

## Scales of variation: their distinction and ecological importance

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This paper, with field data on ground beetles, describes results of various analyses performed at different spatio-temporal scales of resolution to indicate that different phenomena emerge at each of these scales. First, spatial distribution patterns are described, beginning at a fine, local scale of a 40 ha Dutch polder meadow and ending at the geographical range structure of carabids. Similarly, description of temporal variation in species occurrence starts with seasonal variation and ends with a geological scale covering millions of years. As part of the temporal variation concerns factors determining dietary composition, the ecological implications of variation at different scales are considered in the context of optimal foraging.

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### 1. Introduction

Robinson (1956) considered variation of ecological processes at various spatio-temporal scales the “ecological fallacy”, meaning that sampling different scales gives different and often uncomparable results. The difficulties this gives are twofold. (1) Finding a particular process at one level, usually predicts little about processes at other levels, if at all. Much confusion may therefore result from unjustified generalizations. For example, although local dispersion may be explained by differences in soil type, ground-water level, or competition, their effects should not be generalized to another scale to explain the species' range location or size, which may, for example, be temperature dependent. Conversely, temperature may, among other factors influence the level of local fluctuation, but the pattern of fluctuation may be determined by, say, fluctuations in ground-water level. (2) Models describing interference between species, be they competitors, predators and their prey, or hosts and parasites, should account for their specific, scale-dependent responses to factors external to the system concerned. For example, predator abundance not only depends on prey availability and this, in turn, on predation pressure, but also on species-specific responses to temperature or humidity.

One aspect of the specificness of these responses concerns the species' sensitivity to the scale of variation of the factor concerned, which will differ between a great tit as a predator and a caterpillar as its prey. The specificity of responses to external factors thus easily upsets the species' numerical responses relative to each other as expected from model systems, and hence their supposed mutual dependence, or the community structure in general. Therefore, considerations of scale concern two aspects, one methodological (1), and the other the biological system itself (2), which I call the level of resolution and the scale of variation, respectively.

The present paper describes, for ground beetles, phenomena found at several spatial and temporal levels of resolution, as well as effects of variation at different scales on the co-occurrence or co-adaptation of species. First, several spatial levels are considered, ranging from a local field of 40 ha to that of the range structure. Second, several temporal resolution levels are considered, starting from a within-year level to that covering hundreds of millions of years.

Yet, the processes detected that vary on different levels of resolution may have biological implications. One example, putting long-term variation, the determination of the species' dietary composition, into the context of short-term optimum-foraging models, illustrates that the assumptions that these models make

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2	5	3	.	.	.	.	.	.	.	.	.
33	21	29	16	7	2	.	.	.	5	.	.
29	8	9	19	10	1	2	.	.	1	.	.
57	13	12	22	16	47	9	1	.	.	.	.
6	45	10	35	40	24	64	4	1	.	.	.
37	44	27	34	66	63	60	16	4	.	.	.
13	17	28	44	55	57	86	27	11	.	.	.
8	17	47	30	46	52	75	11	2	.	.	.
18	23	10	12	11	49	110	26	11	.	.	.
4	1	4	6	16	19	58	13	19	.	.	.
1	.	8	2	7	6	31	11	1	4	.	.
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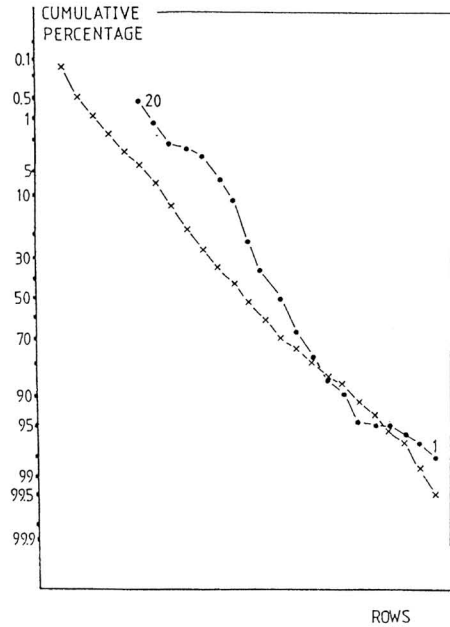


