Ecological diversity, assemblage structure and life cycles of ground beetles (Col., Carabidae) in the forest of Ename (Eastern Flanders, Belgium)

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Abstract

Continuous pitfall trapping during a complete year cycle on 13 sites of the forest of Ename revealed 3861 carabid beetles and 1241 larvae, belonging to 59 species. Although the observed species richness is high, stenotopic woodland carabid species, typically occurring in ancient forests, are represented by few species only and limited in their occurrence to dark forest patches. The high species diversity is primarily due to the presence in this forest of ground beetle species from many other habitats, marshland in particular. Analysis of the faunal assemblages shows that these can be explained at least partly by ecological as well as historical data. Most of the sampling sites can be characterised based on their carabid assemblages. The data illustrate how ground beetles are ideal ecological indicators for the comparison of recent and ancient forest faunas. Nature development experiments to restore gradients at the interface of woodland edges and grassland vegetation do not seem to increase total carabid diversity: an experimental plot along such a gradient contains some eurytopic woodland as well as grassland species, but no additional species limited to the woodland-grassland interface. Details are also given on the life cycle of the most abundant woodland species *Abax ater, Agonum assimile, Asaphidion curtum, Nebria brevicollis, Pterostichus cristatus* and *Pterostichus madidus.*

Key words: Carabidae, forest, diversity, assemblage structure, ecological indicators, life cycle

Résumé

Lors d'un échantillonnage continu à l'aide de pièges durant une année à 13 sites de la forêt d'Ename nous avons obtenus 3860 coléoptères carabiques et 1241 larves, appartenant à 58 espèces. Quoique la diversité observée est élevée, nous n'avons retrouvés que peu d'espèces forestières sténotopes, typiques pour des forêts anciennes, et ceux-la surtout dans des microhabitats sombres de la forêt. La grande richesse spécifique est surtout due à la présence dans ce bois d'espèces de coléoptères carabiques d'une multitude d'autres habitats, de marais en particulier. L'analyse des communautés démontre que leur présence peut être expliquée par des facteurs écologiques aussi bien que historiques. Les résultats obtenues montrent comment ces coléoptères peuvent servir comme indicateurs écologiques pour comparer les faunes de forêts récentes et anciennes. Des experiments de développement de nature pour restorer des gradients à l'interface des limites de forêts et de prairies ne semblent pas augmenter la diversité totale de coléoptères carabiques. Les résultats démontrent la présence de quelques espèces forestières eurytopes, aussi bien que des espèces de prairies, mais pas d'espèces additionelles qui seraient typiques pour l'interface entre ces deux habitats. Des détails concernant le cycle de vie des espèces forestières abondantes *Abax ater, Agonum assimile, Asaphidion curtum, Nebria brevicollis, Pterostichus cristatus* et *Pterostichus madidus* sont visualisés sur des grafiques.

Mots-clefs: Carabidae, forêt, diversité, structure de communautés, indicateurs écologiques, cycle de vie

Introduction

Between March 1994 and April 1995 the forest of Ename was sampled for spiders and carabid beetles, as part of a larger project on terrestrial arthropods of this woodland area (e.g. ALDERWEIRELDT, 1997; DE BAKKER & MAELFAIT, in prep.). The study site is famous for its high floral diversity (484 plant species), extremely well documented with respect to its historical ecology (cf. TACK et al., 1996), but has never been studied before for its terrestrial arthropods. In this contribution, we will discuss the general results obtained during a complete year cycle of sampling on 13 sites in this forest, including an experimental plot where a smooth transition between forest and surrounding grassland has been restored through recent management.

In this paper, we will (1) comment upon the ground beetle species diversity and the presence of carabids of special faunistic interest, (2) describe the observed assemblages and species identities as compared to recent and historical ecology, (3) evaluate the outcome of a nature development experiment to restore smooth gradients at the edges of the forest aimed at increasing total floral and faunal diversity and (4) illustrate details on the life cycle of the most abundant ground beetle species.

More comprehensive comparisons of the observed carabid assemblages with those from other forests in Flanders, as well as population genetic aspects of some carabid species collected in different parts of this study area will be published in future contributions.

Material and methods

1. Study site and history

The forest of Ename is situated in the southern part of the province of eastern Flanders. The forested area is shown on Figure 1 along with elevation lines and the location of the 13 sampling sites for this study (A-M, see further). The historical forest nowadays is divided in three different parts, separated by agricultural land, but more or less interconnected by some important hedges or rows of trees. Sampling sites were chosen in all of the main parts. The total surface of the forest area is about 61 ha.

The forest of Ename is a characteristic type of forest situated on a relatively steep slope, which is the eastern edge of the river Schelde valley. Sampling sites were chosen:

(1) on the slope itself (relatively dry forest patches; sampling stations I, J; more humid forest patches B, G),

(2) in very humid to wet valley forest (C, K, L, including the edges of a large forest pond: M) and also

(3) in a small spring forest (A),

(4) in a large hedge linked to the forest (H) close to the forest site B and

(5) in a transition of forest edge to grassland (D = forest edge, E = interface, F = grassland).

The exact location of the 13 sampling sites is shown in Figure 1, whereas data on soil texture, vegetation cover and vegetation height are summarised in Table 1. Most stations can be characterised as having a clay soil.

Tree cover is highest in sites B, J and G with a dominance of *Castanea sativa* (B), *Fagus sylvatica* (J), and *Carpinus betulus, Fraxinus excelsior* and *Populus canadensis* (G) , respectively.

Shrubs are most pronounced in stations E, I, K and L and dominated by *Prunus spinosa* and *Rubus fruticosus* (E), *Carpinus betulus* and *Rubus fruticosus* (I), *Fraxinus excelsior, Acer pseudoplatanus* and *Rubus fruticosus* (K) and *Rubus caesius* and *Ulmus minor* (L), respectively.

The herb layer is well developed in F, A, C and H with a dominance of *Anthoxanthum odoratum, Holcus lanatus, Lysimachia numullaria* and *Veronica chamaedrys* (F), *Urtica dioica* and *Lamium galeobdolon montanum* (A), *Aegopodium podagraria* and *Urtica dioica* (C) and *Hedera helix* (H), respectively.

Mosses are mostly less abundant except in L, E, K and D, where there is a dominance of *Eurhynchium praelongum*, combined with *Eurhynchium striatum* in K and L.

For additional descriptive information on the sampling sites, including more abiotic and more extensive plant lists and vegetation mapping data, we refer to VANDEN BUSSCHE (1995).

The history of the forest of Ename complex is very well documented (TACK et al., 1993, 1996): the forest area was exploited already since the early Medieval, but gradually replanted from the 13th until about the 18th century. In the 19th century the woodland however was nearly completely cleared. Many forest plant species apparently were able to survive this adverse period, supposedly in hedges and some very small woodland remnants (TACK et al., 1993). Partial reforestation of the area took place between 1886 and 1898 and resulted more or less in the actual situation. Below, we will try to evaluate whether or not typical woodland carabid species were able to survive the ''crisis'' during the 19th century, a phenomenon observed for many typical woodland plant species (TACK et al., 1993).

2. Sampling, meteorology and analysis of the data

Each sampling site was studied by means of three pitfall traps (glass jam jars, diameter = 9,5 cm; filled with a 10% formalin solution with some detergent added to reduce surface tension), emptied at fortnightly intervals between 13 April 1994 and 15 April 1995.

