

Competition in a carabid beetle community: a field experiment

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A 4-yr field experiment tested the significance of intra- and interspecific competition in a carabid beetle community in a beechwood in Lembeek (Belgium). The effects of both manipulating the population density of *Abax ater* – the ecologically dominant species in this forest – and introducing *Pterostichus madidus* – a species occupying a similar niche in a nearby successional forest – were measured on the population dynamics of all large species.

In six fenced plots with different densities of *A. ater* and *P. madidus*, adult beetles were sampled at regular intervals using funnel traps. Population dynamics was followed using individual marking and capture-recapture techniques.

In 3 out of 4 enclosures, the populations of *A. ater* converged towards the same density, suggesting competitive regulation around an equilibrium density. The main variable affected negatively by density was recruitment rate. Body mass was affected by density only in males. Trappability – a measure of individual locomotor activity – was negatively correlated with density in males, but not in females.

Introduced populations of *P. madidus* did poorly, but eventually persisted at low levels in all enclosures, without being affected by intra- or interspecific competition. *Pterostichus oblongopunctatus* and other resident species showed no sign of ecological release in the absence of *A. ater*.

In both *A. ater* and *P. madidus*, differences between individuals introduced from different regions were found to be great enough to significantly affect their ecological performance.

In conclusion, the results of the experiment provide weak evidence for intraspecific competitive regulation in the dominant species *A. ater*, and no evidence for intra- or interspecific competition in the other species.

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Introduction

During the last decade or so, the importance of competition in natural animal communities has been severely questioned. A positive result of this has been a dramatic increase in field experiments designed to test predictions of competition theory (see reviews in Schoener 1983 and Connell 1983).

Carabid beetles have traditionally been regarded as an example of the lack of competition in animal communities (Lindroth 1949, Thiele 1964, 1977, den Boer 1980, 1985). Insects are usually thought to experience strong predation and spatial and temporal variability of the environment because of their relatively small size

and their moderate life span, and, hence, to show few competitive effects (Hutchinson 1961, Schoener 1983, Connell 1983). But carabids are among the largest and longest-lived insects, and among the most important polyphagous invertebrate predators of the soil fauna in the temperate regions. Thus competition may play a more significant role in carabids than in most other insects.

Recently several works have provided some evidence for food limitation and competition in carabids. Heessen (1980) and Baars and van Dijk (1984) showed egg production to be density-dependent. Heessen and Brunsting (1981) and Brunsting and Heessen (1983) pointed out the regulatory power of larval starvation

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and cannibalism on population density. Lenski (1982, 1984) documented a negative effect of population density on body mass and suggested that interspecific competition also reduces body mass. Brunsting and Heessen (1984) suggested density regulation in field experimental populations. Loreau (1986, 1989) and Müller (1985) interpreted patterns of niche differentiation in climax communities as evolutionary outcomes of competitive processes. Although some of these works revealed several potential processes of competition (decreasing foraging success and fecundity, and increasing mortality through larval starvation and cannibalism with increasing density), only in one case were they shown experimentally to be strong enough to significantly influence population dynamics and result in an apparent population regulation (Brunsting and Heessen 1984). On the other hand, no such experimental confirmation has been attempted as yet for interspecific competitive interactions.

The purpose of this paper is to report on a 4-yr field experiment designed to test the significance of both intra- and interspecific competition in a forest carabid community, by investigating the effects of density on population dynamics at the scale of several annual generations.

Hypotheses

A previous study (Loreau 1986) was devoted to niche differentiation in forest carabid beetles in Lembeek (Belgium). The habitats and the carabid communities were described extensively in Loreau (1984a). In conclusion to that study, I put forward the following hypotheses regarding the competitive processes liable to structure the carabid communities.

(1) In a near climax beechwood, clear niche differentiation was found. Competitive interactions between species seem minimized in this old habitat, and, thus, ongoing interspecific competition should be difficult to detect. On the other hand, *Abax ater* (Villers), the ecologically dominant species (in biomass as in activity: Loreau 1984a,b) in this habitat, is a suitable candidate for testing the significance of intraspecific competition, because of its high biomass, its fairly constant population density and its homogeneous large-scale spatial distribution.

(2) In a nearby successional forest, *A. ater* shares the dominant position with *Pterostichus madidus* (Fabr.). The two species have similar diets and annual activity cycles, as well as negatively correlated catch numbers. I hypothesized a process of competitive exclusion between them, the outcome of which would be *A. ater* winning in a later successional stage. Thus, *P. madidus*, which is present only occasionally in the beechwood, might be partly prevented from colonizing this habitat by the dominance of *A. ater*. This is not unlikely as it is abundant in other forest habitats.

To test these hypotheses, I set up an experiment in

the beechwood which assessed the effects of both increasing the population density of *A. ater* and introducing *P. madidus* in the presence and in the absence of *A. ater*. Under the hypothesis of significant competitive interactions, the predictions were:

(1) The populations of *A. ater* with supplemented densities would decline to natural densities in the following generations, while the populations with natural densities would fluctuate around these densities.

(2) *P. madidus* would successfully colonize the plots from which *A. ater* was absent, but not those in which *A. ater* was present.

Note that the second hypothesis was a strong one: *P. madidus* might simply not succeed in colonizing any plots because environmental conditions in the beechwood do not suit it.

Additionally, other effects were investigated: possible intraspecific competitive effects in *P. madidus* in case it succeeded in settling, and possible competitive effects of *A. ater* or *P. madidus* on other large carabid species (> 10 mm). Also, for each species several demographic variables (see below) were followed in addition to density, to assess which of these, if any, would be affected by competition.

Material and methods

Experimental design

Since experimental populations had to be enclosed to prevent migrations between plots, two alternatives were possible for the design of such an experiment: either favouring replicability of the plots at the expense of their size, or favouring their size at the expense of their replicability. The alternatives were incompatible for technical reasons (time, material). The second alternative was adopted because too small enclosures are likely to greatly alter the beetles' behaviour, and, hence, their long-term population dynamics. Biological realism was given precedence over statistical confidence.

Six enclosures of 16 × 14 m (224 m²) were set up in April 1984. The fences were made of galvanized steel sheets 2 m long and 50 cm high, the upper 5-cm edge of which was folded at right angle on one side, while another sheet 10 cm high folded in the same way was riveted on the other side, to prevent the beetles from getting over the fences from both sides. The sheets were riveted together and sunk 20–25 cm into the ground. The enclosures were adjoining to minimize the number of sheets required as well as to make it possible to estimate rates of migration between enclosures.

