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Comparative study of the Terrestrial Isopod Faunas of Ancient Forests and Afforested Former Agricultural Fields

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Abstract

Diversity, composition and species abundances of the terrestrial isopods sampled in 15 forest sites, differing in age, afforestation type and forest developmental stage, in the Voeren region (Belgium), are assessed. Higher numbers of especially rare and very rare woodlice species are only observed in the ancient forests. The young spontaneous forests on former agricultural fields have an eurytopic and common isopod fauna. On former grasslands we find a larger number of eurytopic grassland species. Close to ancient forest, far from open field, some rare and typical ancient forest species appear to start colonizing recently planted forest but populations are still very small. Very typical rare "ancient forest woodlice" found during the present study appear to be absent in other parts of Flanders and are therefore not useful for a region-wide evaluation of the effects of afforestation on former agricultural sites. Important environmental variables are forest age, vegetation structure and soil conditions.

Key words: woodlice, diversity, community structure, afforestation, former agricultural fields, forest age.

Introduction

In western and central Europe terrestrial isopods mainly live in and from dead plant material and they are very important in the biological decomposition of dead organic material (HASSALL, 1977; SUTTON & HOLDICH, 1985; HAMES & HOPKIN, 1989; BERG & WIJNHOVEN, 1997; HASSALL & DANGERFIELD, 1997; ZIMMER & TOPP, 1997; 1999; SZLÁVECZ & MAIORANA, 1998). Woodlice also live on fungi, bacteria and dung and they are an eminent food source for a lot of other invertebrates and vertebrates (SUTTON & HOLDICH, 1985; HASSALL & RUSHTON, 1982; 1984; BAUER & CHRISTIAN, 1995; BERG & WIJNHOVEN, 1997). Especially in forests they can represent an important part of the soil active arthropods (HASSALL *et al.*, 1987; BERG & WIJNHOVEN, 1997; PONSARD *et al.*, 2000). Despite their importance and sometimes impressive abundances in soil ecosystems, woodlice are often neglected in ecological studies. In the present study, the terrestrial isopod faunas of 15 forest and afforested sites in the Voeren region (Belgium) are compared. These sites differ in age, type of afforestation and forest developmental stage. This paper presents part of the results of a large project to evaluate the effects of afforestation of former agricultural land, either spontaneously under a regime of low density grazing or by tree plantation, by comparing the faunas of both types of afforestation with the target habitat, i.e. well developed, ancient forest (DEKONINCK *et al.* 2005a,b). Here we focus on the terrestrial isopod order Oniscoidea or woodlice. We search indicator species for well developed (ancient) forest and assess the importance of several environmental variables.

Material en methods

Study area

The oldest sites in Flanders where afforestation was carried out on former arable fields and grasslands on loamy soils, are situated in the Voeren region. In the vicinity of two old forest relics (the Altenbroek and the Alserbos), relatively large areas were selected for spontaneous afforestation or for afforestation by plantation of indigenous trees (VERSTRAETEN *et al.* 2001; DEKONINCK *et al.*, 2005a,b). This occurred on small scale plots where different species of trees were planted or where spontaneously afforestation was allowed. These plots were sampled for their invertebrate fauna of which we report here the findings for woodlice.

Sampling and identification

Woodlice were sampled in six sites in the Altenbroek, eight sites in the Alserbos and one site in the Veurbos. General characteristics of the sampling sites are given in Table 1. Details on their soil and vegetation can de found in DEKONINCK *et al.* (2005a,b). At each sampling site 3 pitfall traps with a diameter of 9.5 cm were placed in a row, spaced 4 to 5 m apart. A 4 % formaldehyde solution was used as fixative and some detergent added to lower the surface tension. Pitfalls were emptied each fortnight and sampling lasted from April till October 2003. All species were identified using BERG & WIJNHOVEN (1997).

Table 1 — List of the sampled forests with indication of the used numbers, forest name, description of the site management, age (years), distance to ancient forest and distance to open field with AF= ancient forest, SP=spontaneous forest, PL=plantation, Ar=former arable field, Gr= former grassland, val=forest in valley and OF=open field.

Site code	Forest	History	Description of the site	Forested since	Dist. AF (in m)	Dist. OF (in m)
Site01 Voer01	Altenbroek	AF	Ancient oak-birch forest	<1775 de Ferraris	0	37.5
Site02 Voer02	Altenbroek	SP Ar	Afforestation and low density grazing (Galloways), *Salix* sp. and birch.	1996	65	7.5
Site03 Voer03	Altenbroek	SP Gr	Afforestation and low density grazing (Galloways), no shrubs or trees	1996	90	0
Site04 Voer04	Altenbroek	SP Ar	Afforestation and low density grazing, *Salix* sp. and birch	1996	43	7
Site05 Voer05	Altenbroek	PL Ar	Plantation of *Quercus robur*	1989	43.5	43
Site06 Voer06	Altenbroek	AF val	Additional site: ancient mixed deciduous forest	<1775 de Ferraris	0	48
Site07 Voer07	Alserbos	AF	Ancient oak-birch forest	<1775 de Ferraris	0	100
Site08 Voer08	Alserbos	SP Gr	Afforestation of birch	1980	165	217
Site09 Voer09	Alserbos	SP Ar	Afforestation of birch	1980	202	178
Site10 Voer10	Alserbos	PL Gr	Plantation of *Prunus avium* with fragments of *Calluna vulgaris*	1985-1990	158	203
Site11 Voer11	Alserbos	SP Ar	Afforestation of birch	1980	255	135
Site12 Voer12	Alserbos	PL Gr	Plantation of *Quercus robur*	1985-1990	65	97
Site13 Voer13	Alserbos	AF val	Additional site: ancient mixed deciduous valley forest	<1775 de Ferraris	0	26
Site14 Voer14	Alserbos	AF val	Additional site: ancient mixed deciduous valley forest	<1775 de Ferraris	0	15
Site15 Voer15	Veursbos	AF	Additional site: ancient oak-beech forest	<1775 de Ferraris	0	238