General meteorological data were obtained from the nearest meteorological station at Kruishoutem (about 8 km NW from Ename; monthly bulletins of the KMI,
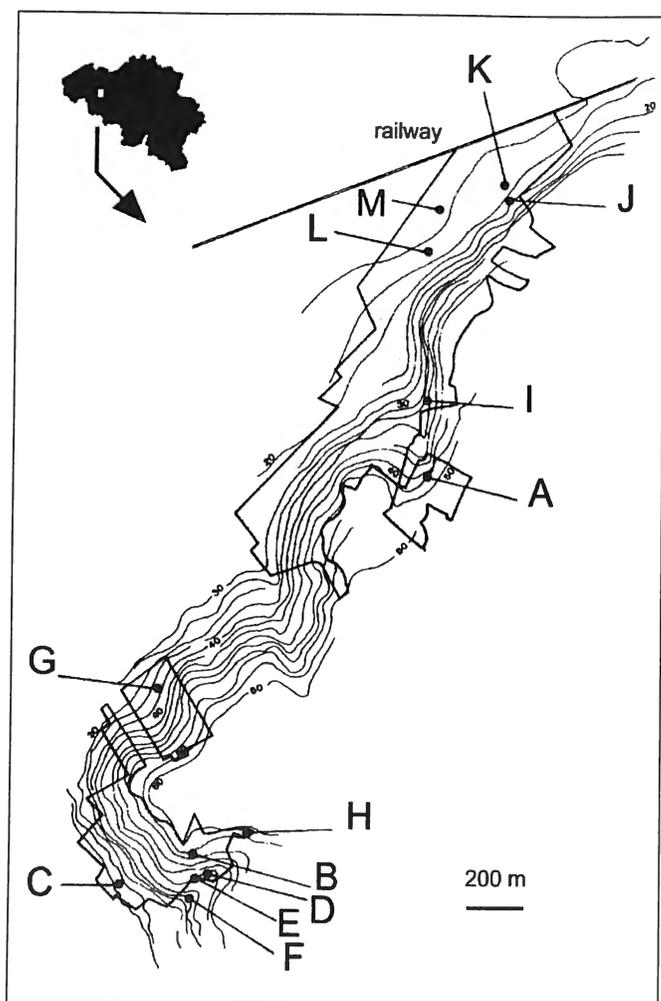
Fig. 1. – Map of the forest of Ename with location of the 13 sampling sites (A-M); elevation lines (20, 30, 40, 50 and 60m) added.

Table 1. – Site characteristics of the sampling sites in the forest of Ename: soil texture fractions, estimates of vegetation cover (%) and vegetation height measured between June 21th and July 7th 1995.

Site	Soil texture (fraction %)			Vegetation cover (%)				Vegetation height (m)		
	sand	loam	clay	tree	shrub	herb	moss	tree	shrub	herb
A	42.9	26.4	30.7	50	50	70	1	30	< = 6	< = 1
B	42.0	29.8	28.2	85	5	55	< 1	25-30	< = 2.5	< = 0.35
C	19.2	64.1	16.7	40	30	70	10	20-30	< = 8	< = 1. 1
D	43.0	22.6	29.4	65	40	60	20	15-25	< = 7	< = 0.5
E	43.6	25.9	30.5	0	70	10	50		5-7	0.15-0.25
F	35.2	37.0	27.8	0	0	95	10			0.6-1
G	44.0	26.3	29.7	70	15	8	1	12-30	< = 1	< 0.1
H	–	–	–	45	45	65	5	25	< = 10	< = 0.3
I	51.8	29.2	19.0	50	70	30	< 1	15-30	< = 12	< = 0.4
J	45.7	32.7	21.6	80	5	25	< 1	25	< = 6	< = 0.3
K	38.9	42.2	18.9	20	70	50	30	25	< = 14	< = 0.8
L	34.8	32.6	32.6	55	75	30	80	25	1-6	< = 0.
M	24.0	36.8	39.2	5	60	40	< 1	25	< = 7	< = 2.3

Ukkel, Belgium). Mean monthly values of maximum and minimum temperature and total precipitation for the complete sampling year cycle are given in Table 2 and have been compared to reference norm values for a long period of observations (1921-1993). Meteorological conditions during this sampling year in general appeared to be rather normal, except for some warmer en wetter months at the end of the sampling cycle, eventually having influenced beetle populations appearing during the next spring (not sampled). Conditions are therefore not expected to have influenced our sampling results very

differently as compared to normal years. Long term carabid samplings during several years in woodland sites of the forest of "Zoniën" (DESENDER, unpublished data) have shown relatively few differences in species composition and diversity from one year to another, in contrast to results obtained from more open habitat types (DESENDER, 1996). We therefore assume that our one year survey in the forest of Ename gives a reliable picture of the local carabid assemblages, especially for what concerns its most abundant species.

All carabid beetle adults and larvae were sorted, iden-

Table 2. – Meteorological data (mean monthly maximum and minimum temperature in °C, total precipitation in mm) from the KMI station at Kruishoutem (monthly bulletins KMI, Belgium) as compared to reference norms from 1921-1993.

month / year	temp. max.	temp. min.	precipitation (mm)	deviation from norms
April 1994	12.9	4.8	74.5	normal
May 1994	16.9	8.0	78.9	normal
June 1994	20.6	10.9	56.4	normal
July 1994	26.5	15.0	94.2	warmer
August 1994	22.5	13.1	45.8	normal
September 1994	17.4	10.3	122.4	colder and wetter
October 1994	14.9	5.6	61.1	normal
November 1994	13.2	7.6	26.1	warmer and dryer
December 1994	8.6	2.4	123.7	warmer and wetter
January 1995	7.8	1.6	152.4	wetter
February 1995	10.2	4.1	78.6	warmer and wetter
March 1995	9.9	2.0	72.4	normal
April 1995	13.2	4.8	41.2	normal

tified to species level and sexed (adults mainly identified by means of LINDROTH, 1974; larvae by making use of several publications and a comprehensive reference collection). Wing polymorphic ground beetles species were checked for their wing development. Larvae were measured (head width) in order to identify the larval instar (3 instars in most carabids). To illustrate details on the phenology of the life cycle in adults and larvae of the most abundant species, numbers caught were recalculated by interpolation to equal halfmonthly intervals of exactly 15 days each.

Species composition and abundance was compared between sampling series by means of a Two Way Indicator Species Analysis (TWINSPAN program: HILL, 1979). TWINSPAN performs a two-way divisive and hierarchical classification whereby the original group of samples and species is split into two groups at each division based on indicator species (HILL, 1979). Species relative abundance, habitat preference, community structure and composition were also compared in Detrended Correspondence Analyses (DCA; detrended by segments; software CANOCO (v. 3.12);TER BRAAK, 1988).

Both the TWINSPAN and DCA analysis were performed on two separate data-sets:

(1) most abundant species from all forest sampling stations (20 species from 11 sites occurring with a total of at least 11 individuals) and

(2) results from the forest-edge experiment separately (sampling sites D, E, F with 9 more or less abundant carabid species).

Data were transformed to percentage occurrence within each species (thus equal-weighting the species) prior to TWINSPAN and DCA analysis. Transformation was preferred for two reasons: (1) pitfall trap data yield only very approximate or possibly biased abundance ratio's between species and (2) to avoid an overruling influence in the analysis of a few very numerous species which may not possess obvious habitat preferences. One possible drawback of this transformation technique is an increasing influence of sampling errors for species caught in relatively low to very low numbers. Therefore the above-mentioned restrictions were applied to the data-set prior to analysis. Species caught in very low numbers in many cases can be interpreted as accidental immigrants anyway (cf. DESENDER & BAERT, 1995; DESENDER, 1996). Additional DCA runs however showed the same overall pattern in ordination diagrams irrespective of the exact size of the data-set.

Results and discussion

1. Carabid diversity, dispersal power and species of special faunistic interest

On the whole, 3861 beetles, belonging to 59 species, and 1241 larvae, from 10 species only, were caught. Many carabid beetles indeed are known to possess larvae living in the soil and thus not easily caught in pitfall traps. Table 3 summarises the total number of adults and larvae obtained in each of the 13 sampling sites. Although the observed species richness is high, stenotopic carabid species, typically occurring in old forests, are represented by few species only (see further). The high species diversity is primarily due to the presence in this forest of ground beetle species from many other habitats, marshland in particular (see further).

