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# Diversity and assemblages of Carabid beetles in ancient forests and afforested former agricultural land

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## Abstract

During 2003, ground beetles were sampled in 15 forest sites of the Voeren region (Flanders, Belgium). 45 Pitfalls were therefore installed in three ancient forests and associated afforested former agricultural fields, including some very young (less than 10 years old) spontaneous afforestations as well as plantations of some 25 years on former arable grasslands and fields. We identified 9584 carabid beetles belonging to 73 species, 14 of which are mentioned on the Red list for Flanders. These include many stenotopic forest species, restricted to a high degree to ancient forest sites. They indicate that the region of Voeren is still of special faunistic interest in this respect. Ground beetle assemblages are highly structured, as revealed by a DCA analysis and mainly related to forest developmental stage. Very young spontaneous afforestations show a high number of ground beetle indicator species, mainly from open landscape habitats. Most of these are common species from arable land and only of little conservation interest. At the other end, ancient forest sites are regrouped with several *Abax* and *Carabus* species as significant indicator species. Somewhat older afforestations and plantations take an intermediate position relatively close to the ancient forest sites, but without strong peculiarities in their assemblage structure. In general, the results show that ground beetle communities from afforestation or plantation need a high number of years to converge towards ancient forest carabid assemblages. Most of the concerned species show a low power of dispersal and need adjacent ancient forest in order to be able to reach and possibly colonize more recent forests in our highly fragmented landscape.

**Key words**: Carabidae, dispersal power, afforestation, ancient forest fauna, habitat fragmentation, nature conservation

## Résumé

Durant l'année 2003, nous avons échantillonné les coléoptères carabiques de 15 sites forestiers de la région de Voeren (Flandre, Belgique). 45 pièges à fosse ont été installés dans trois forêts anciennes et dans d'anciennes zones d'agriculture associées récemment reboisées, de façon naturelle ou artificielle, dans lesquelles sont inclus quelques reboisements très jeunes aussi bien que des plantations sur champs de cultures ou prairies. Au total, nous avons identifié 9584 carabes appartenant à 73 espèces, dont 14 sont mentionnées sur la Liste Rouge des Carabidae de Flandre. Beaucoup d'espèces sténotopiques de forêts sont recensées, dont plusieurs espèces inféodées aux forêts anciennes. Ces espèces indiquent que la région de Voeren possède encore une faune forestière particulière et intéressante. Une analyse DCA démontre que les assemblages des coléoptères carabiques sont bien structurés, principalement en relation avec le stade de développement de forêt. Les très jeunes reboisements spontanés comportent un grand nombre d'espèces indicatrices, surtout d'habitats de milieux ouverts. La plupart de ces espèces sont communes dans différents habitats liés à l'agriculture et ainsi n'ont qu'une valeur limitée pour la conservation de la nature. A l'autre extrémité de l'analyse DCA, les sites de forêts anciennes se regroupent, par la présence de plusieurs espèces d'*Abax* et *Carabus* comme espèces indicatrices significatives. Les reboisements ou plantations un peu plus âgées prennent une position intermédiaire, relativement proche des forêts anciennes, mais sans espèces typiques dans leurs assemblages. En général, les résultats montrent que les communautés de carabes de forêts récentes nécessitent un grand nombre d'années pour converger vers les assemblages de forêts anciennes. La plupart des espèces de carabes concernées possède un pouvoir de dispersion réduit et exige, dans notre paysage fortement fragmenté, des forêts anciennes tout de suite à coté pour pouvoir coloniser des forêts plus récentes.

**Mots clés**: Carabidae, pouvoir de dispersion, reboisement, faune de forêts anciennes, fragmentation d'habitat, conservation de la nature

## Introduction

At present, forest cover in Flanders remains at less than 7% and consists of very small, irregularly spaced and highly fragmented woodlots, mainly as a consequence of intensive agricultural and urban land use (TACK *et al.*, 1993; DEKEERSMAEKER *et al.*, 2001; DUMORTIER *et al.*, 2003). The increasing need to enlarge existing forests or to create new woods, has become a high priority for the Flemish government, who decided some years ago to provide 10.000 ha of new forest on former agricultural sites between 1994 and 2007. In most cases, the only locations in Flanders that can be transformed into new forests are former arable grasslands or fields. During afforestation, spontaneous processes are encouraged, because these are assumed to yield greater natural values (especially floristic) than transformation by plantation (VERSTRAETEN *et al.* 2001). When plantations are conducted, only autochthonous tree species should be used. To compare classical and spontaneous forest extensions, a case-study was set up in the region of 'Voeren' (Flanders) in order to evaluate afforestation by means of different entomofauna groups. Aims and methodology of this study are presented in detail by DEKONINCK *et al.* (in press). The oldest sites in Flanders where afforestation was planned and carried out on formerly arable fields and grasslands on loamy soils are situated in the 'Voeren' region, an area at the extreme eastern border of Flanders near Germany. In the vicinity of two forest relics (the 'Altenbroek' and the 'Alserbos'), large areas were predestined for afforestation or plantation with indigenous trees. Soil-dwelling arthropods, including carabid beetles, spiders, isopods, ants and myriapods, were sampled and studied in 15 sites of this region.

In this paper, we focus on carabids or ground beetles, and their importance to evaluate afforestation on former agricultural fields. Carabids have already been used many times in such studies and their distribution, habitat preference, nature conservation value and importance in monitoring studies in Flanders have been mentioned repeatedly before (e.g. DESENDER, 1996; DESENDER *et al.*, 2004; TURIN, 2000). Another aim of this contribution is to present useful information on colonisation potential and dispersal capacity of carabid species with high conservation value (Red data book species).

We will first focus on general results and evaluate observed species quality through Red data book species and dispersal power of ground beetles. Secondly, we will look at carabid diversity by means of species richness and rarefaction and within the context of possible edge effects in our Flemish highly fragmented landscape. Finally, afforestation or plantation on former agricultural sites will be compared with ancient forests by means of their ground beetle assemblages, and these assemblages will be evaluated by ground beetle indicator species analysis.

## Material en methods

### *Study area, sampling, identification, dispersal power and species diversity*

The oldest sites in Flanders where afforestation was planned and carried out on former arable land on loamy soils are situated in the Voeren region. In the neighbourhood of two forest relics (the Altenbroek and the Alserbos), relatively large areas have been designated for