Six experimental conditions were assigned randomly to the plots as described in Fig. 1. Three density levels were defined for both *A. ater* and *P. madidus*: absent, normal density, and double density. "Normal" density was defined as the yearly maximum mean density (seasonal maximum of the mean density in several enclosures, which was constant from year to year: see Fig. 10)

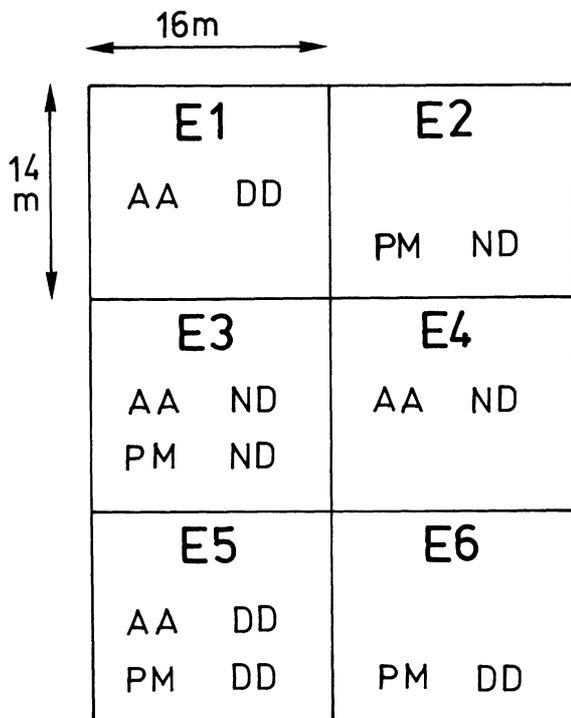


Fig. 1. Experimental design. E = enclosure; AA = *A. ater*; PM = *P. madidus*; ND = normal density; DD = double density.

of adult *A. ater*, as estimated previously (Loreau 1984b), i.e. the equivalent of 70 individuals per enclosure. "Double" density was defined accordingly as 140 individuals per enclosure. I imposed the "normal" density level because I thought that the installation of the fences (which lasted several days) could have disturbed the resident populations, part of which could have left the plots. Using the combinations of densities as shown in Fig. 1, enclosures E4 and possibly E3 could serve as controls for a density effect in *A. ater*; E2 as a control for a possible density effect in *P. madidus*; E2 and E6 as controls for a competitive effect of *A. ater* on *P. madidus*; and E1 and E4 as controls for a possible competitive effect of *P. madidus* on *A. ater*.

It was impossible to implement this design at once. While many carabids have a quite specific annual life cycle, *A. ater* breeds from spring to autumn, soil-dwelling larvae develop from summer till the beginning of the following summer, and new adults emerge from autumn till the following summer (Loreau 1985). Consequently, it was necessary to remove new adult *A. ater* continuously from E2 and E6. Also, in *P. madidus* there are two partly overlapping generations (Luff 1973), so that a balanced population could not be introduced at once. Therefore, the design was set up progressively during the summer 1984 until the total number of marked individuals reached the specified population size in each enclosure. All *A. ater* individuals caught in E2 and E6 were transferred to E1 and E5, respectively; *P. madidus*

individuals were caught in a forest where they were abundant in Treignes (100 km south of Lembeek); and *A. ater* individuals further added to E3, E4 and E5 were also caught in the latter forest. Because few *P. madidus* survived the first year, respectively 6, 5, 6 and 12 individuals caught in the successional forest in Lembeek were further added to enclosures E2, E3, E5 and E6 during the summer 1985, so as to restore viable populations in the same density ratios as in 1984. All the *A. ater* trapped in E2 and E6 after 1984 were released outside the experimental site.

Sampling procedures

Only adult beetles were studied. They were sampled using funnel traps, consisting of a plastic pot 8 cm in diameter equipped with a funnel to prevent predation by small vertebrates. Twelve such traps were evenly spaced along the interior border of each enclosure, such that their rim touched the steel fence. This arrangement allowed me to sample while trampling the plots as little as possible and with a maximum efficiency, because beetles tend to walk along the fence when they come in contact with it.

The traps were closed or removed (in winter) between trapping sessions. From late April or early May to late September or early October during the four years 1984–87, trapping sessions were spaced out every 3–4 wk. A trapping session lasted 1 wk (5 d when catches were scarce): the traps were opened the first day, emptied 3 times every two days in the morning, and closed again the last day.

The beetles collected in the traps were brought to a nearby field laboratory, where their sex and mark was recorded. The individuals captured for the first time were marked individually following the method described in Southwood (1978). Pits were ground in the elytra and the pronotum, using a pointed grindstone, fitted in a drill-chuck driven by a flexible wire. From June 1985 onwards, each individual was weighed to the nearest milligram. The beetles were then released into their respective enclosures on the day of their capture; those individuals which had migrated from one enclosure to another were released in their enclosure of origin.

Analysis of data

The data were processed by computer using the CMR package of Le Boulengé (1985). This package provided estimates of the following variables:

- (1) Population size, estimated per trapping session by the method of Manly and Parr (1968) or, when trappability was zero, by the minimum number of individuals present (number of individuals that were caught during that session or at least once before and after that session).
- (2) Trappability, calculated per day or per session

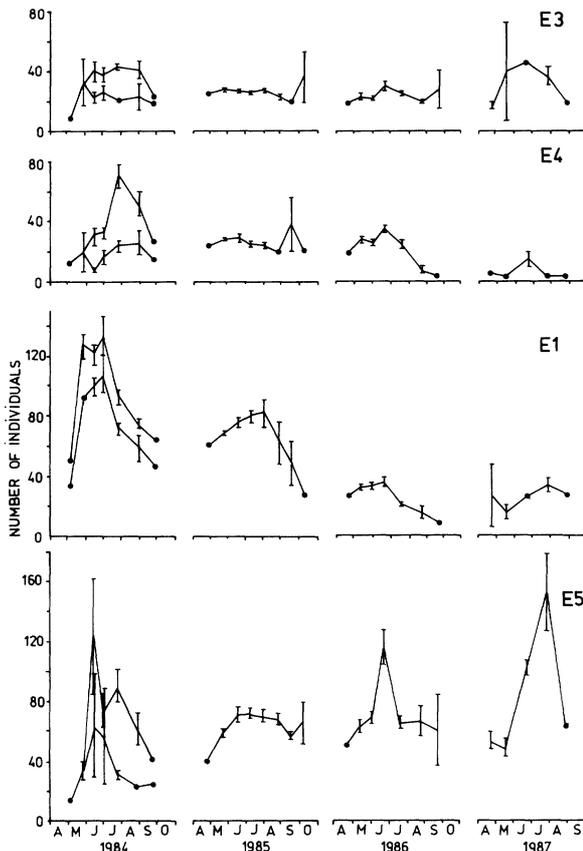


Fig. 2. Changes in the size of the four experimental populations of *A. ater* (Manly-Parr estimates per session ± 1 standard deviation). Upper curves in each enclosure in 1984: total populations; lower curves: resident individuals only (added individuals excluded).

according to Manly and Parr (1968) as the number of individuals recaptured at least once during that day or session, divided by the total number of individuals liable to recapture (first and last captures excluded).