Fourteen wing dimorphic or polymorphic species were observed (Table 4): apparently most of the species occurred in brachypterous morph, a phenomenon observed in many other studies (e.g. DESENDER, 1989, 1996); one exception is *Notiophilus biguttatus*, a species well known from clearer spots in woodland and probably therefore regularly able to fly in search of forest patches with higher light intensities at soil surface (DESENDER, 1989). Four other species from the total list are known as constantly brachypterous carabids: *Abax ater, Patrobus atrorufus, Pterostichus cristatus* and *Pterostichus madidus*. These are all known as more or less forest inhabiting species, *Pterostichus cristatus* even as stenotopic woodland carabid species. The remaining 40 ground beetle species from this species list are constantly macropterous. Nevertheless, many of these species do not necessarily show a high dispersal power because even in these species wing development can be reduced to a certain degree (e.g. *Agonum assimile, Badister sodalis*) and also because in many macropterous species functional flight muscles are regularly or nearly always absent (cf. DESENDER, 1989).

Three species from this inventory are mentioned from the Red list of carabid beetles in Flanders (DESENDER et al., 1995): all are more or less restricted to woodlands: *Agonum livens* (category 2: endangered), *Dromius bifasciatus* (category B: probably endangered) and *Pterostichus cristatus* (category Z: rare). Although the observation of the *Dromius* species concerns one individual only, this is the first data from our country (DESENDER & MAES, 1995). It was taken in a rather humid mixed deciduous forest with oak and ash and some old poplar varieties. The species has a special way of life because it is arboricolous and therefore only rarely caught in pitfall traps. *Agonum livens* is known from relatively few other sites in our country (Fig. 2), mainly very humid forest sites. In the forest of Ename it was only caught in the humid valley forest sites K, L and M. *Pterostichus cristatus* is a brachypterous species mainly occurring in humid and dark forest habitats of ancient woodland (DESENDER, 1989). The species is very rare in Flanders but relatively more common in the Ardennes (Fig. 3). In the forest of Ename it occurs mainly in sites A, B and G, all relatively humid and dark forest patches. It is interesting to note that the species did not occur in station H, which is a hedge linked to the forest near site B: apparently the special habitat preference of this species excludes its occurrence in the relatively less dark and possibly somewhat warmer microclimate of hedges and of forest edges in general.

Table 3. – Number of carabid beetles (males + females) and larvae caught per species and sampling station in the forest of Ename during a complete year cycle (April 1994- April 1995)

Sampling station Species:	A	B	C	D	E	F	G	H	I	J	K	L	M	Total
1 Abax ater	30	55	16	35	3	29	41	6	14	10	12	14	2	267
2 Agonum albipes	1	0	0	0	0	0	0	0	0	0	0	0	0	1
3 Agonum assimile	13	0	0	0	0	0	0	0	1	12	64	5	59	154
4 Agonum dorsale	0	0	0	0	4	0	0	0	0	0	0	0	0	4
5 Agonum livens	0	0	0	0	0	0	0	0	0	0	9	18	3	30
6 Agonum micans	0	0	0	0	0	0	0	0	0	0	0	0	3	3
7 Agonum muelleri	0	0	0	3	2	23	0	0	0	0	6	1	2	37
8 Agonum obscurum	0	0	0	0	0	0	0	0	0	0	0	0	2	2
9 Agonum viduum	0	0	0	0	0	0	0	0	0	0	0	0	8	8
10 Amara aenea	0	0	0	0	0	0	0	1	0	0	0	0	0	1
11 Amara communis	0	0	0	0	0	4	0	0	0	0	0	0	0	4
12 Amara familiaris	0	0	0	0	0	0	0	2	0	0	0	0	0	2
13 Amara lunicollis	0	0	0	0	0	18	0	1	0	0	0	0	0	19
14 Amara plebeja	0	1	1	0	0	2	0	1	1	0	0	0	0	6
15 Amara similata	0	0	0	0	1	6	1	0	0	0	1	1	0	10
16 Anisodactylus binotatus	0	0	1	0	0	11	0	0	0	0	0	0	0	12
17 Asaphidion curtum	1	8	22	3	5	0	7	38	0	2	2	0	1	89
18 Badister bullatus	0	0	0	1	0	1	2	0	0	3	0	0	0	7
19 Badister dilatatus	0	0	0	0	0	0	0	0	0	0	0	0	4	4
20 Badister lacertosus	0	0	0	1	0	0	0	0	0	0	0	0	0	1
21 Badister sodalis	4	7	0	3	7	3	0	1	0	0	1	2	6	34
22 Badister unipustulatus	0	0	0	0	0	0	0	0	0	0	0	0	3	3
23 Bembidion biguttatum	1	0	0	0	0	0	0	0	0	0	0	1	3	5
24 Bembidion deletum	0	0	0	0	0	0	0	1	0	0	0	0	0	1
25 Bembidion dentellum	0	0	0	0	0	0	0	0	0	0	0	0	18	18
26 Bembidion lampros	1	7	0	0	14	13	0	2	1	0	4	1	0	43
27 Bembidion lunulatum	0	0	0	0	0	0	0	0	0	0	1	3	11	15
28 Bembidion obtusum	1	0	0	0	0	2	0	0	0	0	1	0	0	4
29 Bembidion properans	0	0	1	0	0	2	0	0	0	0	0	0	0	3
30 Bembidion quadrimaculatum	1	0	0	0	1	1	0	0	0	0	0	1	0	4
31 Bembidion tetracolum	0	4	1	1	1	0	0	4	0	0	0	0	0	11
32 Clivina fossor	0	0	0	0	0	7	0	1	0	0	16	1	7	32
33 Dromius bifasciatus	0	0	0	0	0	0	0	0	1	0	0	0	0	1
34 Dromius linearis	0	0	0	0	1	0	0	0	0	0	0	0	0	1
35 Dromius spilotus	0	0	0	0	0	0	0	0	1	0	0	0	0	1
36 Dyschirius aeneus	0	0	0	0	0	0	0	0	0	0	0	0	1	1
37 Dyschirius globosus	0	0	0	0	0	0	0	1	0	0	0	0	2	3
38 Elaphrus cupreus	0	0	0	0	0	0	0	0	0	0	2	0	0	2
39 Harpalus latus	0	0	0	0	0	0	0	1	0	0	0	0	0	1
40 Harpalus rufipes	0	0	0	0	0	2	0	1	0	0	0	0	0	3
41 Leistus ferrugineus	0	0	1	0	1	0	0	0	0	0	0	0	0	2
42 Leistus fulvibarbis	0	0	2	1	3	1	1	0	0	0	5	4	14	31
43 Leistus rufomarginatus	0	12	0	0	0	0	23	4	0	0	0	0	0	39
44 Leistus terminatus	0	0	0	0	0	0	0	0	0	0	2	0	0	2
45 Loricera pilicornis	3	20	20	6	0	2	2	0	5	0	2	6	8	74
46 Nebria brevicollis	19	46	37	8	36	337	717	18	10	32	41	25	17	1343
47 Notiophilus biguttatus	7	0	9	9	2	0	28	12	5	1	0	0	1	74
48 Patrobus atrorufus	6	7	0	0	0	0	0	1	0	0	1	2	1	18
49 Pterostichus anthracinus	0	0	0	0	0	0	0	0	0	0	0	1	3	4
50 Pterostichus cristatus	132	73	0	0	0	0	67	0	0	2	1	0	0	275
51 Pterostichus cupreus	0	0	0	0	0	10	0	0	0	0	1	1	0	12
52 Pterostichus madidus	6	57	8	8	4	85	499	243	34	80	4	5	1	1034
53 Pterostichus melanarius	0	1	0	0	0	1	0	2	0	0	0	0	0	4
54 Pterostichus minor	0	0	0	0	0	0	0	0	1	0	0	0	6	7
55 Pterostichus nigrita	10	1	0	0	0	0	0	0	0	0	1	4	16	32
56 Pterostichus strenuus	1	17	3	0	2	0	0	0	1	2	8	0	11	45
57 Pterostichus vernalis	0	0	1	2	0	1	0	1	0	0	0	1	0	6
58 Pterostichus versicolor	0	0	0	0	0	5	0	0	0	1	0	0	0	6
59 Trechus quadristriatus	0	0	1	0	0	1	0	4	0	0	0	0	0	6
sum adults:	237	316	124	81	87	567	1388	346	75	145	185	97	213	3861
LARVAE:														
Abax ater instar I	0	1	0	0	0	2	0	12	1	1	0	0	1	18
Abax ater instar II	0	1	0	1	0	0	0	6	0	0	0	1	1	10
Abax ater instar III	1	2	0	0	1	4	8	3	1	2	0	0	0	22
Agonum assimile	3	0	0	0	0	0	0	0	0	0	0	0	0	3
Agonum muelleri	0	0	0	0	0	0	0	0	0	0	4	0	11	15
Leistus ferrugineus	1	4	4	0	12	1	10	0	1	0	3	5	4	45
Leistus fulvibarbis	0	0	0	0	1	0	0	0	0	0	0	1	2	4
Leistus rufomarginatus	0	6	0	0	0	0	7	3	0	3	0	0	0	19
Leistus terminatus	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Loricera pilicornis	0	0	0	0	1	0	0	0	0	0	0	1	4	6
Nebria brevicollis instar I	0	8	2	0	23	88	62	0	2	0	4	8	1	198
Nebria brevicollis instar II	3	4	11	0	15	62	40	2	4	0	2	11	1	155
Nebria brevicollis instar III	15	21	14	3	21	168	343	3	13	5	73	34	30	743
Notiophilus biguttatus	0	0	0	0	0	0	2	0	0	0	0	0	0	2
sum larvae:	23	47	31	4	74	325	473	29	22	11	86	61	55	1241

