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Species abundance patterns and the structure of ground-beetle communities

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Various theoretical models have been put forward to describe and explain species abundance patterns in ecological communities. Causal models present these as a result of a competitive niche structure, while statistical models emphasize the interplay of many more or less independent factors. The theoretical premises of causal models are tested using data on niche and competitive relationships in ground beetles. The total 4-year catch in pitfalls was shown to be a good predictor of mean biomass, and was consequently used as a measure of the quantitative importance of species. The first premise of causal models, i.e. the quantitative importance of species should be closely correlated with their niche breadth, was found to be valid for the dominant species, but not for the other species. This was also the case for the second premise, i.e. dominance relations are governed by competition. A more unified view of community structure is discussed, which integrates both deterministic and statistical aspects of previous models.

1. Introduction

Biologists have long been intrigued by a prevalent pattern in nature. In most ecological communities, a few species proliferate while most others are more or less rare. Such differences in quantitative importance among the species in a community are found irrespective of the measure used, be it the number of individuals or measures like biomass and productivity, which are of greater ecological significance in the case of organisms with wide size differences (Whittaker 1965). The resulting patterns of species quantitative importance, usually referred to as "species abundance patterns", are often regular and similar among communities, even though these may have quite different species. Ecologists have sought to explain such patterns by some common underlying community structure and biological processes. Indeed, if such a universal structure and processes could be found, they could provide a powerful tool to help understand the diversity of communities, and thus such crucial aspects as their evolution or the effects of man's interventions.

Various mathematical distributions have been put forward to describe species abundance patterns, the most widely known and used being the geometric series (Motomura 1932), the logarithmic series (Fisher et al. 1943), the lognormal distribution (Preston 1948, 1962), and the broken-stick distribution (MacArthur 1957, 1960). Except for that of MacArthur, these distributions were elaborated more to fit empirical data than from theoretical premises regarding underlying ecological processes. But explanatory models were soon proposed for all of them (see Whittaker 1965, 1972; May 1975, 1981; Frontier 1985).

Curiously enough, these explanatory models are of two essentially contradictory types:

1) The first type is causal. All these models share the same basic assumptions: first, that the quantitative 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.
2) The second type of explanatory model 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, which generates a lognormal distribution (May 1975).

It was commonly accepted that the geometric and 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 (Whittaker 1965, 1972; May 1975, 1981).

This conventional view is no longer tenable today. On the one hand, it is known that all species abundance distributions can be generated by various stochastic processes (Cohen 1968; Caswell 1976; Engen, 1978). On the other hand, the lognormal distribution too can be generated by a causal model based on the same assumptions as the others (Sugihara 1980, 1989). Lastly, it is possible to make the lognormal curve reasonably fit most species abundance distributions from the near-geometric to the broken-stick form by varying the values of the parameters (Whittaker 1972; Taylor 1978; Frontier 1985). As a result, new approaches are now emerging (e.g., Kolasa 1989).

Most ecologists have discussed the usefulness of the various distributions and models from the viewpoint of their ability to fit data. Although this clearly is of interest for descriptive and comparative purposes, it is essential to go to the root of the problem, that is, to test the validity of the premises of the explanatory models. Surprising as it is, there have been very few attempts at doing so. There are two ways to achieve this goal. One is to compile data from a great number of communities but with a low definition of the species' niches, e.g. by considering only spatial distributions (Kolasa 1989). Another is to focus on a few communities, but with thorough data on niche and competitive relationships. I shall here adopt the latter approach and analyse detailed data from a few forest ground-beetle communities (Coleoptera, Carabidae).

My objectives will be threefold:

1) first, to provide evidence for the use of pitfall catches as a measure of a species' quantitative importance in a community;
2) to synthesize scattered data from my own field studies to test the premises of the causal models;
3) lastly, to argue for a more unified view of community structure.

