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Dynamics of regional distribution: the core and satellite species hypothesis

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A new concept is introduced to analyse species' regional distributions and to relate the pattern of distributions to niche relations. Several sets of data indicate that average local abundance is positively correlated with regional distribution, i.e. the fraction of patchily distributed population sites occupied by the species. This observation is not consistent with the assumptions of a model of regional distribution introduced by Levins. A corrected model is now presented, in which the probability of local extinction is a decreasing function of distribution, and a stochastic version of the new model is analysed. If stochastic variation in the rates of local extinction and/or colonization is sufficiently large, species tend to fall into two distinct types, termed the "core" and the "satellite" species. The former are regionally common and locally abundant, and relatively well spaced-out in niche space, while opposite attributes characterize satellite species. This dichotomy, if it exists, provides null hypotheses to test theories about community structure, and it may help to construct better structured theories. Testing the core-satellite hypothesis and its connection to the r-K theory and to Raunkiaer's "law of frequency" are discussed.

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Предлагается новая концепция для анализа регионального распределения видов и для сравнения характера распределения с соотношением ниш. Несколько серий данных показали, что величина средней локальной численности положительно коррелирует с региональным распространением, то есть с относительным количеством мозаично расположенных видовых стаций, занятых данным видом. Это наблюдение не соотвествует модели регионального распределения, предложенной Левинсом. Здесь предлагается исправленная модель, в которой обсуждается вероятность локального исчезновения вида, как уменьшающаяся функция распространения и стохастическая версия новой модели. Если стохастические колебания скоростей локального исчезновения и/или колонизации достаточно велики, проявляется тенденция разделения видов на два четких типа, называемых "основным" и "сателлитным". Первые обычны в своем регионе, локально многочисленны, а сателлитные виды характеризуются противоположными признаками. Эта дихотомия если она существует, позволяет использовать нуль-гипотезу для проверки теории структуры сообщества и она может помочь в создании более совершенной теории. Обсуждаются результаты проверки гипотезы "основных-сателлитных" видов и ее связи с r-K теорией и биологическими спектрами Раункиера.

1. Introduction

It has been popular to define ecology as the study of abundance and distribution of organisms (e.g. Andrewartha and Birch 1954, Krebs 1972), to the extent that MacArthur and Wilson (1967) state there is no real distinction between ecology and biogeography. For the purposes of this paper, I define *abundance* as the number of individuals at a local population site (for other definitions see Hengeveld 1979). There are good reasons to express abundance as a fraction of the possible maximum numbers sustainable at the site (Andrewartha and Birch 1954), but this may be difficult particularly when dealing with multispecies communities. *Distribution* refers to the number of population sites occupied by the species; this again may be given as the fraction out of the suitable ones within an arbitrary or natural region. Population sites can be discrete units, like true islands; or, like habitat islands, they may have been delimited more arbitrarily from the rest of the environment; or they may be contagious, in which case distribution is simply the proportion of total area occupied. This definition of distribution does not specify the type of spatial patterns, i.e. the locations of the (occupied) sites in space, which is a related but different question.

Theoretical ecology has largely modelled local abundance (e.g. May 1976), while distribution has been left, until recently, to biogeographers, with the exception of the largely descriptive statistical work on animal and plant distributions (Patil et al. 1971, Bartlett 1975, Taylor et al. 1978, Ord et al. 1980). An exception to this rule is Levins's (1970, see also 1969a) model on extinction, which has been followed by a number of studies on interspecific competition (Cohen 1970, Levins and Culver 1971, Horn and MacArthur 1972, Levin 1974, Slatkin 1974, Hanski 1981a; see also Skellam 1951) and predation (Vandermeer 1973, Zeigler 1977) in patchy environments, all of which apply Levins's approach to regional population dynamics and underline the difference between local and regional interactions.

The spatial aspect of population interactions has recently received increasing attention (reviewed by Levin 1976; see also Smith 1974, Levin 1977, 1978, Gurney and Nisbet 1978a, b, Taylor and Taylor 1977, Crowley 1979, Comins and Hassell 1979, Hanski 1981b), and it has become clear that understanding of both spatial processes (distribution of the species in physical space) and resource partitioning (distribution of the species in niche space) are essential components to a satisfactory explanation of the perennial questions: Why are there so many species? Why are there so many rare species? (Wiens 1976, Yodzis 1978, Hanski 1979a). Indeed, some ecologists (e.g. Simberloff 1978) have gone so far as to maintain that, in many or most cases, spatial dynamics in independently developing populations explain most of the "community patterns" (see also Caswell 1976). This contrasts with the approach initiated by MacArthur (summarized in his 1972 book).