DCA community analysis and correlations with environmental variables

Detrended Correspondence Analysis was used to compare sites with respect to their overall species composition. 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. Two species, of which in total less than 45 individuals were caught, were omitted from the analyses.

At each pitfall trap (n=45) the ground cover of the most abundant plant species were recorded (Londo-scale on a 2x2 m area). We also estimated the cover of grasses, herbs, shrubs (height < 5 m), trees (height > 5m), leaf-litter, mosses and bare ground. These estimates should allow us to assert the importance of horizontal and vertical vegetation structure. For vegetation and litter characteristics at site level, average values obtained for the 3 pitfalls were used. At each site a soil sample (mixture of three samples per site taken during installation of each pitfall) was taken for which ten soil variables were measured (for more details: Dekoninck *et al*, 2005a,b).

INDVAL (Dufrêne & Legendre, 1997)

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. Such *a posteriori* groups which were tested are: history of the sites (i.e. ancient forest, former arable land, former grassland), afforestation type (i.e. spontaneous, plantation) and age of forest succession (7 years, 20-25 years and ancient forest).

Results and discussion

General results

In total 11111 specimens belonging to 10 species were collected. The most abundant species was *Ligidium hypnorum* (CUVIER, 1792) (4014 specimens). Four of the five most widely distributed woodlice species in Belgium (according to WOUTERS *et al.*, 2000), were found: *Porcellio scaber* LATREILLE, 1804; *Philoscia muscorum* (CUVIER, 1792); *Oniscus asellus* LINNAEUS, 1758 and *Trichoniscus pusillus* BRANDT, 1833. Only *Armadillidium vulgare* LATREILLE, 1804 a common open landscape species was missing. In the dry ancient forest site of the Alserbos, one of the two ancient valley forest sites of the same forest complex and the ancient forest site of the Veursbos complex, 9 species were collected which is about 1/3 of the Belgian woodlice fauna (WOUTERS *et al.*, 2000).

Some woodlice species found in our study are very rare in Belgium (WOUTERS *et al.*, 2000): *Armadillidium pulchellum* (ZENCKER, 1798), *Armadillidium opacum* (KOCH, 1841), *Armadillidium pictum* Brandt, 1833 and *Porcellium conspersum* (KOCH, 1841) For all these species their distribution in Flanders and Belgium is poorly known. Also, comments on their ecology are scarce and can only be obtained from literature from neighbouring countries, which can be summarised as follows. *A. pulchellum* is very rare in the Netherlands where it is only known from humid forest on calcareous, loamy soils (BERG & WIJNHOVEN, 1997). In Ireland this species is rare and restricted to calcareous undisturbed soils (DOOGUE *et al.*, 1979). *A. opacum* is also very rare in the Netherlands and known from calcareous, humid forests (BERG & WIJNHOVEN, 1997). In France, *A. opacum* is rather common and can be found in large forest complexes (VANDEL, 1962). In the Netherlands *A. pictum* is a rare species from humid ancient forests and shrubs on calcareous, loamy soils (BERG & WIJNHOVEN, 1997). According to VANDEL (1960) this species can be catalogued as a 'real forest' species. *P. conspersum* is very rare in the Netherlands and restricted to humid forest with a preference for *Alnus glutinosa* forests (BERG & WIJNHOVEN, 1997; SOESBERGEN, 1999). In France the distribution of this species is restricted to the eastern regions (VANDEL, 1960) occurring in pine, spruce, and beech forests where it lives in very humid situations and in rotten wood (VANDEL, 1962).

Table 2 — Species and number of individuals collected in each site AF= ancient forest, SP=spontaneous forest, PL=plantation, Ar=formerly arable field, Gr= formerly grassland, val=forest in valley.