Fig. 1a. — a: Numbers of *Dyschirius globosus* caught during 1976 in a 800 x 500 m<sup>2</sup> meadow in the Dutch inland polder Oostelijk Flevoland. For an explanation see the text. — b: Cumulative percentage of numbers of *Dyschirius globosus* plotted on normal probability paper. The continuous line represents the numbers in the rows in Fig. 1a; the dashed line the numbers in columns perpendicular to the main trend in the distribution pattern at an angle of 45° relative to the original columns.

relate to the wrong temporal scale. As optimal-foraging models are part of a complex of theories collectively known as the “balance of nature” and pertain to processes operating on fine scales (Hengeveld 1986), explanations in terms of long-term variation thus contradict current ideas of balanced, equilibrium species compositions.

To illustrate scale-dependent variation, I mainly draw on material I have collected myself as examples. Other examples can be found in Dayton & Tegner (1984) for marine ecology, Harris (1980) and Reynolds (1984) for freshwater ecology, Delcourt et al. (1983) and Birks (1986) for palynology, Wiens (e.g. 1981) for ornithology, chapters in Diamond & Case (1986) for community ecology, or Hengeveld (1982) for ecology in general. Most of these examples discuss the methodological aspects of analysis and representativity of levels of resolution only, rather than concentrate on consequences to the species concerned, which I stress here.

## 2. Levels of resolution

### 2.1. Spatial variation

Fig. 1a shows the distribution of *Dyschirius globosus* in a 40 ha meadow during 1976 (Hengeveld 1979, Kooijman & Hengeveld 1979). Its highest densities occur at the edge of a sand layer in one corner of the field on top of clay, which is uniform throughout the field. Artesian water from underneath the sand forms a gradient in both directions from the edge, determining the beetle’s local density. This density is distributed like a Gaussian distribution at right angles to the sand edge (Fig. 1b) and is stable within the year. The highest numbers of another species, *Pterostichus versicolor* (= *P. coerulescens*), occur in the clay part of the field, particularly in the left bottom corner of Fig. 1a. Its dispersion over the field, however, varies seasonally; the young, callow

beetles prevail in this corner, suggesting that this is the main area of reproduction for this species, to which the population contracts before reproduction and after which it extends over the field again (Hengeveld 1979). A third species, *Trechus obtusus*, is more uniformly distributed, but seems even more dynamic, both within and between years. Moreover, the two wing forms, macropters and brachypters, as well as the sexes, show independent dynamic behaviour, apparently responding differently to the same ecological factors (Hengeveld, in prep.).

Thus, these three species are distributed differently over this field, and respond individually to local factors and in their dynamism through time, a feature of the species analysed (Hengeveld 1979, Kooijman & Hengeveld 1979). Their response to environmental factors, expressed by their local distribution, can be described using the Gaussian distribution as a model.

The model used for describing the beetle's non-linear response to environmental factors assumed a Poisson-distributed error. This means that within the scale of the 252 individual sampling sites of the 21 x 12 grid system, the beetles were assumed to move randomly rather than according to some finer-scale environmental factor. But when the numbers of beetles caught in each of the five pitfall traps constituting a sampling site are averaged and these averages plotted against within-site variance, the scatter does not follow a linear 45° line characteristic of Poisson-distributed data, but bends upwards (unpublished data), similar to Taylor et al.'s (1978) findings. This indicates that at low densities the beetles are randomly distributed, but cluster at high densities. This, in turn, implies that finer-scale, within-site variation is heterogeneous, indicating a response to the same or another environmental factor operating at that scale as well.