The first objective is prerequisite because of the considerable controversy over the usefulness of pitfall-catch data. Baars (1979) showed that the total year-catch in pitfalls is approximately proportional to population density when different populations of the same species are compared, but this proportionality does not hold when different species are compared, because a wide array of factors influences each species' catch efficiency (Luff 1975; Adis 1979). Other authors (Schaefer 1971; Thiele 1977; Loreau 1984a) have argued that pitfall catch in fact provides a more meaningful measure of a species' ecological importance than does population density, because it also integrates body mass and time of activity. Since these arguments have been widely ignored (e.g. den Boer 1986, 1989), it is necessary to provide evidence for the use of pitfall catches as a measure of a species' ecological importance before using them as such.

2. Study sites and methods

Three forest sites were studied in Lembeek (Belgium): a near-climax beech forest, a pine plantation, and a young successional forest with a highly diversified vegetation (described in Loreau 1984a). Adult carabids were sampled continuously from 1978 to 1981 using pitfall traps (Loreau 1984a). Population density and biomass of the most abundant species in the beech forest were estimated independently by capture-recapture methods during 10 periods from May 1978 to October 1981. During each period, enclosures were set up; carabids were captured on several occasions using pitfall traps within the enclosures and marked individually; population density was estimated by both the Lincoln-Chapman index and the Leslie-Davis catch-effort method; and biomass was estimated as the product of population density and the mean individual fresh mass (Loreau 1984c).

Table 1. Species composition and total 4-year pitfall catches in the three forest ground-beetle communities (beech forest, pine plantation, successional forest). Data from Loreau 1984a.

	Beech	Pine	Succ.
Abax ater	1694 [ab]	832 [b]	901 [c]
Pterostichus oblongopunctatus	217 [ab]	4	
Cychrus attenuatus	195 [ab]	21 [b]	1
Carabus problematicus	178 [ab]	222 [b]	25 [c]
Leistus rufomarginatus	55 [ab]	82 [b]	
Nebria brevicollis	21 [ab]		
Abax parallelus	20 [ab]	3	
Trichotichnus laevicollis	18 [b]	4	29 [c]
Asaphidion flavipes	16 [b]	4	1
Carabus purpurascens	13 [c]		
Notiophilus biguttatus	12 [b]	91 [b]	1
Badister bipustulatus	11 [ac]	2	1
Lorocera pilicornis	10 [b]	40 [b]	16 [c]
Pterostichus madidus	1	4	490 [c]
Harpalus latus		1	110 [c]
Amara lunicollis			52 [c]
Bradycellus collaris			39 [c]
Trechus obtusus	6	1	30 [c]
Bembidion lampros	3	1	8 [c]
Leistus ferrugineus			8 [c]
Others (number of species)	9 (8)	8 (5)	27 (12)

[a] species included in the analysis of biomass-catch correlation (Fig. 1).

[b] species for which the full 3-dimensional niche analysis was carried out (Figs. 2 and 3, Table 2).

[c] species for which only 2 niche dimensions were analysed (annual activity and spatial distribution; Fig. 2, Table 2).

Six niche components were investigated, which represent all the major potential dimensions of resource partitioning in forest ground beetles (Loreau 1984b, 1987):

1) type and
2) size of prey eaten, by examination of the digestive-tract content and laboratory experiments on feeding preferences;
3) annual activity pattern, using pitfall traps;
4) daily activity rhythm, using live traps;
5) horizontal spatial distribution of activity, using pitfall traps;
6) vertical distribution of activity, using traps with windows open at various depths.

Niche breadth and overlap were computed for each niche dimension using Levins's (1968) indices. The relative niche breadth of species i was calculated as B_i/k, where B_i is Levins's absolute niche breadth index and k is the number of resource categories. The mean niche overlap of species i on the other species was calculated as

$$\sum_{j \neq i} a_{ij} / (n - 1),$$

where a_{ij} is Levins's niche overlap index and n is the number of species.

3. Results

The main species in the communities studied and their total catches in pitfalls are listed in Table 1.

