have a permanent impact on the forest soil global biogeochemistry.

7.4. Conclusions

Besides a better understanding of key ecological factors for various wood-dependent forest taxa, perhaps a major finding of our research is that there exist critical thresholds for those different factors below which risks of population depletion and species extinction are greatly increased. Such non-linear responses of organisms to habitat loss (see Connor & McCoy 1979) are of course species- or group-specific, with threshold values depending on the species ecology, dispersal capability or population structure. Species or group responses will also be scale-dependent, depending on what habitat features are important for their vital demographic parameters, namely their reproduction, mortality/survival, immigration and emigration. Local dead wood supply is one of them, especially for saproxylic insects, wood-decaying fungi and cavity-nesting birds. But evidence suggest also that other factors, maybe not so obvious, can be particularly important in explaining the contemporary distribution of forest biodiversity in Belgium, such as the extent of fragmentation and transformation of its original temperate forest cover into exotic conifer plantations and its likely influence on crucial population processes operating over the landscape.

By providing threshold values for diverse habitat parameters shown to be important for numerous saproxylic species, this project calls for forest management procedures that also take into account their biological requirements in the management plans. Moreover, the retention of key habitats for biodiversity, such as overmature, cavity-bearing or dead trees, does not contradict with wood production for economical purposes, as shown for example by our estimates of soil fertility or bark beetle population size at the highest dead wood volume. As long as they are present in a supply large enough to meet the minimum population requirements of the species.

Habitat features to be retained for biodiversity conservation purposes, such as dead wood or overmature trees, can be incorporated into management plans and their financial impact for forest owners, which can be evaluated by using simulation models that are based on available estimates of tree growth and decay. As a result, the accuracy of the models will depend on how informative the forest inventories are.

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SPSD II (2000-2005)

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SPSD II

A RESEARCH PROJECT TO STUDY PATTERNS, ROLES AND DETERMINANTS
OF WOOD-DEPENDENT SPECIES DIVERSITY IN BELGIAN DECIDUOUS FORESTS (XYLOBIOS)

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