Whatever view one holds on the importance of competitive and other biotic interactions in structuring communities, it is an indisputable fact that communities consist of different kinds of species: some are widely distributed while others occur patchily; there exist locally abundant and locally rare species; and in some communities species are, at least apparently, well spaced-out in niche space, while in other communities guilds of similar species coexist. One is tempted to pose the question: Is it possible to find unifying factors to simplify this diversity?

I suggest some narrowing down of this question. It will first be shown that dynamics in local abundance and regional distribution are interdependent. Incorporating this observation into the type of models of regional distribution suggested and first analysed by Levins (1969a, 1970, Levins and Culver 1971) leads to an important structural change in the basic model. The key question in the analysis of the revised model is whether there is an internal equilibrium point on the distribution scale, which most species are approaching, or whether the species are just heading towards either maximal distribution and superabundance, or regional extinction.

2. Local abundance and regional distribution are interdependent

Four examples from different invertebrate taxa are put forward to answer the question, are local abundance and regional distribution independent of each other? The answer is no.

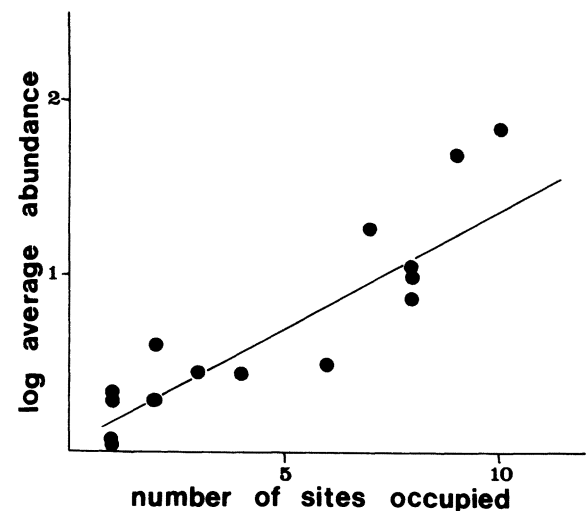Fig. 1. Relationship between average local abundance and distribution in Anasiewicz's (1971) data on bumblebees from Lublin, Poland. While calculating average abundance only those sites were included from which the species was collected (note logarithmic y-axis). Distribution is the number of sites, maximally 10, occupied by the species. Each dot in this figure represents one species (the line has been drawn by eye).
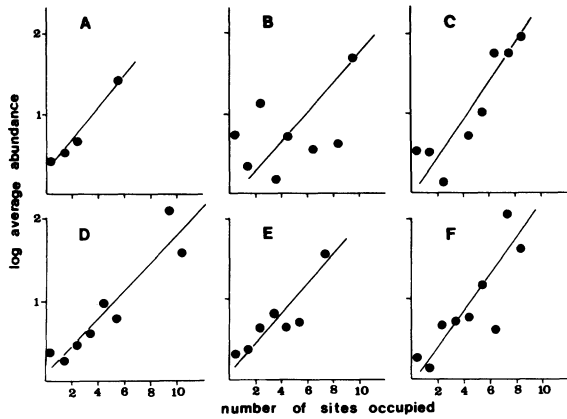
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Fig. 2. Relationship between average local abundance and distribution, like in Fig. 1, in Kontkanen's (1950) data on leafhoppers from meadows in East Finland. Each dot in this figure is the average for several species, which had the same distribution. Figures A to F refer to different "communities", representing wet to dry meadows (from left to right) at early (upper row) and late summer (lower row).

Anasiewicz (1971) studied bumblebees in the parks, squares, lawns, etc. of Lublin in Poland – all good examples of discrete habitat islands in the man-made environment. Average local abundance increased with the number of sites from which the species was recorded (Fig. 1; only sites in which the species was present are included in the calculation of average local abundance).