Extending the spatial scale, the distribution patterns of all polder immigrants were analysed, using principal components analysis (Haecck et al. 1980). In an earlier study, Haecck (1971) reported that these immigrants represent a subset of the total Dutch carabid fauna, consisting of macropters and wing-dimorphic species only. Later studies suggested that brachypterous species did not occur in those polders surrounded by water and that the brachypterous individuals of wing-dimorphic species, which did not occur, may be offspring of winged parents. Contrary to plants (Nip et al. 1977), carabid distribution within the polders is determined by habitat factors, flying beetles apparently being able to find their preferred

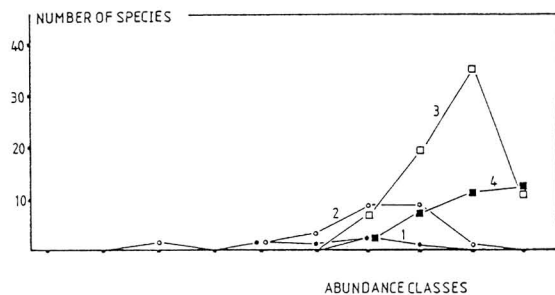


Fig. 2. Numbers of immigrant species in the Dutch inland polders in logarithmic abundance classes and divided into four geographical categories. Category 1 comprises geographically marginal species in the Netherlands, category 4 geographically central species, and categories 2 and 3 species of intermediate relative range locations.

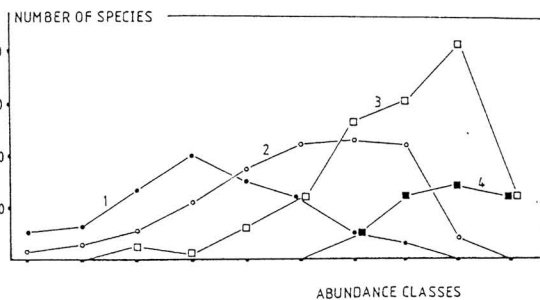


Fig. 3. The same as Fig. 2, for all of the Netherlands.

habitats easily. Moreover, on a national scale, brachypters prevail in the drier, eastern parts of the Netherlands, whereas macropters are common in the lower, wetter parts in the west. Preference for wet habitats as a factor apparent on a broad spatial scale, may also determine a beetle's colonization chance.

Apart from dispersal capacity, the species' general intensity of occurrence in the Netherlands adds to the probability of them colonizing the new area. This intensity, in turn, depends on the location of the Netherlands relative to that of the species' geographical distribution. Fig. 2 shows that species occurring in the Netherlands only at or near their range margins are underrepresented relative to those occurring near or at their range centres. This underrepresentation may be the result of various intensity components, such as the general level of occurrence in the Netherlands, or the number of habitats preferred. These and other parameters are described in more general papers on range structure (Hengeveld &

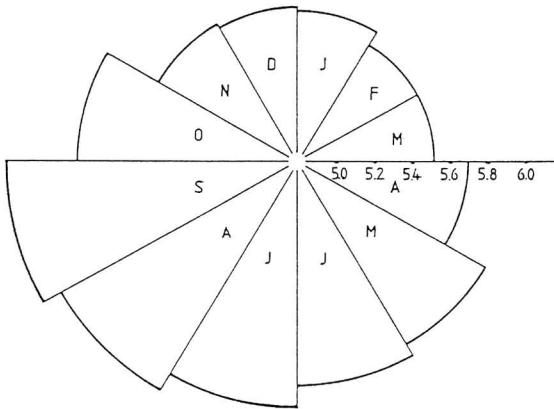


Fig. 4. Monthly geometric mean body size in mm of ground beetle immigrants in the Dutch inland polders.

Haeck 1981, 1982). For carabids and other taxa, several ecological parameters comprise the general concept of a species' intensity of occurrence reaching its highest values in the range centre and decreasing towards the margins. This trend determines both national and local density levels as one of the intensity components (Fig. 3). Thus, even in their so-called preferred habitats, carabids fluctuate statistically at lower mean levels at their range margins than in more central areas.