Table 4. – Number of brachypterous (b) and macropterous (m) carabids in wing dimorphic or polymorphic species from the forest of Ename.

station:	A		B		C		D		E		F		G		H		I		J		K		L		M		total	
wing development: / species:	b	m	b	m	b	m	b	m	b	m	b	m	b	m	b	m	b	m	b	m	b	m	b	m	b	m	b	m
Agonum obscurum																									2		2	
Bembidion lampros	1		7						14		13				2		1				4		1				43	
Bembidion obtusum	1										2											1					3	1
Bembidion properans					1						2																3	
Bembidion tetracolum			4		1		1		1						4												11	
Clivina fossor											7				1						16		1		7		32	
Dromius linearis									1																		1	
Dyschirius globosus															1										2		3	
Notiophilus biguttatus	2	5			2	7	1	8	2				10	18		12		5		1						1	17	57
Pterostichus anthracinus																								1	1	2	1	3
Pterostichus melanarius			1								1				2												4	
Pterostichus minor																		1							3	3	3	4
Pterostichus strenuus	1		17		3				2								1		2		8				11		45	
Pterostichus vernalis						1		2				1				1								1				6
Total (b/m)	5	5	29		7	8	2	10	20		25	1	10	18	10	13	2	6	2	1	28	1	2	2	26	6	168	71

■ Before 1950

□ Since 1950

▣ Both time periods
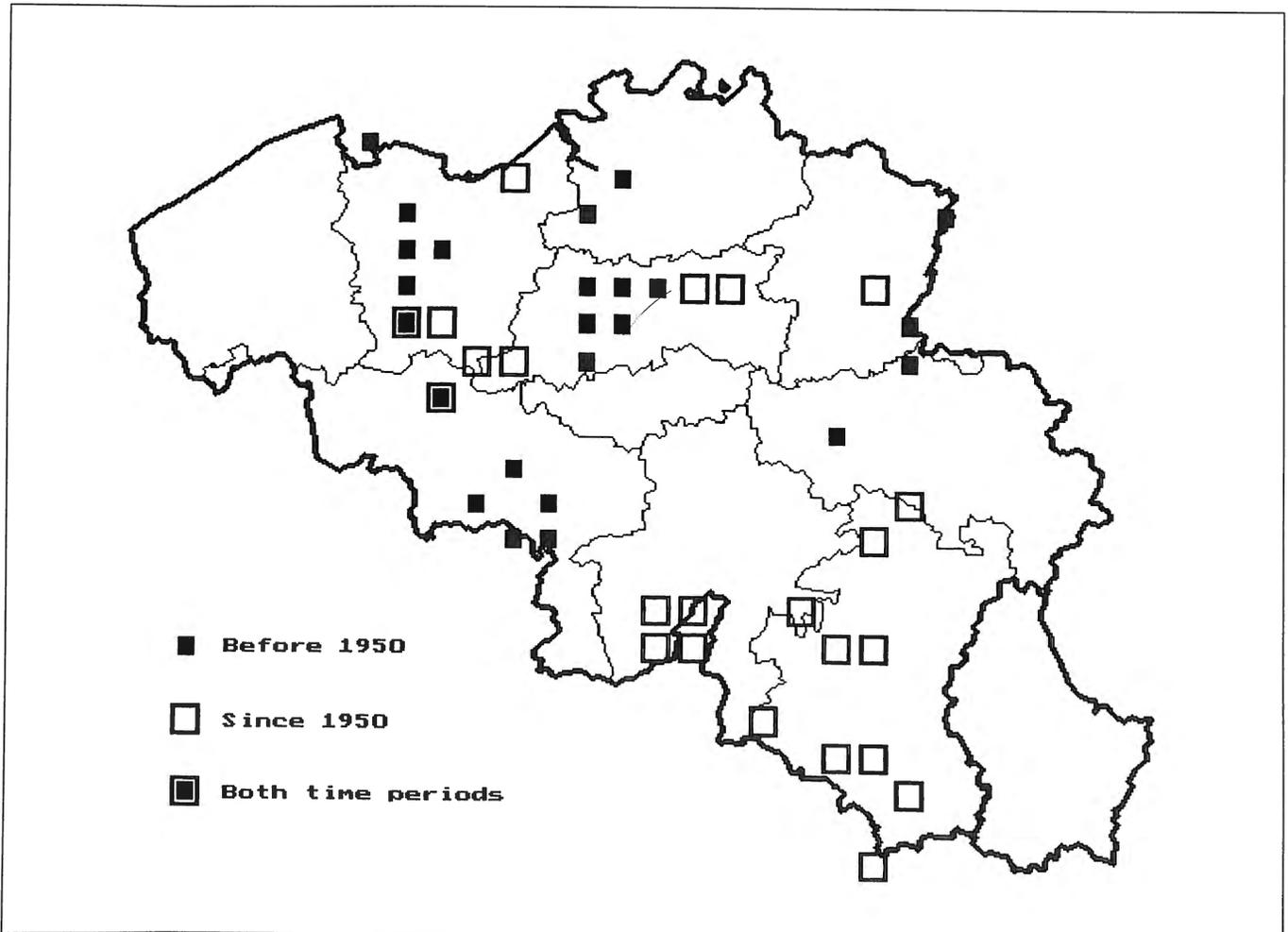
Fig. 2. – Distribution of *Agonum livens* in Belgium (UTM 10km-grid)

2. Species composition and carabid assemblage structure: the influence of ecological and historical factors

DCA and TWINSPAN results based on all sampling stations except the woodland-grassland transition zone (D, E, F; see further) are shown in Figure 4 and 5, respectively. In general, and for both analyses, individual trap results are mostly grouped within their respective sampling station. DCA axis 1 explains 22.9% of the total variation, whereas axis 2 adds 10.6% to this explained variance. Higher order axes do not raise this total much more (e.g. axis 3 explains only 5% more).