Kontkanen (1950; see also 1937, 1957) sampled leafhoppers from meadows in East Finland. He delimited six "communities" of coexisting species, and, in
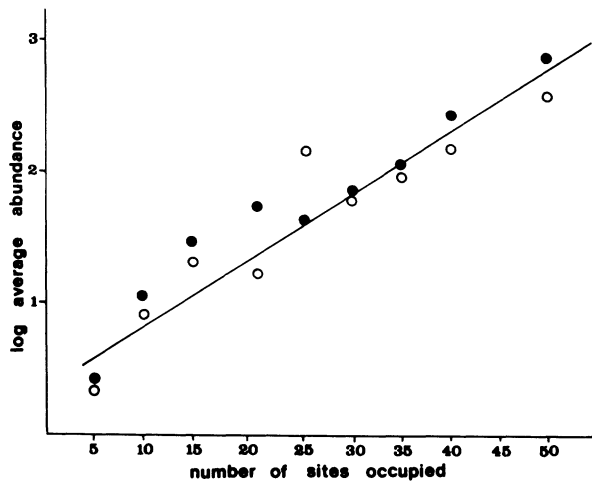
each community, a positive correlation exists between average local abundance and distribution (Fig. 2).

The third example is from Karppinen's (1958) study on soil mites (Oribatei) in two forest types in North Finland. In both habitats, a positive correlation between abundance and distribution is apparent (Fig. 3).

The final example is from my studies on dung and carrion beetles in lowland rain forest in Sarawak (Hanski unpubl.). Trapping was carried out with 10 traps for 4 nights at 12 sites, situated at least 0.5 km from each other in homogeneous virgin forest. I have restricted the analysis to the species-rich genus *Onthophagus* (Scarabaeidae). Once again, a positive correlation exists between the number of trapping sites from which the species was caught and the average catch from one site (Fig. 4). I conclude from these examples that a correlation between abundance and distribution is the rule in nature.

It is beyond the scope of this paper to go into details about the causes of this relationship, but it may be pointed out that the level of between-site movements is clearly of crucial importance. It appears to be common in nature that emigration takes place much before local carrying capacity has been reached, perhaps because of reasons discussed by Lidicker (1962) and Grant (1978).

Datum points in Figs 1 to 4 result from sampling, but because both abundance and distribution are underestimated, an increase in sample size should not change the picture qualitatively. There are, of course, truly rare yet widely distributed species, like the crane *Grus grus* in Finnish marshlands (Järvinen and Sammalisto 1976), but if communities consisting of reasonably similar species are studied, true distribution is expected to be correlated with true average abundance. The contrary

Fig. 3. Relationship between average local abundance and distribution, like in Fig. 1, in Karppinen's (1958) data on soil mites (Oribatei) from two forest types in North Finland. Each dot in this figure is the average for several species, which have been grouped into 10 distribution classes (total number of sites was 50 in both forest types). The two kinds of symbols refer to the two forest types.
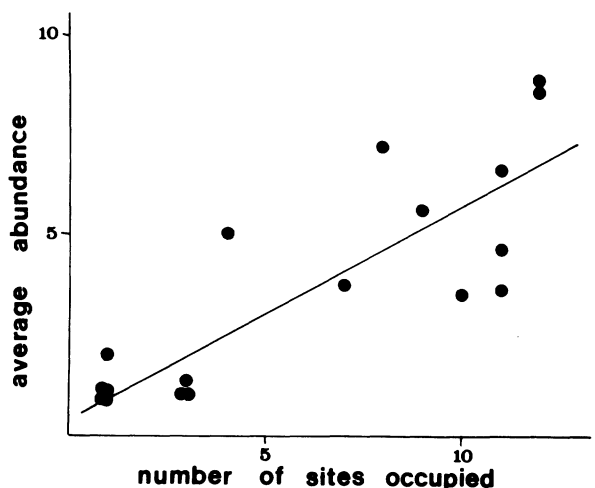

Fig. 4. Relationship between average local abundance and distribution, like in Fig. 1, in *Onthophagus* (Scarabaeidae) in the alluvial forest in Sarawak (Hanski unpubl.). A total of 12 sites was studied in homogeneous virgin forest. Each dot in this figure represents one species (note that y-axis is not logarithmic).

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would require spatial variance to decrease by a factor greater than approximately the squared proportional decrease in average abundance, which most certainly is not the case at least in moths and aphids (Taylor et al. 1980, see also 1978). Accepting that spatial variance is proportionally as large in rare as in abundant species, local extinctions are bound to occur (MacArthur and Wilson 1967), and distribution is, at least in rare species, less than the possible maximum.

3. Models of distribution

The paradigm for the dynamics in local abundance is still the logistic equation (Lotka 1925)

$$\frac{dN}{dt} = rN(1-N/K), \tag{1}$$

while perhaps the only similarly general model proposed for distribution is Levins's (1969a)

$$\frac{dp}{dt} = ip(1-p)-ep, \tag{2}$$

where p, a measure of distribution, is the fraction of population sites occupied by the species ($0 \le p \le 1$), and i and e are constants for a given species in a given environment. The first term in this equation is the rate of colonization of empty sites, and the second term is the rate of local extinctions. When all suitable sites in the region are occupied, p equals 1. The single internal equilibrium of Eq. (2) is stable, $\hat{p} = 1-e/i$, and regional extinction follows if $e \ge i$.

