

## Chapter 5: Ground beetles in a changing environment : determinants of species diversity and community assembly

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### INTRODUCTION

The exponential increase of human activities has reached the point where man alters the natural environment on a global scale and threatens unintentionally to drive to extinction half of the species with which he shares his planet within a century; that is, at a rate about a million times greater than the rate at which new species are formed (May 1988). The most direct cause of species extinction is the destruction of their habitat, but even in protected habitats indirect factors, notably atmospheric or water pollution and climate change, might lead to profound changes in plant and animal communities.

Faced with this potential unprecedented ecological catastrophe, ecology is still ill-armed theoretically. Ecology is a young science confronted with levels of complexity that have no equivalent in other sciences. Community ecology in particular, whose object is to understand the processes governing the diversity and organization of species assemblages, is in the midst of what may be called a crisis. During previous years the prevailing view was the deterministic one developed by the Hutchinson-MacArthur school based on equilibrium competition theory (*e.g.* MacArthur 1972) - actually the first generally consistent theory of community organization. Despite partial successes, this theory failed to provide a satisfactory general explanation of the diversity and coexistence of species. The emphasis has now shifted to the significance of regional biogeographic processes (*e.g.* Ricklefs

1987; Cornell & Lawton 1992) and non-equilibrium coexistence (*e.g.* Levins 1979; Chesson 1986; DeAngelis & Waterhouse 1987; Huston 1993). But this shift has not resulted in a new unified theory; the tendency has rather been to identify different kinds of communities (*e.g.* Schoener 1986a). If the competitive exclusion principle is analogous to Newton's first law of motion (Hardin 1960), then community ecology is still lacking the analogue of Einstein's theory of relativity.

What is a community, how does it assemble and how does it respond to environmental changes? These fundamental questions have not yet received final answers, and the present paper certainly does not pretend to provide them. But it attempts to shed light on these questions by examining factors that determine the diversity and structure of ground beetle communities (Coleoptera, Carabidae). Diversity is the hallmark of all life forms, but in no other group is it as spectacular as in insects, and more especially in beetles. Southwood (1978) identified three biological features responsible for this extreme diversity of insects: their small size, which allows them to occupy many special niches, their wings, which provide them with a great power of dispersal among temporary patches, and their metamorphosis, which allows them to partition time. The first two features, together with a moderate life span and intermediate positions in trophic chains, also contribute to the potential for non-equilibrium and non-competitive coexistence (*e.g.* Hutchinson 1961; Schoener 1986b). In this respect ground beetles are of special interest, because they are extremely diversified with about 40,000 described species; they are mostly predators, they span a wide range of sizes, and a number of large forest species have lost their ability to fly and can live for several years. The latter species can thus be viewed as making a transition with small vertebrates from an ecological viewpoint, and their study is likely to reveal more continuities between the ecological processes affecting small invertebrates and large vertebrates than is a comparison between extreme forms of these two groups.

## REGIONAL VERSUS LOCAL PROCESSES

How local is a local community? Both the Hutchinson-MacArthur school emphasizing biotic interactions and the ecophysiological school emphasizing individual

adaptations to abiotic factors have traditionally sought to explain the composition and diversity of communities in terms of local deterministic factors. For ground beetles, the most famous representative of the ecophysiological school was Thiele, who presented a remarkable synthesis on habitat selection by adaptations in physiology and behaviour in his 1977 book. A different perspective emerged from den Boer (*e.g.* 1977), who considered extinction of carabid populations a continually occurring process, compensated for by re-founding of populations through dispersal. On this view, the composition and diversity of local communities, especially in unstable biotopes, should be dependent on stochastic, regional dispersal processes. Empirical evidence in several taxonomic groups and theoretical arguments have now accumulated to show that regional and historical factors can profoundly influence local diversity (*e.g.* Ricklefs 1987; Cornell & Lawton 1992).

By way of example, Figure 1 summarizes the composition and species richness of ground beetle communities I studied intensively in three forest biotopes in Lembeek, Belgium: a young successional forest, which is intermediate between a meadow and a forest, a pine plantation, and a climax beechwood (Loreau 1984a). Though artificial, the pinewood harbours a carabid community which is in many respects intermediate between those of the other two biotopes; the three forests can thus be viewed as representing a succession to the climax stage. Ground beetles were sampled continuously using pitfall traps from 1978 to 1981. The total catch in pitfall traps was shown to be a good predictor of mean biomass, and hence of the ecological importance of species (Loreau 1992). In Figure 1 the species are ranked from the most important (rank 1) to the least important (highest rank) in terms of catch numbers, and their rough habitat type was determined from previous studies in Europe. In the climax beechwood all the main species were typical forest species, whose presence and abundance may be ascribed to local deterministic factors. But many of the rare species were typical for more open habitats and were probably occasional immigrants. On the other hand the successional forest contained a mixture of species of all habitat types. Since the biotope itself is heterogeneous, it is difficult in this case to separate regional from local effects, but it is likely that even the