The main separation in the data is observed between sites K, L and M and the remaining sampling stations, both in the DCA and TWINSPAN results. These three sites are situated in the more humid valley forest, where tree cover is relatively low. Indicator species for these sites are the hygrophilous *Bembidion dentellum*, *B. lunulatum* as well as *Agonum livens*; Except for *A. livens*, these carabids however are not exclusive woodland species but more typical for many kinds of very humid habitats (such as marshland) with at least some shade. Many other carabid species from these sampling stations (cf. Fig. 4 species scores and Fig. 5) are euryto-

pic carabids known from different kinds of disturbed habitats, including cultivated fields and pastures (e.g. *Clivina fossor* and *Agonum muelleri*). Whether there occurrence here is due to human disturbances caused by recent or historic forest management practices or simply because of external influences (edge effects) in this relatively narrow forest patch remains an open question.

A next division is visible in the TWINSPAN results between A and B (humid forest and spring forest with indicator species such as *Patrobus atrorufus*, *Pterostichus cristatus* and *Pterostichus nigrita*) and the other remaining stations. This distinction is less clear in the ordination diagram. In general, the first DCA axis seems to coincide with a gradient from (at the left in Fig. 4) relatively dry forest (with more or less eurytopic woodland species such as *Asaphidion curtum*, *Leistus rufomarginatus*, *Abax ater* and *Nebria brevicollis*) to more open and very humid valley forest including marshland (at the right). The second ordination axis mainly reveals variation between the stations K and L, on the one hand, and M, on the other hand, and can be interpreted as a gradient from somewhat more shaded humid forest (A, B) with a ground cover dominated by mosses (and *Agonum livens* as indicator species) to more open humid riparian sites

Fig. 3. – Distribution of *Pterostichus cristatus* in Belgium (UTM 10km-grid)

species, stenotopic *Abax* species, ...) appear to be lacking here, despite the relatively high total species richness. This absence of many typical woodland beetles in the forest of Ename possibly can be explained by the historically very well documented large scale deforestation which took place in this area from 1780 until 1880. During that period habitat destruction and extreme fragmentation must have depauperated the local forest ground beetle fauna. Typical woodland ground beetles apparently have not been able to recolonise the area since its more recent reforestation, presumably because of a continuous isolation from other large forest complexes ever

Fig. 4. – DCA ordination diagrams (species scores and sample scores) along the first and second axis based on ground beetles in 11 forest sampling stations of the forest of Ename (species labels are abbreviated genus and species name; see text and Table 3 for further explanation)

along the large forest pond (site M with a.o. *Bembidion dentellum* and *Bembidion lunulatum* as ecological indicators).

Most of the sampling sites can thus be characterised based on their carabid assemblages (sampling units are indeed mostly grouped within each sampling station separately, cf. Fig. 5). The observed differences in assemblages mainly can be interpreted by means of ecological factors. Comparison of these data with those from older and larger forest complexes in our region (e.g.. the "Zoniënwoud", DESENDER et al., 1987) reveals, however, that several stenotopic forest carabids (which are to be found in ancient forests, such as *Carabus* species, *Cychrus*

Fig. 6. – DCA ordination diagrams (species scores and sample scores) along the first and second axis based on ground beetles in a gradient from forest edge (D), transition zone (E) to adjacent grassland (F) near the forest of Ename (species labels are abbreviated genus and species name; see text and Table 3 for further explanation)

```
                         SITE
          SPECIES    DMMMLLLKKK|CCDIC JD IJJ HHGGG AAABBBHI

      7  Bemb dent   -555-----|-------------------------  111
      9  Bemb lunu   -455-43--3|-----------------------  111
      3  Agon live   -222352424|---------------------  111
      4  Agon muel   333--3-53-|-----4---------------  111
     10  Cliv foss   -343--2535|----------2----------  111
      2  Agon assi   -443-21444|---1--2-12------13-----  110
     11  Leis fulv   -354--4422|222-----------2--------  110
     19  Pter nigr   -544-232--|---------------324-2---  110
      6  Badi soda   4432-222--|----------------44242-  10
     20  Pter stre   -234---33-|22-2--2---------2542--  011
      8  Bemb lamp   ------3-44|----------------344343  010
     16  Patr atro   ---3-4-3--|----------------4545-3-  010
     13  Lori pili   132112211-|433331------11--1253--1  010
     17  Pter cris   ---------1|--------1---421445441--  001
     12  Leis rufo   ----------|---------3-355---4243-  001
     18  Pter madi   ---1-11-11|1-11112122344541112221  000
     15  Noti bigu   --1-------|3223131---32533--3---2-  000
      5  Asap curt   -1------11|51--222---52212-1-2213-  000
     14  Nebr brev   -111-11111|21-11111111155311121-1-  000
      1  Abax ater   1--1-22121|2132232111-12333-333312  000

                     00000000000111111111111111111111111
                     00001111110000000000000000011111111
                     01110011110000000000001111100011111
```

Fig. 5. – TWINSPAN ordered two-way table based on ground beetles in 11 forest sampling stations of the forest of Ename (see legend Fig. 4 for further explanation)

since and because the majority of these ground beetle species is known as brachypterous with a low dispersal power (DESENDER, 1989).

These data illustrate how ground beetles are ideal ecological indicators also for the comparison of recent and ancient forest faunas. The fact that many typical woodland plant species of the forest of Ename were able to persist the large scale deforestation can a.o. be explained by the fact that many plant species can much easier survive prolonged periods of adverse conditions in a site through their stored seed banks, which can stay vital for many years. In contrast, most terrestrial invertebrates, including the beetles studied by us, have to reproduce at least once every year to persist on a given site. As a result, terrestrial invertebrates are expected to be even more useful candidates for evaluating the historical ecology of different sites.

3. Diversity and ground beetle assemblages at the interface of a woodland edge to grassland transition

The DCA ordination diagram (Fig. 6) as well as the TWINSPAN ordered two-way table (Fig. 7) show that each sampling station (woodland edge (D), transition zone (E), and grassland (F)) easily can be characterised by its ground beetle assemblage. The DCA first axis explains as much as 51.6% of the total variation (and indeed separates the three sampling stations nearly completely), whereas the second axis adds only 8.1% more to the total explained variance. A detailed look at the species and their relative abundance shows, however, that there is no additional increase in the total species diversity which could be attributed specifically to the transition zone. The species assemblage there is composed of both (eurytopic) woodland species (such as *Abax ater* and *Notiophilus*
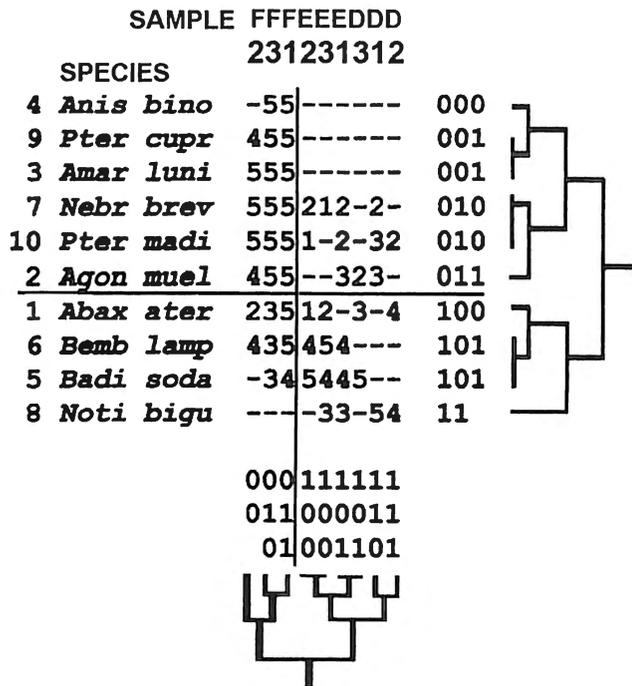
```
         SAMPLE  FFFEEEDDD
                 231231312
      SPECIES
   4  Anis bino    -55|------  000  ┐
   9  Pter cupr    455|------  001  │
   3  Amar luni    555|------  001  │
   7  Nebr brev    555|212-2-  010  │
  10  Pter madi    555|1-2-32  010  │
   2  Agon muel    455|--323-  011  ┘
   1  Abax ater    235|12-3-4  100  ┐
   6  Bemb lamp    435|454---  101  │
   5  Badi soda    -34|5445--  101  │
   8  Noti bigu    ---|-33-54  11   ┘

               000|111111
               011|000011
               01 |001101
```

Fig. 7. – TWINSPAN ordered two-way table based on ground beetles in a gradient from forest edge (D), transition zone (E) to adjacent grassland (F) near the forest of Ename (see legend Fig. 6 for further explanation)

biguttatus), apparently infiltrating into the grassland, whereas some (eurytopic) grassland species (such as *Agonum muelleri*) also merge into the woodland edges; there are no additional species found, which would be limited to the woodland-grassland interface.