Species	code	Altenbroek						Alserbos								Veursbos
		Site 01	Site 02	Site 03	Site 04	Site 05	Site 06	Site 07	Site 08	Site 09	Site 10	Site 11	Site 12	Site 13	Site 14	Site 15
		AF	SP Ar	SP Gr	SP Ar	PL Ar	AF val	AF	SP Gr	SP Ar	PL Gr	SP Ar	PL Gr	AF val	AF val	AF
Armadillidium opacum	ARMOPA	40	0	0	0	0	25	133	0	1	0	0	0	1177	962	0
Armadillidium pictum	ARMPIC	17	0	0	0	1	1	81	1	0	0	0	0	292	173	4
Armadillidium pulchellum	ARMPUL	157	0	0	0	3	0	2	0	0	0	0	0	0	2	1
Ligidium hypnorum	LIGHYP	0	0	0	3	21	19	197	245	23	697	249	74	1593	826	67
Oniscus asellus	ONIASE	71	1	0	2	11	60	126	7	71	2	5	21	674	252	69
Philoscia muscorum	PHIMUS	7	10	46	123	26	38	82	91	19	168	31	37	162	355	1
Porcellium conspersum	PORSCA	0	0	0	0	0	0	11	0	0	0	0	0	0	2	1
Porcellio scaber	PORCON	10	4	1	6	0	26	8	1	3	3	1	6	14	10	2
Trachelipus rathkii	TRARAT	0	0	0	3	1	0	0	0	0	0	0	1	2	0	2
Trichoniscus pusillus	TRIPUS	15	0	0	3	90	51	14	436	7	141	148	105	119	51	158
Number of species		**7**	**3**	**2**	**6**	**7**	**7**	**9**	**6**	**6**	**5**	**5**	**6**	**8**	**9**	**9**
Number of specimens		**317**	**15**	**47**	**140**	**153**	**220**	**654**	**781**	**124**	**1011**	**434**	**244**	**4033**	**2633**	**305**

As can be seen in Table 2, if the above mentioned rare species are found in high numbers this only occurs in the ancient forest stands. In two young developing forest sites near the Alserbos (site 02 and 03) we also collected a specimen of one of the rare species (resp. *A. pictum* and *A. opacum*). This is also the case for *A. pictum* in the plantation near the Altenbroek forest complex (site05). Probably these individuals are only accidental records. We think they could reach the new forest sites from the ancient forest stands where we found dense populations of *A. pictum* and *A. opacum* (maximum distance to ancient forests ± 200m), but did not yet establish a good vital population. The environmental conditions of these the young forest stands are seemingly not yet favourable enough to allow permanent settlement and a building-up of local populations and of these species. There is no direct relation between distance to ancient forest and chance to find rare forest species that arrive in the new forest sites. For example in site 12 only 65 m away from the ancient forest stands in the Alserbos none of these rare forest species were found.

Diversity, communities and indicators

In sites 02 and 03, the most recent forests (agricultural fields abandoned in 1997), we observed a low woodlice species richness with very few specimens despite the fact these sites are very close to ancient forest stands of Altenbroek. The average species richness of the ancient forests is significantly higher (8.17 ± 0.98 (n=6)) than in all former grasslands (4.75 ± 1.89 (n=4) and Mann-Whitney U-test, Z=2.61, p=0.009) and arable fields (5.4 ± 1.52 (n=5) and Mann-Whitney U-test, Z=2.56, p=0.009).

The DCA diagram (axis 1 and 2) based on the distribution of the 8 most abundant species over 45 pitfalls is presented in Fig. 1. The first two axes account for the largest part of the total variance (eigenvalues: $\lambda=0.76$ for axis1 and $\lambda=0.19$ for axis2). Eigenvalues of higher axes