(3) Disappearance rate from sessions i to $i+1$, calculated as:

$$D_i = 1 - N_{i+1}/N_i$$

where N_i is the minimum number of individuals present at session i , and N_{i+1} is the number of those among them which are still present at the next session.

For comparison of unequal intervals between sessions, disappearance rate was then expressed as a mean rate per day, calculated as:

$$\delta_i = 1 - (1 - D_i)^{1/\Delta_i}$$

where Δ_i is the interval between the first days of sessions i and $i+1$.

(4) Average as well as between- and within-individual variances of body mass per session. Only the between-

individual variation was used in the analysis of variance for comparison between enclosures.

As carabids have annual generations, comparisons between years are of special interest, and the following additional variables were estimated:

(1) Year-to-year disappearance rate, calculated as above by:

$$D_i = 1 - N_{i+1}/N_i$$

where now N_i is the total number of individuals present in year i , and N_{i+1} is the number of those among them which are still present in the next year.

(2) Year-to-year recruitment rate, calculated as the number of newly marked individuals in year $i+1$, divided by the number of females present in year i .

(3) Fraction of the population lost to emigration over a year, estimated as follows:

(a) The mean emigration rate from an enclosure across one side of the fence between sessions i and $i+1$ was estimated as the number of individuals that were recaptured in other enclosures at session $i+1$, divided by the total number of individuals recaptured in the enclosure and by the number of sides adjoining other enclosures.

(b) This mean rate was multiplied by the number of non-adjoining sides and by the minimum number of individuals present at session i to give the number of individuals lost to emigration between sessions i and $i+1$ (since the individuals that had crossed an adjoining side were recaptured and released in their enclosure of origin, only those which had crossed a non-adjoining side were lost from the experimental plots).

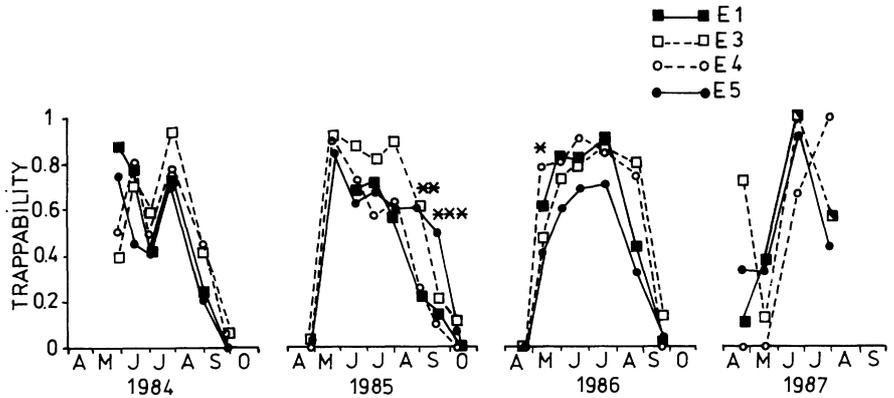
(c) The latter numbers were summed over all sessions in a year, and divided by the number of individuals present in that year, to provide the estimated fraction of the population lost to emigration during that year.

Laboratory experiment on the decrease in body mass after feeding

A laboratory experiment was carried out in May–June 1988 on the changes in body mass of *A. ater* as a function of the time after feeding to satiation, to make it possible to interpret field data on body mass in terms of degree of satiation.

Ten males and 10 females of *A. ater* were caught in the Lembeek beechwood and placed individually in plastic pots on a moist filter paper. After having been starved for a week, they were given pieces of earthworms, slugs and insect larvae at nightfall and allowed to feed during the night. The next morning, and every morning during two weeks, they were weighed at 8 a.m. to the nearest milligram.

Fig. 3. Changes in the trappability per session of *A. ater* in the various enclosures. A significant difference between enclosures at a particular session (χ^2 test) is indicated by: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.



Results

1. *Abax ater*

Population size

From the first to the second year of the experiment, the four populations of *A. ater* decreased (Fig. 2). However, if only resident individuals are considered (added individuals excluded), the populations remained fairly constant in the two enclosures with normal density (E3 and E4) throughout the experiment, although more variation appeared during the last year. This means that the resident populations were probably not disturbed by the installation of the fences and that the density level imposed as "normal" was slightly too high for the experimental plots. In one of the enclosures with double density (E1), the population continued to decrease until it reached the same density as in the enclosures with normal density. These results conform to the predictions.

However, the population in E5 increased instead of decreasing during the last two years, in contradiction to the predictions.

Apparently, the presence of *P. madidus* had no effect on the populations of *A. ater*.

Trappability

Trappability – a measure of individual locomotor activity – varies more widely than density (Fig. 3) and explains most of the phenological pattern of the species.

No clear-cut difference between enclosures appears at first sight. However, when results are pooled by year, highly significant effects emerge. Locomotor activity was generally greater in males than in females (Tab. 1), and, more importantly, it differed markedly between enclosures in males but not in females (Tab. 2).

Density effects seem to account for most of the differences in males, but, surprisingly, in a direction opposite to that predicted by the hypothesis of density-dependent food limitation (Grüm 1971, Lenski 1984): trappability was generally lower in the enclosures with high density (E1 and E5 in 1984 and 1985, E5 in 1986 and 1987).

Note that the significance of the differences in Tabs 1 and 2 may be overestimated because each occasion of recapture was regarded as an independent observation in the χ^2 tests. Should there be consistent differences in activity between individuals in each enclosure, the number of independent observations would have been overestimated. However, the regularity of the density effects observed makes it unlikely that these are artefacts.

Another comparison whose relevance will be discussed later, is between local individuals, native to Lembeek, and introduced individuals, native to Treignes (Tab. 3). Introduced individuals were distinctly more active than local individuals in the enclosures with normal density. This effect, however, does not fundamentally affect the comparisons between enclosures.

