

The nature of the structuring of ecological communities : the example of carabid beetles

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Summary

Various theoretical models have been put forward to describe and explain the structure and diversity of ecological communities. Some emphasize interspecific competition, others, the interplay of many more or less independent factors.

A series of works on the structuring of forest carabid communities in Belgium allows one to glimpse a synthesis on this issue. A carabid community shows a well-defined niche structure, in which the dominant species fills a central place. This species is distinguished by a very broad niche, a quasi-homogeneous spatial distribution, a stable population, and apparently a competitive regulation. On the other hand, other species display a greater dependence on spatial and temporal variability of the environment, and do not seem to be governed by competitive interactions.

This suggests a quite general model of structuring of communities where competition operates in a more or less restricted group of dominant species, while the abundance of many species is governed by different factors which vary in space and time.

Key-words : community structure, niche, competition, theoretical models, carabid beetles.

Résumé

Nature de la structuration des peuplements écologiques: l'exemple des coléoptères carabides.

Divers modèles théoriques ont été avancés pour décrire et expliquer la structure et la diversité des peuplements écologiques. Certains mettent l'accent sur la compétition interspécifique, d'autres, sur l'action conjuguée d'une multitude de facteurs plus ou moins indépendants.

Un ensemble de travaux sur la structuration des peuplements forestiers de carabides en Belgique permet d'entrevoir une synthèse sur ce point. Un peuplement de carabides montre une structuration nette des niches écologiques des diverses espèces, dans laquelle l'espèce dominante occupe une place centrale. Cette espèce se distingue par une niche très large, une répartition spatiale quasi-homogène, une population stable et, semble-t-il, une régulation compétitive. D'autres espèces, par contre, témoignent une plus grande dépendance à l'égard de l'hétérogénéité spatiale et temporelle de l'environnement et ne semblent pas gouvernées par des interactions compétitives.

Ceci suggère un modèle de structuration des peuplements de valeur assez générale, où la compétition intervient dans les rapports d'un groupe plus ou moins restreint d'espèces dominantes, tandis que l'abondance de nombreuses espèces est gouvernée par des facteurs différents, variables dans l'espace et dans le temps.

Mots-clés : structure de peuplement, niche, compétition, modèles théoriques, carabides.

Introduction

Anyone who studies more than one species at a time is brought to ask questions like: what explains the

diversity of species in a community? is a community structured, and how? to what extent is this structure determined by competitive relations between species? Much ink has flowed on these questions which have been and still are pervasive in ecology. The purpose of this paper is not to make a general synthesis or to settle once and for all questions that are still expanding. It is rather to attempt to articulate an answer to these questions founding upon a series of thorough works on carabid beetle communities.

For ten years I have studied the ecology of a few forest carabid communities in Lembeek (Belgium), especially of a stable community living in a nearly climax beechwood. These studies have gone from a descriptive study of the general characteristics of the communities (LOREAU 1984a), to a detailed analysis of the ecological niches of the species (LOREAU 1984b), then to a study of the factors determining the niche structure, especially available food resources (LOREAU 1988), and lastly to an experimental study of the population dynamics and competitive relations of the species (LOREAU in press). Synthesizing all this material can help to illuminate the above questions.

Theoretical models of species abundance patterns and niche structure

Natural communities are not made up of species with roughly equal quantitative importances. As a rule one or a few species - the dominants - prevail in abundance, biomass or activity, while most species are more or less rare. Various theoretical distributions have been brought forward to describe such patterns mathematically: MOTOMURA's (1932) geometric species, FISHER et al.'s (1943) logarithmic series, PRESTON's (1948, 1962) lognormal distribution, and MACARTHUR's (1957, 1960) broken-stick distribution. Except for the latter, these distributions were elaborated more to fit empirical data than from theoretical premises regarding underlying ecological processes. However, such explanatory theoretical foundations have not been long to

appear, and are still commonly accepted by ecologists (WHITTAKER 1965, 1972; MAY 1975, 1981). Curiously enough, they are of two essentially contradictory types. The first type of explanatory theories is strictly causal and based on specific models of community structure. All these models assume, first, that the numerical importance of a species is related to the fraction of the niche space it appropriates, and, second, that this niche space has a fixed volume which is split up between competing species. Depending on the rule of this split, at one extreme the geometric and logarithmic series would be indicative of a scramble competition, leading to strong inequalities of species abundances; while at the other extreme the broken-stick distribution would be typical for a contest competition involving territorial behaviour, leading to less unequal abundances.