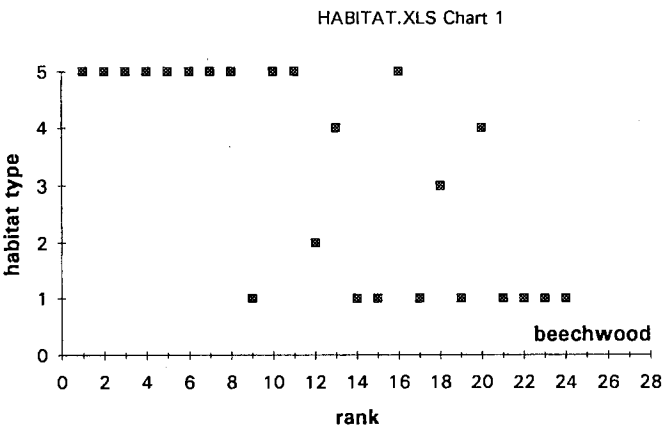
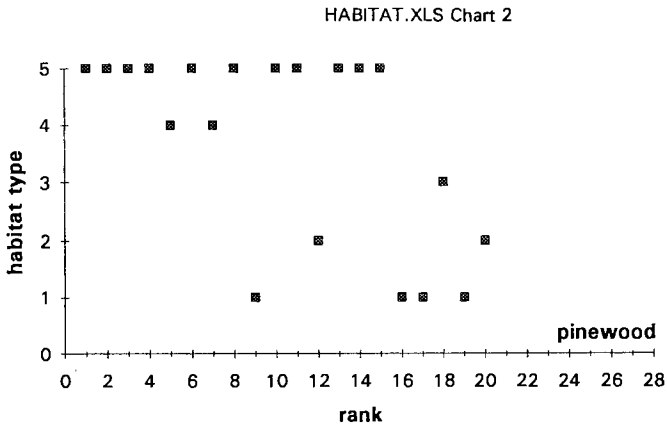
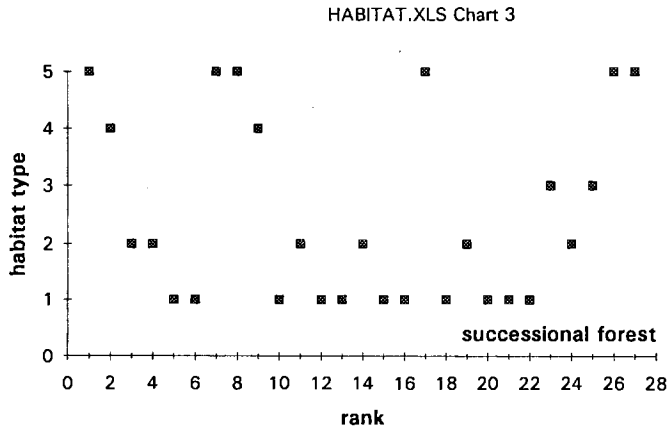


Figure 1. Habitat type of the species composing three forest carabid communities in Lembeek, Belgium, against their rank of ecological importance as obtained from pitfall trapping. Habitat types: open (1), intermediate (2), humid (3), non-specific (ubiquitous species) (4), and forest (5) habitats. Data from Loreau (1984a).

abundance of the dominant species was affected by immigration from the surrounding forests, where it was dominant too. Thus although regional processes affect local species diversity in all cases, the extent to which they affect the core species and community structure is likely to differ among sites, and to be greater in unstable biotopes (*e.g.* a successional stage) and lower in stable biotopes (*e.g.* a climax stage) (see also den Boer 1977). Another factor liable to affect the extent of regional influences is the area of the biotopes: the smaller their area, the greater the regional influences due to edge effects (*e.g.* Niemelä 1988). Other authors have recently presented evidence that biogeographic processes determine local ground beetle diversity. Thus Heijerman & Turin (1989) suggested that geographical position is more important than forest type in determining the composition of forest carabid communities in the Netherlands. Eyre & Luff (1993) were not able to ascribe differences in forest carabid communities from northeast England to environmental factors. However, caution must be exerted to avoid unwarranted generalizations. The relative importance of biogeographic factors in these studies may be explained by the fact that most of the forested areas considered were young, hence in a successional stage (Turin et al. 1991), or by the high similarity of the various forests in the region.

#### NICHE DIFFERENTIATION AND COMPETITION

The foregoing suggests that while local deterministic factors do not explain the whole diversity of communities, they do play a role in the presence and abundance of the main species. According to niche and competition theory, only those species will coexist which have sufficiently different niches to avoid competition for shared resources (*e.g.* Hutchinson 1957; MacArthur 1972). Community organization thus results from resource partitioning generated by interspecific competition. Can this theory explain the diversity of the main species in carabid communities?