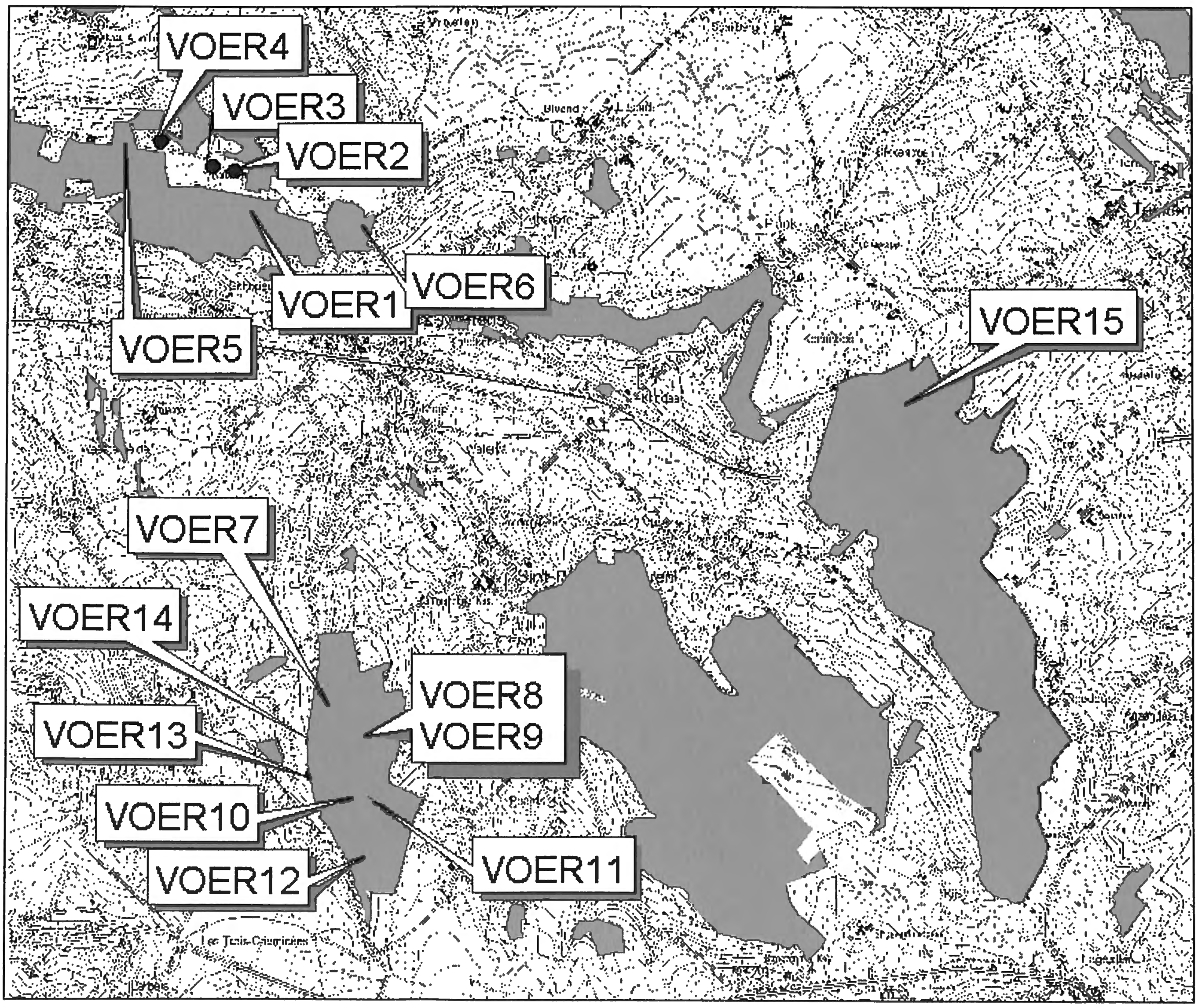



Fig. 1 — Location of the 15 sampling sites in the three forest complexes of the Voeren region: Altenbroek: sites 1-6, Alserbos: sites 7-14, Veursbos: site 15.

Table 1 — Code, history, description and age of the sampling sites. (additional sites with only pitfalls are marked with *)

| Site code | Forest | History | Description of the site | Forested since |
|---|---|---|---|---|
| VOER01 | Altenbroek | Ancient forest | Ancient oak-birch forest | <1775 de Ferraris |
| VOER02 | Altenbroek | Arable field | Afforestation and low density grazing (Galloways), *Salix* sp. and birch. | 1996 |
| VOER03 | Altenbroek | Grassland | Afforestation and low density grazing (Galloways), no shrubs or trees | 1996 |
| VOER04 | Altenbroek | Arable field | Afforestation and intensive summer grazing, *Salix* sp. and birch | 1996 |
| VOER05 | Altenbroek | Arable field | Plantation of *Quercus robur* | 1989 |
| VOER06* | Altenbroek | Ancient forest | Additional site: ancient mixed deciduous forest | <1775 de Ferraris |
| VOER07 | Alserbos | Ancient forest | Ancient oak-birch forest | <1775 de Ferraris |
| VOER08 | Alserbos | Grassland | Afforestation of birch | 1980 |
| VOER09 | Alserbos | Arable field | Afforestation of birch | 1980 |
| VOER10 | Alserbos | Grassland | Plantation of *Prunus avium* with fragments of spontaneous *Calluna vulgaris* | 1985-1990 |
| VOER11 | Alserbos | Arable field | Afforestation of birch | 1980 |
| VOER12 | Alserbos | Grassland | Plantation of *Quercus robur* | 1985-1990 |
| VOER13* | Alserbos | Ancient forest | Additional site: ancient mixed deciduous valley forest | <1775 de Ferraris |
| VOER14* | Alserbos | Ancient forest | Additional site: ancient mixed deciduous valley forest | <1775 de Ferraris |
| VOER15* | Veursbos | Ancient forest | Additional site: ancient oak-beech forest | <1775 de Ferraris |

spontaneous afforestation or to be altered to forest by plantation of indigenous trees (VERSTRAETEN *et al.* 2001; DEKONINCK *et al.*, in press). At present, these two forests consist of many small plots with different age, structure and history and as such are ideal to evaluate current ongoing afforestation.

Carabidae were sampled in six sites of the Altenbroek, eight sites of the Alserbos and one site in the Veursbos, a larger forest in the same region, added as reference ancient forest site. The sampling sites are situated on Fig. 1. Characteristics of all 15 sampling sites are given in Table 1, whereas details on soil and vegetation characteristics can be found in DEKONINCK *et al.* (in press). In 11 sampling sites (VOER01-VOER05 and VOER07-VOER12) 3 pitfalls, 3 white water traps and one Malaise trap were installed. In sites VOER06 and VOER13-VOER15, on the other hand, only 3 pitfall traps were in operation. All pitfalls (glass jam jars, diameter of 9.5 cm) and white water traps (17x10 cm and 5 cm high) were installed in a row, spaced 3-5 m apart. A 3.5% formaldehyde solution was used for killing and fixation and some detergent was added to lower surface tension. Each Malaise trap collecting vial was filled with a 75% alcohol solution. All traps were emptied 12 times from 02-IV-2003 until 08-X-2003.

All carabid beetles were identified, sexed and checked for the presence and development of their hind wings (macropterous or full-winged versus brachypterous or short-winged beetles).

Species diversity was evaluated by species richness and by rarefaction. Rarefaction curves for each site were calculated based on the actual number of individuals per species (HECK *et al.*, 1975; HURLBERT, 1971; JAMES & RATHBUN, 1981).

### *Assemblage Analysis (DCA), correlations with environmental variables and Indicator Species Analysis*

Detrended Correspondence Analysis (DCA) was used to compare sites with respect to overall species composition based on the most abundant ground beetles. DCA is a multivariate technique that positions samples along orthogonal axes that sequentially explain the greatest amount of inter-sample variation (MCCUNE & GRACE, 2002). Default settings were used, i.e. detrending by 26 segments and non-linear rescaling. All ground beetle species with at least 45 individuals (= number of sampling units) were used in the analyses (24 species), with transformed data (equal-weighting the species). Interpretations were based on available knowledge on the biology and ecology of the individual species.

Equal-weighting of the most abundant species in the analysis was preferred for several reasons: to include pitfall trap data (yielding only very approximate or possibly biased abundance ratios between species) and to avoid an overruling influence in the analysis of a few very numerous species yet possibly without obvious habitat preference. One possible drawback of the applied technique is an increasing influence of sampling errors for species caught in relatively low numbers. Therefore, only species with at least 45 individuals were retained for analysis.

At each sampling unit (n=45) the most abundant plant species were noted (Londo-scale on a 2x2 m area). We further assessed the cover of grasses, herbs, shrubs, trees (> 5 m), leaf-litter, mosses and bare ground. Estimated vegetation height was averaged from 30 random measurements, whereas the calculated standard deviation was used as a measure of vegetation structure.

With the INDVAL technique (DUFRENE & LEGENDRE, 1997), hypotheses were tested in order to detect and describe the value of different species for indicating forest developmental stage, here conceptualized as groups of sample units (sites) with similar developmental stage, history or type of forest expansion. The groups tested for were mainly derived from the DCA results. This method gives information on the concentration of species abundance in a particular group of samples and on the faithfulness of occurrence of a species in this particular group. Indicator values are tested for statistical significance using a randomization (Monte Carlo) technique.

## Results and discussion

### *General results on sampling techniques and an overview of endangered carabid species*

A total of 9584 carabid beetles from 73 species were collected during the entire sampling period. This is a high number of individuals and more than 25% of the complete Flemish carabid fauna. All species and their abundance on each site are given alphabetically in Table 2, along with Red data book classification for Flanders (DESENDER *et al.*, 1995).

Pitfalls collected 8733 specimens. Four species were exclusively collected with the other sampling techniques: *Calosoma inquisitor* (1 ind. in VOER01) collected with white water trap, *Dromius agilis* (1 ind.), *D. linearis* (2 ind.) and *D. quadrimaculatus* (6 ind.), all collected with Malaise traps. In contrast to most other carabids