Range size and location, in turn, seem to be determined by geographical factors, the latter of which also determines where a species occurs within the Netherlands. Hengeveld & Hogeweg (1979) performed two cluster analyses for Dutch species, one on a national scale and one on a European scale. Clusters of both correlate, implying that Dutch clusters comprise geographical elements of broader-scale geographical variation extending over at least Europe, Africa north of the Sahara, and the western part of the Middle East. This correlation is most clearly explained ecologically.

## 2.2 Temporal variation

Fig. 4 shows the seasonal variation in mean body size for carabid immigrant species in the Dutch inland polders (Haeck & Hengeveld, 1974). On average, beetle size is smaller in winter, increasing gradually until September, after which it decreases again. This trend may be explained ecologically and confirms Mossakowski's (1970) findings that larger species

preferentially occur in drier habitats and smaller ones in both dry and wet ones. On average, species in the west of the Netherlands are smaller than those in the drier, eastern parts (Haeck & Hengeveld 1974).

At the broader scale of decadal variation during the present century, two types of variation can be distinguished, that of particular species groups and that of species per se (Hengeveld 1985b). The first type shows that species with different preferences for temperature and humidity, for different habitats, and belonging to different geographical elements, fluctuate independently of each other. Two trends are superimposed, a long-term one, covering the whole period investigated from the end of the last century to the mid-1970s (axis II), and a short-term one from the mid-1930s to the 1950s (axis III). (N.B. Axis I contains the variance due to interspecific variation in relative species abundances.) The points in a decade-to-decade comparison are aligned to both trends (Fig. 5); the first shows up from an almost perfect sequence of nine decades along axis II. The second trend shows up from the first and last few points lying below and the intermediate points above this axis. The first trend represents one from drier to more humid conditions, as suggested by the moisture and habitat preferences of species in the species-to-species comparison and from a gradual rise in annual precipitation over this period. The last two decades are inverted, according to the faunistic composition and to climatic conditions. The second trend represents one in temperature, as the climate of the 1930s, 1940s, and 1950s was more continental than the decades before and after. During this period southern species, preferring warm and dry conditions, prevailed and species of wet, northern conditions declined. This accords with the faunal elements Hengeveld & Hogeweg (1979) described for the European distributions. It also agrees with broad ecological characteristics of the genera to which the species belong. The second, broader type of variation, concerning the species per se independent of their taxonomic identity or eco-physiological or geographical characteristics, indicated that this variation is random (Fig. 6). This follows from the fact that their distribution in the two-dimensional factor-space (II, III) approaches normality.

## 2.3. Conclusion

These examples of variation showing up at various levels of resolution, suggest that species' co-

Fig. 5. Generalized results of the species-to-species comparison of the faunal composition of Dutch ground beetle species during the nine decades 1890–1975. The inserted graphs show the trends over those decades by species in the part of the scatter concerned. The species' eco-physiology, habitat preferences, and geographical range locality are also indicated. The points represent the decadal composition of the Dutch beetle fauna of 365 species. Point 1 represents the decade 1890–1900 and point 9 that of 1970–1975. Above axis II lie the points representing the warm 1930s, 1940s, and 1950s, below it the cooler decades among which that of the cold 1920s (point 3).