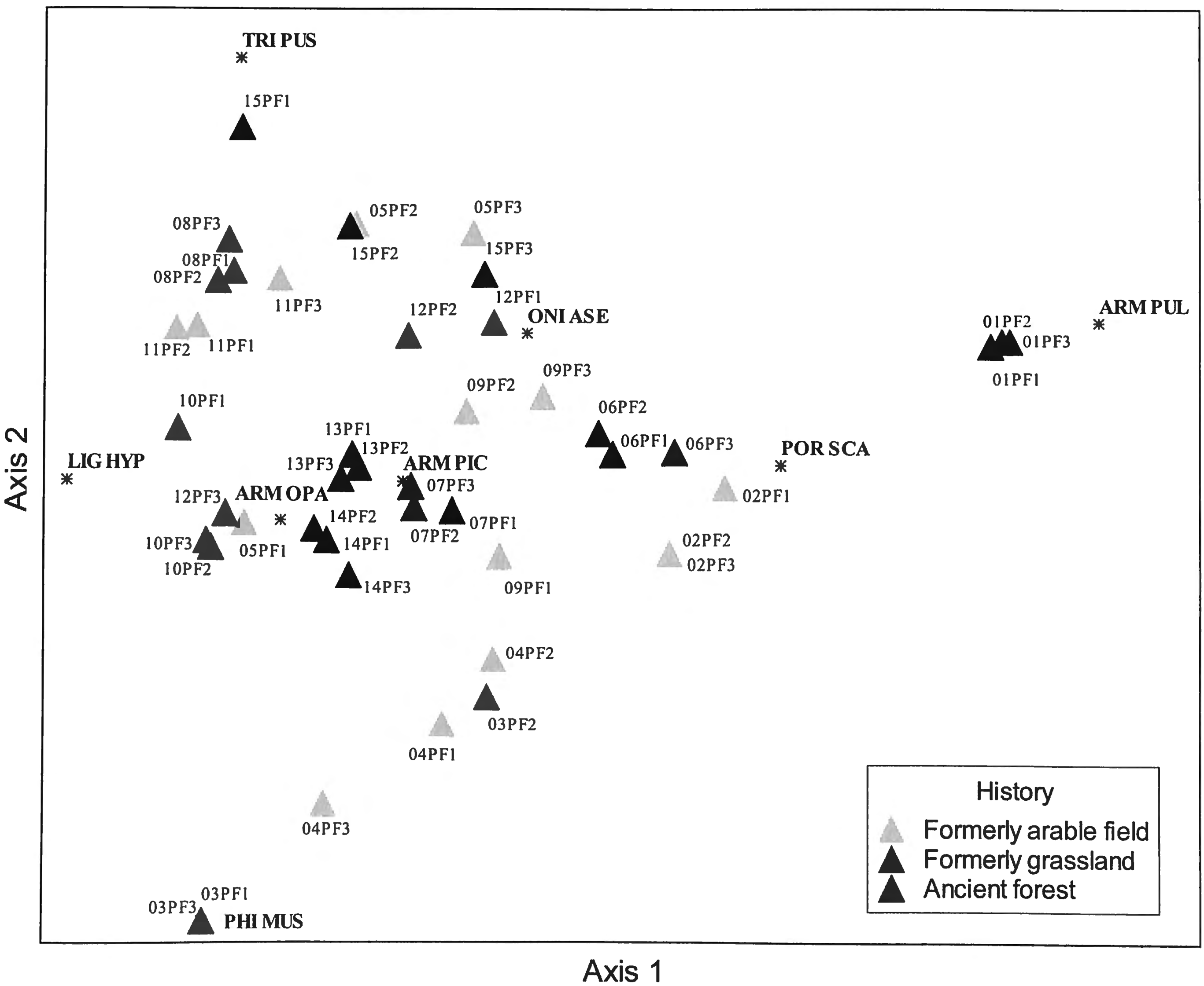

Fig. 1 — DCA diagram (axis1 $\lambda=0.76$ and axis 2 $\lambda=0.19$) of all pitfall traps based on collected individuals for n= 45 pitfalls and 8 species. Pitfalls (PF) are presented by ▲ and their history. Species codes are listed in Table 2.

Table 3 — Indicator species, indicator values and significance levels for here used groups of pitfalls.

Groups of pitfalls	GROUP	Indicator species	Indicatorvalue	Significance p
Ancient forest Formerly arable field Formerly grassland	Group of the ancient forest pitfalls	*ONIASE* *ARMOPA* *ARMPIC* *PORSCA*	89.0 83.3 77.4 56.1	0.001 0.001 0.001 0.002
Young afforestation Old afforestation Ancient forest – Plantation	Group of the ancient forest pitfalls	*ARMOPA* *ONIASE* *ARMPIC*	83.3 80.3 76.7	0.001 0.001 0.001