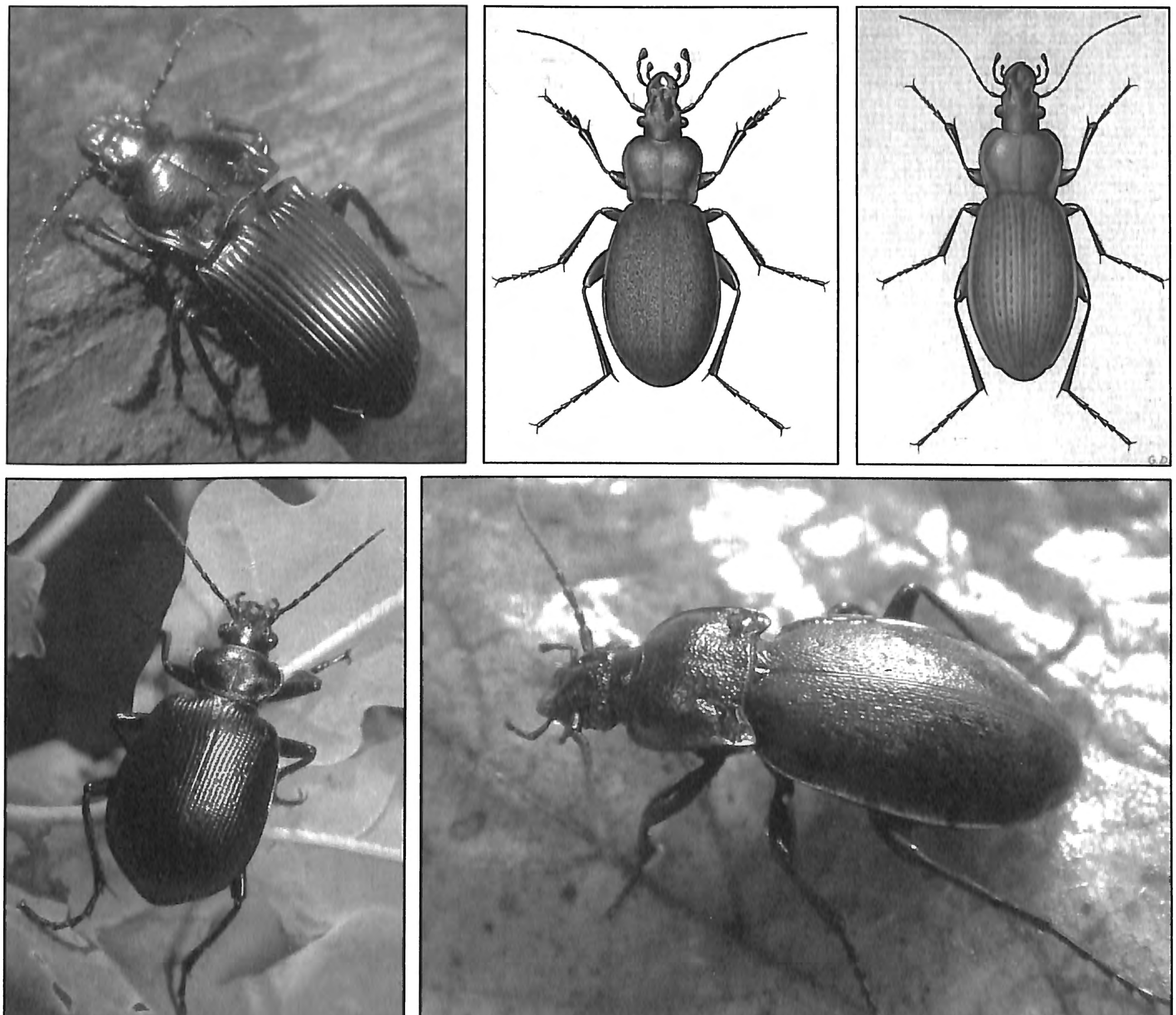


Fig. 2 — Some Red data book ground beetles obtained in the 15 sites sampled in the Voeren region: from upper left to lower right: *Abax parallelus, Carabus coriaceus, Carabus monilis, Calosoma inquisitor* and *Carabus nemoralis.*

Table 2 — Carabid beetles obtained in 15 sites from 3 forests in the Voeren region, with indication of Red list species (R=rare, V=vulnerable, T=threatened, D=decreasing).

| SPECIES / SITE | Altenbroek | | | | | | Alserbos | | | | | | | | Veurs | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | VOER01 | VOER02 | VOER03 | VOER04 | VOER05 | VOER06 | VOER07 | VOER08 | VOER09 | VOER10 | VOER11 | VOER12 | VOER13 | VOER14 | VOER15 | Total | RDL |
| | OB ref | SP Ak1 | SP Gr | SP Ak1 | AP Ak | OB val | OB ref | SP Gr | SP Ak1 | PL Gr1 | SP Ak2 | PL Gr2 | OB val1 | OB val2 | OB ref | | |
| *Abax ater* | 268 | 8 | 1 | 7 | 58 | 42 | 318 | 168 | 190 | 24 | 167 | 88 | 207 | 115 | 76 | **1737** | |
| *Abax parallelus* | 23 | | | | | 19 | 54 | | | | | | 59 | 27 | 1 | **183** | *R* |
| *Agonum assimile* | | | | | | | | | | | | | 1 | 1 | 4 | **6** | |
| *Agonum dorsale* | | | 3 | 3 | | | | | | | | | | | | **6** | |
| *Agonum muelleri* | | 12 | 1 | | | | | | | | | 1 | | | | **14** | |
| *Agonum viduum* | | | | | | | | | | | | 1 | | | | **1** | |
| *Amara aenea* | | 5 | 4 | 1 | 1 | | | | | | 1 | 1 | | | | **13** | |
| *Amara aulica* | | 22 | 5 | 8 | | | 2 | 1 | | | | | | | | **38** | |
| *Amara communis* | | 2 | 23 | 3 | | | | | | | | | | | | **28** | |
| *Amara convexior* | | 1 | | | | | | | | | | | | | | **1** | *V* |
| *Amara familiaris* | | | 2 | 5 | 1 | | | | | | | | | | | **8** | |
| *Amara lunicollis* | | | 51 | | 1 | | | | | 5 | | | | | | **57** | |
| *Amara ovata* | | | | | | | | | | | | | 10 | 2 | | **12** | |
| *Amara plebeja* | | | 1 | 1 | 4 | | | | | | | | | | | **6** | |
| *Anisodactylus binotatus* | | 3 | 36 | 26 | 1 | | | | | | | | | | | **66** | |
| *Asaphidion curtum* | | 3 | | | | 1 | | | | | 1 | | | | | **5** | |
| *Asaphidion flavipes* | | 56 | 4 | 12 | 1 | | | | | | | | | | | **73** | |
| *Asaphidion stierlini* | | 14 | 2 | 5 | | | | | 1 | | | | | | | **22** | *R* |
| *Badister bullatus* | | | | | 2 | | 4 | 3 | 1 | | 1 | 2 | | 1 | | **14** | |
| *Badister lacertosus* | | | | | | | | 1 | | | | | | | | **1** | |
| *Badister sodalis* | | | 1 | | 1 | | | | | | | | 1 | | | **3** | |
| *Bembidion lampros* | 7 | 125 | 21 | 220 | 15 | | | | | | 2 | | | | | **390** | |
| *Bembidion obtusum* | | 5 | 2 | 2 | | | | | | | | | | | | **9** | |
| *Bembidion properans* | | 11 | | 1 | 3 | | | | | | | 2 | | | 1 | **18** | |
| *Bembidion tetracolum* | | 2 | | 9 | | | | | | | | | | | | **11** | |
| *Bradycellus harpalinus* | | | | 3 | | | | | | | | | | | | **3** | |
| *Bradycellus sharpi* | | | | | | | | | 2 | | | | | | | **2** | *R* |
| *Bradycellus verbasci* | | 3 | | 3 | | | | | | | | | | | | **6** | |
| *Calathus rotundicollis* | 4 | | | | 1 | | | | | | | | | 2 | | **7** | |
| *Calosoma inquisitor* | 1 | | | | | | | | | | | | | | | **1** | *T* |
| *Carabus coriaceus* | 7 | 3 | | | 5 | 14 | 30 | 9 | 8 | 1 | 4 | 13 | 31 | 11 | 19 | **155** | *V* |
| *Carabus granulatus* | | 41 | 18 | 24 | | | | | | | | | | | | **83** | |
| *Carabus monilis* | | 80 | 115 | 6 | 1 | | 1 | 3 | 2 | 2 | 1 | | 4 | 3 | 1 | **219** | *D* |
| *Carabus nemoralis* | 4 | 7 | 23 | 12 | 7 | 5 | 91 | 38 | 27 | 12 | 13 | 25 | 19 | 9 | 1 | **293** | *D* |
| *Carabus problematicus* | 7 | | | | 11 | 3 | 33 | 6 | 12 | 5 | 36 | 60 | 16 | 47 | 33 | **269** | |
| *Carabus violaceus purpurascens* | 45 | 4 | 5 | 5 | 25 | 148 | 67 | 34 | 19 | 18 | 77 | 85 | 34 | 25 | 46 | **637** | |
| *Chlaenius nigricornis* | | | | | | | | | | | | 1 | | | | **1** | *T* |
| *Clivina fossor* | | 44 | 35 | 23 | | | | 2 | 1 | | | | | | | **105** | |
| *Dromius agilis* | | | | | | | | | | | 1 | | | | | **1** | *R* |
| *Dromius linearis* | | | | | | | | | | | 2 | | | | | **2** | |
| *Dromius quadrimaculatus* | 1 | | | | | | 2 | | 2 | | 1 | | | | | **6** | |
| *Dyschirius globosus* | | 11 | 48 | 42 | | | | | | | | 4 | | | | **105** | |
| *Harpalus affinis* | | | | 3 | | | | | | | | | | | | **3** | |
| *Harpalus distinguendus* | | | | 1 | | | | | | | | | | | | **1** | |
| *Harpalus griseus* | | | | 1 | | | | | | | | | | | | **1** | *T* |
| *Harpalus rubripes* | | | 1 | | | | | | | | 1 | | | | | **2** | |
| *Harpalus rufipes* | | 19 | 99 | 41 | 6 | | | | | | 1 | | | | | **166** | |
| *Leistus ferrugineus* | | 1 | | | | | | | 2 | | 4 | 3 | 3 | | | **13** | |
| *Leistus fulvibarbis* | | | | | 1 | | | | | | | 1 | 2 | 2 | | **6** | |
| *Leistus rufomarginatus* | 6 | | | | | 1 | 3 | | | 0 | 4 | 1 | | 1 | 3 | **19** | |
| *Loricera pilicornis* | 1 | | 1 | | 1 | | 2 | 2 | | | | | | | | **7** | |
| *Molops piceus* | | | | | | | | | | | | | | 1 | | **1** | *V* |
| *Nebria brevicollis* | 17 | 1 | 26 | 3 | 4 | 65 | 9 | 4 | | 4 | 5 | 42 | 61 | 51 | 3 | **295** | |
| *Notiophilus biguttatus* | 4 | | | | 1 | 1 | 6 | 18 | 20 | | 3 | 4 | 9 | 8 | 3 | **77** | |
| *Notiophilus palustris* | | | | | | | | 1 | 1 | 2 | 1 | 1 | | | | **6** | |
| *Notiophilus rufipes* | 1 | | | | | | | | | | | | | | | **1** | |
| *Parophonus maculicornis* | | | 4 | 3 | | | | | | | | | | | | **7** | *V* |
| *Pterostichus cupreus* | 1 | 9 | 35 | 2 | 2 | | | | | 4 | | 1 | 3 | 1 | | **58** | |
| *Pterostichus madidus* | 125 | | 4 | 222 | 47 | 146 | 30 | 148 | 638 | 239 | 537 | 286 | 153 | 124 | 30 | **2729** | |
| *Pterostichus melanarius* | | 23 | 12 | 162 | 6 | | 1 | 40 | 28 | 1 | 19 | 6 | 9 | 17 | 2 | **326** | |
| *Pterostichus niger* | | 62 | 21 | 57 | 5 | 1 | 49 | 11 | 1 | 3 | 37 | 8 | 4 | 4 | | **263** | |
| *Pterostichus nigrita* | | | | | | | | | | | | | | | 1 | **1** | |
| *Pterostichus oblongopunctatus* | 67 | | | | 3 | | 46 | 15 | 5 | | 2 | 1 | | 1 | 49 | **189** | |
| *Pterostichus strenuus* | | 6 | 9 | 18 | 1 | | | 14 | 7 | 1 | 10 | 3 | | | | **69** | |
| *Pterostichus vernalis* | | 31 | 34 | 38 | | | 1 | | | 3 | 1 | 7 | 2 | | | **117** | |
| *Pterostichus versicolor* | | 130 | 132 | 60 | 2 | | | 4 | 1 | 12 | 1 | 8 | | 2 | | **352** | |
| *Stenolophus teutonus* | | | | 1 | | | | | | | | | | | | **1** | |
| *Stomis pumicatus* | | 2 | 5 | | 1 | | | | | | 1 | | | | | **9** | |
| *Synuchus nivalis* | | 1 | | 9 | 1 | | | | | 1 | 1 | 2 | | | | **15** | |
| *Trechus micros* | | 1 | | | | | | | | | | | | | | **1** | |
| *Trechus obtusus* | | | | | 18 | | | 9 | 3 | | 4 | | | | 1 | **35** | |
| *Trechus quadristriatus* | | 3 | | 2 | | 1 | | | 2 | | | | | | | **8** | |
| *Trichotichnus laevicollis* | | | | | | | 49 | 78 | 48 | | 10 | 3 | | 1 | | **189** | *R* |
| *Total individuals* | 589 | 751 | 784 | 1044 | 237 | 447 | 798 | 609 | 1021 | 337 | 949 | 660 | 628 | 456 | 274 | **9584** | |
| *Species richness* | 18 | 35 | 34 | 38 | 32 | 13 | 19 | 21 | 22 | 17 | 30 | 27 | 19 | 22 | 17 | **73** | ***14*** |