Disappearance rate

The differences in year-to-year disappearance rates between enclosures (Tab. 4) were generally correlated with the differences in changes in density. From 1984 to 1985, density dropped in all enclosures, and there were no significant differences in disappearance rates. From 1985 to 1986, density further dropped in E1, and the heterogeneity between disappearance rates is explained by a higher rate in E1. From 1986 to 1987, density decreased in E4 and increased in E3 and E5, and these

Tab. 1. Summary of the comparisons between the yearly average trappabilities per day of male and female *A. ater*.

	E1	E3	E4	E5
1984	+*	+*	+**	-ns
1985	+ns	+*	+ns	-ns
1986	+**	+*	+ns	+*
1987	+ns	+*	+***	-ns

+ : trappability higher in males than in females;
 - : trappability lower in males than in females.
 Significance levels of the differences using χ^2 tests:
 ns not significant ($P > 0.05$);
 * $P < 0.05$;
 ** $P < 0.01$;
 *** $P < 0.001$.

Tab. 2. Yearly average trappabilities per day of male and female *A. ater* (numbers of occasions of recaptures in parentheses), and overall χ^2 comparisons among enclosures.

	E1	E3	E4	E5	χ^2
Males					
1984	0.301 ^b (574)	0.422 ^c (173)	0.410 ^c (173)	0.218 ^a (225)	26.50***
1985	0.277 ^b (697)	0.394 ^c (259)	0.253 ^b (300)	0.251 ^a (578)	20.09***
1986	0.349 ^b (255)	0.346 ^b (191)	0.435 ^b (161)	0.260 ^a (503)	19.48***
1987	0.356 ^{ab} (118)	0.413 ^{bc} (109)	0.577 ^c (26)	0.302 ^a (398)	11.82**
Females					
1984	0.237 (316)	0.276 (116)	0.241 (108)	0.272 (195)	1.18 ^{ns}
1985	0.241 (344)	0.315 (216)	0.248 (157)	0.253 (475)	4.24 ^{ns}
1986	0.174 (86)	0.227 (141)	0.294 (102)	0.199 (347)	5.26 ^{ns}
1987	0.250 (60)	0.253 (83)	0 (12)	0.323 (161)	6.73 ^{ns}

When the overall comparison shows a significant difference, values that do not differ at the 0.05 significance level by pairwise χ^2 tests have the same letters (a, b, or c). Significance levels as in Tab. 1.

changes were again reflected in different disappearance rates. However, there is on the whole little evidence for density effects; only the high rate in E1 in 1985–86 is consistent with such effects.

Females have generally higher disappearance rates than do males (Fig. 4; 2-tailed Wilcoxon matched-pairs signed-ranks test: $P < 0.02$). Furthermore introduced individuals have distinctly higher disappearance rates than do local individuals (Fig. 5).

Emigration and survival rates

The estimated fraction of the population lost to emigration over a year was generally low (Tab. 5), indicating

that enclosures were efficient in isolating populations. Whenever significant emigration was observed between two enclosures, it was related to the abundance of small-mammal holes (which were consequently filled up) under the fence separating those two enclosures. Thus, small-mammal activity seems the main factor responsible for the beetles clearing the fence.

Because of the rather low fraction of the population lost to emigration, year-to-year disappearance rates are essentially mortality rates. When corrected for emigration, year-to-year survival rates proved to be generally quite high (from 0.33 to 0.45 in 1984–85, from 0.35 to 0.63 in 1985–86, and from 0.11 to 0.47 in 1986–87), close

Tab. 3. Average trappabilities per day (over the two years 1984 and 1985) of local and introduced *A. ater* in the enclosures where individuals were introduced (numbers of occasions of recaptures in parentheses), and χ^2 comparisons among enclosures (rows) and according to the individuals' origin (columns).

	E3	E4	E5	χ^2
Males				
Local	0.328 (305)	0.221 (249)	0.234 (710)	11.75**
Introduced	0.669 (136)	0.454 (251)	0.289 (166)	43.50***
χ^2	44.61***	30.41***	2.23 ^{ns}	
Females				
Local	0.242 (248)	0.203 (182)	0.258 (566)	2.24 ^{ns}
Introduced	0.448 (87)	0.353 (119)	0.299 (147)	5.30 ^{ns}
χ^2	13.17***	8.32**	1.02 ^{ns}	

Significance levels as in Tab. 1.

Tab. 4. Year-to-year disappearance rates of *A. ater* (numbers of individuals present during the first of the two years in parentheses), and overall χ^2 comparisons among enclosures.

	E1	E3	E4	E5	χ^2
1984-85	0.58 (143)	0.64 (69)	0.66 (71)	0.70 (140)	4.54 ^{ns}
1985-86	0.69 ^b (87)	0.49 ^a (37)	0.42 ^a (33)	0.40 ^a (87)	16.24 ^{**}
1986-87	0.76 ^{ab} (38)	0.56 ^a (32)	0.90 ^b (39)	0.60 ^a (99)	14.87 ^{**}

When the overall comparison shows a significant difference, values that do not differ at the 0.05 significance level by pairwise χ^2 tests have the same letters (a or b). Significance levels as in Tab. 1.

to or sometimes higher than the upper estimates for other species (den Boer 1979). Some adults marked at the beginning of the experiment were still alive at the end, which means that they were at least 4 yr old.

Recruitment rate

From 1984 to 1985, all year-to-year recruitment rates were quite low (Tab. 6), which may be a density-dependent effect since density was above the natural level in all enclosures. The low rate in E1 from 1985 to 1986 may also be a density effect, but this was absent in E5. No density effect was apparent from 1986 to 1987.

Body mass

Females always weighed more than males, but there was no clear-cut difference either between seasons or between enclosures (Fig. 6). When data are pooled by year, however, the analysis of variance reveals significant differences between enclosures in males, but not in females (Tab. 7). In 1985 and 1986, the data supported the hypothesis of reduced body mass in males at high densities: planned comparisons between enclosures with normal densities (E3 and E4 in 1985; E1, E3 and E4 in 1986) and enclosures with high densities (E1 and E5 in 1985; E5 in 1986) show a significantly lower body mass at high densities ($P < 0.01$ in both years). On the other hand, density effects do not explain the differences in 1987, since the enclosure with the lowest density (E4) was also that with the lowest mean body mass.

Note here again that the number of independent observations might be slightly overestimated in the analy-

sis because each mean individual body mass per session was assumed to be an independent observation. This assumption is justified by the fact that no regular differences in body mass were found between sessions.