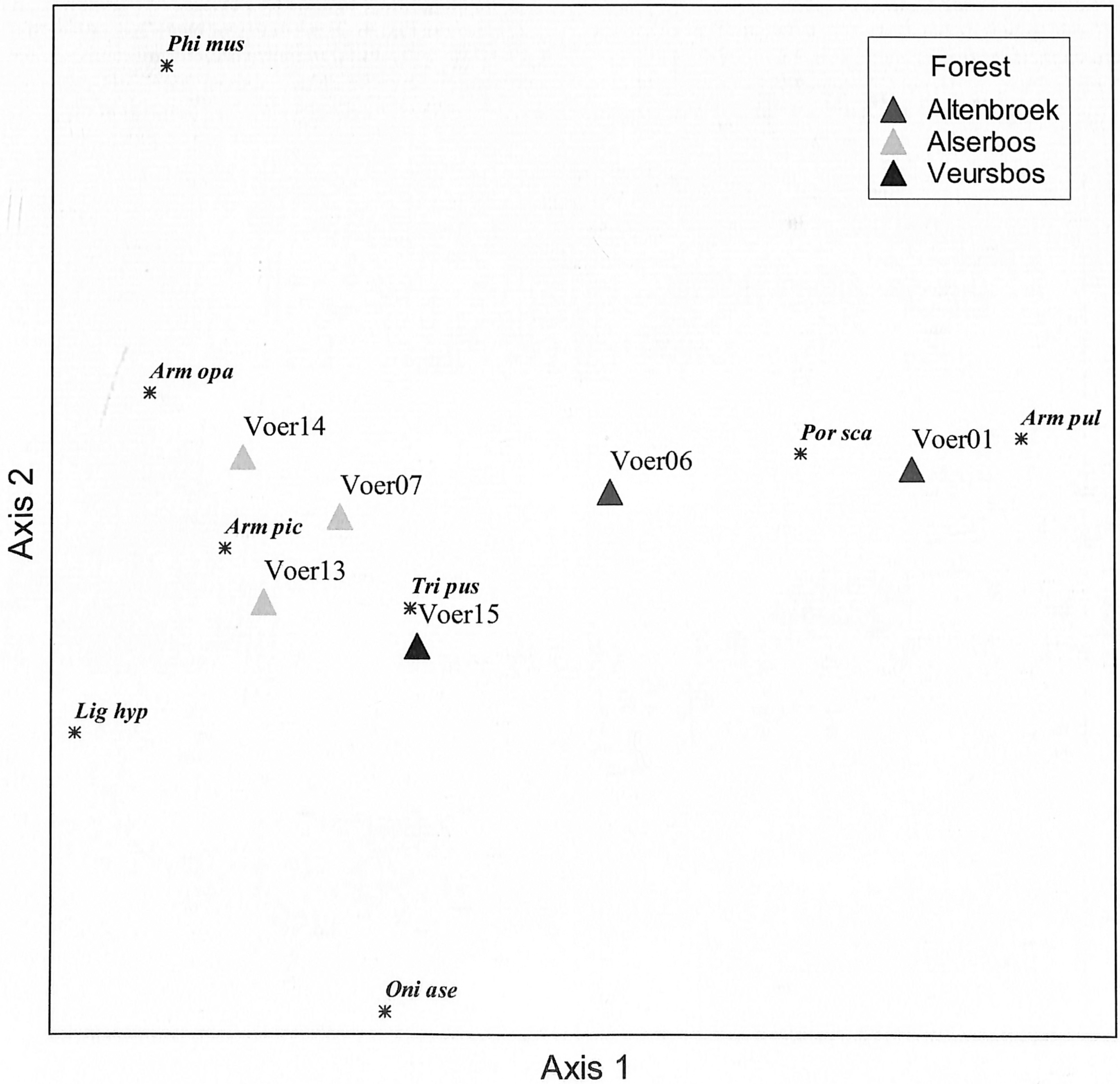

Fig. 2 — DCA diagram (axis1 λ=0.73 and axis 2 λ=0.06) of all ancient forest sites based on collected individuals for n=6 sites and 8 species. Sites are presented by ▲ and their forest complex. Species codes are listed in Table 2.

are lower than 0.05 and therefore these axes are not considered. The spreading along the first axis is determined by the presence of *L. hypnorum* in most of the sites from the Alserbos and by the high abundance of *A. pulchellum* in site 01. None of the here considered vegetation variables seem to explain this first axis. The spreading along the second axis is related to a lower cover of the grass layer ($r=-0.654$ and $p<0.001$), higher cover of the tree layer ($r=+0.594$ and $p<0.001$) and higher cover of the litter layer ($r=+0.573$ and $p<0.001$) i.e. decreasing habitat openness.

As *L. hypnorum* has a preference for very wet localities (BERG & WIJNHOVEN, 1997) the first axis might coincide with a dry-humid-wet gradient. That would imply however that *A. pulchellum* occurs in drier habitats. But according to VANDEL (1962) *A. pulchellum* has a similar ecological preference as *A. pictum* and both species avoid dry habitats. Site 01 has the lowest C/N ratio of all sites. As *A. pulchellum* is only found in high numbers at that site, a low C/N of the leaf litter might be the limiting factor for the occurrence of that rare species.

By applying the INDVAL test in two possible groupings of the samples (Table 3) the following species come out as indicators of ancient forest: ONIASE, ARMOPA, ARMPIC for both groupings and PORSCA for only one. This result can be better understood by considering Table 2. *Armadillidium opacum* is found in high to very high numbers in all ancient forest sites of the two forest complexes Altenbroek en Alserbos, whereas it is not found in any of the afforested sites there (apart from the exceptional individual discussed above). It is however not found in the ancient forest site of the Veurbos complex. If it is completely absent from this forest complex is not known. Its absence in the Veursbos ancient woodland site can thus be a landscape ecological effect as a result of insufficient habitat quality. More extensive sampling of Veursbos would be needed to test between these two possibilities. *Armadillidium pictum* is not found in high numbers in only one or two ancient forest sites (site 06 and site 15). *Porcellio scaber* is found in almost all