We can conclude that this single nature development experiment to restore gradients at the interface of woodland edges and surrounding grassland vegetation does not seem to increase total carabid diversity, at least not (yet?) in this case. Whether this holds also for other faunal or floral elements remains to be answered.

4. Life cycle timing in the most abundant woodland species

Details are given on the phenology of the life cycle (one complete year cycle interpolated in 24 equal periods) of the most abundant woodland species *Abax ater* (adults and larvae, cf. Fig. 8), *Agonum assimile* (Fig. 9), *Asaphidion curtum* (Fig. 10), *Nebria brevicollis* (adults and larvae, Fig 11, 12), *Pterostichus cristatus* (Fig. 13) and *Pterostichus madidus* (Fig. 14). In these graphs pooled data are given from all forest sampling stations (total – E, F) or, if available, separately also for the grassland and woodland-grassland transition (F, E).

Abax ater (Fig. 8) reproduces mainly in summer-autumn and probably hibernates mostly as larva III. Apparently some adults also hibernate and reproduce during spring (first activity peak) giving rise to a small peak of first instar larvae at the end of spring. This corresponds more or less to the results of THIELE (1977) who further mentioned that the cycle of this species shortened when moving North in Europe. Results for the 'Zoniënwoud' (DESENDER et al., 1987) showed an additional third adult activity peak during early summer corresponding to the appearance of a new generation of beetles (tenerals). *Abax ater* shows some parental care, where the female prepares a cocoon from loamy soil, where eggs are deposited and protected until larvae appear (LÖSER, 1969).

Agonum assimile (Fig. 9) illustrates the pattern of a typical spring breeding carabid (cf. THIELE, 1977), with spring-summer larvae and hibernation by the new generation of adults. Apparently reproductive activity is highest in early spring (April). A low number of larvae was caught indeed between May and July.

Asaphidion curtum (Fig. 10) has only recently been recognised as a distinct species and formerly was not distinguished from *Asaphidion flavipes* (MUILWIJK & HEIJERMAN, 1991; SPEIGHT et al., 1986). Both species have a distinct habitat preference, *Asaphidion curtum* occurring in light forests, *Asaphidion flavipes* more in open landscapes such as cultivated fields, and there is a corresponding difference in their functional morphology related to their specialised predatory behaviour (BAUER et al., 1998). As far as we know, there are no older literature data on the life cycle of *Asaphidion curtum*. Apparently the species is especially active to reproduce during spring, whereas hibernation most probably takes place in the adult stage.

Nebria brevicollis (Fig. 11, 12) is a very eurytopic ground beetle with some preference for shaded habitats, such as light forests and orchards. It was the most abundant carabid in this study, but occurred as well in the forest as in the nearby grassland sampling stations, thereby enabling an interesting comparison of the life cycle timing in two very different but adjacent habitat types. Large numbers of active larvae were also obtained for this species.

Clearly the adults of this species show two activity peaks during one year (both in grassland and in woodland sites): the spring activity corresponds to the appearance of the new generation (cf. presence of tenerals), whereas the second peak corresponds to the reproductive activity (cf. appearance of first instar larvae). Hibernation mainly takes place as second and third larval instar, but these remain active, even during colder periods. A detailed comparison between the phenology in both habitats shows that the reproductive activity in the grassland is somewhat delayed as compared to the forest (regulated by temperature? lower temperatures reached somewhat earlier in forest as compared to grassland?), but that both cycles are synchronised again with the appearance of third instar larvae and/or the appearance of the new generation of beetles (regulated by daylength?).

Fig. 8. – Phenology of the life cycle in adult *Abax ater* (top figure) in forest sampling stations of the forest of Ename, along with activity curves for larvae of instar I, II and III (all numbers interpolated to equal halfmonthly intervals)
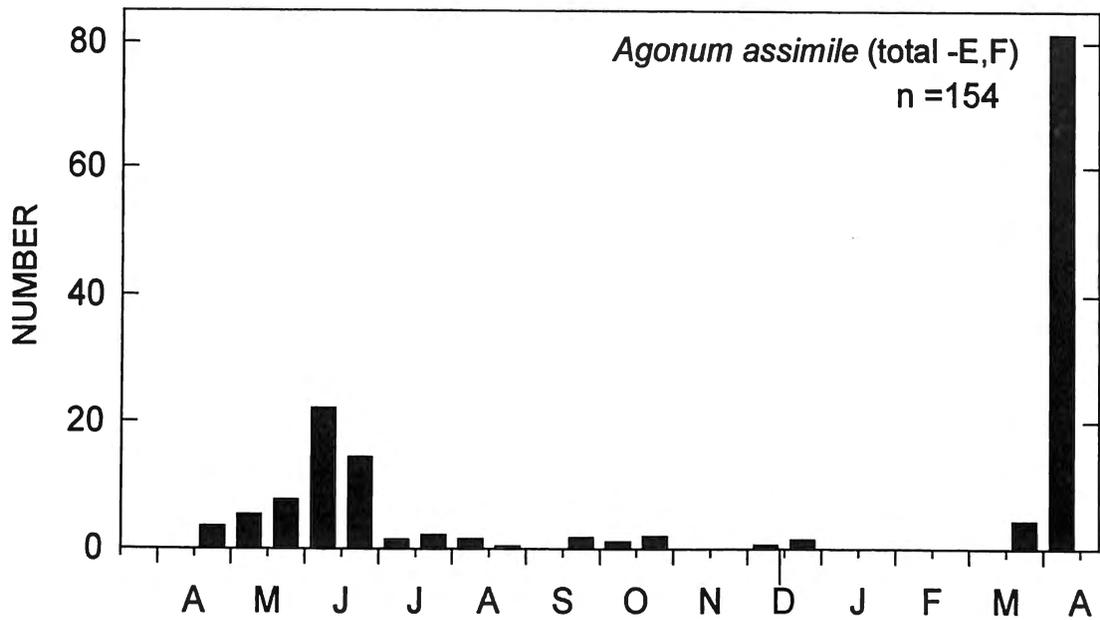
Fig. 9. – Phenology of the life cycle in adult *Agonum assimile* in forest sampling stations of the forest of Ename (numbers interpolated to equal halfmonthly intervals)
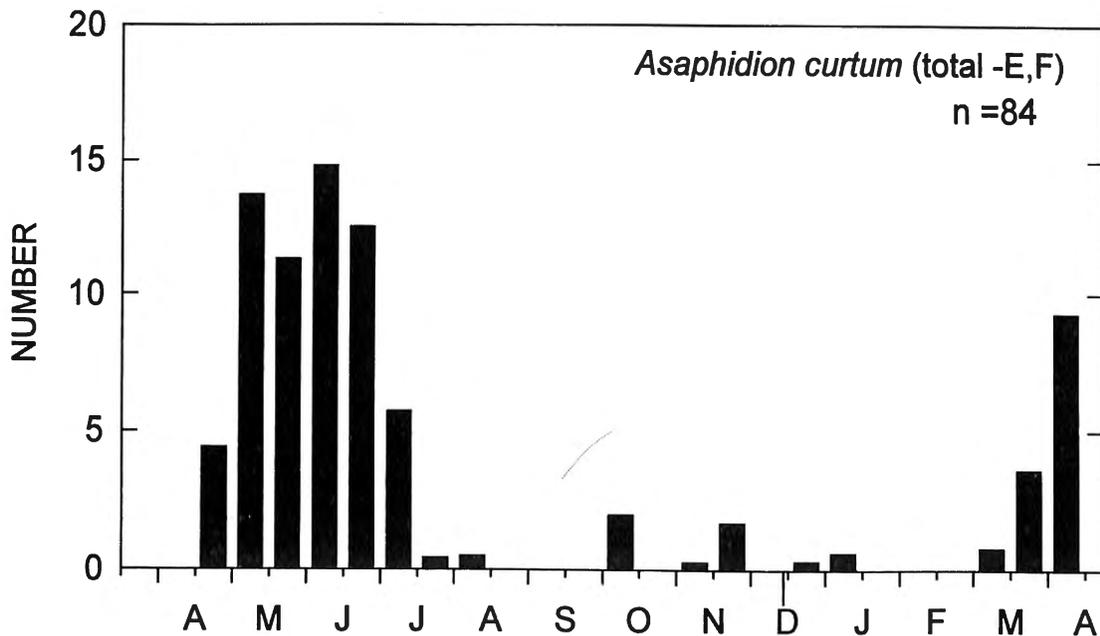
Fig. 10. – Phenology of the life cycle in adult *Asaphidion curtum* in forest sampling stations of the forest of Ename (numbers interpolated to equal halfmonthly intervals)