I investigated this issue in great detail in the forest ground beetle communities from Lembeek. I first analyzed all the niche components likely to be involved in resource partitioning for the various species: annual and daily activity rhythms, type and size of prey eaten, and horizontal and vertical spatial distributions of activity. The two main components leading to niche differentiation (low niche overlaps) in the

beechwood and the pinewood were found to be the annual activity pattern and the type of prey (Figure 2). There was a nice seasonal succession of periods of maximum activity of the various species (which also appears in Figure 5), as well as clear-cut differences in feeding preferences despite the fact that almost all species proved to be polyphagous predators on primary consumers. The combination of these two niche dimensions resulted in a remarkable overall niche differentiation, in contradiction with the view generally held before. Furthermore, temporal niche differentiation was much less in the successional forest, where the annual activity cycles of the dominant species appeared actually to converge rather than diverge; this finds expression in a consistently higher mean niche overlap whatever the number of species considered (Figure 2). These results are those predicted by competition theory: niche differentiation is achieved provided that the environment is stable enough for competitive relationships to stabilize in turn. They were further confirmed by tests against null models, but niche divergence was found to be statistically significant only among the four dominant species in the climax beechwood (Loreau 1989).

Horizontal spatial distribution of activity relates probably more to a species' habitat than to its niche (*sensu* Whittaker et al. 1973). For this component, niche overlap increased from the successional forest to the climax beechwood (Figure 2), which expresses the growing spatial homogeneity of the environment. Spatial distributions of ground beetles are usually contagious, but an interesting feature of large dominant species was that their distribution tended to be random at large spatial scales in those biotopes where they were most abundant, as if they saturated the environment (Loreau 1984b, Loreau & Nolf 1993). Detailed capture-recapture data further showed a considerable mixing of the population of the dominant species in the beechwood, *Abax ater* (Loreau & Nolf 1993).

A long-term (4 years) field experiment was then carried out to test the significance of intra- and interspecific competition in the beechwood (Loreau 1990). Intraspecific competition in the dominant species *A. ater* was tested by a convergence experiment in fenced plots with either normal or double population density; interspecific competition was tested by experimental introduction of a species

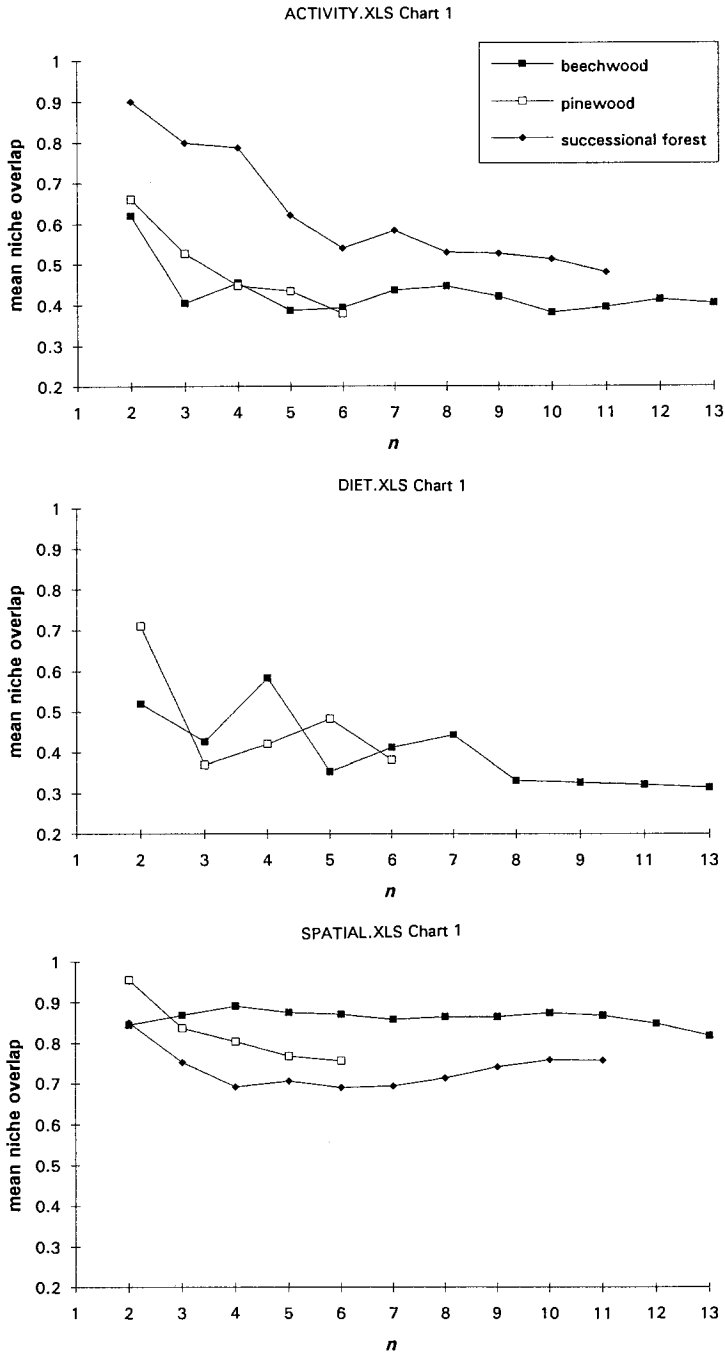


Figure 2. Mean niche overlap of the first  $n$  species in the three forest carabid communities of Lembeek (species ranked according to their ecological importance), for the three main niche components: annual activity cycle (top), diet (middle), and horizontal spatial distribution of activity (bottom). Data from Loreau (1984b, 1984c).

occupying a similar niche in the successional forest, *Pterostichus madidus*, either with or without *A. ater*, and by monitoring the effects of different densities of *A. ater* on the other local large-sized species. This experiment provided some evidence for competitive regulation in the dominant species *A. ater*, but no evidence for intra- or interspecific competition in the other species. The introduced populations of *P. madidus* did poorly, but persisted at low densities apparently without being affected by the presence of *A. ater*. The other resident species, among which was the second dominant species *P. oblongopunctatus*, also showed no sign of ecological release in the absence of *A. ater*. It must be noted, however, that the experimental plots were too small to harbour viable populations of the third and fourth dominant species, which are large-sized and highly mobile.