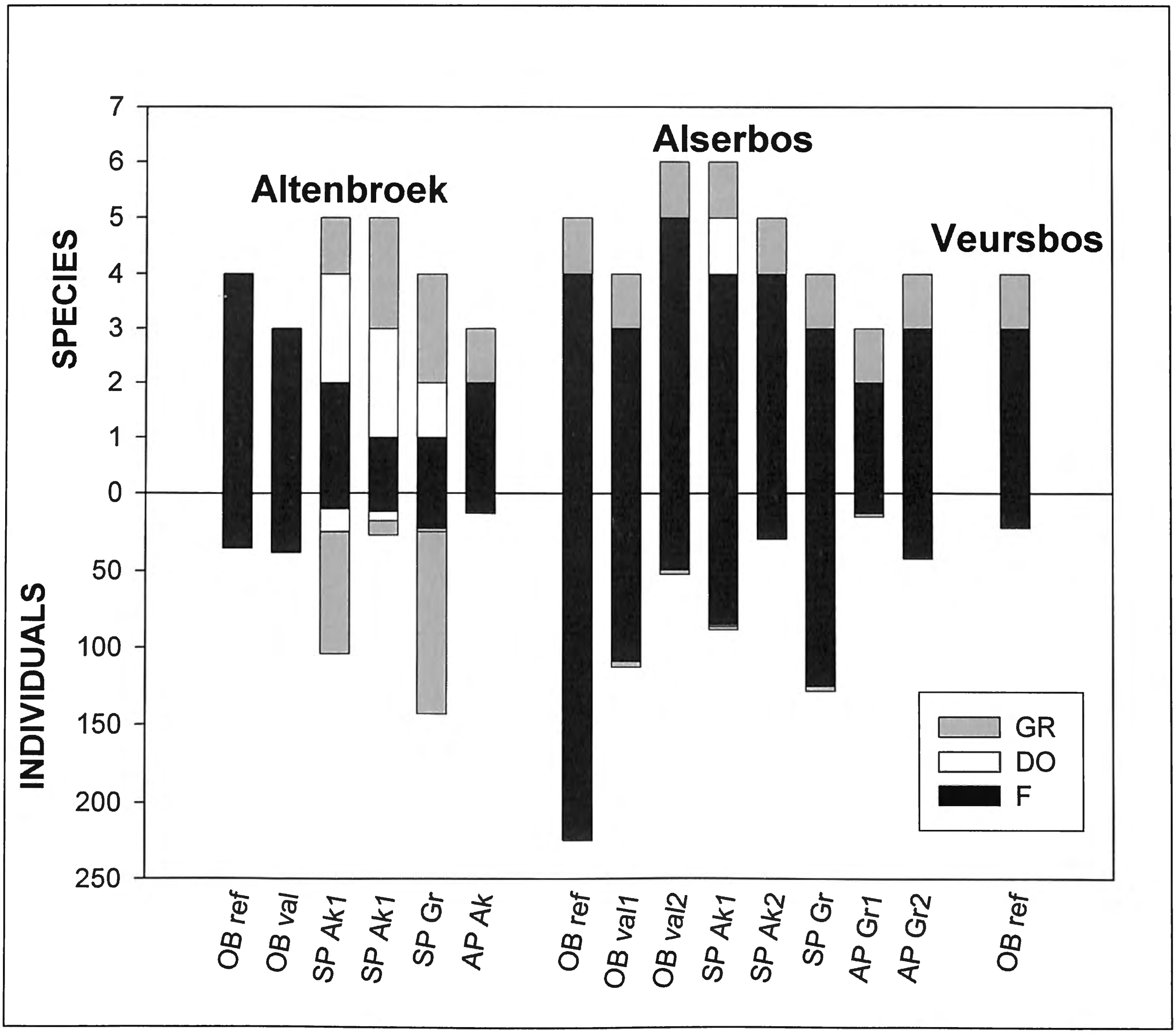



Fig. 3 — Red data book carabid species and individuals in the 15 sampling sites, arranged per forest complex and major habitat preference. Abbreviations: OB=ancient forest, SP=spontaneous afforestation, AP=plantation, ref=reference site, val=-valley site, Ak=former agricultural field, Gr=former grassland; habitat preference codes: F=forest species, DO=species from dry open habitat, GR=grassland species.

which are exclusively soil-dwelling arthropods, these 4 carabid species are known as arboricolous or at least as regularly climbing in vegetation. This behaviour is also expressed in different morphological characteristics. The bodies of *Dromius agilis* and *D. quadrimaculatus* are extremely flattened dorso-ventrally, allowing them to shelter during inactivity under bark or in tree fissures. *Calosoma inquisitor* feeds exclusively on caterpillars and pupa living on oak. Arboricolous *Dromius*-species, as also *Calosoma inquisitor,* are provided with well-developed flight wings and always possess functional flight muscles (cf. DESENDER, 2000).