Body mass decreases strongly after feeding (Fig. 7). Thus, changes in body mass due to feeding prevail over individual variability during the first days after feeding. From Fig. 7, it can be estimated that the mean body mass observed in the field corresponds usually to 3 fast days. Thus, the frequency of feeding and the degree of satiation are quite low in the field, which confirms earlier observations from examination of digestive-tract contents (Loreau 1983).

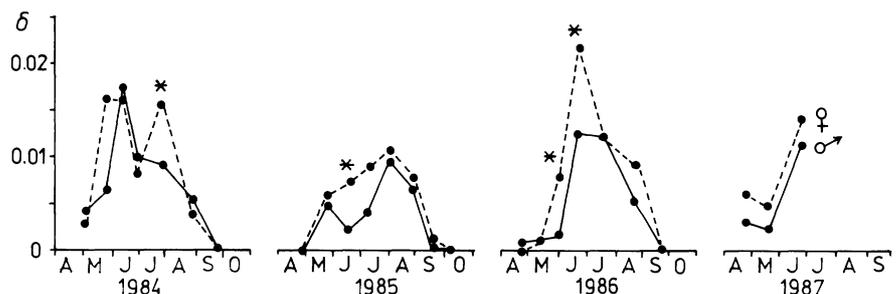
2. *Pterostichus madidus*

P. madidus populations did poorly in all enclosures (Fig. 8). They seemed eventually to persist at low levels, independently of their initial density or of the density of *A. ater*.

Unlike in *A. ater*, the mean trappabilities in *P. madidus* were different between enclosures in both sexes (Tab. 8). Again they tended to be lower at higher densities. Males were always much more active than females ($P < 0.001$ in all enclosures).

A massive mortality seems to have occurred after the introduction of the beetles into the experimental plots during the first year, resulting in especially high year-to-year disappearance rates (Tab. 9). The estimated fractions of the populations lost to emigration in 1984 were low (from 0.01 to 0.12) and, thus, emigration cannot be responsible for the high disappearance rates. The latter

Fig. 4. Changes in the mean disappearance rate per day of male and female *A. ater* (pooled data of all enclosures). A significant difference between enclosures at a particular session (χ^2 test) is indicated as in Fig. 3.



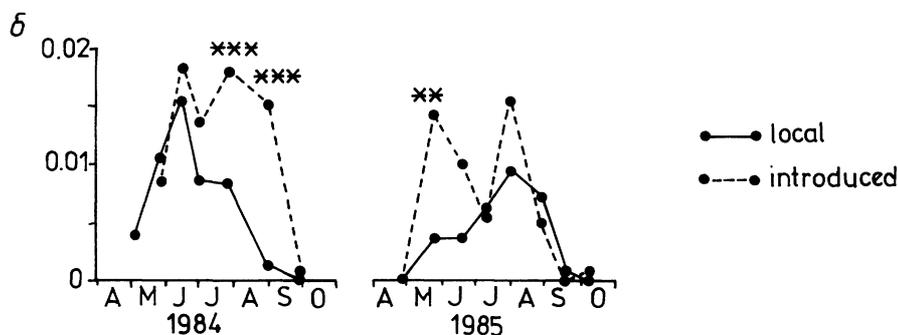


Fig. 5. Changes in the mean disappearance rate per day of local and introduced *A. ater* (pooled data of all enclosures). A significant difference between enclosures at a particular session (χ^2 test) is indicated as in Fig. 3.

were somewhat lower in the following years. No significant differences were found between enclosures.

Recruitment rates were very low during the first years but increased dramatically in three enclosures during the last year (Tab. 10). Figures were usually too low to test for differences between enclosures, but, if anything, they suggest contingent variations in recruitment rates rather than any intra- or interspecific density effects.

Body mass did not differ significantly between enclosures in either males or females.

3. Other species

Pterostichus oblongopunctatus (Fabr.) was the most abundant carabid after *A. ater* in the beechwood (Lo-reau 1984a,b). Its populations declined in all enclosures but E5 (Fig. 9).

No differences in trappability were found either between enclosures (pooled data over 4 yr and 2 sexes: $\chi^2 = 10.37$, 5 df, $P > 0.05$) or between sexes (pooled data over 4 yr and 6 enclosures: $\chi^2 = 2.30$, 1 df, $P > 0.05$).

Year-to-year disappearance rates were similarly high in all enclosures (generally above 0.8). Recruitment rates were low on average, but the 4-yr mean rate in E5 was higher than that in the other enclosures ($\chi^2 = 5.95$, 1 df, $P < 0.05$).

Body masses in males were significantly different between enclosures (4-yr averages: $F = 2.87$, $k_1 = 5$ and $k_2 = 31$, $P < 0.05$), but this difference cannot be ascribed to any intra- or interspecific density effect.

The populations of *Carabus problematicus* (Herbst), *Cychrus attenuatus* (Fabr.), *Abax parallelus* (Duftschmid) and *Nebria brevicollis* (Fabr.) were too scarce to provide interpretable results. The experimental plots were apparently too small for the highly mobile, large-sized *Carabus* and *Cychrus* species. It is sufficient to note that the removal of *A. ater* did not lead to an increase in the population of any of those species.

Discussion

The results of this experiment provide weak evidence for intraspecific competition in the ecologically dominant species *A. ater*, and no evidence for any intra- or

interspecific competitive effects in the other species. As mentioned earlier (Experimental design), the experimental approach followed here relied on biological realism at the expense of replication. This generally allowed only statistical comparisons between particular plots, not between treatments (see the discussion in Hurlbert 1984). This limitation also applies to the previous experiment of Brunsting and Heessen (1984), which had no replication at all. Accordingly, the conclusions of this experiment are necessarily qualitative and tentative.

Intraspecific competition in *A. ater*

The evidence for intraspecific competition in *A. ater* is ambiguous. In one of the enclosures with high density (E5), the population increased during the last two years, in contradiction to the predictions. However, it seems reasonable to interpret this increase as a result of particularly favourable conditions in that enclosure, since the latter was also favourable to the populations of *P. madidus* and *P. oblongopunctatus*, mainly through high recruitment rates. In the other enclosures containing *A. ater*, population changes were in accordance with the hypothesis of density limitation by competition. The relative stability of these populations indicated not only by their constancy (see also below) but also by their tendency to return to their previous density further suggests competitive regulation around an equilibrium density.

Two surprising results were the negative correlation between individual locomotor activity and population density in males, and the absence of density-dependent

Tab. 5. Estimated fractions of the populations (numbers of individuals in parentheses) of *A. ater* lost to emigration over a year.