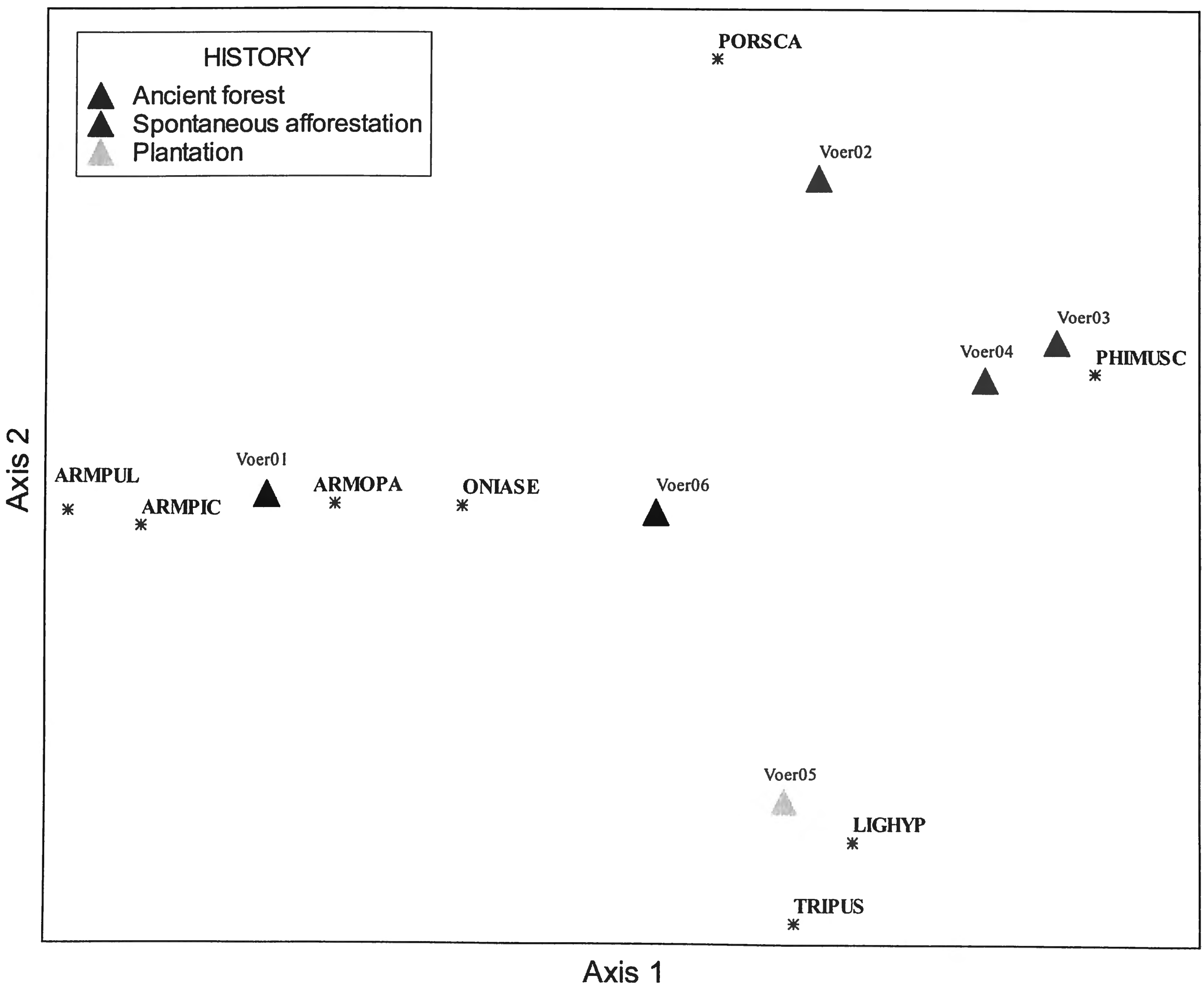

Fig. 3 — DCA diagram (axis1 λ=0.60 and axis 2 λ=0.06) of all Altenbroek forest sites based on collected individuals for n=6 sites and 8 species. Sites are presented by ▲ and their history. Species codes are listed in Table 2.

sampling sites, but in slightly (though significantly) higher numbers in the ancient forest sites. *Oniscus asellus* occurs in quite high numbers in all ancient forest sites. Also in the older afforestations it seems to have become relatively well represented.

Ancient forest sites

A DCA analysis using only ancient forest sites and their isopod communities results in Fig. 2 (axis1 $\lambda=0.73$ and axis 2 $\lambda=0.06$). The spreading along the first axis is related to a high percentage of soil covered with leaf litter ($r=+0.636$ and $p<0.001$) and a low cover of the grass layer ($r=-0.634$ and $p<0.001$) and the herb layer ($r=-0.643$ and $p<0.001$). The ordination along the second axis coincides with variation in the cover of the bush layer ($r=-0.754$ and $p<0.001$) and the tree layer ($r=+0.642$ and $p<0.001$). The sites cluster according to forest complex suggesting that we should evaluate the effects of afforestation on the composition of isopod communities for each forest complex separately.

Woodlice communities in the Altenbroek forest complex (Fig. 3)

Sites from the Altenbroek cluster according to their forest developmental age. The ancient forests with typical forest species as *O. asellus*, *A. opacum*, *A. pulchellum* and *A. pictum* have a totally different isopod fauna than those of the recently abandoned agricultural fields (sites 02, 03, and 04) dominated by the eurytopic *P. scaber* and *P. muscorum*. In site 05 where forest succession is already going on for more than 10 years these common species seem to have been replaced by *L. hypnorum* and *T. pusillus*.

Woodlice communities in the Alserbos (Fig. 4)

As for the Altenbroek, the sites of the Alserbos cluster according to their developmental age. The ancient forests, with typical forest species as *O. asellus*, *A. opacum*, and *A. pictum*, are still very different in isopod fauna from the sites abandoned 20-25 ago which are dominated by the

