BEETLE DIVERSITY AND HISTORICAL ECOLOGY
OF WOODLANDS IN FLANDERS

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Abstract. Extensive data on the present-day carabid beetle fauna occurring in woods of Flanders were compared with a unique data-set of archaeological carabid remains from a Late and Post-Roman forest at Velzeke (Eastern Flanders), within the framework of a study on the historical ecology of woodlands in Flanders. Integration of these data on 14 woods revealed that most have been significantly impoverished with respect to their stenotopic woodland beetle fauna. The carabid species' diversity is higher in several small and relatively recent woodlands compared to that in larger ancient forests, regardless of whether this diversity is evaluated by rarefaction or by mean species richness per standardised year sample data. This pattern is primarily caused by the presence, in forest fragments, of many species from surrounding open habitats. Typical woodland beetles show a reduced dispersal power (constant brachyptery) and appear to be strongly linked to larger ancient woods. Knowledge of historical ecological factors, other than actual size of the forests, further aids the explanation of the observed ground beetle assemblages in the specific forests or sites. Preliminary results of population genetics, for the eurytopic forest carabid beetle *Abax ater*, showed significant genetic differentiation between populations (due to reduced gene flow) at a relatively large spatial scale, although genetic erosion cannot (yet?) be observed for this species.

Key words: woodland, biodiversity, historical ecology, deforestation events, woodland area, wood exploitation, archaeology, habitat fragmentation, ground beetles (Carabidae), ancient woodland indicators, dispersal power, population genetics, *Abax ater*, region of Flanders

INTRODUCTION

A short history of woodland in Flanders

It is a safe assumption that, at the beginning of the Holocene, there was more woodland in Flanders than there is now. However, the history of woodlands in Flanders cannot be described by a simple model of linear decline, but is characterised by periods of regression and expansion (BLOEMERS & VAN DORP, 1991; TACK *et al.*, 1993; TACK & HERMY, 1998). A first regression period started with the introduction of Neolithic cultures into our regions. At that moment, two processes initiated the decline of the original forest, *i.e.*,

deforestation due to woodland being turned into fields, and degradation due to areas being used as grazing grounds for large herds of domestic animals. The former process had a particularly severe impact during that period, and this is demonstrated by the finds of Neolithic Michelsberg sites (BLOEMERS & VAN DORP, 1991) in areas that are now under forest and which, as is suggested by the absence of younger sites, were never inhabited again.

How woodland evolved during the Bronze and Iron Ages is still largely unknown, but it can be assumed that the processes of forest degradation and disappearance continued, reaching a peak during the Roman period, as a result of large scale agricultural exploitation. After the fall of the Roman Empire, political instability caused a reduction of the human population and a decline of agricultural exploitation. Therefore, during the Early Medieval period, woodland recovered to a certain extent. During the High Middle Ages, however, renewed deforestation took place (VERHULST, 1990), in many cases precisely in those areas that had become woodland again during Early Medieval times.

From the end of the 13th century onwards, gradual deforestation was occasionally interrupted by renewed cultivation of woodland, mostly for economic purposes, such as the demand for firewood. During the 19th century, a final large scale deforestation took place in Flanders. As a result, woodlands in Flanders nowadays are extremely fragmented and/or reduced in size (compare Fig. 1 around 1000 AD, before the extensive Late Medieval deforestation, and Fig. 2 based on a recent map for Western and Eastern Flanders).
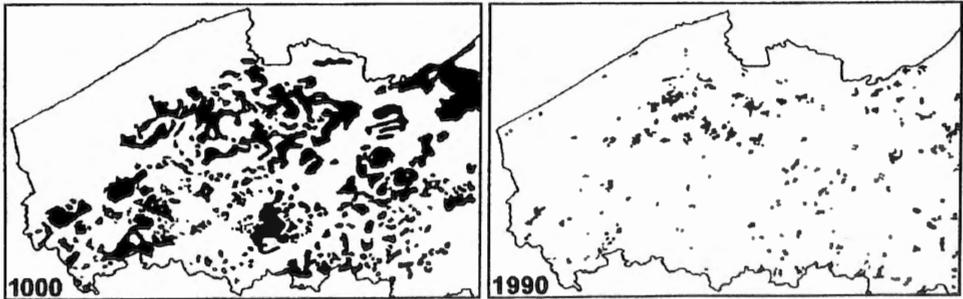
Figs 1-2. – Fragmentation in woodlands of Western and Eastern Flanders : Fig.1 : situation around 1000 AD, before extensive Medieval deforestation (after TACK et al., 1993, modified) ; Fig. 2 : based on a recent map.