The second type of explanatory theories is strictly statistical in nature. If the number of species is sufficiently large, the species abundance pattern will be determined by the interplay of a multitude of more or less independent factors. Since in general ecological factors affect population dynamics and compound multiplicatively, the statistical Central Limit Theorem ensures that a lognormal distribution of the number of species as a function of their abundance will result.

Consequently, it is commonly accepted that the geometric or logarithmic series and the broken-stick distribution apply to relatively small and homogeneous communities where a single factor predominates, and reflect features of community biology, while the lognormal distribution applies to large and heterogeneous communities where many factors act together, and reflects purely statistical properties. The situation is however much more complex. For instance, the lognormal distribution can reasonably fit most empirical distributions from the near-geometric to the broken-stick form (WHITTAKER 1972). TAYLOR (1978) in particular showed that the logarithmic series is indistinguishable in practice from a "small sample" condition of the lognormal distribution. On the other hand, the lognormal distribution itself can be generated by a causal model based on the same assumptions as the others (SUGIHARA 1980). Thus theoretical arguments alone are unable to decide which actual processes underlie species abundance patterns.

Species abundance patterns and niche structure in carabids

Forest carabid communities are relatively small and homogeneous; they comprise a few tens of species, most of which are predatory on primary consumers, active at the surface of the litter, and nocturnal (LOREAU 1984b, 1987). Thus according to the causal models, one should expect a species abundance pattern obeying a geometric or logarithmic series, and interspecific relations governed by competition.

Fig. 1 shows the dominance-diversity curves for three communities in Lembeek. Their aspect is indeed that of a logarithmic series. In the near-climax beechwood, the dominance relationships are also rather constant from year to year among the dominant and subdominant species. Thus the niche structure and interspecific relations should be relatively stable, which makes investigation in this biotope especially interesting.

A thorough niche analysis was carried out in the beechwood, involving five niche components (LOREAU, 1984b, 1987): diet, annual activity cycle, daily activity rhythm, horizontal spatial distribution of activity, and vertical distribution of activity. The three most informative components were found to be diet, annual activity cycle and spatial distribution of activity; they are also roughly independent, which allows one to estimate 3-dimensional niche parameters. The other two components are less informative - as mentioned above, most species are mainly surface- and night-active; they are also not independent of the first three ones.

It turned out that niches are well differentiated in the 3-dimensional niche space, and distributed according to a well-defined structure, with the niche of the dominant species, *Abax ater*, being broadest and occupying a central position. Table 1 compares the various 1-dimensional and the 3-dimensional niche breadths for *A. ater* with the average niche breadths of the other species, and shows that *A. ater's* niche is significantly broader than the average of the other species in all the dimensions considered, and a fortiori in the 3-dimensional space. A good indication of the central position of a species' niche is given by its mean overlap on the other species, since the more a niche is central, the more it overlaps other niches. Table 2 shows that *A. ater* again has a mean niche overlap that is significantly greater than the average of the other species in all the dimensions, and thus also in the 3-dimensional space.

Thus the breadth and central position of the niche of the dominant species is a well-marked feature, which conforms to one of WHITTAKER'S (1965) models of community structure. It is also consistent with the first hypothesis underlying the causal models, i.e. that the numerical importance of a species is correlated with the fraction of the niche space it appropriates. However, this hypothesis is not supported by the data for the other species: the correlation between the 3-dimensional niche breadth (after angular transformation) and the numerical importance (log 4-year catch) of the other species is weak and not significant ($r = 0,338$; 8 df; $P > 0,05$).

Competitive relations within and among species

The second hypothesis underlying the causal models is that dominance relations are governed by competition.

In order to test this hypothesis, I carried out a 4-year field experiment (LOREAU in press). Its principle was as follows. Several experimental plots were isolated by steel enclosures of 16 x 14 m, and the population dynamics of all large-sized species was followed during four years in each enclosure using capture-recapture techniques. The population density of two species were manipulated experimentally during the first year. First, the density of the dominant *A. ater* was doubled in some enclosures in order to test the importance of intraspecific competition. If the latter was significant, the expected effect was a convergence towards natural densities in all plots in the following generations. Second, *Pterostichus madidus*, a species with a niche similar to that of *A. ater*, was introduced either in the presence (control condition) or in the absence (experimental condition) of *A. ater* in some enclosures. Since *P. madidus* is common in the successional forest but very rare in the beechwood of Lembeek, the hypothesis was that its quasi-absence in the beechwood was partly due to competition with *A. ater*. Thus the expected effect was that *P. madidus* would successfully colonize the plots from which *A. ater* was absent, but not those in which *A. ater* was present. Finally, one could expect that some of the resident species in the beechwood would become more abundant in the absence of *A. ater*.