3.1. Pitfall catches as a measure of a species' quantitative importance

Since biomass was here estimated at each period for the whole active carabid population, the mean biomass over all periods integrates biomass and time of activity and can thus be regarded as a good measure of a species' quantitative importance from an ecological standpoint.

Mean biomass is plotted in Fig. 1 against the total 4-year catch for the most abundant me-

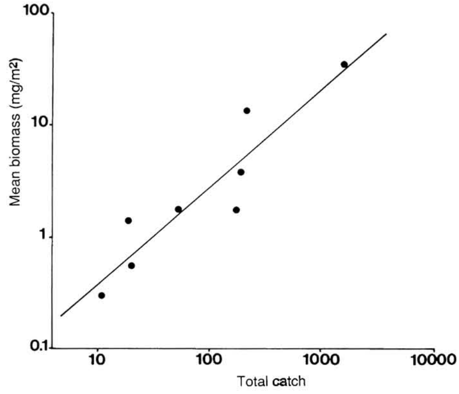

Fig. 1. Mean biomass plotted against total catch in pitfalls (log scales). Results from the 4 years 1978–1981 for 8 medium- and large-sized carabid species in the climax beech forest, and regression line fitted by the least squares method. Pitfall-catch data from Loreau (1984a), and mean biomass from biomass data in Loreau (1984c). See Table 1 for species names.

dium- and large-sized carabid species (> 6 mm) in the beech forest. There is a very good correlation between mean biomass and total catch on a log-log scale ($r = 0.926$, 6 *df*, $P < 0.001$), as compared with the poor correlation between mean density and total catch (log-log scale, $r = 0.537$, 6 *df*, $P > 0.05$). Moreover, the slope of the regression line in Fig. 1 is close to 1 (0.865, 95% confidence interval: 0.513–1.217). Thus total catch in pitfalls is a good predictor of mean biomass, and hence of the quantitative importance of species. This is true at least for the medium- and large-sized, predominantly nocturnal species which prevail in most forests. Note, however, that the correlation might be poorer if small diurnal species were included, because these might be better able to avoid traps.

In the remainder of the paper, I shall accordingly use total catch as a measure of a species' quantitative importance.

3.2. Test of the premises of causal models

Forest carabid communities are relatively small and homogeneous: they comprise a few tens of species (Table 1), most of which are predatory on primary consumers, active at the surface of the litter, and nocturnal (Loreau 1984b, 1987).

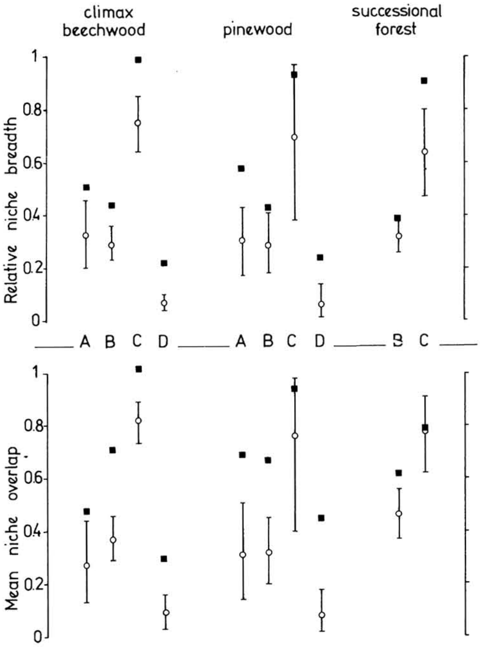

Fig. 2. Relative niche breadth and mean niche overlap of the dominant *Abax ater* (filled squares) and average relative breadth and mean overlap of the other species (open circles, with 95% confidence interval) in the major niche dimensions in the three forest ground-beetle communities. A = type of prey; B = annual activity; C = spatial distribution; D = 3 dimensions together. The data (from Loreau 1984b) were normalized using an angular transformation prior to the estimation of the 95% confidence intervals. Data on the type of prey eaten are missing for the successional forest. See Table 1 for the species included in this analysis.