Many other authors have already described the characteristic life cycle of *Nebria brevicollis*, which reproduces during autumn after a summer diapause of the adults (e.g. DULGE, 1994; KALAS, 1985; POLLARD, 1968). Larvae overwinter (LOREAU, 1984, 1985), sometimes also a small part of older adult beetles (LINDROTH, 1945). According to THIELE (1977), the summer diapause would be necessary to ensure that larvae, which are adapted to cold conditions only, appear during winter.

Pterostichus cristatus is a stenotopic carabid from humid and dark forest habitats. Reproductive activity (Fig. 13) culminates in summer/autumn and hibernation probably takes place in larval stage(s) (DESENDER, 1989; THIELE, 1977).

Pterostichus madidus (Fig. 14) is another eurytopic species preferring relatively dark forests, but regularly also found in more open habitats. According to the literature,
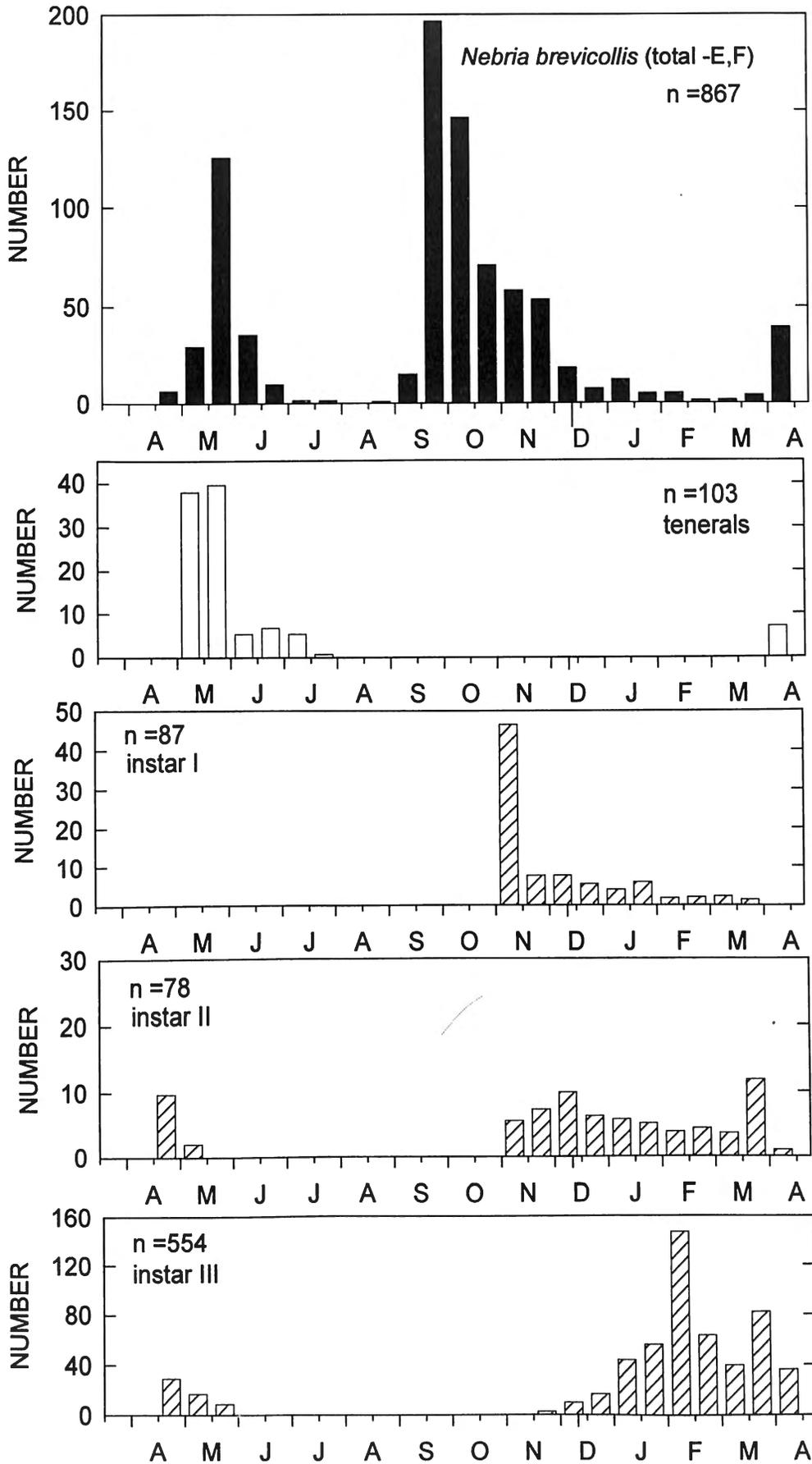
Fig. 11. — Phenology of the life cycle in adult and teneral *Nebria brevicollis* (top figures) in forest sampling stations of the forest of Ename, along with activity curves for larvae of instar I, II and III (all numbers interpolated to equal halfmonthly intervals)
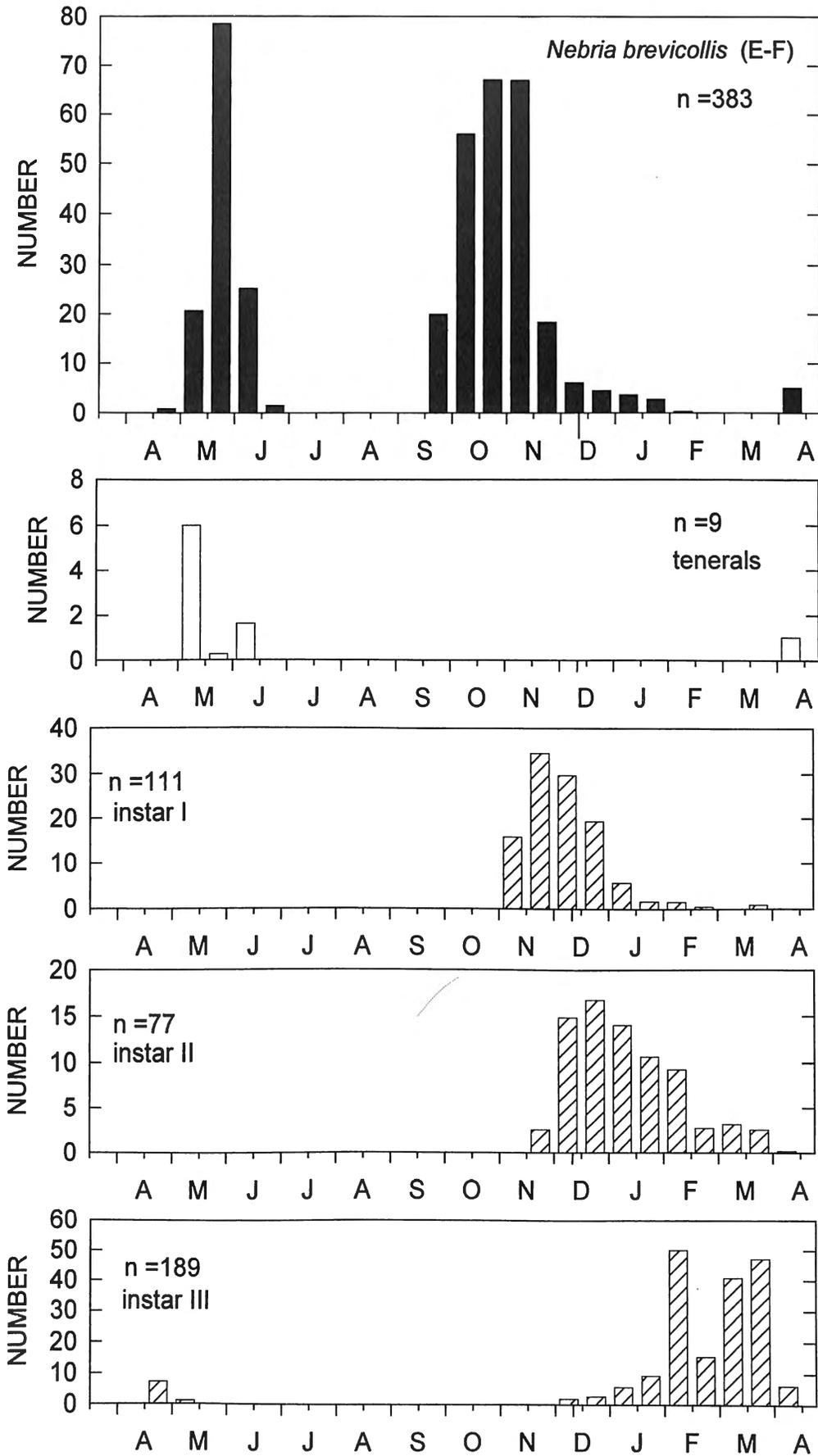