	E1	E3	E4	E5
1984	0.06 (9)	0.01 (1)	0	0.10 (14)
1985	0.12 (10)	0.17 (6)	0.09 (3)	0.05 (4)
1986	0	0.06 (2)	0.08 (3)	0.08 (8)
1987	0	0.04 (2)	0.21 (3)	0

Tab. 6. Year-to-year recruitment rates of new adult *A. ater* (numbers of females present during the first of the two years in parentheses), and overall χ^2 comparisons among enclosures.

	E1	E3	E4	E5	χ^2
1984-85	0.40 (58)	0.40 (30)	0.30 (33)	0.52 (61)	2.74 ^{ns}
1985-86	0.33 ^a (33)	0.76 ^b (17)	1.67 ^c (12)	1.24 ^{bc} (42)	24.60 ^{***}
1986-87	2.07 ^b (14)	2.47 ^b (17)	0.58 ^a (19)	1.96 ^b (50)	21.27 ^{***}

In the χ^2 tests of homogeneity of recruitment rates among enclosures, the observed distribution of recruits among enclosures is compared with the expected distribution under the hypothesis of equal recruitment rates. When the overall comparison shows a significant difference, values that do not differ at the 0.05 significance level by pairwise χ^2 tests have the same letters (a, b, or c). Significance levels as in Tab. 1.

effects on activity and body mass in females. Previous works using food supplementation experiments showed that adult activity is reduced when additional food is provided (Grüm 1971, Lenski 1984), indicating that activity is partly associated with the search for food in limited supply. If adult competition for food were significant, one should expect that locomotor activity is positively correlated with population density (Lenski 1984). Here there was a negative correlation in males, and no correlation in females. In *P. madidus*, a negative correlation was also found in both sexes. The most likely explanation of these results is that adult competition for food is not significant, and that the main factor determining differences in activity is the search for sexual partners. Males are more actively involved in this search than are females, which explains their higher locomotor activity, while females spend much time laying eggs. Since encounters are more frequent at higher densities, one would indeed expect that activity is reduced at high densities especially in males, and less so in females, as was observed.

This does not necessarily imply that adult competition for food is totally absent, however. Body mass was

found to be strongly dependent on feeding, and, thus, should be related to foraging success (Lenski 1982, 1984, Sota 1985, van Dijk 1986). The reduced body mass at high densities in males seems consistent with the existence of competitive effects. Since the two sexes were found to have somewhat different diets (Loreau 1983) and probably to forage in different places (Loreau 1987), it is possible that females are less dependent upon those food resources which are limiting for males, and this might explain the absence of differences in body mass in females.

The lack of evidence for competition for food in females contrasts with the potential regulatory role of food limitation through its effect on egg production, as stressed by several authors (Heessen 1980, Baars and van Dijk 1984, Lenski 1984, Sota 1985, van Dijk 1986; but see den Boer 1986). Note that food limitation does appear to be important in natural populations of *A. ater*, as shown by the low frequency of feeding in the field (Loreau 1983, and this study). What the present results suggest is that food limitation acts mainly in a density-independent way, as was also suggested by Juliano (1986a,b). However, egg production was not mea-

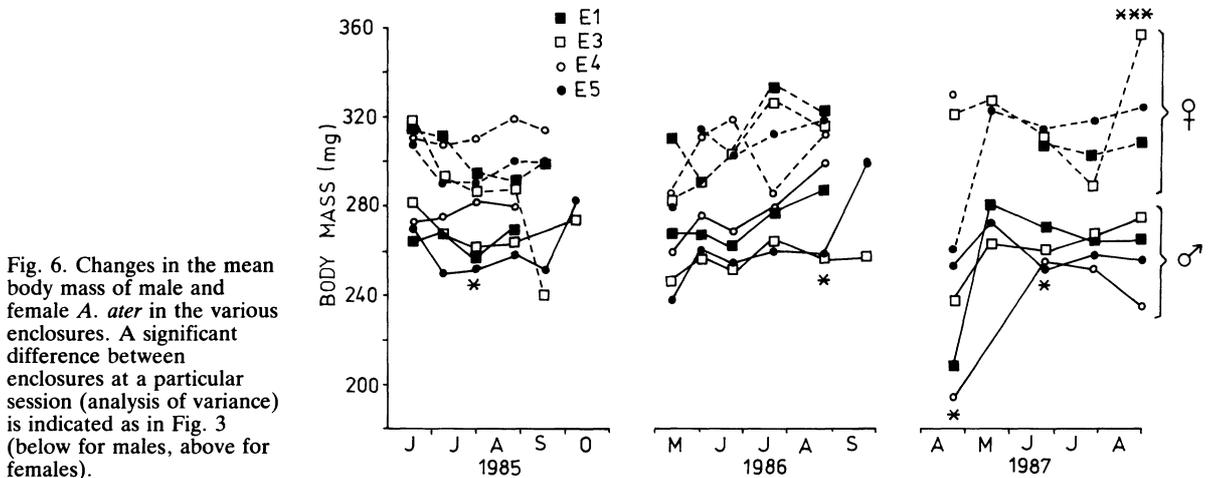


Fig. 6. Changes in the mean body mass of male and female *A. ater* in the various enclosures. A significant difference between enclosures at a particular session (analysis of variance) is indicated as in Fig. 3 (below for males, above for females).

Tab. 7. Yearly average body masses (in mg) of male and female *A. ater* (numbers of observations in parentheses), and analyses of variance.

	E1	E3	E4	E5	F
Males					
1985	263 ^{ab} (119)	269 ^b (51)	275 ^b (36)	257 ^a (112)	4.54**
1986	269 ^b (76)	256 ^a (54)	271 ^b (62)	255 ^a (120)	7.64***
1987	265 ^b (54)	259 ^{ab} (61)	248 ^a (19)	255 ^a (169)	3.44*
Females					
1985	306 (57)	294 (40)	310 (23)	299 (95)	1.23 ^{ns}
1986	309 (27)	308 (39)	305 (40)	306 (92)	0.10 ^{ns}
1987	308 (26)	316 (40)	320 (4)	299 (77)	2.28 ^{ns}

When the analysis of variance shows a significant difference, values that do not differ at the 0.05 significance level by pairwise t-tests have the same letters (a or b). Significance levels as in Tab. 1.

sured in this experiment; it is possible that body mass and activity are more weakly related to food limitation than is fecundity in this species.