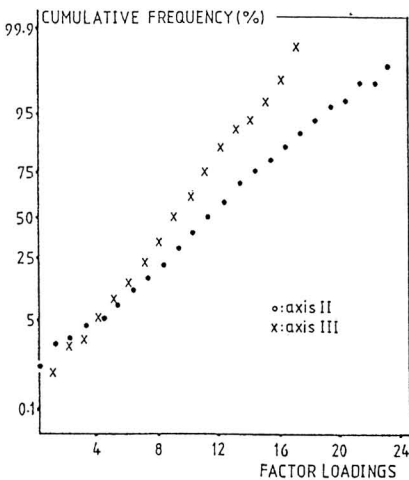
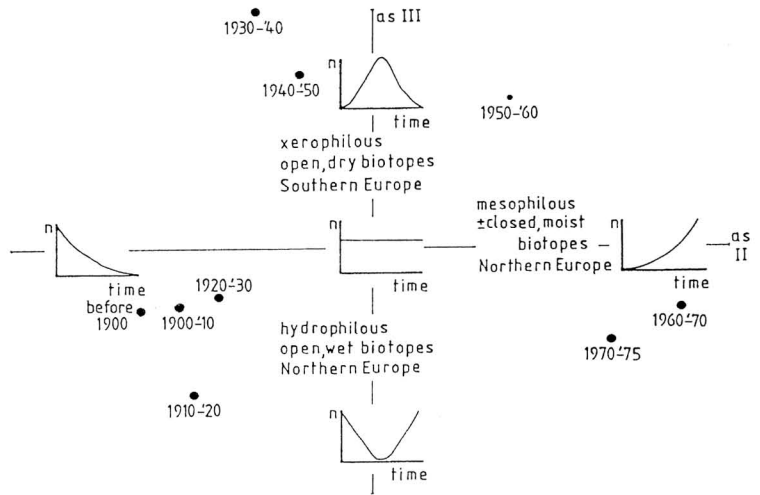


Fig. 6. Cumulative number of species along axes II and III plotted on normal probability paper.

adaptations cannot be expected to occur in carabid beetles, neither among each other, nor between them and species of other taxa. They show individualistic behaviour in space and time, as well as with regard to abiotic factors as far as these are known. This behaviour, moreover, pertains to variation at the various levels separately and among these levels. Their ecological responses and rates of spatial adaptation vary independently, rather than according to clusters of shared species properties. This is significant when interpreting ecosystems or biogeographic provinces as natural, coherent units.

### 3. Ecological implications

The implication of species varying on several spatio-temporal scales and responding to factors that operate on those scales is that they behave individually and do not form stable, persisting ecosystems or communities. The species in an assemblage are neither qualitatively, nor quantitatively co-adapted to each other. Variation in dietary composition in carabid species and its underlying morphology substantiates this first aspect, namely that within the short time-scales of spatially heterogeneous faunal variation as described above, species cannot possibly adapt new feeding strategies because of the intricacy of the complex of the many properties involved. First, I will show short-term variation in dietary composition among three ecologically related species, of which two are also taxonomically close. Then I discuss the dietary composition of 24 species, together with properties related to feeding and digestion. This should be viewed from the concept of optimal-foraging models, describing qualitative species adaptations in terms of competition for food.

Comparing three ground beetle species, *Pterostichus versicolor*, *P. lepidus*, and *Calathus erratus*, in the Netherlands all living on heathland, Hengeveld (1985a) found that their dietary composition varies both within and between the six years investigated. Competition cannot allow for dietary composition, rather, temporal variation in prey fauna explains the differences between these species. Nor can differences in dietary composition be ascribed to optimal foraging, as this difference is externally imposed by the changing faunal composition.

Comparing the dietary composition of 24 species, but not allowing for temporal variation, Hengeveld (1980a, 1980b, 1980c, 1981) showed that these species can be divided into two main groups, feeding specialists and generalists. These clusters coincide with two subfamilies within the Carabidae, the Carabinae and the Harpalinae, respectively. The first of these taxa can be subdivided again into those eating snails, worms and caterpillars, the Carabini and Cychrini, and the remainder, specializing on the microfauna of collembolids, mites, etc. (cf. also Forsythe 1983b). Coincidence of the dietary composition of adult beetles and even their larvae (Ishikawa 1973) with taxonomic classification suggests a long-term, phylogenetic background of feeding habits rather than short-term adaptation to changeable community compositions, particularly when competition cannot be shown in the three species mentioned. To the contrary, classificatory relationships may, in part, represent a complex of co-adapted properties related to feeding with a long phylogenetic history. Then, evolutionary rates may not be as high as is assumed for community adaptations through optimal foraging, but low because of the complexity of the required reconstruction of behavioural, morphological, anatomical, physiological, and ontogenetic traits, apart from purely ecological ones, such as habitat preference, or diurnal versus nocturnal activity for hunting.