Levins (1970) subsequently analysed the stochastic version of Eq. (2): the extinction parameter, e, was assumed to be a random variable, with mean $\bar{e}$ and variance σ_e^2. Assuming no autocorrelation ("white noise"), the diffusion equation method (Kimura 1974) may be used to analyse the distribution of p, and gives (Levins 1970),

$$\Phi(p) = Cp^{2(i-\bar{e})/\sigma_e^2-2} \exp(-2ip/\sigma_e^2), \tag{3}$$

as the limiting ($t \to \infty$) distribution of $\Phi(p,t)$. This does not depend on the initial value, $p(0)$. Constant C is necessary to guarantee that $_0\int^1\Phi(p)dp = 1$. Critical points of Eq. (3) may be found from the equation,

$$2M_{\delta p} - d/dp \; V_{\delta p} = 0, \tag{4}$$

where $M_{\delta p}$ and $V_{\delta p}$ are the mean and variance of the rate of change in the stochastic version of Eq. (2). This gives the condition,

$$i > \bar{e} + \sigma_e^2, \tag{5}$$

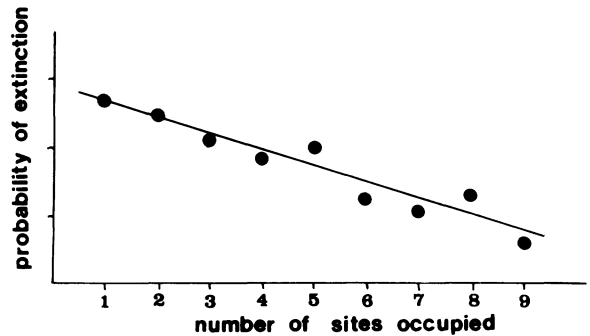for a unimodal distribution $\Phi(p)$ with a peak at $p =$

Fig. 5. Relationship between the probability of local extinction (per year) and distribution in Simberloff's (1976) data on mangrove island insects. Maximum number of sites (small mangrove islands) was nine. Each dot represents the average for several species (the line has been drawn by eye).

$1-(\bar{e}+\sigma_e^2)/i$. If (5) does not hold, $\Phi(p)$ is a decreasing function between 0 and 1. The deterministic equilibrium, obtained when $\sigma_e^2 = 0$, is always equal to or greater than the stochastic mode. It should be noted that there are two interpretations for $\Phi(p)$ (Kimura 1964). $\Phi(p)$ gives the distribution of p both for a single species during a long period of time, and for a community of similar species at a given moment.

The assumption that all the local populations are the same, implicit in model (2), is very unrealistic. To model local dynamics at each population site explicitly is out of question (though see DeAngelis et al. 1979), but the relationship found in Sect. 2 provides us with an approximative, yet qualitatively correct, non-constant relationship between p and the "average state" (abundance) in a local population: average local abundance increases with increasing p.

Probability of local extinction increases with decreasing population size (e.g. MacArthur and Wilson 1967, Christiansen and Fenchel 1977). One would expect, therefore (see Sect. 2), that e in Eq. (2) is not constant, but decreases with p. I have found 3 sets of data to test this prediction.

A re-analysis of Simberloff's (1976) results on extinction of local (island) populations of mangrove island insects shows that e in Eq. (2), a parameter related to the probability of local extinction, decreases with increasing p (Fig. 5). The same result was obtained from a similar analysis of Kontkanen's (1950) data on leafhoppers in meadows in East Finland (Fig. 6).

The third example is from Boycott's (1930, see also 1919 and 1936) study on fresh-water molluscs in small ponds in the parish of Aldenham in England. Almost a hundred ponds were surveyed for molluscs and plants in 1915 and 1925. This example is particularly important because the small size of the ponds enabled Boycott (1930: 2–3) to make accurate censuses. The extinctions observed are thus real. (Simberloff (1976) also tried to document all the populations of each island, while

Fig. 6. Relationship between the probability of local extinction and distribution in Kontkanen's (1950) data on leafhoppers in East Finland. Maximum number of sites (meadows) was three. Black dots represent the average for several species and the probability of extinction in five years; open circles give the corresponding annual extinction probabilities (these results indicate that "re-colonization" was frequent, which is partly an artefact of the relatively small sample size, leaving some small populations unnoticed; cf. Kontkanen 1950).