The results of this experiment were again rather contrasted. On the one hand, the populations of *A. ater* did converge towards the same density except in one enclosure, in partial accordance with the hypothesis of population regulation around a constant equilibrium density. On the other hand, the populations of *P. madidus* did poorly, but eventually seemed to persist at low densities in all enclosures, apparently without being affected by the presence or absence of *A. ater*. The other, resident species also showed no sign of ecological release in the absence of *A. ater*. Furthermore, the most abundant of them, *Pterostichus oblongopunctatus*, was apparently in non-equilibrium conditions. It thus seems that competition does not govern population dynamics in species other than the dominant.

Towards a more unified view of community structure

The two hypotheses underlying the causal models of community structure are both confirmed for the dominant species only, and at best insufficient for the other species. Therefore they cannot account for the numerical relations in the communities, and an alternative theoretical model is needed. The essence of this model must derive from the recognition that competition does not affect all species equally. Note that if

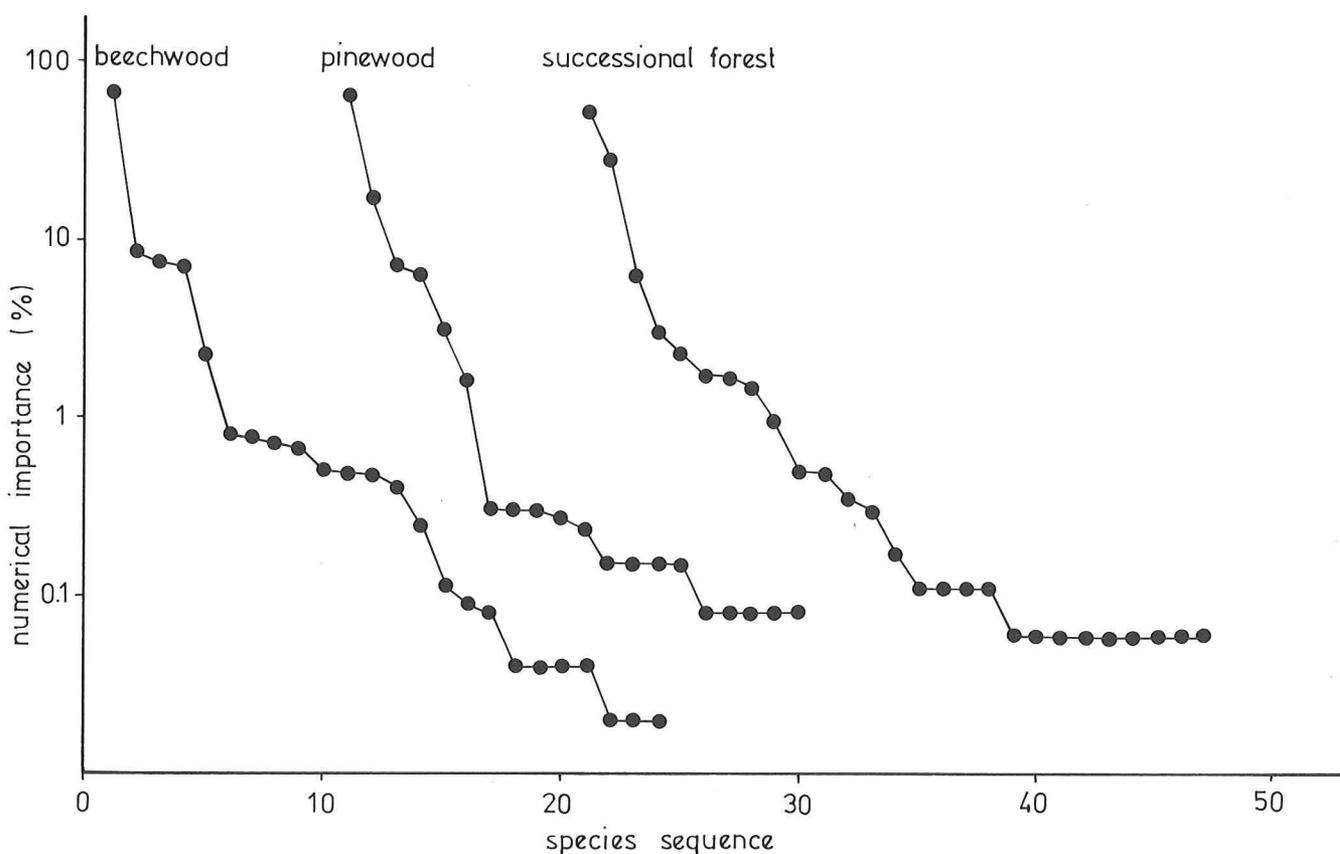


Fig. 1. Dominance-diversity curves for forest carabid communities in Lembeek. Points represent species, plotted by numerical importance (4-year catch in pitfalls, expressed as a percentage of the total catch for all species) against the species' rank in the sequence of species from most to least important. For the sake of graphic clarity, the curves have been spaced out by 10 units along the abscissa. See LOREAU (1984a) for a discussion on the adequacy of year-catch as a measure of the numerical importance of carabids in these communities.

competition exists within the dominant species, then it has also to exist in some way within and between the non-dominant species. But it must be too weak to have a predominant influence on their overall population dynamics. What distinguishes the dominant *A. ater* from most other species in the communities studied is its broader niche in all the significant dimensions, its quasi-homogeneous spatial distribution and its constancy from year to year. This species probably successfully escape the overwhelming influence of other factors because of its good adaptation to the environment. The other species are more specialized, have a more heterogeneous distribution and fluctuate more in time, and thus are probably each more subject to different local and immediate factors such as predation, availability of favourable microsites, availability of specific prey, etc. These are the conditions giving rise to a lognormal distribution, i.e. the interplay of many more or less independent factors. Competition is one of these factors, which is liable to play an important role more especially in one or a few dominant species.

Several arguments suggest that such a situation is not specific to the particular carabid communities studied, but is quite general. First, the hypothesis that niche space has a fixed volume which is split up between competing species, which is central to the causal models, is somehow contradictory to the very concept of the niche, which describes the specific way each species responds to the environment. Since different