The overall conclusion suggested by these studies is that competition does play a role in ground beetle communities, but a much more restricted role than assumed in equilibrium competition theory. Competition seems to determine population density and dynamics only in a single or a few dominant species in the climax forest. This does not necessarily mean that competition is absent in the other species, but at least that, if present, it is too weak or variable to govern the presence, abundance and overall population dynamics of these species. In other, more unstable and heterogeneous biotopes, its role should be even more limited. This conclusion is not inconsistent with those of a recent extensive review of interspecific competition in ground beetles (Niemelä 1993).

The questions now are: how to explain that competition is significant in one species but not in others, and how to explain community-wide patterns such as niche differentiation in the climax forest? The answers to these questions, I suggest, lie in the coexistence of both equilibrium and non-equilibrium populations and the structuring influence of the lower trophic level, which will be examined in the next sections.

## NON-EQUILIBRIUM VERSUS EQUILIBRIUM POPULATIONS

The equilibrium view of the world has a long tradition in science, and ecology is no exception. The idea that populations and communities reach some sort of



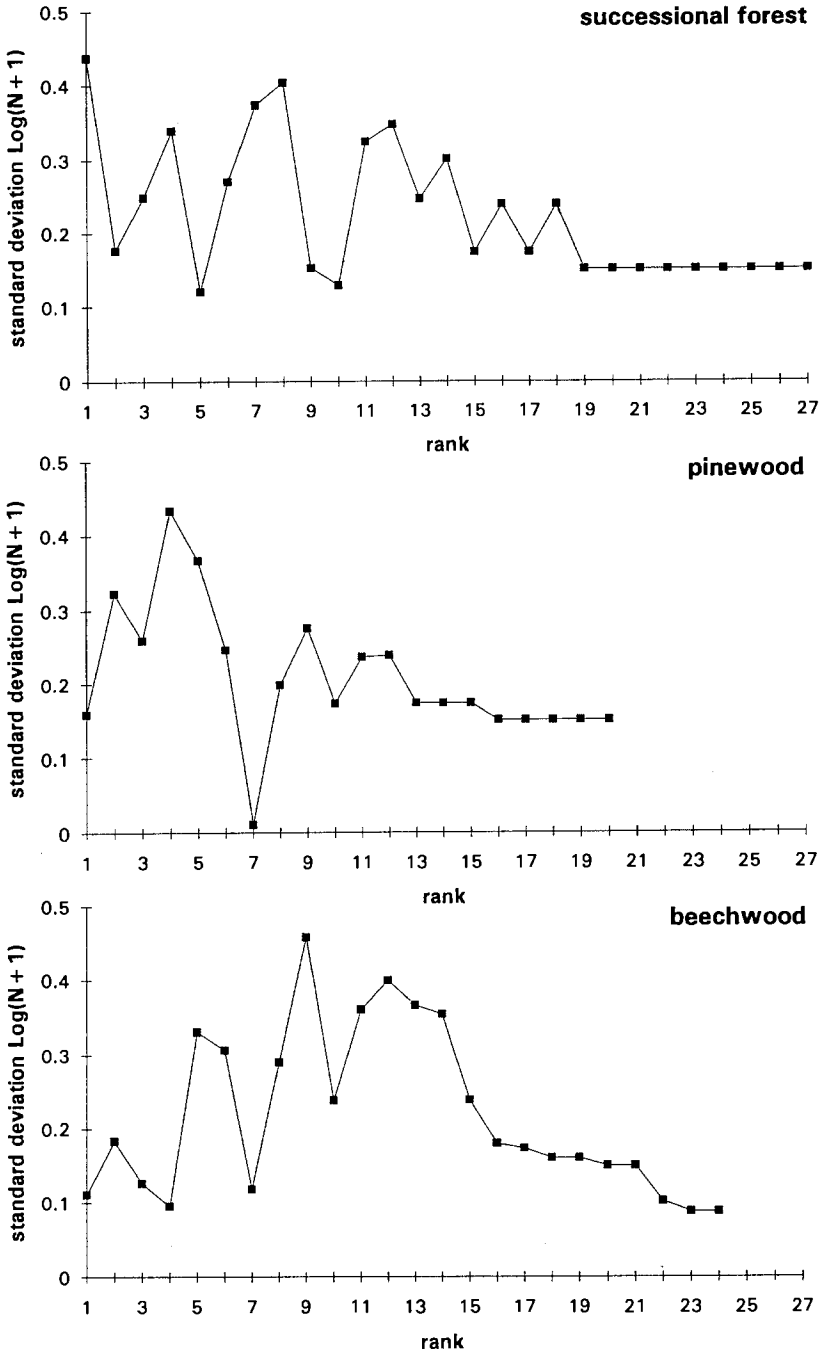


Figure 3. Population variability, as measured by the standard deviation of log-transformed year-catches ( $N$ ), against the species' rank of ecological importance in the three forest carabid communities of Lembeek. Data from Loreau (1984a).