The variable mostly affected by density was the recruitment rate of new adults. Therefore the main factor liable to regulate the populations of *A. ater* is competition and cannibalism at the larval stage, as stressed by Heessen and Brunsting (1981) and Brunsting and Heessen (1983, 1984).

Parmenter and MacMahon (1988) recently emphasized the potential role of predation by rodents. However, like Brunsting and Heessen (1984) or Baars and van Dijk (1984), I found no evidence for a significant role of predation on adult *A. ater*. First, the high year-

to-year survival rates are not consistent with the impact of predation as reported in Parmenter and MacMahon (1988). Second, some insight into the differential predation pressures in the various experimental plots can be gained from the estimated fractions of the populations lost to emigration. As mentioned earlier, emigration resulted mainly from small-mammal activity and, thus, should be correlated with predation pressure. There was no correlation between estimated fractions of the populations lost to emigration (Tab. 5) and disappearance (Tab. 4) or survival rates.

It is worth mentioning the significant role of spatial heterogeneity. Local factors were strong enough to prevail over density effects in E5 during the last two years

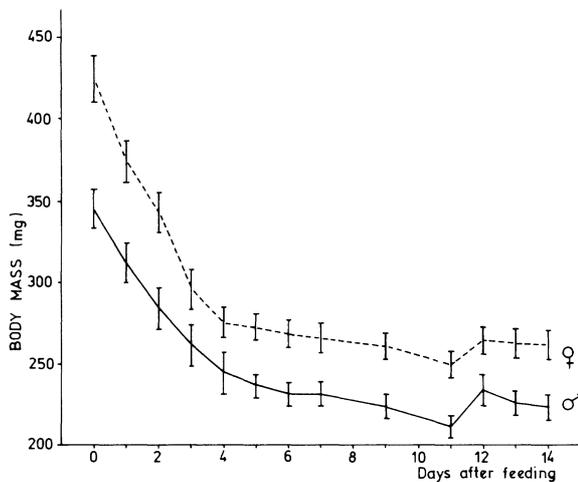


Fig. 7. Changes in the body mass of male and female *A. ater* after feeding to satiation in the laboratory (average \pm 1 standard error). Time 0 = first morning after feeding.

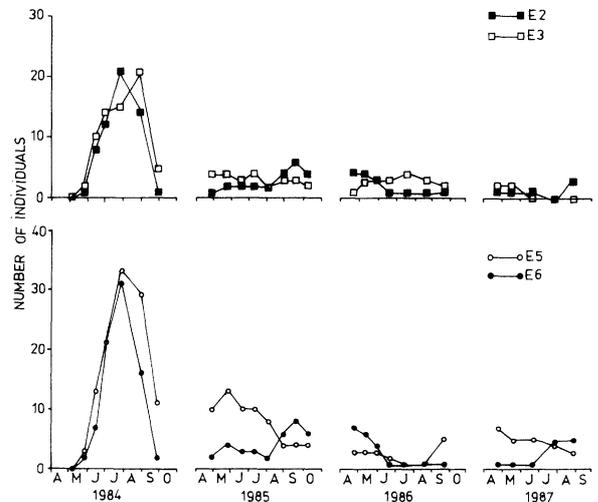


Fig. 8. Changes in the size of the four experimental populations of *P. madidus* (minimum numbers of individuals present).

Tab. 8. 4-year average trappabilities per day of male and female *P. madidus* (numbers of occasions of recaptures in parentheses), and overall χ^2 comparisons among enclosures.

	E2	E3	E5	E6	χ^2
Males	0.473 ^a (110)	0.608 ^b (148)	0.480 ^a (221)	0.416 ^a (166)	12.15**
Females	0.208 ^b (72)	0.146 ^{ab} (157)	0.093 ^a (364)	0.085 ^a (213)	11.51**

Values that do not differ at the 0.05 significance level by pairwise χ^2 tests have the same letters (a or b). Significance levels as in Tab. 1.

of the experiment, and to depress all demographic variables (survival, recruitment, body mass) simultaneously in E4 from 1986 to 1987. Since there was no obvious alteration in the physical environment of the experimental plots and the role of predation was apparently not significant, these local factors were probably heterogeneously changing prey populations. The significance of spatial heterogeneity has long been emphasized in carabids (den Boer 1968, 1971). The point of some interest here is that the beechwood in which this experiment was carried out is an especially homogeneous habitat in which *A. ater* has a homogeneous large-scale distribution (Loreau 1984c). Even under such homogeneous conditions heterogeneity still has a significant influence. It must be noted, however, that the use of enclosures enhances spatial heterogeneity artificially. The natural area of activity of *A. ater* is no doubt greater than the area of an enclosure, and, thus, enclosures prevent natural movements that tend to homogenize the conditions experienced by the various individuals.

Lack of evidence for intra- and interspecific competition in other species and significance of local adaptations

The results of the experiment fail to support the second main hypothesis under test, i.e. that interspecific competition from *A. ater* partly prevents *P. madidus* from colonizing the beechwood. *P. madidus* did poorly in all enclosures; mortality was high and recruitment of new adults was low. Thus, the very occasional presence of this species in the beechwood results from a lack of

adaptation to some basic physical or biotic conditions in this habitat.

However, *P. madidus* populations did persist at low levels, and survival and recruitment improved during the last two years of the experiment. The reason for this change is to be found in the origin of the introduced individuals. During the first year, the experimental populations of *P. madidus* were formed of individuals caught in Treignes, a locality situated 100 km away. Before starting the experiment, I did not expect that this distance would have a large effect on the performance of these individuals. But the results for *A. ater* clearly demonstrate that the origin of the individuals has a significant effect on their activity and mortality: the individuals native to Treignes were more active and disappeared at higher rates than did local individuals, which means that they were less adapted to the conditions prevailing in Lembeek and probably had escape reactions. Thus, differences – probably local adaptations – between populations 100 km apart are great enough to significantly affect their ecological performances. The massive mortality suffered by *P. madidus* individuals after their release in the plots during the first year is likely due to this factor. Those individuals which had survived the first year and those native to Lembeek which were added in the second year were better adapted, which led to a greater persistence of the populations. Since the latter are naturally present only very occasionally in the beechwood, their persistence was probably transient. Nonetheless, it was observed, and apparently was not affected by either intraspecific competition or interspecific competition with *A. ater*.

The same conclusion holds for *P. oblongopunctatus*

Tab. 9. Year-to-year disappearance rates of *P. madidus* (numbers of individuals present during the first of the two years in parentheses), and overall χ^2 comparisons among enclosures.