Carabid beetles from Flemish woodlands

Within the framework of several projects, including a long-term insect monitoring study, quantitative data on the carabid beetle fauna from many Flemish woodlands have recently been accumulated. When ecological data about carabids are gathered through actual sampling and collecting in the field, or through the study of museum collections,

the time-span covered is generally restricted to the last two centuries. Through archaeo-logical analysis, however, it is possible to gain zoogeographic and ecological information about insect communities from much older periods. At some archaeological sites, specific man-made structures, such as wells, ditches or cesspits, have acted as pitfalls in the past, and have given rise to an accumulation of insect remains. These assemblages can be dated by the association of artefacts that are found in stratigraphic connection with them, or by physico-chemical dating techniques. The importance of the archaeological samples lies in the fact that they can originate from biotopes or environments that have disappeared today. Abundant archaeological carabid remains of a Late and Post-Roman forest at Velzeke (Eastern Flanders) have revealed a unique example of a woodland faunal composition around 500 AD (DESENDER et al., unpubl.). Besides the investigation of recent and archae-ological woodland carabid faunas, an independent study has been performed on the his-torical ecology of woodlands in Flanders (see TACK et al., 1993). This study included aspects of fragmentation and site history, such as changes in area, de- or reforestation and forest exploitation.

In this paper, an attempt is made to integrate data from 14 Flemish woods, in order to analyse the current ground beetle diversity and faunal quality (values for conservation), within the framework of the historical ecology of these woods, and to compare them with faunal assemblages of Late and Post-Roman date from the same region.

Recently, population genetic studies on selected species of woodland ground beetles were undertaken, in order to evaluate the role of historical and present-day ecology and population characteristics in the observed genetic differentiation and diversity. Such stu-dies may throw light on the mechanisms (apart from habitat quality decline or the loss of suitable habitat *per se*) responsible for the loss of typical species during woodland frag-mentation, *e.g.*, by genetic erosion or reduced gene flow. Eventually, this may lead to an increased understanding of the actual conservation values of Flemish woodlands and sug-gest remedies for future woodland rehabilitation. In the present report, only preliminary population genetic results for the eurytopic forest carabid species *Abax ater* are sum-marised.

MATERIAL AND METHODS

Study sites

Fig. 3 shows the geographical locations of the 14 Flemish woods, from which faunal data have been used in the present paper. These locations have been superimposed on a recent map locating the woodlands in the region (see also Table 1). Two of the woods investigated are situated at the border of the Flemish region and continue into adjacent regions, i.e., the « Zoniënwoud » (located on the territories of Flanders, Brussels and Wallonia), and the Flemish « Bos Ter Rijst » at Edingen (which continues on Wallonian territory where it is called « Bois du Strihoux »). Obviously, most of the studied woods are situated relatively close to each other (except for the two woods at Wijnendale, cf. nrs 1 and 8 on Fig. 3). The forests are predominantly located on loamy soils, a higher sandy soil component being present only in most parts of the « Meerdaalwoud » (Fig. 3, nr 12), and at Wijnendale (Fig. 3, nrs 1 and 8). The archaeological site (Fig. 3, nr 14) is situated near

the centre of the entire study area and very close to about half of the studied woods. The central location of the archaeological study site ensures a more straightforward comparison and evaluation of historical ecological influences (see further). At present, woodland no longer exists on the exact location of this site, and there is some discussion as to how large the wood might have been at the time of the accumulation of the beetle remains (see further and DESENDER *et al.*, unpubl.).

Although, by now, data have been accumulated on the occurrence of ground beetles in many of the other woodlands of Flanders, i.e., from the coastal region (mostly relatively recent plantations on sandy soil) and from the Campine region (mostly pine woods on poor sandy soil), these have been deliberately excluded from the present analysis. Indeed, because of the different ecological conditions in these woods, comparison with the archaeological woodland samples and other (deciduous) forests situated on loam or sandy loam soil is difficult.

TABLE 1

Characterisation of study areas, according to deforestation events (A, B, C: see text), size class (S: small, M: medium-sized, L: large and XL: «extra large» (see text)) and exploitation history (DS: disturbed soil, US: mostly undisturbed soil); added numbers as used in Fig. 3

Woodland study areas	nr	deforestation	size class	exploitation
Wijnendale (satellite forest patch)	1	A	S	DS
Parikebos	2	A	S	DS
Zegelsem - Burreken	3	B(C)	S	DS
Schorisse (Bos Ter Rijst)	4	B	M	DS
Bos t'Ename	5	B(A)(C)	M	DS
Neigembos	6	A	M	DS
Brakelbos	7	A	L	DS
Wijnendalebos	8	A(B)	L	DS
Edingen (Bos Ter Rijst-Bois du Strihoux)	9	A	L	DS
Kluisbos	10	A	L	DS
Walenbos	11	C(A)	S-L*	DS
Meerdaalwoud	12	A	L	DS
Zoniënwoud	13	A	XL	US
Velzeke (archaeological samples)	14			