Their patterns of species quantitative importance are typically distributed as in a logarithmic series, or even a geometric series among dominant species (Table 1, Loreau 1984a). According to the conventional view, this might indicate hierarchical competitive relations obeying a rule of pre-emption of the niche space by the successive dominant species (Whittaker 1972).

The first premise of the causal models is "that the fraction of environmental resources utilized and the fraction of total community production realized by the species will be closely related to (though not identical with) the fraction of niche space occupied" (Whittaker 1965:254). In other words, the quantitative importance of species should be positively correlated with their niche breadth.

Among the six niche dimensions investigated, the three most discriminating ones were found to be type of prey eaten, annual activity cycle and within-habitat spatial distribution of activity; they were also roughly independent, which allowed estimation of 3-dimensional niche parameters (Loreau 1984b). In all these major niche dimensions, the first premise is met by the dominant species (Fig. 2): the niche breadth of *Abax ater*, which is clearly dominant in the communities investigated, is significantly greater than the average niche breadth of the other species in the climax forest, and generally so in the other forests as well. Furthermore, it occupies a central position in the niche structure. An indication of the central position of a species' niche is given by its mean overlap of the other species' niches, since a central niche is likely to overlap more other niches. *A. ater* has a mean niche overlap that is significantly greater than the average of the other species in all the dimensions in the climax forest, and in the other forests as well except for spatial distribution. This conforms to one of Whittaker's (1965) models of community structure.

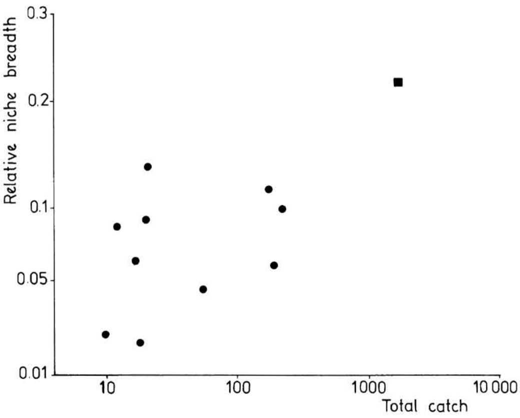

Fig. 3. Correlations between 3-dimensional relative niche breadth (angular scale) and quantitative importance (total 4-year catch, log scale) of species in the beech forest. The correlation is significant when the dominant species (square) is included, but is not significant when it is excluded.

Table 2. Correlations, with significance levels and degrees of freedom, between niche breadth and quantitative importance (total 4-year catch) of species in the major niche dimensions in the three forest ground-beetle communities, with and without the dominant *A. ater*.

	with			without		
Beech forest						
type of prey	0.263	ns	9	0.080	ns	8
annual activity	0.458	ns	11	0.358	ns	10
spatial distribution	0.687	*	11	0.511	ns	10
all 3 together	0.653	*	9	0.338	ns	8
Pine plantation						
type of prey	0.982	***	4	0.961	**	3
annual activity	0.618	ns	4	0.356	ns	3
spatial distribution	0.680	ns	4	0.639	ns	3
all 3 together	0.900	*	4	0.767	ns	3
Successional forest						
annual activity	0.553	ns	9	0.534	ns	8
spatial distribution	0.449	ns	9	0.281	ns	8

Pitfall-catch data (from Loreau 1984a) were log-transformed, and niche breadth data (from Loreau 1984b) were angular-transformed. Significance levels: ns = not significant ($P > 0.05$); * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. See Table 1 for the species included in this analysis.

On the other hand, this agreement with the first basic assumption of causal models cannot be extrapolated to the community as a whole. Although there are some overall correlations between niche breadth and quantitative importance, they tend to vanish and lose their statistical significance when the dominant species is excluded, except in one case (Table 2 and Fig. 3). This lack of significance might be due to the relatively low number of degrees of freedom, but the data do not support this interpretation since overall the correlations do not increase with increased numbers of degrees of freedom.