	E2	E3	E5	E6	χ^2
1984–85	0.97 (73)	0.91 (70)	0.88 (141)	0.94 (141)	7.12 ^{ns}
1985–86	0.67 (12)	0.67 (12)	0.83 (23)	0.68 (22)	–
1986–87	0.75 (4)	0.60 (5)	0.67 (9)	0.88 (8)	–
Total	0.92 (89)	0.86 (87)	0.86 (173)	0.91 (171)	3.36 ^{ns}

Significance levels as in Tab. 1.

Tab. 10. Year-to-year recruitment rates of new adult *P. madidus* (numbers of females present during the first of the two years in parentheses), and overall χ^2 comparisons among enclosures.

	E2	E3	E5	E6	χ^2
1984–85	0.17 (30)	0 (28)	0 (57)	0.04 (57)	–
1985–86	0 (6)	0.17 (6)	0.39 (13)	0.11 (9)	–
1986–87	3.00 (1)	0 (2)	3.33 (3)	1.50 (4)	–
Total	0.22 (37)	0.03 (36)	0.21 (73)	0.13 (70)	6.25 ^{ns}

Significance levels as in Tab. 1.

and the other resident species – although for the latter the numbers of individuals were probably too low to have any significance. Niches are well differentiated among the resident species in the beechwood (Loreau 1986), so that no dramatic effect was expected. However, some signs of ecological release might have appeared in the form of increased abundance in the absence of the dominant species *A. ater*. None was observed. It seems that the effects of competition are too weak to be detected in the overall population dynamics of the other species, that they are overwhelmed by the effects of other factors. What these factors are is not known: it may be predation, availability of favourable microsites, or availability of specific prey. Many factors or combinations of factors can reduce populations to levels such that competition with the dominant species, between each other and within each of them is usually too weak to have detectable effects.

Equilibrium and non-equilibrium populations

It may not be fortuitous that density regulation was suggested in the ecologically dominant species both in this experiment and in Brunsting and Heessen's (1984), while no significant competition was suggested within and between other species. Moreover, the same species that was dominant and showed density regulation in Brunsting and Heessen (1984) – *P. oblongopunctatus* – provides no evidence for competitive effects in the present study where it was not dominant.

A comparison between the long-term changes in density in *A. ater* and *P. oblongopunctatus* in Lembeek is also enlightening (Fig. 10): the yearly maximum mean density was remarkably constant in *A. ater* over a 10-yr period while it declined continuously in *P. oblongopunctatus* over the same period. The total year-catches of *P. oblongopunctatus* from 1978 to 1981 indicated the same downward trend (Loreau 1984a). This further suggests that the population of *A. ater* is in stable equilibrium conditions, while that of *P. oblongopunctatus* is in non-equilibrium conditions. Of course, one cannot rule out the possibility that *P. oblongopunctatus* remains in equilibrium with declining resources, but so wide variations in resources seem unlikely given the polyphagy of this species. Thus, in the same community, different species seem to be subject to fundamentally different types of population dynamics, relating to the two broad

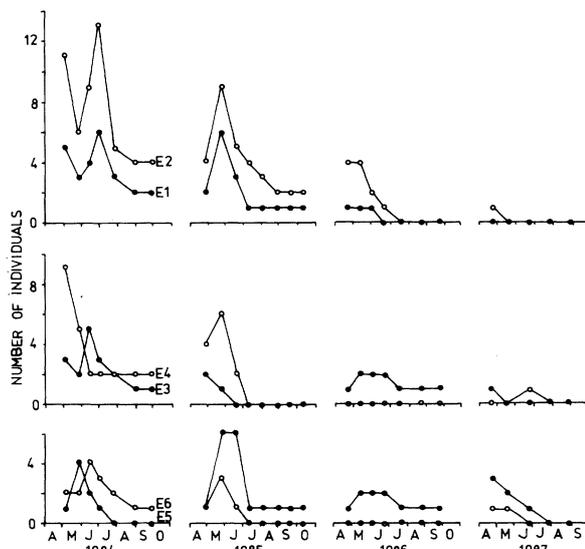


Fig. 9. Changes in the size of *P. oblongopunctatus* populations in the various enclosures (minimum numbers of individuals present).

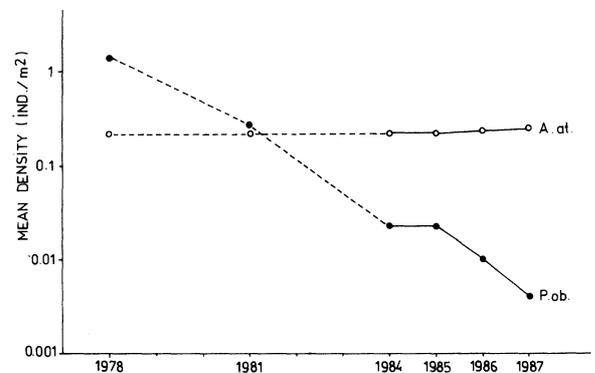


Fig. 10. Long-term changes in the yearly maximum mean population density in *A. ater* and *P. oblongopunctatus*, as estimated within enclosures. Data for 1978 and 1981 from Loreau (1984b).

concepts of equilibrium and non-equilibrium (see DeAngelis and Waterhouse 1987).

I suggest that dominant species in climax communities will more often approach equilibrium conditions and competitive regulation, while most of the less abundant species will be in non-equilibrium conditions and weakly or episodically affected by competitive interactions, because dominant species will be precisely those species which are especially well adapted to the environment and escape the overwhelming influence of predation and spatial and temporal variability of physical and biotic factors. This suggestion is closely akin to the core and satellite species hypothesis of Hanski (1982).

The present work questions the deterministic, equilibrium view which underlies much of the classical theory of interspecific competition and which permeated my previous interpretation of the pattern of niche differentiation (Loreau 1986). But the pattern is real (Loreau 1989), and a field experiment, even if it is carried out over several years, has intrinsic limitations in its time and space scales (Diamond 1986). The time and space scales of the process of niche differentiation are those of long-term interactions and evolution. Even in non-equilibrium conditions, populations can reach high densities episodically (as is the case with *P. oblongopunctatus*) and be then subject to relatively intense competitive pressures (MacArthur 1972, Wiens 1977, Schoener 1984). Also, the Lembeek beechwood is only a small – and not undisturbed – remnant of much larger forests. It is impossible from its study today to extrapolate the general conditions under which the past interactions and evolution of the species have taken place. However, the above discussion makes it very unlikely that interspecific competition can have generated niche differentiation among more than a few dominant species in a biotope.

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