equilibrium or steady state has been one of the central tenets of the Hutchinson-MacArthur school. Others have strongly opposed this view, among them carabidologists like den Boer (*e.g.* 1968, 1981). Today non-equilibrium processes are accepted as significant components of species coexistence and diversity (*e.g.* Levins 1979; Chesson 1986; Huston 1993), and the opposition between equilibrium and non-equilibrium concepts has been largely resolved by noting that these generally apply to different scales (*e.g.* DeAngelis & Waterhouse 1987). What is perhaps less appreciated is the fact that equilibrium and non-equilibrium populations can coexist within a single community, in such a way that a community may consist of a core of equilibrium dominant species and a large set of non-equilibrium species (Caswell 1978; Hanski 1982; Loreau 1992).

This is strongly suggested by patterns of variability of population sizes in the carabid communities from Lembeek. If one plots population variability, as measured by the standard deviation of log-transformed year-catches, against the species' rank of ecological importance (Figure 3), the expected pattern for a non-equilibrium community is a widely and irregularly oscillating curve without detectable trend, because standard deviation after log transformation should be independent of the mean and variability should be distributed randomly. That is what was found in the successional forest (Figure 3). Note that the tail of the curve bends downward and becomes flatter due to low catch numbers (in particular the rarest species are those which are caught only once; thus they must have identical low variabilities because of identical series of zero catches). This reduced variability of small populations can be regarded as real when populations are censused exhaustively (*e.g.* Schoener & Spiller 1992), but has to be regarded as a statistical artefact when populations are only sampled as is the case here with pitfall trapping. On the other hand, the curve in the beechwood was very different from that "null" pattern: it tended to be bell-shaped with low variabilities in the dominant species. The situation was somewhat intermediate in the pinewood.

After elimination of the species with too low catch numbers (total 4-year catch 5 individuals) which contribute to the tail of the curves in Figure 3, the correlation

Table 1. Correlations between population variability [standard deviation  $\text{Log}(N+1)$  where  $N$  is the total year-catch], average ecological importance [average  $\text{Log}(N+1)$ ], and body size in the three ground beetle communities from Lembeek. Highly significant correlations ( $P < 0.01$ ) are indicated by \*\*; other correlations are not significant ( $P > 0.05$ ).

correlation	successional forest (10 df)	pinewood (4 df)	beechwood (12 df)
average - SD $\text{Log}(N+1)$	0.077	-0.519	-0.755**
body size - SD $\text{Log}(N+1)$	0.548	-0.388	-0.775**
average $\text{Log}(N+1)$ - body size	0.496	0.502	0.519

between population variability and average ecological importance (average log-transformed year-catch) varied from zero in the successional forest to a highly significant negative value in the beechwood (Table 1). Body size also seemed to play a significant part in the pattern, since the correlation between population variability and body size varied from a positive value (just under the 0.05 significance level) in the successional forest to a significant negative value in the beechwood. The correlation between body size and ecological importance was positive though not significant in all cases. All this suggests that the succession to the climax stage is accompanied by a tendency for large dominant species to stabilize around an equilibrium state.

The results presented in Figure 3 actually underestimate the contrast between equilibrium and non-equilibrium populations because they are based on data from only four years of pitfall trapping. Over longer periods of time, the contrast is much more striking. Thus the average population density of the dominant species in the beechwood, *A. ater*, was remarkably constant over a 13-year period, while that of the second dominant species, *P. oblongopunctatus*, declined by three orders of magnitude over a 10-year period (Figure 4). Although population fluctuations alone are not sufficient to discriminate between equilibrium and non-equilibrium conditions, this kind of contrast is a strong argument for such a discrimination, all the more so since