Malaise traps only collected 16 carabid species and 51 individuals whereas white water traps yielded 43 species and 800 specimens. Most of these beetles were also found in pitfalls.

Amongst the total number of 73 carabid species, 14 are mentioned in the Red data book for Flanders (DESENDER *et al.*, 1995) and are marked with their category in Table 2. It concerns 5 Rare, 4 Vulnerable, 3 Endangered and 2 Decreasing species. Some of these beetles are illustrated in Figure 2, whereas their habitat preference is summarised in Figure 3. Although the number of Red list species is similar between all sites, highest numbers of individuals of forest species coincide with the ancient forest reference sites in each of the sampled forests. The youngest afforestation sites (in the Altenbroek) are dominated by dry open landscape or grassland species (Fig. 3).

A majority of the 14 Red list beetles appear to be stenotopic forest species: *Abax parallelus, Bradycellus sharpi, Carabus coriaceus, Carabus nemoralis, Caloso-*

*ma inquisitor, Molops piceus* and *Trichotichnus laevicollis.* Except for *C. inquisitor*, all of these forest species have highly reduced hind wings and as such a low dispersal power. Several of these ground beetles were nearly restricted to ancient forest sites within our study area, where they were found in high abundances: *Carabus coriaceus, C. nemoralis* and *Abax parallelus.* The last-mentioned species was, without exception, limited in its occurrence to ancient forest and has indeed been noted before as a powerful indicator for ancient forests (ASSMANN, 1999, DESENDER *et al.*, 1999). At this moment, ecological and genetic studies are ongoing at the RBINSc, within the context of a recently started project, in different eco-regions from our country, in order to define with more precision region-specificity of possible indicator-ground beetles for ancient forests (cf. DESENDER *et al.*, 2005).

The remaining Red list carabid species that were found include *Carabus monilis*, a beetle sporadically found in forest but preferring grasslands on heavy soil. Especially in the province of Brabant and the Voeren region it is still largely distributed (DESENDER, 1986a), whereas in other parts of Flanders *C. monilis* has completely disappeared in recent decades. The other Red list species are typically open landscape species. Remarkable amongst them are three more or less thermophilic species, which appear to be expanding in Flanders very recently: *Asaphidion stierlini, Harpalus griseus* and *Parophonus maculicornis*. The latter two carabids are especially found in oligotrophic, rather dry and thermophilic grasslands. Probably they feed on seeds and are not carnivorous or omnivorous as many other carabids. An increasing number of recent discoveries of these carabids suggest they have become more abundant and widespread in Flanders, probably at least partly due to recent climatic warming. For example, during a recent survey along the motorway verges of the ring road around Brussels, high numbers of *Parophonus maculicornis* were found on south-facing slopes (DESENDER *et al.*, 2004).

***Dispersal power***

Figures 4 and 5 summarize the dispersal power of ground beetles in each of the sampling sites (brachyptery versus macroptery, with separate indication of wing polymorphic species) respectively on species and on individual level, and at the same time with absolute and relative numbers of the distinguished categories.

As expected, wingless ground beetles dominate in the ancient forest reference plots, this trend being more strongly visible on the graphs based on numbers of individuals (cf. DESENDER, 1989). On the other hand we can clearly observe that especially the youngest afforestation sites (in the Altenbroek) show a much higher amount of species and individuals belonging to wing polymorphic and constantly macropterous carabids. At the same time, a large part of brachypterous individuals from afforestations or plantations appear to belong to wing dimorphic or polymorphic species. Previous studies in Belgium have shown that in this category of ground beetles there is a

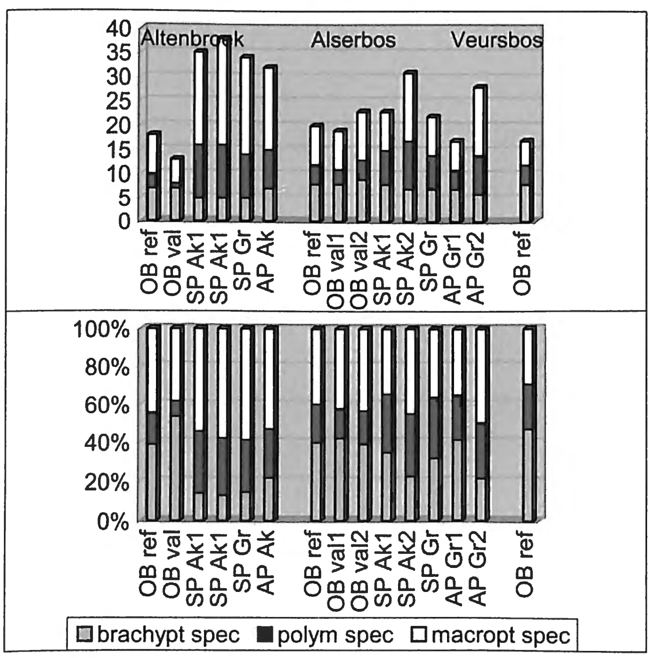



Fig. 4 — Ground beetle hind wing development on species level (higher graph: absolute number of species; lower graph: relative contributions) for the 15 sampling sites, arranged per forest complex.

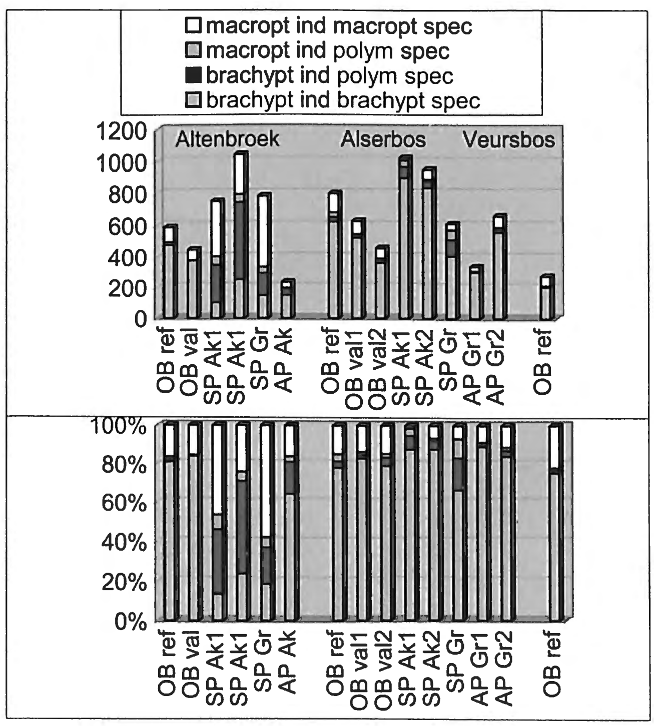



Fig. 5 — Ground beetle hind wing development on individual level (higher graph: absolute number of individuals; lower graph: relative contributions) for the 15 sampling sites, arranged per forest complex.

significantly higher amount of eurytopic species with lower value for nature conservation (DESENDER, 1986b). *Trichotichnus laevicollis* and *T. nitens* are the only known carabids in Belgium displaying sex-linked wing dimorphism: males always have wings, whereas females are invariably wingless (cf. DESENDER, 1987).

These results on the other hand do not prove that all macropterous individuals or species from our samples were able to fly, as flight muscles were not checked and are not necessarily functional in such beetles (cf. BEN BOER; *et al.*, 1980; DESENDER, 2000).