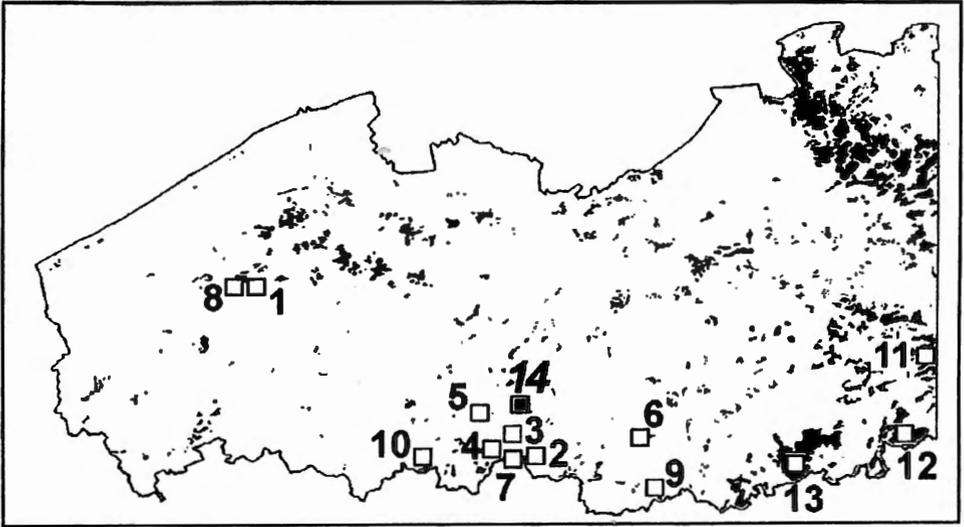* Walenbos was formerly small but has recently been expanded to a large woodland.

Fig. 3. – Location of the studied woods in Flanders; archaeological site at Velzeke (nr 14) labelled differently; numbers refer to the woods as mentioned in Table 1.

A historical approach to recent woods in Flanders

Considering their history, woodlands in Flanders can be described according to three basic factors: deforestation events, changes in dimensions resulting in actual size, and exploitation history. Considering the historical data that allow reconstruction of deforestation history in some detail, the maps by de Ferraris, drawn around 1775, are the oldest, more or less reliable source. Starting from these maps, present day woodlands have been subdivided into three categories: (A) woods that are drawn by de Ferraris, are still present today, and have known a continuous existence (« ancient forests »), (B) woods that are present on de Ferraris' maps, are extant today, but have not known a continuous existence in the intermediate period (« exploitation forests »), and (C) areas that show no woodland cover on de Ferraris' maps but are woodland today (« recent forests »).

Considering surface cover, four groups can be discriminated (see TACK *et al.*, 1993). The category of « small woods » comprises forests that at present cover less than 20 hectares (ha) and that covered less than 50 ha around 1775 AD, when the maps of de Ferraris were drawn. « Medium sized woods » cover at present 20 to 200 ha, and covered 50 to 500 ha around 1775. The group of « large woods » unifies forests that today cover more than 200 ha, and covered more than 500 ha at the end of the 18th century. Within the latter group, an exception must be made for the Zoniënwoud, which nowadays still covers an area of more than 4000 ha. Because of its extremely large size (according to Flemish standards), this forest must be placed in a fourth group.

The exploitation history of Flemish woodlands has been very diverse. Within the context of carabid (« ground beetle ») ecology, however, woodlands must mainly be subdivided according to former disturbances of the soil. In most of the Flemish forests, the soil

layers have been severely affected by human activities in the past, *e.g.* extraction of tree roots for firewood and grazing by domestic animals. Only in a few forests, of which the Zoniënwoud is an example, were such practices limited.

The forests, used as case-studies within the present analysis, can be described according to the criteria explained above. A summary of these characterisations is given in Table 1. For most of the carabid beetle sampling sites (forest plots) within these woods (see further), detailed historical data were also gathered on deforestation events and exploitation history. More comprehensive case studies and analyses based on these detailed data are beyond the scope of this paper but will be presented in future contributions.

Recent woodland carabid faunas in Flanders: sampling, diversity and population genetic case studies

Within the framework of several projects, including a long-term insect monitoring study in several habitats of Flanders, carabid beetles have been studied at many natural, semi-natural and cultivated sites since approximately 1980. Sampling campaigns have mostly been undertaken by means of at least one year cycle of pitfall trapping. Sampling involved at least 3 traps (glass jam jars, partly filled with a fixative, and with a diameter of approx. 10 cm) per site or micro-habitat (data from occasional year samplings with more than 3 traps per site were standardised by rarefaction to 3 sampling units). The traps were continuously in operation during a complete year cycle and emptied at fortnightly or three-weekly intervals.

Several of the larger or medium-sized woods, mentioned in Table 1 (*e.g.*, Zoniënwoud, Walenbos, Wijnendalebos and Bos t'Ename) have by now been sampled at some 10 to 20 different plots, sometimes during multiple year cycles (*e.g.*, DESENDER *et al.*, 1987; DESENDER & VANDEN BUSSCHE, in press). The data-set from most of the smaller woods by now includes replicate complete year cycle samples from at least 2 to 3 different sites, except for the extremely small satellite forest patch at Wijnendale (Fig. 3, nr 1), which could only be sampled as a single sampling station. Most of the year cycle sampling campaigns have been performed since 1985. Several of the woods were also recently sampled or resampled. As a result, today, the total data-set on the 13 woods from Table 1, has grown to around 100 site-year-samples and includes more than 60,000 ground beetles belonging to around 120 species.