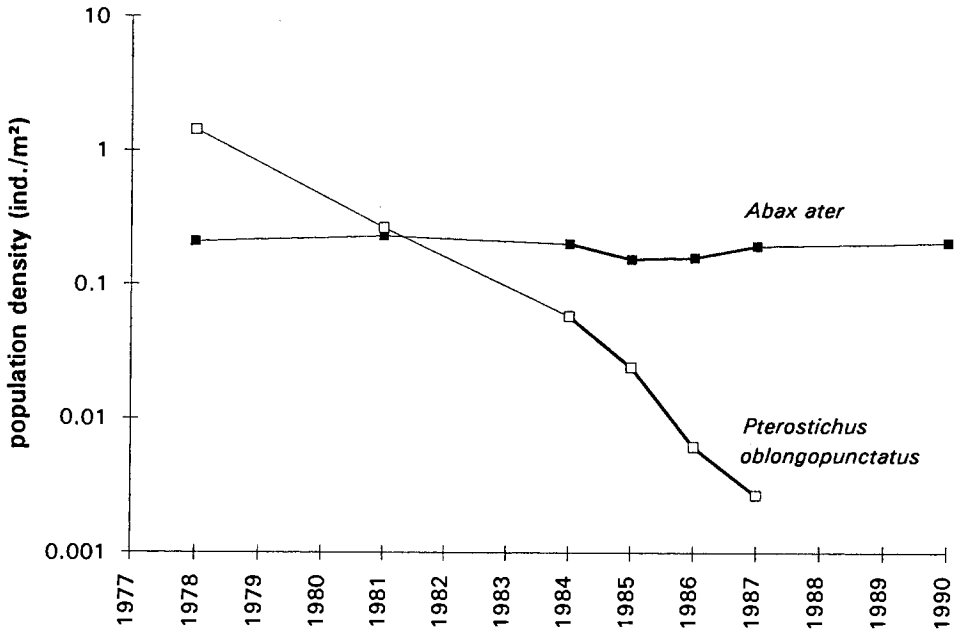


Figure 4. Long-term changes in the population density of the two dominant species in the beechwood of Lembeek, during their period of maximum density (late April to late June for *P. oblongopunctatus*, mid-May to late July for *A. ater*). Capture-recapture data from Loreau (1984d, 1990) and Loreau & Nolf (1993).

it is consistent with field experimental data on competition (see previous section) and does not seem to be consistent with alternative explanations. For instance, the population stability of *A. ater* cannot be ascribed to a spatial "spreading of risk" (den Boer 1968, 1981) because of the spatial homogeneity of the population and its environment (Loreau & Nolf 1993). Also widely fluctuating populations such as that of *P. oblongopunctatus* can hardly be assumed to be in a moving equilibrium with widely fluctuating resources because ground beetles are polyphagous and should not generally be strongly influenced by fluctuations of any particular prey species.

The tendency for large dominant species to reach equilibrium conditions in the climax forest while most other species and even dominant species in the successional forest do not, can be explained plausibly as follows. Most species are adapted to only part of the conditions experienced in their local environment and accordingly are sensitive to spatial and temporal variations in these conditions; the smaller their body size and the more unstable and heterogeneous the environment, the greater generally their sensitivity. Such species therefore reach neither an equilibrium nor generally a very high biomass. A few species can be especially well adapted to the whole range of conditions experienced in the local environment; this seems to be the case, for instance, with *A. ater* in the beechwood where its activity spans the whole biotope spatially and most of the year temporally. Favourable conditions for this to occur are a large body size and a stable and homogeneous environment. Such species accordingly reach a high biomass and stabilize at their carrying capacity through competition. These reflections are likely to apply to many other organisms; thus the tendency for large dominant species more often to approach equilibrium conditions and competitive regulation in stable environments while less abundant species are more often in non-equilibrium conditions and weakly affected by competition; this tendency is likely to be quite general.

On the other hand, the concrete realization of this tendency depends heavily on species- and site-specific characteristics. Therefore it comes as no surprise that no consistent effect of body size on population variability was found by Gaston & Lawton (1988) in a large-scale analysis of patterns in insect populations. What is more surprising is that they did find high positive correlations between population variability and abundance or ecological importance in all groups including carabids, in contradiction with the above arguments and results. These correlations are most probably due to the inclusion of species with low catch numbers in the correlations, and hence, as argued above, artefacts. I recalculated these correlations for carabids using the same data as in Gaston & Lawton (1988) (data from den Boer 1977) and did not find them to be significant in any of the four sites considered when species with too low catch numbers (total 8-year catch 8 individuals) are eliminated.

## STRUCTURING INFLUENCE OF RESOURCES

The previous two sections make it clear that while competition can have a significant influence in one or a few dominant species in the climax stage, it cannot explain patterns at the level of whole ground beetle communities. Some of these patterns have been known for long and explained by abiotic factors. Thus most ground beetles from open biotopes are active in the spring while forest species tend to be active later in the year. This trend was explained by microclimatic factors: forests have buffered microclimates, they warm up and cool off less and later than do open biotopes; as a result they tend to harbour more autumn breeders than do open biotopes (Thiele 1977). Furthermore spring and autumn breeding are correlated with diurnalism and nocturnalism respectively, and this trend towards increasing night activity through the year was explained by the same microclimatic factors: the preference for a high humidity leads to nocturnalism - to ensure a high humidity - and to autumn activity, because nights are too cold in spring, while spring breeders must be diurnal and tolerate low humidity to enjoy high enough temperatures (Thiele 1977).

These explanations owe their success to their being straightforward and in keeping with the known microclimatic requirements of the various species. For this reason, however, they were accepted uncritically, without confrontation with alternative explanations. The main problem with such explanations is that they are unilateral; they merely express correlations between isolated aspects of a species' niche or habitat and isolated environmental factors. But there are manifold interrelations between the various components of a species' niche, which implies that the latter has to evolve and be considered as a totality (Loreau 1988). For instance, diurnalism was shown to be correlated also with body size, which prompts explanations in terms of biotic interactions (predation pressure, prey availability) (Southwood 1978; Loreau 1988).