The second premise of causal models is that dominance relations are governed by competition. I tested this premise in a field experiment in the climax beech forest. This experiment is reported elsewhere (Loreau 1990). In brief, it provided some evidence for competitive regulation in the dominant *A. ater* through density convergence of several experimental populations, but provided no evidence for competition within or among the other species. Furthermore, the most abundant of them, *Pterostichus oblongopunctatus*, was apparently in non-equilibrium conditions. It thus seems that competition is not the principal factor governing population dynamics in species other than the dominant.

4. Discussion

In the ground-beetle communities studied, the two premises of the causal models of community structure were both confirmed for the dominant species, but are at best insufficient for the other species. It is thus obvious that they cannot account for the whole species abundance pattern in a community, and that an alternative theoretical framework is needed. The essence of this new framework must derive from the recognition that competition does not affect all species equally. In the communities studied, the dominant *A. ater* seems to escape the overwhelming influence of other factors because of its especially good adaptation to the overall environment (Loreau 1984b). 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. I have suggested accordingly that competition plays an important role in one or a few dominant species in a community, while the abundance of most species is determined by the interplay of many more or less independent factors (Loreau 1990). Note that these are the conditions underlying the statistical view of species abundance patterns (May 1975). Therefore even relatively homogeneous communities should not depart from the statistical conditions giving rise to a lognormal distribution of species abundances, or to its small-sample approximation, the logarithmic series (Taylor 1978).

This hypothesis reconciles the conflicting deterministic and statistical views of species abundance patterns as two views pertaining to different scales: on the scale of the few dominant species, the deterministic influence of competition may prevail, while on the scale of the community as a whole, the description of the pattern has to become essentially statistical. This hypothesis and also the results presented above are consistent with aspects of the core and satellite species hypothesis of Hanski (1982), the theoretical views articulated by Brown (1984), and in part the model of Kolasa (1989) with regard to the presence of breaks in community structure. These theories, however, have a spatial dimension that is beyond the scope of the present study, because my focus here was on the structure and processes acting within a community, i.e. on niche relationships strictly speaking (Whittaker et al. 1973).

To what extent can this hypothesis be generalized? It is generally admitted that insects and other arthropods as a rule show fewer competitive effects and regularities than other organisms because of their relatively small size, their moderate life span and their intermediate position in trophic chains (Hutchinson 1961, Connell 1983, Schoener 1983, 1986). These factors should affect ground beetles less than most other insects, because carabids are among the largest and longest-living insects, and among the most important predators of the soil fauna in temperate regions. However, there is little doubt that competition is stronger and more widespread, for instance, in large organisms competing for space, like plants and terrestrial vertebrates. Nevertheless, several lines of argument suggest that the view presented here is quite general and should apply to communities of such organisms as well.

First, the hypothesis that niche space has a fixed volume that 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 (Whittaker et al. 1973). 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 describe closed systems, while the basic theories and facts of biogeography show that communities change continuously under the effects of extinction and colonization. Regional processes can profoundly influence local diversity, especially among rare species (Ricklefs 1987). Third, these models are based on a strict equilibrium view (MacArthur 1960) and do not incorporate non-equilibrium phenomena, which are receiving increasing recognition in ecology (DeAngelis and Waterhouse 1987). It is quite likely that dominant species in climax communities will more often approach equilibrium conditions, while many less abundant species will be in non-equilibrium conditions and thus weakly or episodically affected by competitive interactions, as suggested by several authors (Caswell 1978, Hanski 1982). This is indeed what has been observed in some recent work on plants (Grubb 1986). Therefore, what is liable to vary among communities is perhaps not so much the basic model outlined here, as the size of the group of dominant species subject to significant competition, depending on the type of organisms and the type of biotopes. This number might vary from zero in the case of organisms suffering heavy predation in strongly disturbed environments to many in the case of large sessile or territorial organisms in stable environments.

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