All carabid beetles from the samples were identified to species level, counted and checked for their dispersal power (hind wing development and flight muscle development). Whether species are constantly brachypterous, macropterous or showing wing dimorphism or polymorphism, and to what degree they are able to disperse by flight, has been well documented in earlier papers (*e.g.*, DESENDER, 1989). Moreover, data from neighbouring regions and countries allow most species, recorded in Flemish woodlands, to be classified independently according to habitat preference (*e.g.*, ASSMANN, in press; BAGUETTE, 1993; LINDROTH, 1945; LUFF, 1998; THIELE, 1977; TURIN *et al.*, 1991). Detailed knowledge of geographical distribution and recent expansion or regression of individual species is available for Belgium (DESENDER, 1986a-d) and a documented Red

Data Book has recently been published for the region of Flanders (DESENDER *et al.*, 1995). For the purposes of the analysis described in this paper, a distinction was made between (1) stenotopic and (2) eurytopic woodland species, (3) ubiquists (also occurring in forest as in open landscape habitats), and (4) species from different types of open landscape habitats, mainly marshland, humid grasslands or cultivated fields.

Carabid diversity was assessed in three different ways: (1) total species richness per wood (obviously a biased diversity estimator due to an inevitably lower mean number of individual plot-year cycles in small to very small woods), (2) mean species diversity per sampling site (plot-year cycle) for a given wood and (3) rarefaction: calculation of the mean number of species for 100 individuals per sampling site, based on the actual number of individuals per species, for a given wood (cf. HECK *et al.*, 1975; HURLBERT, 1971; JAMES & RATHBUN, 1981). Habitat preference coding (see above) was then used for a more detailed comparison of the diversity observed and the data from historical ecology.

Preliminary population genetic data were gathered by cellulose acetate electrophoresis for the eurytopic woodland carabid beetle *Abax ater*, sampled from all 13 woods in this study (except for the small satellite forest patch at Wijnendale due to insufficient sample size). For each population, at least 40 beetles were analysed for 5 allozymes. More details on the technique and the statistical software used are given by HEBERT & BEATON (1989) and by DESENDER *et al.* (1998). Analysis of the preliminary data on *Abax ater* was restricted to a simple assessment of genetic diversity (mean number of alleles/locus, cf. BERG & HAMRICK, 1997) and of genetic differentiation between the study woods in relation to geographic location (isolation by distance?, reduced gene flow?). More extensive analyses based on these and additional data, and on other species, will be given in future publications.

Archaeological woodland fauna in Flanders: unique ground beetle data from a Roman well at Velzeke

In 1988, the Provincial Archaeological Museum of south-east Flanders excavated a stone well of Roman type at Velzeke (Eastern Flanders, Belgium), at the edge of a Roman site that flourished from the first to the third century AD (Van der Plaetsen, pers. comm.). The lower 3.5 m of the well's fill consisted of a deposit of organic debris that was subdivided in 11 sampling units and sieved on 0.5 mm meshes. The residues proved to be rich in zoological remains, i.e., bone, mollusc shells and the chitinous remains of insects. From the latter group, only the carabid remains were used in an attempt to reconstruct the former landscape around the well. Justification for this selection can be found elsewhere (ERVYNCK *et al.*, 1994), as well as a detailed account of the ground beetle results from the study (DESENDER *et al.*, unpubl.).

From each subunit, the remains of at least 100 carabids could be identified, yielding a total sample of more than 1100 ground beetles, belonging to 58 species. Most of the subunit samples (especially subunit 2-9) yielded a carabid faunal assemblage indicative of woodland habitat. They were dominated by stenotopic and eurytopic woodland species, implying that woodland surrounded the well at the time of deposition. Radiocarbon dating indicates the existence of this fauna around 500 AD, covering a time span of around 150

years (VAN STRYDONCK, pers. comm.). These carabid faunal data were compared to present-day data from the 13 woods previously described. Diversity was assessed in similar ways to that outlined above, but here, each subunit sample was considered a replicate sample for this wood in order to estimate mean values and associated standard errors.