Resource availability in fact seems to be a key determinant of the niche structure of carabid communities but has been rarely investigated. Ground beetles were regarded traditionally as broadly polyphagous, but, as mentioned above, their feeding preferences turned out to be much more differentiated than was assumed before, at least in forests. When I compared the niche structures of the carabid

communities from the beechwood and the pinewood in Lembeek, I arrived at the conclusion that the only difference between them was the elimination of species with intermediate niches in the pinewood, and this appeared to correspond exactly to the impoverishment of the available prey spectrum and the simplification of the litter (Loreau 1984c). Thus the diversity of niches in a community seems to be directly dependent on the diversity of available resources.

A quantitative study of seasonal changes in prey availability further showed that available resources determined the temporal structure of the beechwood community. A distinct pattern emerged when body size was plotted against the period of maximum activity for the various species in the beechwood: large species tended to have a maximum body size towards late summer (Figure 5). This pattern was nicely explained by seasonal changes in the availability of the various prey types in which each carabid was most specialized: large insect larvae for *Carabus* species, annelids for *Abax* species (though *A. ater* was the most generalist species and also readily ate large insects and molluscs), molluscs for *Cychrus attenuatus*, and small and medium-sized insects for *P. oblongopunctatus* and *Nebria brevicollis*. The correspondence between the periods of maximum activity of large ground beetles, especially dominant species, and their preferred prey types was extremely good (Figure 5); even more so since within these periods the activity of dominant species was correlated with that of their preferred prey (Loreau 1988). Thus there was strong evidence that the seasonal niche structure is tightly adapted to available resources among large species in the climax forest. Note that this conclusion was not true for small species.

Much of the diversity and structure of carabid communities appears to be accounted for by the combined effects of abiotic factors and resource availability, and probably much more could further be accounted for were one to know better the ecology of larvae, which are likely to be the critical stages on account of their great ecological requirements and energetic needs. This suggests that a significant part of the organizing process of carabid communities occurs through the flow of energy and matter coming from the lower trophic level rather than through horizontal (competitive) interactions. The soil trophic web might therefore be organized in a bottom-up or donor-controlled fashion more than in a top-down or recipient-controlled

fashion. This also conflicts with another central, if implicit, assumption of equilibrium competition theory, i.e., trophic interactions are recipient-controlled like in Lotka-Volterra systems (*e.g.* MacArthur 1972). It is now recognized that the control of trophic interactions is generally shared by the donor and recipient populations, with considerable variations from almost complete donor control to almost complete recipient control (*e.g.* Odum & Biever 1984; Hunter & Price 1992; Power 1992; Strong 1992). One important factor that bends trophic interactions towards donor control is spatial and temporal heterogeneity (Smith 1972; Arditi & Ginzburg 1989), and this is generally more significant in terrestrial than in aquatic systems. In particular, invertebrates that hunt at the soil surface such as adult ground beetles forage in an environment in which their prey are ephemeral; these prey either live permanently in the canopy (phytophagous insects) or find refuge in the soil, under bark, etc. (other insects, earthworms, molluscs). As a result, adult ground beetles generally are unlikely to control the abundance of particular prey species even though they may have a profound impact at the soil surface, and the potential for exploitation competition is low. The situation is different for the soil-dwelling larvae, and the most plausible mechanism for competition in ground beetles is food-dependent cannibalism at the larval stage (Heessen & Brunsting 1981).

## CONCLUSIONS AND PERSPECTIVES ON BIOINDICATION

This (non-exhaustive) overview of determinants of species diversity in ground beetle communities shows that the assumptions on which equilibrium competition theory is based are not met on the scale of whole communities. The view presented here is that of communities as dynamic assemblages in which only some dominant species can reach equilibrium conditions and competitive regulation in sufficiently stable and homogeneous environments; diversity, especially of rare species, is influenced by regional processes, and the main local structuring factors are abiotic constraints and resource availability. I think that this view applies to many communities of other organisms and can accommodate a wide range of situations by letting the balance between local and regional processes, equilibrium and non-