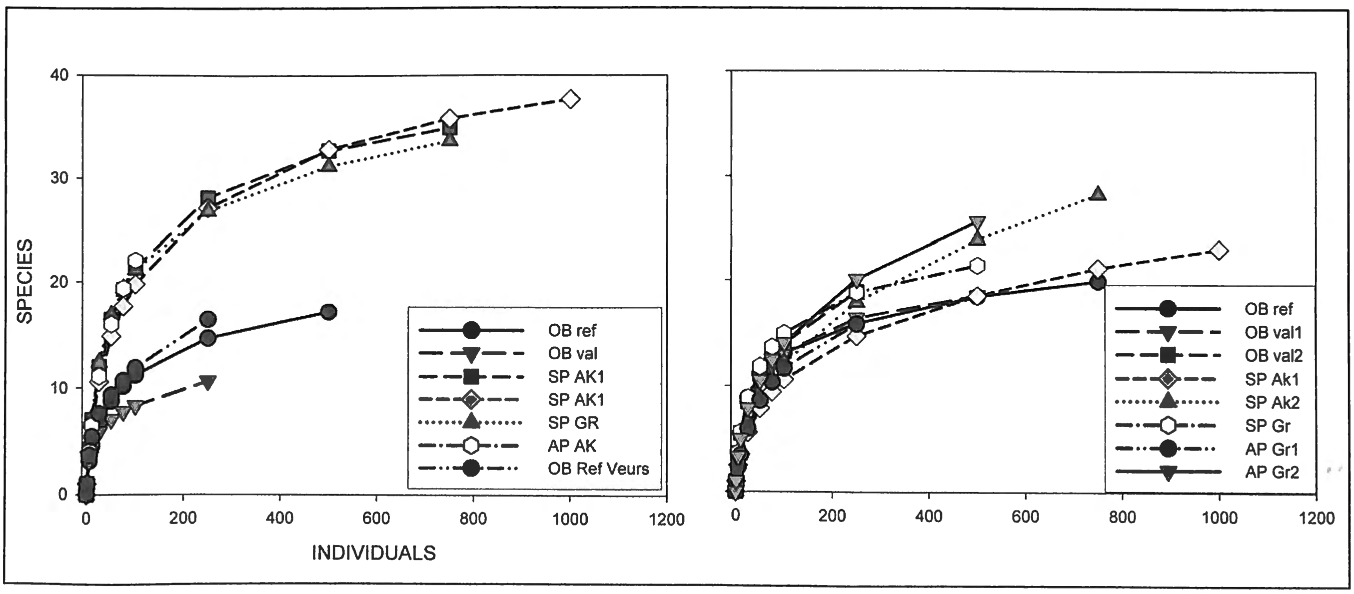
***Understanding ground beetle diversity: species richness, rarefaction and edge effects***

Species diversity, whether evaluated by species richness or rarefaction, differs strongly between the major forest habitats in our dataset (ancient forest, young afforestation or plantation, very young spontaneous afforestation). Rarefaction curves are shown in Figures 6-7, whereas the possible influence of major habitat type as well as distance to nearest other habitat (edge effects) are evaluated in Figure 8.

Regression lines show a negative relationship between distance to nearest other habitat and species richness, but this relation is only significant for recent forest types as compared to ancient forest. Rarefaction diversity estimates (in stead of species richness) yield very comparable results. As compared to ancient forest sites, ground beetle diversity is higher in younger forest as well as in forest nearer to other habitat. The values for the three plantations in this set are somewhat lower than for afforestation sites of similar age (Alserbos). Probably this reflects the observed higher habitat homogeneity in these plantations as compared to increased structural diversity in spontaneous afforestation sites. As mentioned higher, this does not mean that values for nature conservation would necessarily be more important in such situations.

The rarefaction diversity curves also show how ancient forest sites in general are characterized by lower ground beetle diversity. The diversity curves for all afforestations of the Altenbroek appear to be clearly higher as compared to all other series. This is probably the consequence of the above-suggested edge effects, although such effects might interact with the fact that these afforestations are very young habitats, more intermediate-like between open land and young forest. On the other hand, this situation makes a scientifically sound evaluation of beetle diversity between spontaneous afforestation and plantations more difficult, especially between the two studied forest complexes. Future biodiversity studies or monitoring therefore always should try to incorporate potential edge effects within the experimental or sampling setup (cf. DESENDER, 2005), e.g. by sampling at sufficient distance (e.g. 200 m) from other habitats, or, as possibly more realistic in our Flemish highly mosaic landscape, by using a defined minimum distance from other habitats or ecotones, or, at least, by taking such information into account. Anyway, evaluation of species diversity for a specific taxonomic group at a particular site in our highly fragmented landscape appears not always relevant and could even yield misleading conclusions (cf. DESENDER, 1996, 2005). Better alternatives therefore are probably to focus more on species quality (cf. Red list species), or to combine species information of interesting species known to occur in viable, more or less abundant, populations. Species found in very low numbers only, on a given site, will probably in much more cases merely indicate accidentally immigrating individuals from surrounding habitats.

Sustainable conservation and forest management therefore preferably should focus on species quality and




Figs. 6-7 — Ground beetle rarefaction curves for all 15 sampling sites, regrouped per forest complex (left figure: Altenbroek and Veursbos; right figure: Alserbos; see legend figure 3 for abbreviations).

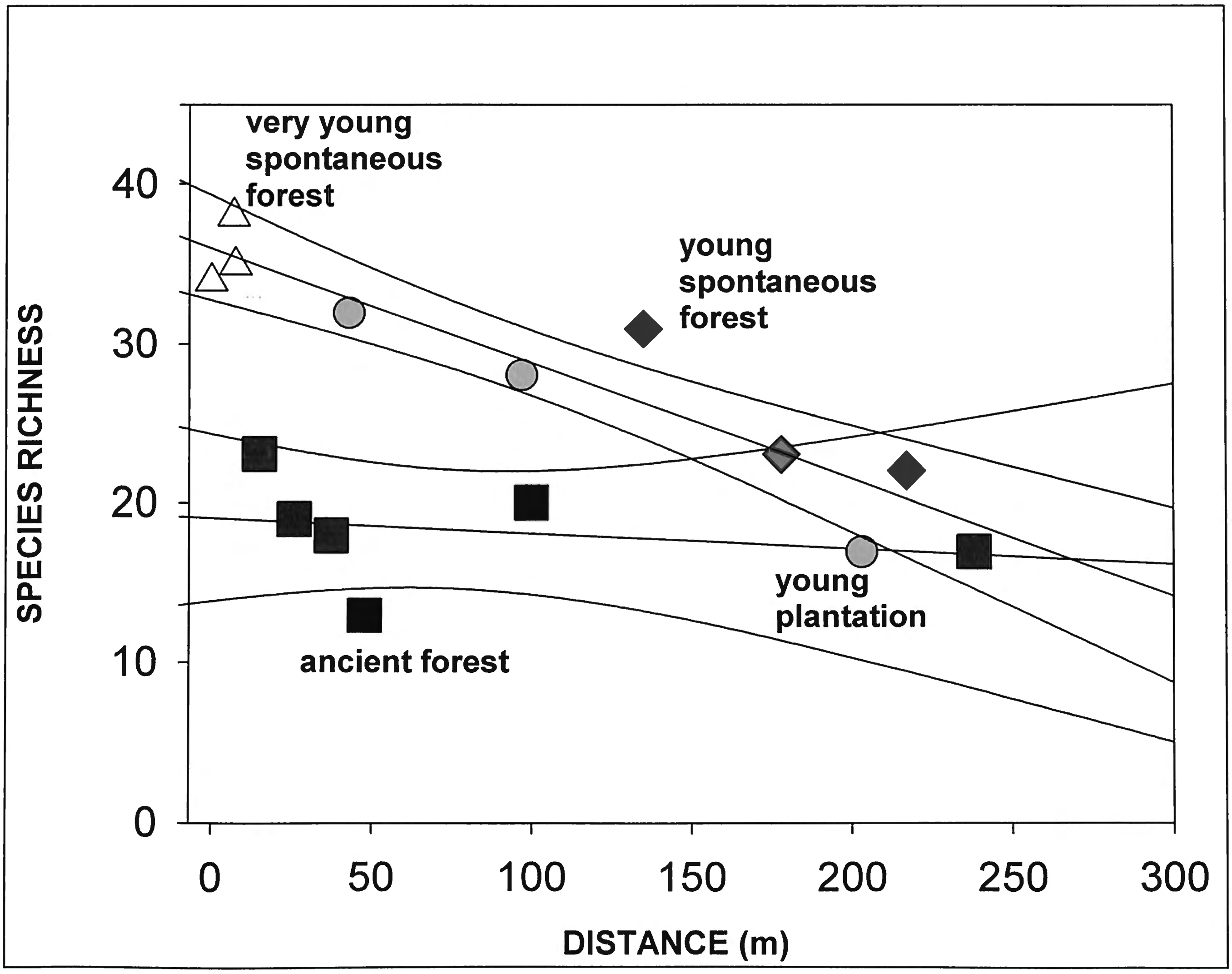



Fig. 8 — Carabid diversity in relation to distance to nearest other habitat (grassland for all sites, except for the three very young sites, where it is ancient forest). Separate regression lines with 95% confidence limits for ancient forest sites and for all afforestations or plantations.

population size in stead of concentrating only on total species richness. Other aspects of target species, such as population genetic diversity and/or dispersal power, are further recommended for valuable additional information in evaluation and monitoring studies.

***Ground beetle assemblages and indicator species in the studied forest sites***

Fig. 9 presents the labelled DCA ordination diagram of all 45 pitfall trap samples and for the 24 most abundant carabid species used for analysis, with an overlay of the main history of the forest sites. The same ordination plot is redrawn in Fig. 10 with added ellipses enclosing well-defined groups of samples and in Fig. 11 with an added plot of vectors for environmental variables significantly related to the two most important ordination axes. Tables 3 and 4 show Pearson and Kendall correlation coefficients between respectively species scores (Table 3) and environmental variables (Table 4) and the major DCA axes. Table 5 summarizes the significant indicator carabid species obtained by INDVAL for different hypotheses, based on groups of sites derived from the DCA analysis.