species utilize different resources or the same resources in different ways, the niche space does not have rigid boundaries, and all its parts are not indifferently accessible to all species. Second, the causal models are based on a strict equilibrium view and do not incorporate the non-equilibrium phenomena which are more and more recognized in ecology (e.g. DE ANGELIS and WATERHOUSE 1987). Third, these models describe closed systems while the basic theories and facts of biogeography show that communities change continuously under the effects of extinction and colonization. Even in organisms where competition is particularly strong and widespread, like plants, it is to be expected that competition is severe among a certain number of dominant and intermediate species, but not among a lot of rare species. This is indeed what has been observed in some recent works (GRUBB 1986). What is liable to vary is probably not so much the basic model outlined here, as the number of species subject to significant competitive effects, depending on the type of organisms.

Community ecology has to integrate the deterministic and statistical aspects of reality more tightly instead of opposing them. The type of description of the structure of ecological communities depends on the field of vision one adopts, and it is very probable that a statistical description has to prevail when whole communities, including rare species, are considered, such as in species abundance patterns.

Table 1. Relative niche breadths of *A. ater* compared with the average breadths of the other species (95% confidence interval in parentheses) in the various niche dimensions and in the 3-dimensional niche space in the Lembeek beechwood.

	<i>A. ater</i>	other species
diet	0,51	0,32 (0,20 - 0,46)
annual activity	0,44	0,29 (0,23 - 0,36)
spatial distribution	0,99	0,75 (0,64 - 0,85)
3 dimensions together	0,22	0,07 (0,04 - 0,10)

From data in LOREAU (1984b). The relative niche breadth of species *i* is calculated as B_i/k , where B_i is LEVINS' (1968) niche breadth index and k is the number of resource categories. Niche breadth data were normalized using an angular transformation prior to the estimation of the 95% confidence intervals.

Table 2. Mean niche overlap of *A. ater* compared with the average mean overlap of the other species (95% confidence interval in parentheses) in the various niche dimensions and in the 3-dimensional niche space in the Lembeek beechwood.

	<i>A. ater</i>	other species
diet	0,48	0,27 (0,13 - 0,44)
annual activity	0,71	0,37 (0,29 - 0,46)
spatial distribution	1,02	0,82 (0,73 - 0,89)
3 dimensions together	0,30	0,09 (0,03 - 0,16)

From data in LOREAU (1984b). The mean niche overlap of species *i* on the other species is calculated as $\sum_{j=1}^{n-1} \alpha_{ij}/(n-1)$ where α_{ij} is LEVINS' (1968) niche overlap index and n is the number of species. The data of mean niche overlap were normalized using an angular transformation prior to the estimation of the 95% confidence intervals.

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