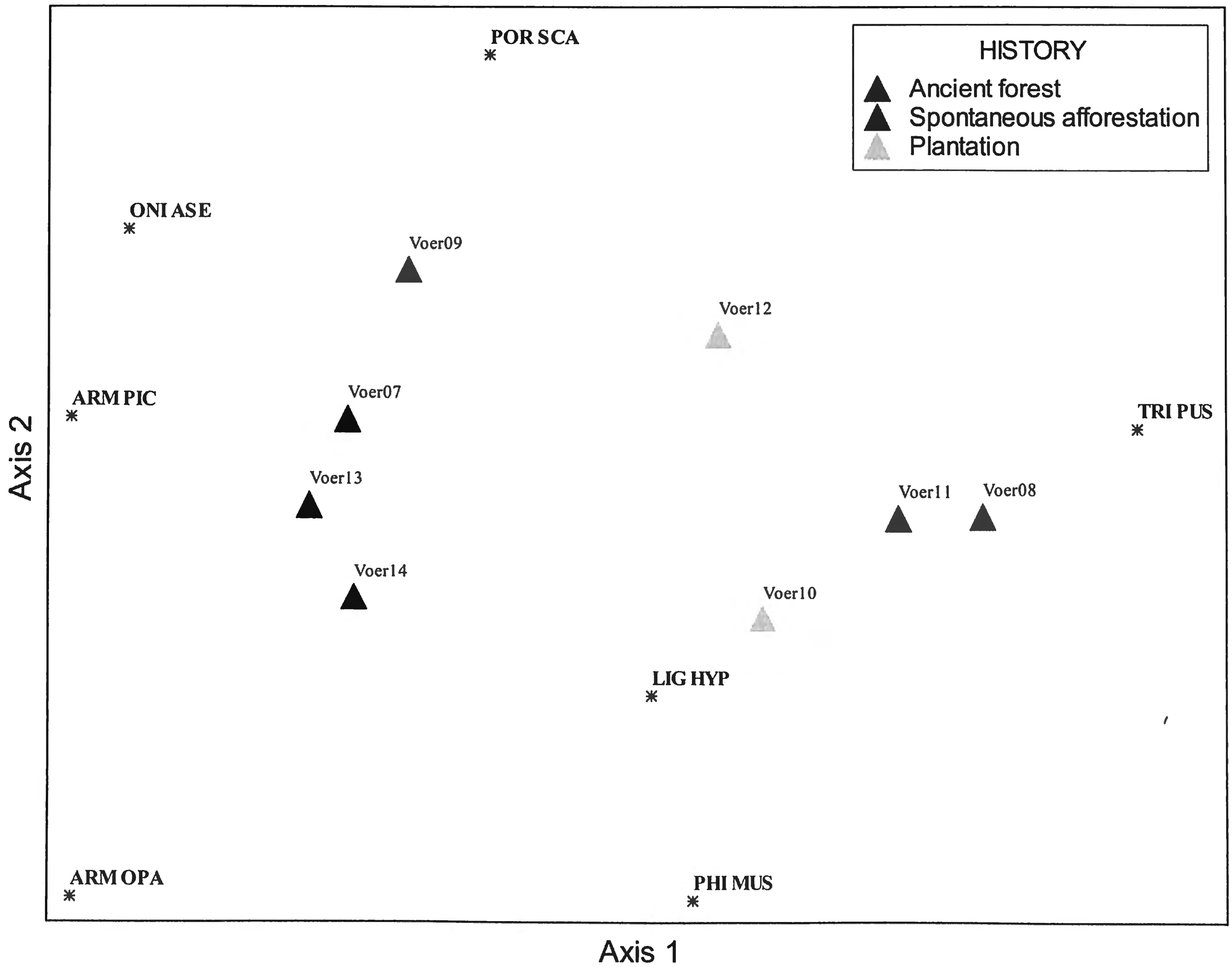

Fig. 4 — DCA diagram (axis1 $\lambda=0.43$ and axis 2 $\lambda=0.04$) of all Alserbos forest sites based on collected individuals for n=8 sites and 7 species. Sites are presented by ▲ and their history. Species codes are listed in Table 2.

more eurytopic and common forest species *P. scaber, L. hypnorum*, *T. pusillus* and *P. muscorum*.

Conclusions

Although woodlice are important in soil ecosystems and sometimes have impressive abundances in forests, their usefulness as bio-indicators in ecological surveys as this study, should be considered in the right perspective. It is not a very species rich group; only therefore already the number of potential indicators is also low.

Used at the appropriate spatial scale they seem to have however good indicator potentialities. In the Voeren region, there are quite some woodlice species which are bound to well-developed forests: *P. conspersum*, *A. pictum*, *A. pulchellum* and *A. opacum*. The occurrence of one or several of these species indicates in the here considered region for a long period undisturbed development of good forest conditions, i.o.w. ancient forest conditions. For other parts of the country, where these rare species do not occur, the abundance of *Oniscus asellus* will be the only indicator for reaching real forest environments. That particular species can only be used as indicators on a restricted geographical scale, was stressed by ZIMMER *et al.* (2000) for *P. conspersum* in German grasslands.

The terrestrial isopod fauna of ancient forests has higher species richness than both young and older afforestations and plantations. After 20-25 years of development we only find less demanding forest species, such as *T. pusillus*, *O. Asellus* and *L. hypnorum*.

To summarize, we can state that it takes apparently long before an interesting ancient forest isopod fauna can settle in abandoned former agricultural sites where a spontaneous forest succession is ongoing or where a new forest was planted. Most probably suboptimal soil and environmental conditions still too dissimilar from those in ancient forests are responsible for this. After 25 years these species are still missing even if distance from ancient forest is not a limiting factor.

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References

BAUER, R. & CHRISTIAN, E., 1995. The effect of enchytraeid faeces and mucus on the food choice of *Porcellio scaber* (Isopoda). *European Journal of Soil Biology*, 31 (1): 49

BERG, M.P. & WIJNHOVEN, H., 1997. Landpissebedden. Wetenschappelijke Mededelingen KNNV, nr 221, 80 pp.