RESULTS AND DISCUSSION

Carabid beetle diversity and historical ecology

Fig. 4 summarises the total carabid diversity from the 14 woods investigated, arranged in 4 size groups according to historical ecological characteristics. The archaeological data are also shown for comparison. Total species richness varies widely between circa 20 to nearly 70 carabid species per wood. Somewhat surprisingly, many large forests as well as the very large «Zoniënwoud» do not show a higher number of species compared to most of the small and medium-sized forests. A regression analysis of species richness on log(area) does indeed show that area is not a significant predictor of total diversity (r^2= 0.029, n.s.). An increased species richness nevertheless would be expected in these larger forests for two reasons. Firstly, large to very large woodlands have received a much higher sampling effort (number of separate sampling sites within one wood). The very large «Zoniënwoud» has, for example, by now been sampled already at more than 25 different sites, all included in this dataset. Secondly, larger woodlands would be expected to include a larger variety of micro-habitats, possibly increasing the total species richness of beetles. More recent woodlands, as well as those exploited relatively recently (cf. Fig. 4, asterisk-labelled bars), do not appear to show consistently lower or higher diversity compared to genuinely ancient forests.
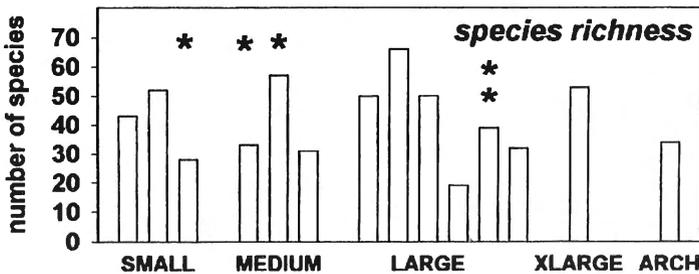

Fig. 4. – Total ground beetle species richness for the investigated woods (*= exploitation forests; **= recent forest; woods are ordered as in Table 1).

Values of much more straightforward and unbiased estimators for the comparison of beetle diversity between the woods are plotted in Fig. 5. These include: (A) mean total number of species per sampling series per wood and (B) mean expected number of species for 100 individuals calculated by rarefaction. Paradoxically, both estimators on average suggest higher diversity values in smaller sized forests. Weighted regressions of diversity on log(area) are highly significant and show a negative relationship based on both diversity estimators (cf. Fig. 7, A and B).
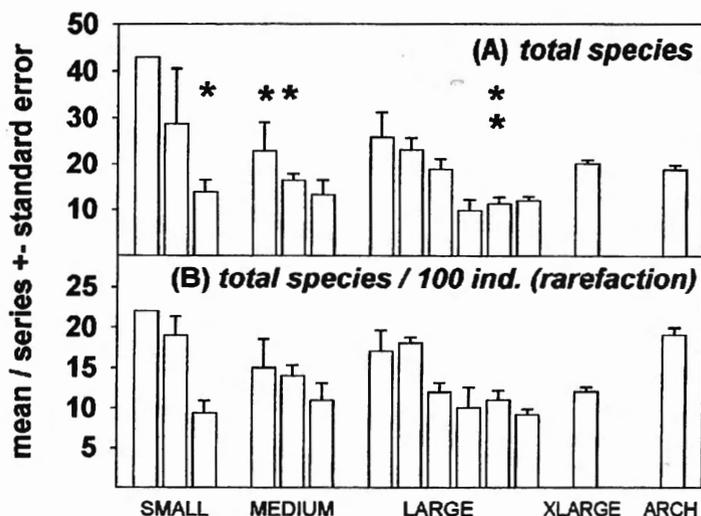
Fig. 5. – Carabid beetle diversity (measured per wood, woods ordered as in Table 1) as (A) mean total number of species per sampling series and (B) species per 100 ind., calculated by rarefaction; ARCH= data from the archaeological samples, added for comparison; *= exploitation forests; **= recent forest.

Disentangling carabid diversity, according to habitat preference of the species involved, clearly shows that increased mean diversity in smaller-sized forests is caused by a pronouncedly higher number of open landscape carabid species (Fig. 6, A). This suggests severe edge effects from forest-surrounding open habitat types, increasing with decreasing forest patch size. A regression of open landscape species diversity on log(area) is indeed highly significant and again negative (Fig. 7, C). Other authors have described how the invertebrate fauna of fragmented woodland is more influenced by surrounding habitats than is the case for more contiguous forest (HALME & NIEMELÄ, 1993; MAELFAIT et al., 1992). In some recent reviews (EHRLICH,1996; ZUIDEMA et al., 1996), it has been suggested that small forest fragments are dominated by edge effects. Much more research is required on this topic, however, especially for invertebrates, since most research has been focused towards birds (EHRLICH,1996).

Whereas eurytopic woodland species or ubiquists (Fig. 6, B and C) do not show an obvious trend (nor any significant species-area relationships), an entirely opposite trend is shown for stenotopic woodland species (Fig. 6, D). Such species appear to be powerful indicators of larger ancient woods. Only the «Zoniënwoud» samples approached the high mean value of stenotopic woodland beetles found in the archaeological assemblages. A regression analysis of these diversity data on log(area) shows a significantly positive relationship (Fig. 7, D). A closer look at somewhat deviating points reveals a number of interesting and suggestive patterns. Without exception, woods, that have been temporarily heavily or partly exploited during the last 200 years, or that can be more or less classified as recent forest (differently-labelled on Fig. 6, D), are situated in the lower part of the plot,