Fig. 12. — Phenology of the life cycle in adult and teneral *Nebria brevicollis* (top figures) in woodland edge (E) and grassland (F) sampling stations of the forest of Ename, along with activity curves for larvae of instar I, II and III (all numbers interpolated to equal halfmonthly intervals)
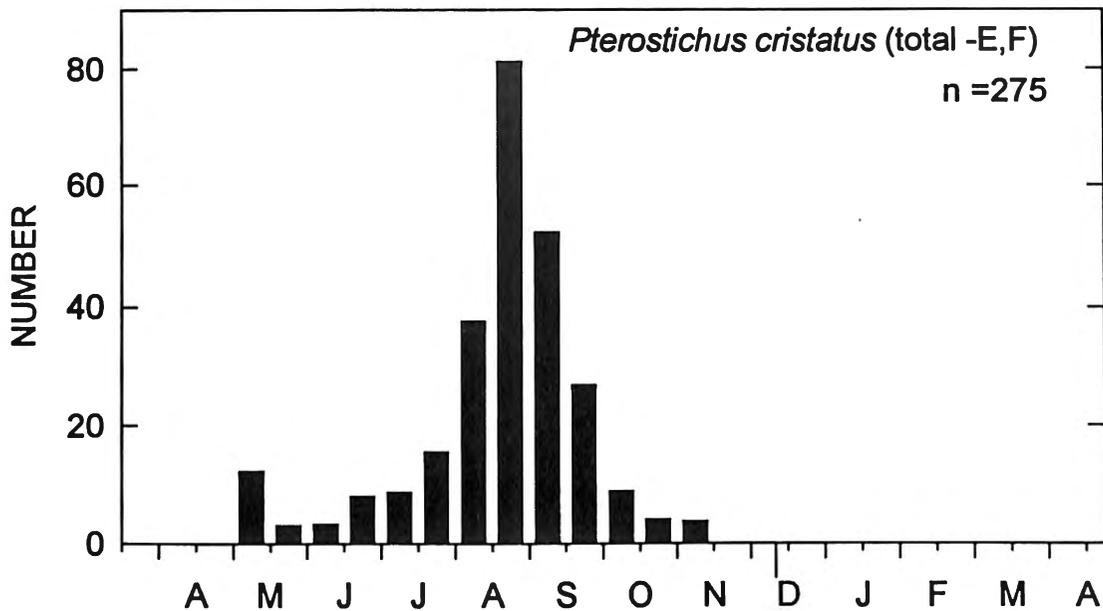
Fig. 13. – Phenology of the life cycle in adult *Pterostichus cristatus* in forest sampling stations of the forest of Ename (numbers interpolated to equal halfmonthly intervals)
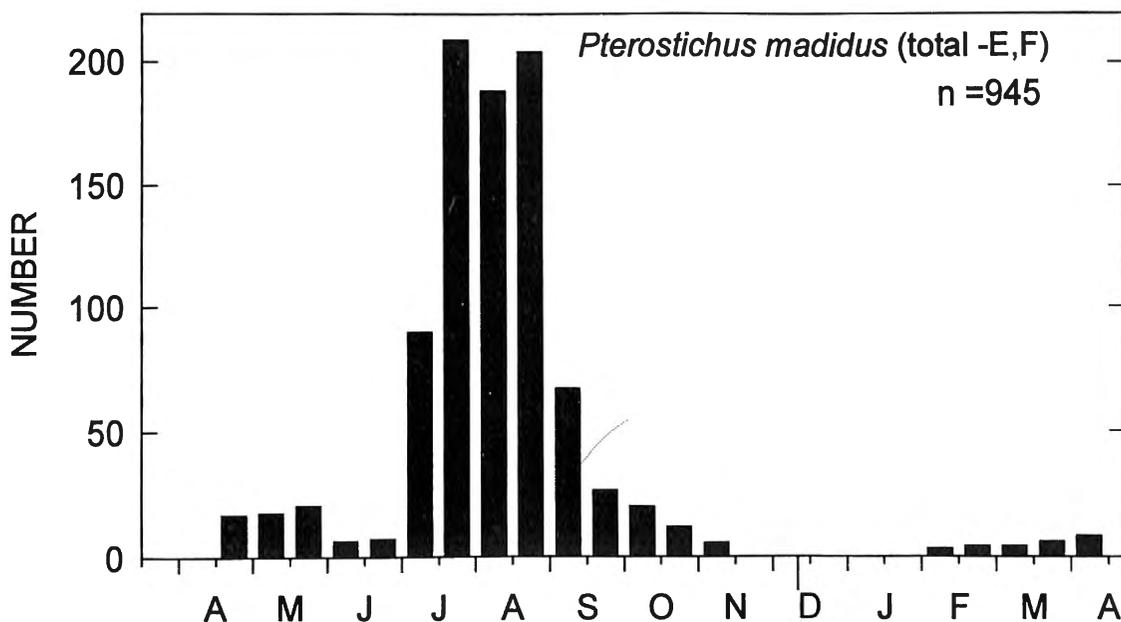
Fig. 14. – Phenology of the life cycle in adult *Pterostichus madidus* in forest sampling stations of the forest of Ename (numbers interpolated to equal halfmonthly intervals)

the life cycle of this species would be composed of multiple and varying reproductive periods, with some part of the population hibernating as larvae, some part as adults (LOREAU, 1984, 1985). In the forest of Ename main reproductive activity probably takes place during summer (cf. DESENDER, 1989). According to GREENSLADE (1965) some adults (mainly females) would survive a first reproductive period and show a small second peak next year during early spring after hibernation. This is prob- ably also the case in our study area (compare with Fig. 14).

G. TACK as the stimulating organiser, kindly assisted in sampling by means of pitfall traps. D. DE BAKKER and J.-P. MAELFAIT assisted in various ways.

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