DCA ordination shows that the largest part of variation in the data resides along the first axis (eigenvalue=0.769), whereas the second axis has already a much lower eigenvalue of 0.220. The first DCA axis corresponds with 'degree of afforestation' or 'forest age' and is positively related to tree cover and litter layer and negatively related to cover of grasses. At the left the very young (less than 10 years) spontaneous afforestations are strongly differentiated from all other study sites (group A). A high number of carabids is significantly related to this group of samples and concerns without exception species from open habitats, more specifically from rather open and rather dry grassland or fields on rather heavy soil. Most carabids from that list are indeed well-known eurytopic, very common and widely distributed species from fields, ruderal sites and arable grasslands: *Anisodactylus bino-*

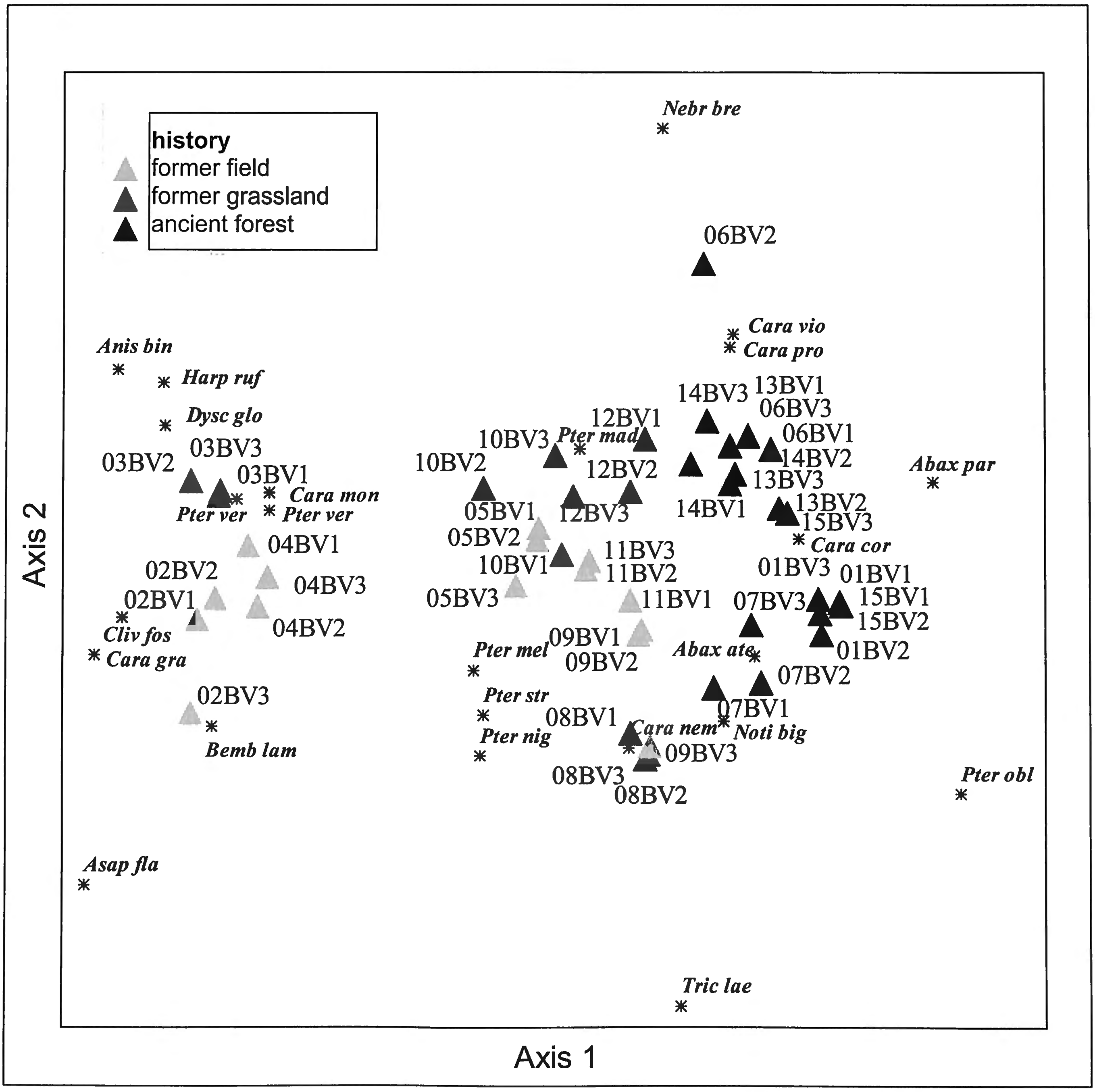
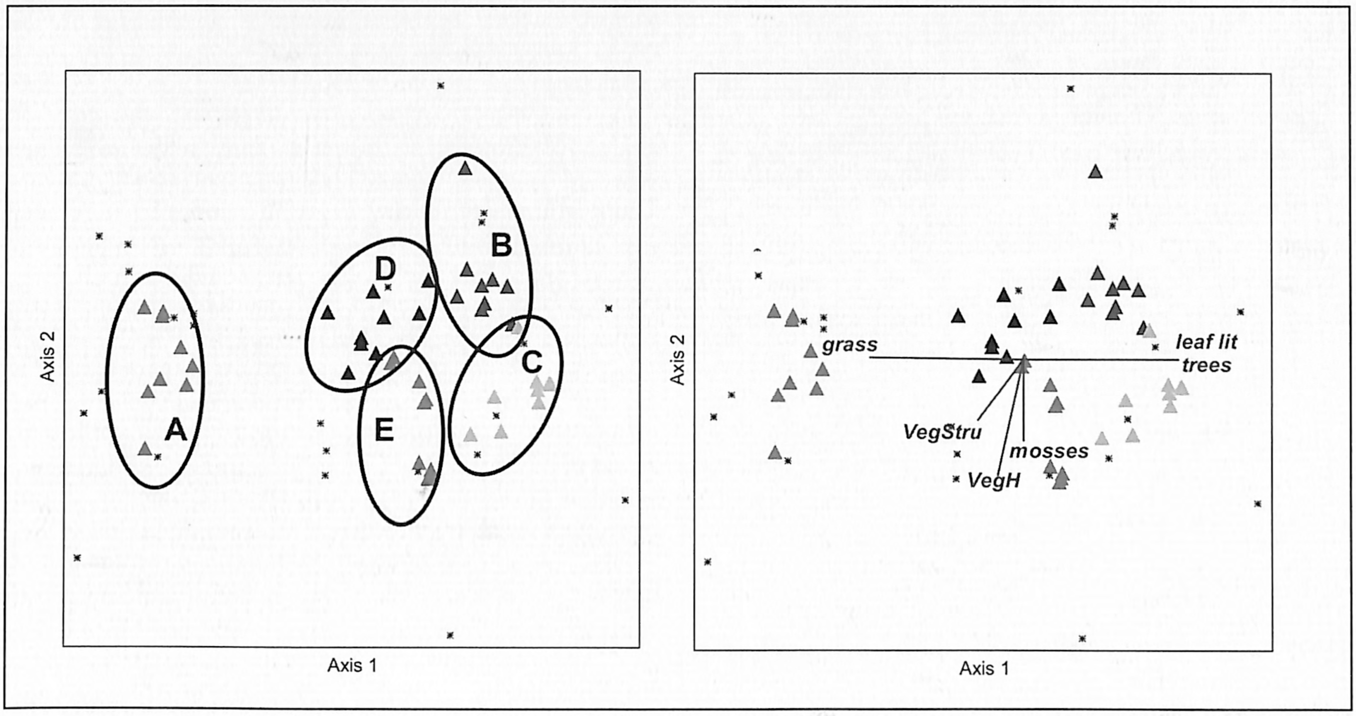



Fig. 9 — DCA ordination species and sample scores based on individual traps (BV) in 15 sampling sites and 24 most numerous ground beetle species (abbreviations show first 4 letters of genus name and first 3 of species name), with overlay of forest history.

*tatus, Asaphidion flavipes, Bembidion lampros, Clivina fossor, Dyschirius globosus, Harpalus rufipes, Pterostichus vernalis* and *P. versicolor*. *Carabus granulatus* and *Carabus monilis* are also found on these sites in relatively high numbers, whereas they are nearly absent from the other sampling sites. *Carabus granulatus* is a common species from nutrient-rich and rather humid vegetation types, especially eutrophic swamps. In Belgium, *C. monilis* is rather numerous in more or less humid grassland on heavy soils, but this species appears to be absent from many other regions in Flanders. Along the other side of the first DCA axis, all sampled ancient forest reference sites from the different forest complexes are regrouped (groups B and C), characterized by well-known forest carabids: *Abax ater, A. parallelus, Carabus coriaceus, C. problematicus, C. violaceus purpurascens* and *Pterostichus oblongopunctatus*. In between these extremes, but already closer to ancient forests, the 25 to 30 years old afforestations are positioned (plantations as well as spontaneous forest; groups D and E). A number of forest beetles already occur in these sites, but in general their numbers are lower, whereas some other carabid forest species are still lacking.