These suspicions are fully substantiated by recent eco-morphological work mainly by Bauer (1971, 1974, 1975, 1981, 1982; Bauer & Bath, 1974; Bauer et al. 1977) and Evans and Forsythe (Evans 1977, 1980, 1982, Forsythe 1983a, 1983b; Evans & Forsythe 1984, 1985). For example, allowing for a different choice of prey to be made, the animal should be able to detect it in another way, requiring particular eyes with a certain resolution or other sense-organs. Then it has to chase it, necessitating certain types of locomotion adapted to pushing its body into snails, or into small crevices, to digging, running, jerking, or to climbing trees. Having caught its prey, special adaptations are needed for chewing and devouring it, which sometimes involves external digestion of soft-bodied prey or sieving out hard particles, or grinding or cutting hard, chitinous exo-skeletons. Finally, the digestive system differs for different food particles, the proventriculus being a masticating or a sieving organ, etc. (e.g. Forsythe 1983, Reichenbach-Klincke 1938). But the animal not only needs eyes, a feeding apparatus, legs or thickness and hairiness of its proventriculus, but more basically,

also a certain musculature, innervation, and digestive juices produced by specialized glands.

As the construction of highly complex, co-adapted structures requires time, simple mathematical optimum-foraging models, assuming population stability and compositional community persistence, fail, at least for the mentally limited carabids with an highly intricate and specialized feeding and digestive apparatus. Distribution patterns of carabids as predators and those of their prey are simply too dynamic for radical or even small reconstructions of the body-plan to be made in a short period of time. Evans' (1982) phylogenetic reconstruction, tracing the origin of various taxa back to the Early Triassic, though involving a process covering several hundreds of millions of years, seems more plausible from a biological viewpoint. On the other hand, however specialized they are as a result, present-day carabids have to be sufficiently flexible to accept different kinds of prey in environments varying for short periods of time or shift their range to other continental regions within relatively short times such as Coope (1975) described. Studying a carabid species' diet, therefore, involves adaptations on different time-scales, among which the long-term ones may be the most significant and restrictive.

#### 4. Conclusions

Most present-day ecological models concern different aspects of a more basic theory, that of the "balance of nature"; they pertain to demographic parameters and assume that populations mutually keep their numbers in equilibrium in climatically constant and uniform environments. Furthermore, communities would be compositionally persistent, the composite species being stable and mutually co-adapted (e.g. Hengeveld 1986, Simberloff 1980). Demographic disequilibria would be short-lived, being adjusted by various community mechanisms operating on the same spatio-temporal scale of the factor that caused the disturbance.

But varying the level of resolution of our analyses shows responses to different and possibly interfering factors, varying on many scales. Thus, disturbances by factors operating on one scale usually cannot easily be compensated for by those operating on other ones, if at all. Moreover, as Davis (1986) emphasized, environmental conditions, particularly temperature viewed on various time-scales up to 100 000 years, do not remain the same, but show trends.



Superimposed on each trend are those on smaller scales, recognized as fluctuations or noise. This means that during the Pleistocene, populations can only be in equilibrium on a scale of 100 000 years. But to be sure, even the couple of million of Pleistocene years are but a phase in a general cooling trend since the Cretaceous (cf. Frakes 1979), the period of origin of the main carabid taxa and hence of the constraints put on their feeding flexibility as a significant demographic and community parameter. Moreover, temporal temperature trends are usually spatially differentiated on various scales as well and differ in both ways from trends in precipitation. Finally, within this spatio-temporal framework, species responses are randomly distributed, at least at the scale of the last nine decades in Europe.

The significance of analysing taxa on various levels of resolution, therefore, is that they put local and short-term phenomena into perspective. This perspective may give another attitude towards population stability and species co-adaptations within ecological communities. Methodologically, this means that observations at one scale cannot be generalized without testing. Biologically it means that species-specific qualitative or quantitative co-adaptations cannot be expected to occur when species respond to factors varying on different scales, or when their response time is too long to attain the fine-scale pattern required. Both aspects require investigations to be made, covering several scales of both time and space.

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