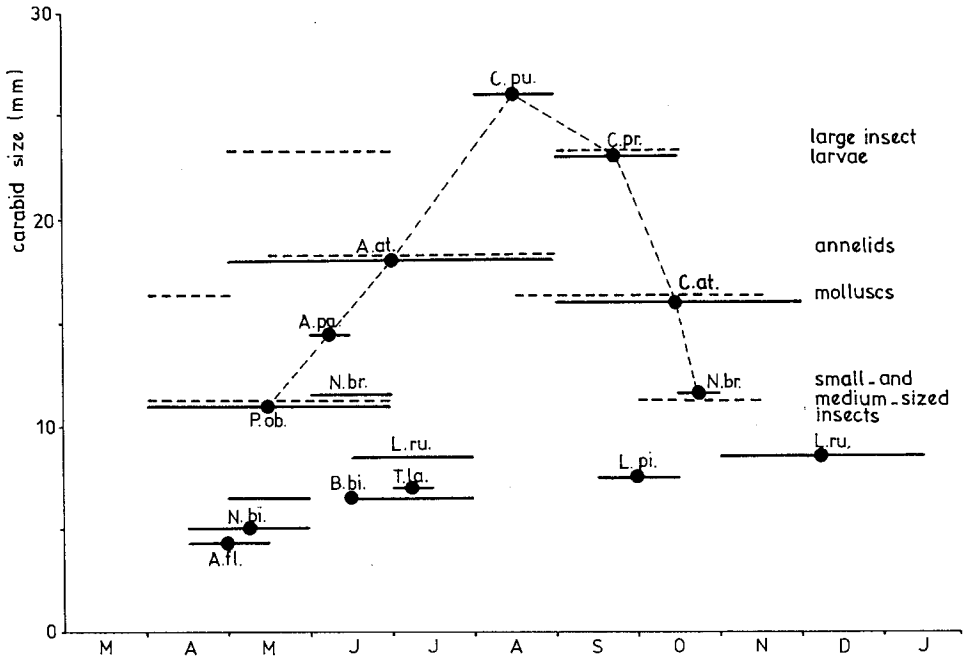


Figure 5. Body size against period of maximum activity (horizontal unbroken line) for the main species in the beechwood of Lembeek. The sloping dashed line joins the successive niche centres of the large species. The periods of maximum activity of the great prey types (horizontal dashed lines) are indicated at the same height as those of the four dominant species of which they are the preferred prey: *Abax ater* (A.at.), *Pterostichus oblongopunctatus* (P.ob.), *Cychrus attenuatus* (C.at.) and *Carabus problematicus* (C. pr.). Other species are *Abax parallelus* (A.pa.), *Carabus purpurascens* (C.pu.), *Nebria brevicollis* (N.br.), *Asaphidion flavipes* (A.fl.), *Notiophilus biguttatus* (N.bi.), *Badister bipustulatus* (B.bi.), *Trichotichnus laevicollis* (T.la.), *Lorocera pilicornis* (L.pi.) and *Leistus rufomarginatus* (L.ru.). Data from Loreau (1988).

equilibrium populations, donor and recipient controls of trophic interactions, vary from one extreme to the other.

This view is general, however, and as such imprecise. An ultimate goal of community ecology should be to formulate testable rules for the process of community assembly. Only then can community ecology relate itself directly to the practical problems raised by increasing environmental changes. Even strongly interacting organisms such as plants respond to long-term climate changes in a species-specific way, which leads to continuous changes in communities. Communities of weakly interacting organisms such as ground beetles are still more labile and change on the time scale of a generation, that is, roughly one year. Ground beetles in particular are highly diversified, they are sensitive to abiotic factors such as microclimate as well as resource availability, and their ecology and systematics is relatively well known. All this makes carabids and their communities potentially good biological indicators of environmental changes.

But much remains to be done, in my opinion, before we can use them efficiently as such. The most convincing application of ground beetles as bioindicators so far is in paleoecology and paleoarchaeology (*e.g.* Coope 1967; Osborne 1969). A lot of information has been accumulated on the habitat types of ground beetles, which allows reliable reconstructions of past environments. Since habitat type is largely determined by, and classified according to, plant communities, it is more disputable whether that kind of information can add much to the direct study of plant communities in present environments. The term bioindicator has been used rather loosely in recent literature, more to emphasize the fact that carabid communities are different in different environments than to show a direct practical use (*e.g.* various contributions in Stork 1990). Changes in carabid communities most probably do indicate changes in the environment, but which ones is not yet clear. In existing predictive models, carabid distributions are inferred mechanically from predicted changes in plant distributions and not the other way round (Rushton et al. 1993; Pizzolotto 1993). Large-scale databases of carabid distributions have been set up recently in several European countries, and have allowed investigation of long-term changes in distributions since the last century. Such changes were first attributed by Hengeveld (1985) to climate

changes, but a much more convincing explanation is direct destruction of natural and semi-natural habitats by human activities (Desender & Turin 1989; Desender et al. 1993). For the time being, monitoring of ground beetle communities appears to be mainly useful for conservation purposes, but its use in bioindication of environmental changes is a reasonable hope for the future (*e.g.* Luff et al. 1992).

Progress in that direction demands more insight into the causal factors that govern the distribution and abundance of species and the assembly of communities. In particular, most studies so far have attempted to explain carabid distributions from correlations with some abiotic factors, but part of these correlations might in fact reflect only indirect effects, the direct causal factors being biotic, *e.g.* resource availability. This further suggests a new potential way of considering ground beetles as bioindicators, namely as indicators of the general state of the soil fauna, hence of ecosystem functioning. If this proved to be the case, ground beetle communities might contain less redundant information in relation to plant communities and would be all the more useful to consider. One of the major challenges for the years to come appears to be the development of an integrated research programme combining investigations on several ecological levels - from the individual organism to the ecosystem - and several spatial scales - from the local to the continental scale.

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