irrespective of their actual size. This is most obvious for the « Walenbos », the single wood in this series which has recently been expanded considerably from a small forest fragment at the time of de Ferraris. Apparently, most stenotopic ground beetle species must have disappeared at least by that time (or earlier) from this wood and were not able to recolonise the area since. The fact that this forest is extremely wet over most of its actual area could have further reduced the possibilities for survival of stenotopic woodland beetles. In the upper part of the regression plot (Fig. 7, D), mean number of stenotopic woodland carabids is higher (as expected from the fitted regression on actual size area) for one wood : the « Zoniënwoud ». This wood is the only one in the series which has retained relatively undisturbed soils over much of its area. The importance of the soil disturbance factor is further substantiated by a more detailed examination of the data from this forest. Indeed,
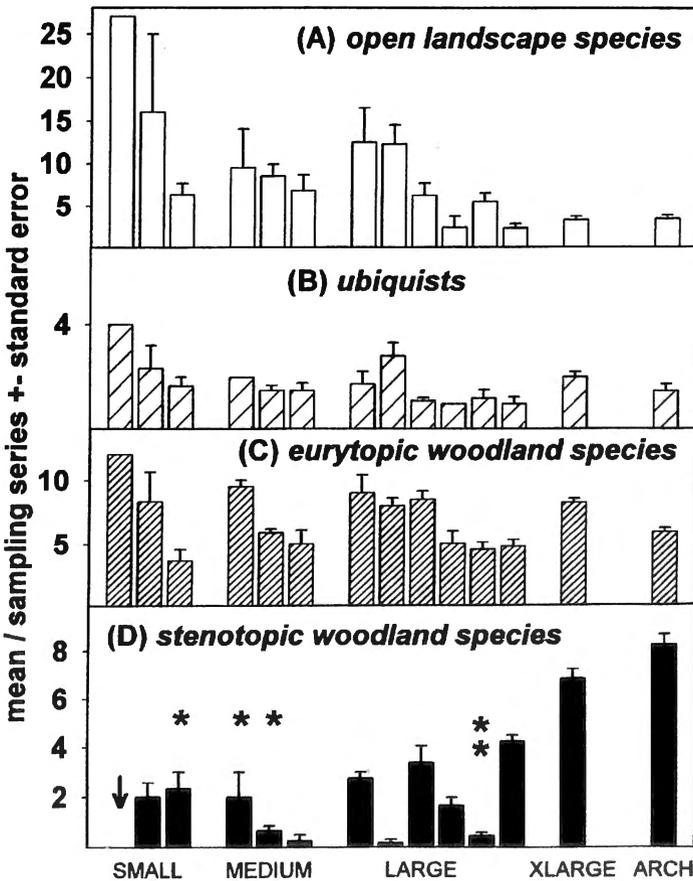
Fig. 6. – Carabid beetle diversity (measured per wood, woods ordered as in Table 1) as mean number of (A) species from open landscape habitats, (B) ubiquists, (C) eurytopic woodland species and (D) stenotopic woodland species ; ARCH= data from the archaeological samples, added for comparison ; *= exploitation forests ; **= recent forest.

some sample series from sites in the « Zoniënwoud», documented to be situated on soil, cultivated from the 14th until the 18th century, have yielded 3.00 ± 1.29 (95% c.i.) stenotopic woodland carabids compared to a significantly higher value of 7.78 ± 0.52 (95% c.i.) obtained for sites on more or less undisturbed soils. In a recent review of invertebrates and boreal forest management, NIEMELÄ (1997) similarly concluded that undisturbed old-growth forest must be set aside to sustain specialist species and to serve as sources for recolonisation.
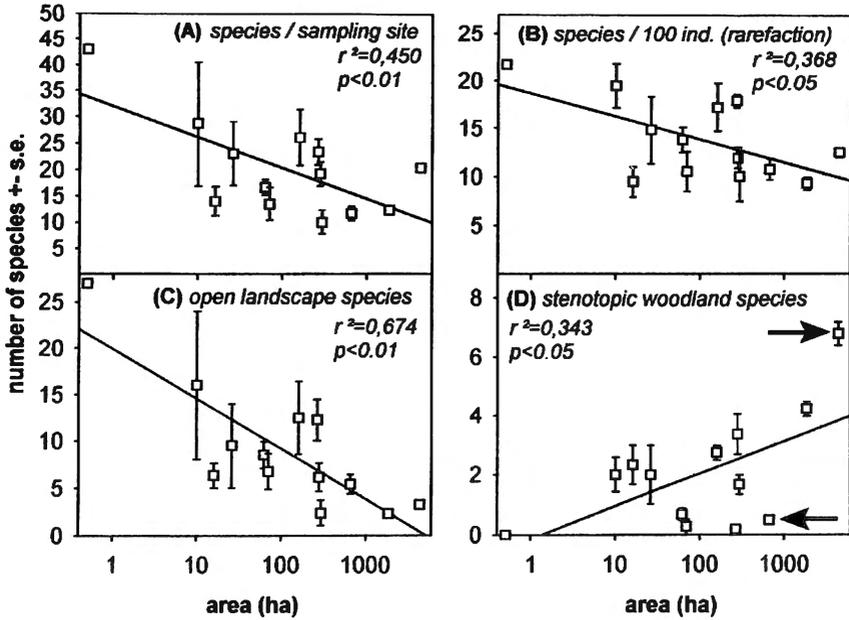
Fig. 7. – Species-area regression analyses: mean species diversity versus log(woodland area) for (A) total carabid species per sampling series, (B) number of species per 100 ind. (rarefaction), mean number of (C) open landscape species and (D) stenotopic woodland species (arrows indicate distinct outliers, further explained in the text).