Figs. 10-11 — DCA ordination species and sample scores with added ellipses (left graph) enclosing well defined groups of samples (A=very young afforestation, B=valley ancient forest, C=plateau ancient forest, D=young plantation, E=young spontaneous afforestation; see text for further explanation); right graph: biplot with overlay of forest type and plot of vectors from environmental variables significantly related to ordination axes (see Table 4).

Table 3 — Pearson and Kendall correlations between the most numerous carabid species and the DCA ordination axes; significant values are marked with shading.

| **Axis:** | 1 | | | 2 | | |
|---|---|---|---|---|---|---|
| ***species*** | **r** | **r-sq** | **tau** | **r** | **r-sq** | **tau** |
| *Abaxater* | .651 | .424 | .506 | -.390 | .152 | -.242 |
| *Abaxpara* | .475 | .226 | .536 | .151 | .023 | .158 |
| *Anisbino* | -.673 | .453 | -.486 | .108 | .012 | .051 |
| *Asapflav* | -.499 | .249 | -.556 | -.248 | .062 | -.094 |
| *Bemblamp* | -.623 | .388 | -.501 | -.175 | .031 | -.105 |
| *Caracori* | .579 | .335 | .520 | -.022 | .000 | -.027 |
| *Caragran* | -.779 | .607 | -.544 | -.143 | .020 | -.071 |
| *Caramoni* | -.728 | .529 | -.402 | -.007 | .000 | -.065 |
| *Caranemo* | .229 | .052 | .068 | -.361 | .130 | -.123 |
| *Caraprob* | .411 | .169 | .361 | .236 | .056 | .104 |
| *Caraviol* | .530 | .281 | .470 | .320 | .103 | .096 |
| *Clivfoss* | -.820 | .673 | -.512 | -.122 | .015 | -.163 |
| *Dyscglob* | -.730 | .534 | -.538 | .070 | .005 | .026 |
| *Harprufe* | -.753 | .566 | -.614 | .118 | .014 | .020 |
| *Nebrbrev* | .200 | .040 | .194 | .629 | .395 | .430 |
| *Notibigu* | .274 | .075 | .344 | -.424 | .180 | -.257 |
| *Ptermadi* | .124 | .015 | .035 | -.048 | .002 | .057 |
| *Ptermela* | -.401 | .161 | -.303 | -.192 | .037 | -.245 |
| *Pternige* | -.486 | .236 | -.359 | -.342 | .117 | -.203 |
| *Pteroblo* | .523 | .273 | .465 | -.401 | .161 | -.417 |
| *Pterstre* | -.461 | .212 | -.420 | -.401 | .161 | -.277 |
| *Ptervern* | -.852 | .726 | -.538 | .005 | .000 | .139 |
| *Ptervers* | -.846 | .715 | -.655 | -.009 | .000 | .048 |
| *Triclaev* | .188 | .035 | .116 | -.689 | .474 | -.469 |

Along the second DCA-axis, plantations (group D) are more or less distinguished from spontaneous afforestations (group E), but the differences are not very pronounced. Along the same axis, there is also some differentiation between valley ancient forests (group B) and plateau ancient forests (group C). In general, the second axis corresponds negatively to cover of mosses, vegetation height and structure. Scores of these variables are indeed lower in the more homogeneous plantations as compared to the more structurally variable spontaneous afforestations. A ground beetle corresponding positively to this axis is *Nebria brevicollis*, an extremely common carabid from disturbed and nutrient-rich forest with a lot

Table 4 — Pearson and Kendall correlations between environmental variables and the DCA ordination axes; significant values are marked with shading.

| **Axis:** | 1 | | | 2 | | |
|---|---|---|---|---|---|---|
| ***variable*** | **r** | **r-sq** | **tau** | **r** | **r-sq** | **tau** |
| bare ground | .296 | .088 | .349 | .368 | .135 | .166 |
| grass | -.746 | .556 | -.507 | .085 | .007 | .132 |
| shrubs | -.201 | .040 | .061 | -.292 | .085 | -.258 |
| herbs | .350 | .122 | .161 | -.230 | .053 | -.120 |
| trees | .749 | .561 | .358 | -.019 | .000 | .016 |
| mosses | .009 | .000 | -.350 | -.550 | .302 | -.264 |
| leaf litter | .672 | .452 | .536 | .030 | .001 | .018 |
| humus | .269 | .072 | .082 | .055 | .003 | -.022 |
| VegH | -.306 | .094 | -.123 | -.654 | .428 | -.367 |
| VegStru | -.406 | .165 | -.278 | -.475 | .226 | -.299 |

Table 5 — Carabid indicator species, indicator values and significance levels for different types of forest in the 15 sampling sites: very young afforestation, young afforestation, ancient forest.

| Species | Habitat type | Indicator value | significance |
|---|---|---|---|
| *Caragran* | very young afforestation | 100 | 0,001 |
| *Dyscglob* | very young afforestation | 98 | 0,001 |
| *Harprufe* | very young afforestation | 97 | 0,001 |
| *Bemblamp* | very young afforestation | 96,7 | 0,001 |
| *Ptervern* | very young afforestation | 93,5 | 0,001 |
| *Ptervers* | very young afforestation | 92,5 | 0,001 |
| *Anisbino* | very young afforestation | 88,9 | 0,001 |
| *Asapflav* | very young afforestation | 88,2 | 0,001 |
| *Clivfoss* | very young afforestation | 87,6 | 0,001 |
| *Amarauli* | very young afforestation | 86,8 | 0,001 |
| *Caramoni* | very young afforestation | 83,3 | 0,001 |
| *Amarcomm* | very young afforestation | 77,8 | 0,001 |
| *Asapstie* | very young afforestation | 75,7 | 0,001 |
| *Pternige* | very young afforestation | 68,3 | 0,001 |
| *Bembobtu* | very young afforestation | 66,7 | 0,001 |
| *Ptermela* | very young afforestation | 66,1 | 0,005 |
| *Pterstre* | very young afforestation | 63,3 | 0,001 |
| *Ptercupr* | very young afforestation | 62,8 | 0,002 |
| *Paromacu* | very young afforestation | 55,6 | 0,001 |
| *Ptermadi* | young afforestation | 63,8 | 0,001 |
| *Trecobtu* | young afforestation | 53,9 | 0,003 |
| *Abaxpara* | ancient forest | 88,9 | 0,001 |
| *Caracori* | ancient forest | 72,7 | 0,001 |
| *Nebrbrev* | ancient forest | 68,8 | 0,003 |
| *Caraviol* | ancient forest | 58,7 | 0,003 |
| *Abaxater* | ancient forest | 58,3 | 0,001 |
| *Caraprob* | ancient forest | 49,1 | 0,021 |

of shade, also numerous in valley forests (whether ancient or not). *Trichotichnus laevicollis* correlates negatively to the same axis, prefers rather open and relatively dry plateau forests, and is supposed to feed especially on seeds, hence its probable preference for rather open ancient forests.

A formal INDVAL-analysis based on the observed groups of samples in the DCA, only indicates on the one hand a lot of carabid indicator species for the very young afforestations, few species for intermediately-aged plantations as well as spontaneous forest, and again more carabid indicators for ancient forest, without a clear indication, however, of species completely restricted to valley or plateau ancient forest.

As the variables related to forest and afforestation history appear not to be totally independent from other characteristics of the different forest complexes investigated in this study, we have to be careful with the extrapolation of our detailed results. Besides the suggestion, already given above, to try to incorporate possible edge effects in future sampling schemes, our results further suggest that it is necessary to try to incorporate data from older afforestations (at least 50 to 100 years) in order to evaluate plantations versus spontaneous forests as well as the comparison between former fields or grasslands. Also, as many typical faunal elements of ancient forests, including carabids, possess only a limited power of dispersal, it will be necessary to compare such data with results from recent forests or afforestations not in contact with or at increasing distances from ancient forests. Interpretations will, however, always have to be performed mainly within the studied eco-region and within the limitations imposed by the sampling setup. Yet, some clear indicator species for ancient forest, such as *Abax parallelus* and *Carabus coriaceus,* appear nevertheless to be qualified for monitoring studies within the context of afforestation management. Future ecological studies or monitoring within the context of forest management would benefit even more from the incorporation of population ecological and population genetic aspects of these ground beetles, which are of special interest for our nature conservation.

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