DEKONINCK, W., DESENDER, K., GROOTAERT, P. & MAELFAIT, J.-P., 2005a. Faunistische evaluatie en vergelijking van bosuitbreiding via bebossing, spontane verbossing, en extensieve begrazing van open terreinen: een case-study in de Voerstreek. Rapport ENT.2005.01, i.o.v. Aminal afdeling Bos & GROEN, BRUSSEL.

DEKONINCK, W., DESENDER, K., GROOTAERT, P. & MAELFAIT, J.-P., 2005. The effects on arthropods of tree plantation and spontaneous afforestation on former agricultural land near old forests in the Voeren region (Belgium). *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Entomologie* 75: 221-234.

DOOGUE, D., READON, N.M. & HARDING, P.T., 1979. Further records of uncommon Irish woodlice (Crustacea: Isopoda), *Irish Naturalists' Journal*, 19 (10): 343-347.

DUFRÊNE, M. & LEGENDRE, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 61: 345-366.

HAMES, C.A.C., & HOPKIN, S.P., 1989. The structure and function of the digestive system of terrestrial isopods. *Journal of Zoology*, 217: 599-627.

HASSALL, M., 1977. Consumption of leaf litter by the terrestrial isopod *Philoscia muscorum* in relation to food availability in a dune grassland ecosystem. *Ecological Bulletin*, 25: 550-553.

HASSALL, M. & DANGERFIELD, J.M., 1997. The population dynamics of a woodlouse, *Armadillidium vulgare*: an example of biotic compensatory mechanisms amongst terrestrial macrodecomposers? *Pedobiologia*, 41: 342-360.

HASSALL, M. & RUSHTON, S.P., 1982. The role of coprophagy in the feeding strategies of terrestrial isopods. *Oecologia* 53: 374-381.

HASSALL, M. & RUSHTON, S.P., 1984. Feeding behaviour of terrestrial isopods in relation to plant defences and microbial decay. In SUTTON, S.L. & HOLDICH, D. *The Biology of Terrestrial Isopods. Proceedings of the Zoological Society of London Symposium*, 53: 487-505.

HASSALL, M., TURNER, J.G., & RANDS, M.R.W., 1987. Effects of terrestrial isopods on the decomposition of woodland leaf litter. *Oecologia*, 72: 597-604.

MCCUNE, B. & GRACE, J.B., 2002. Analysis of ecological communities. MjM. Software Design, Gleneden Beach, OR, US, 300 pp.

PONSARD, S., ARDITI, R. & JOST, C., 2000. Assessing top-down and bottom-up control in a litter-based soil macroinvertebrate food chain. *Oikos*, 89: 524-540.

SOESBERGEN, M., 1999. *Porcellium conspersum*, een in Nederland zeer zeldzame landpissebed van vochtige bossen (Crustacea: Isopoda: Oniscoidea). *Nederlandse Faunistische Mededelingen*, 9: 140-141.

SUTTON, S.L. & HOLDICH, M.D., 1985. The Biology of Terrestrial Isopods (Symposia of the Zoological Society of London), Oxford Univ Pr.

SZLÁVECZ, K. & MAIORANA, V.C., 1998. Supplementary food in the diet of terrestrial isopods. *Israel Journal of Zoology*, 44: 413-421.

VANDEL, A., 1960. Isopodes Terrestres. *Faune de France*, 64: 1-416.

VANDEL, A., 1962. Isopodes Terrestres. *Faune de France*, 66: 417-931.

VERSTRAETEN, A., VANDEKERKHOVE, K. & DE KEERSMAEKER, L., 2001. Praktijkgericht onderzoek naar kansen en belangrijke stuurvariabelen voor natuurontwikkeling op gronden met voormalig intensief landbouwgebruik. Deel III: kansen van spontane verbossing versus actieve bosaanplant. Eindverslag van project VLINA 99/02, studie uitgevoerd voor rekening van de Vlaamse Gemeenschap binnen het kader van het Vlaams Impulsprogramma Natuurontwikkeling in opdracht van de Vlaamse minister bevoegd voor natuurbehoud. IBW Bb R 2001.011., 155 pp.

WOUTERS, K., TAVERNIER, J.M. & MEURISSE, L., 2000. Distribution and bibliography of the terrestrial Isopoda (Crustecea) of Belgium. *Bulletin van het Koninklijk Belgische Instituut voor Natuurwetenschappen, Biologie*, 70: 193-205.

ZIMMER, M. & TOPP, W., 1997. Does leaf litter quality influence population parameters of the common woodlouse, *Porcellio scaber* Latr., 1804 (Crustacea: Isopoda)? *Biology and Fertility of Soils*, 24: 435-441.

ZIMMER, M. & TOPP, W., 1999. Relations between woodlice (Isopoda: Oniscidea), and microbial density and activity in the field. *Biology and Fertility of Soils,* 30: 117-123.

ZIMMER, M., BRAUCKMANN, H.-J., BROLL, G. & TOPP, W., 2000. Correspondence analytical evaluation of factors that influence soil macro-arthropod distribution in abandoned grassland. *Pedobiologia*, 44: 695-704.

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