The general conclusion from these results is that most woodlands in Flanders have been impoverished to a high degree in terms of their stenotopic woodland beetle fauna.

Ancient forest carabids: distribution and dispersal power

Stenotopic carabids from ancient forests apparently have become increasingly rare and now show a highly discontinuous distribution in Flanders. Nowadays, some of these species have probably disappeared entirely from this region (*e.g. Carabus intricatus*), or are only known from one (*Leistus piceus*) or very few relatively large forests (*Abax ovalis, Carabus auronitens, Cychrus attenuatus, Molops piceus*) (DESENDER *et al.*, 1995). All these species indicate(d) a habitat type which can no longer be found in our region: large, dark, cool forest without human interference, with an undisturbed soil and natural decay processes related

to abundant dead wood. In Flanders, there is not a single forest left where all of the afore-mentioned ground beetle species still occur together, not even the large « Zoniënwoud », and yet all of these species co-occurred in the archaeological assemblages, many in vast num-bers. These unique archaeological samples show that it is highly improbable to invoke purely ecological or biogeographic reasons for the recent absence of these stenotopic woodland carabids in Flanders, at least in a region with similar edaphic conditions. Some other steno-topic woodland carabid beetles still appear to survive in a higher proportion of forests in Flanders, all of which are classified as « ancient ». In several sites, such species are known only from relatively small populations (possibly as a result of decreased habitat quality and/or increased edge effects due to forest fragmentation) and they are therefore probably close to extinction (*e.g. Abax parallelus, Carabus problematicus*).
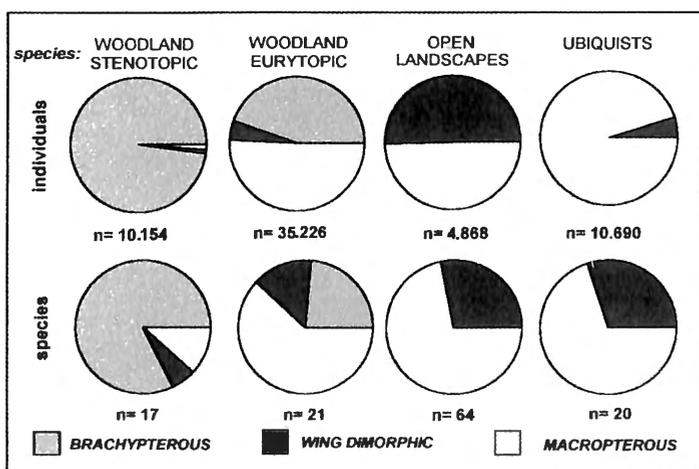
Fig. 8. – Dispersal power and habitat preference in woodland inhabiting ground beetles, based on the total data-set for the studied 13 woods (more than 60.000 carabids, belonging to 122 species). Species are classified into 4 habitat preference categories; dispersal power clearly increases from left to right.

Several of the stenotopic woodland ground beetles have recently been categorised as indicators of ancient woods in other regions also, *e.g.* in many parts of Germany (ASSMANN, 1994, in press; VOSSEL & ASSMANN, 1995), France (BUREL, 1989; TIBERGHIEN, 1981) and the UK (LUFF, 1998). The degree of forest fragmentation, however, is much higher in Flanders, and, as a result, eventual future recolonisation of rehabilitated forests will not eas-ily occur in the region. Most of these stenotopic woodland carabids indeed are constantly brachypterous (cf. Fig. 8) and avoid living near woodland edges, thereby further reducing chances for natural colonisation (ASSMANN, in press). In north-west Germany, for example, woodland cover has increased considerably during the last 200 years (ASSMANN, in press). In the same study, at least some of these typical woodland species appeared to have been able to recolonise recent forest, contiguous to ancient woods. Detailed studies on *Carabus*

auronitens (NIEHEUS *et al.,* 1996; SCHWÖPPE *et al.,* 1998) in the same region have provided population genetic as well as experimental evidence (by translocation experiments) for the historical ecological influence on the actual distribution of this species.

Genetic diversity and differentiation in the woodland carabid *Abax ater*: preliminary results

A simple measure of genetic diversity is compared for the 12 investigated populations of *Abax ater* in Fig. 9. Genetic erosion in fragmented forests cannot (yet?) be concluded from this data, although there are somewhat higher mean values for the ancient woods as compared to the others. The absence of clear evidence for genetic erosion could be due to the eurytopy of this woodland carabid species. Indeed, *Abax ater* has been observed in high population densities in all kinds of forest, also in small fragments. This means that effective population size for such a species will not easily fall below threshold values enhancing the chances for genetic drift (and resulting genetic erosion). It is therefore necessary to enlarge the data-set, if possible with data from even smaller populations. Actual isolation of forests (instead of size *per se*) might also be a more relevant influencing factor for the comparison with genetic diversity.
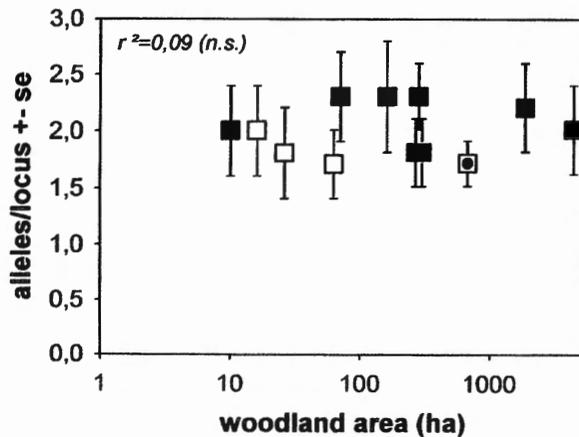

Fig. 9. – Estimates of genetic diversity in *Abax ater* (12 populations; mean number of alleles per locus; 19 alleles for 5 allozymes), plotted against log(woodland area); exploitation woods (open symbols), recent wood (open dotted symbol), ancient forests (black symbols).

The population genetic structure of *Abax ater*, compared between 12 of the woods in this study, shows an overall significant genetic differentiation (for 4 of the 5 allozymes: $X^2(MPI)=50.3$, p=0.0005; $X^2(PEP)=25.6$, p=0.0075; $X^2(G6PDH)=102.0$, p=0.0000; $X^2(PGI)= 21.4$, p=0.93; $X^2(PGM)=87.47$, p=0.0000), although the associated Fst-value is low, amounting only to 0.03. Fig. 10 shows a dendrogram based on Rogers' similarity between allele frequencies for the 12 populations studied. Significant differentiation between pairs of populations (test-results added on Fig. 10) was consistently found

between each of the three forests near Brussels (Zoniënwoud, Meerdaalwoud and Walenbos) and each of 6 other woods investigated in this study. This suggests isolation by distance (reduced gene flow), but only on a relatively large geographic scale (exceeding the size of single forests). Whether this result is linked to the more eurytopic habitat preference of *Abax ater* (which still occurs in many, sometimes very small, forests) or to the influence of a small data-set, remains to be answered.
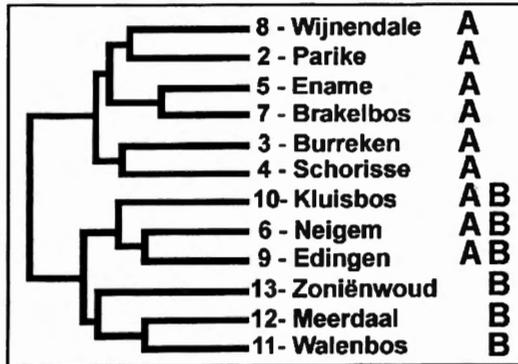

Fig. 10. – UPGMA-dendrogram based on genetic similarity (Rogers' similarity, 5 allozymes) for *Abax ater* from 12 populations; woodland sites, followed by the same letter code, are not significantly different (Bonferroni-corrected pairwise comparisons between all populations).

Because of obvious historical ecological influences on the current distribution of many woodland species (see above), one would expect to find at least some effects of woodland history and fragmentation on actual genetic differentiation and diversity in these beetles. In theory, fragmentation is supposed to increase differentiation among isolated sites and to decrease genetic diversity within populations. This follows from the combined or separate effects of lower effective population size and fewer exchange of individuals (reduced gene flow) (for Flanders, *e.g.* : DESENDER *et al.*, 1998; MATTHYSEN *et al.*, 1995; VAN DONGEN *et al.*, 1994, VAN DONGEN, 1997). Our preliminary results for the eurytopic woodland ground beetle *Abax ater* are not yet conclusive in this respect. Another recent population genetic study of the same species, on a small geographic scale in a region of Germany, yielded a comparable degree of genetic differentiation between populations (BUTTERWECK, 1998). *Abax ater*, although being constantly wingless, has been observed to move from forests into hedgerow networks (CHARRIER *et al.*, 1997). This is an additional explanation as to why population genetics could be less influenced by fragmentation than would be expected for more stenotopic woodland beetles. Where possible, the population genetics of some of these more stenotopic species should now also be studied. Only then will it be possible to evaluate more generally whether historical ecology has influenced the currently observed population genetics of woodland beetles in Flanders.

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