Kontkanen (1950) probably missed many small populations.) My re-analysis (Fig. 7) of Boycott's (1930) data closely agrees with the above results: e is not constant but decreases with p. This result is not quite accurate, because more than one extinction-colonization event may have taken place in 10 years (cf. Diamond and May 1977), but the trend is very clear.

At present we may accept the simplest hypothesis about the rate of extinction: $e'(1-p)p$ (note that $e' \approx e$ when p is small). On this assumption Eq. (2) is replaced by

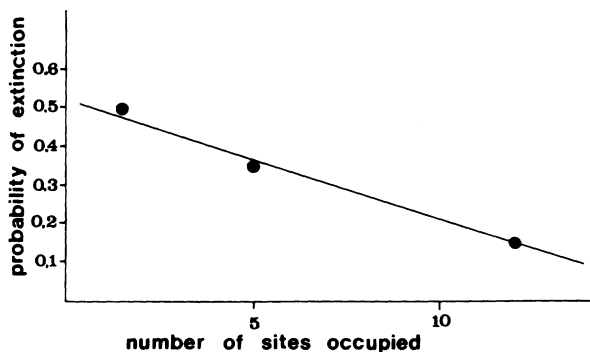$$\frac{dp}{dt} = ip(1-p) - e'p(1-p). \qquad (6)$$

Fig. 7. Relationship between the probability of extinction and distribution in Boycott's (1930) data on fresh-water molluscs in small ponds in England. This figure gives the "net" extinction rate in 10 years. While constructing the figure, I have included the 34 ponds in Boycott's (1930) classes A and B which did not dry up during the study period. Species have been divided into three distribution classes, namely 1 or 2, 3 to 7, and 10 to 14 ponds occupied, and the dots in the figure give the average for each group (altogether there were 16 species).

I shall next explore two simple assumptions about the colonization process.

(1) If i in Eq. (6) does not depend on p, we obtain the logistic equation (1). This has been analysed, in the ecological context, by Levins (1969b; see also May 1973 and Leigh 1975). In the deterministic case, there is one stable equilibrium point, either at $\hat{p} = 1$, if $i > e'$, or at $\hat{p} = 0$, if $i < e'$. For the stochastic version, assume that $s \equiv i - e'$ is a random variable, and that there is no autocorrelation. The diffusion equation method gives,

$$\Phi(p) = Cp^{2(\bar{s}/\sigma_s^2-1)}(1-p)^{-2(\bar{s}/\sigma_s^2+1)}. \qquad (7)$$

$\Phi(p)$ is bimodal if $\sigma_s^2 > \bar{s}$. If, on the other hand, $\bar{s} > \sigma_s^2$, all populations approach maximal distribution, $p = 1$.

(2) Let us assume that the rate of colonization is $(s'p + e')p(1-p)$; the model then becomes,

$$\frac{dp}{dt} = s'p^2(1-p), \quad s' > 0. \qquad (8)$$

Evidently, there is only one stable equilibrium point, $\hat{p} = 1$. If s' is a random variable, and there is no autocorrelation, we can again use the diffusion equation method, which gives,

$$\Phi(p) = C\exp(-2\bar{s}'/\sigma_{s'}^2 p)p^{2(\bar{s}'/\sigma_{s'}^2-2)}(1-p)^{-2(\bar{s}'/\sigma_{s'}^2+1)}. \qquad (9)$$

This distribution is bimodal if $\bar{s}' < \sigma_{s'}^2/3$. If the mean is greater than a third of the variance, all populations become maximally distributed.

A biological justification for assumption (2) about the rate of colonization is the probably increasing number of emigrants with increasing local abundance (e.g. Dempster 1968, Johnson 1969); presumably, more emigrants means more colonizations.

Addendum

During the preparation of this paper it escaped my notice that there may be certain mathematical problems in the use of the diffusion equation technique in the analysis of the models in Sect. 3 (Levins's 1970 analysis is erroneus; see Boorman, S. A. and Levitt, P. R. 1973. Theor. Pop. Biol. 4: 85–128; and see Roughgarden, J. 1979, pp. 384–391. Theory of population genetics and evolutionary ecology: an introduction. MacMillan). A supplementary numerical analysis of a discrete time version of Eq. (6) indicates, nonetheless, that the result presented here is qualitatively correct (Hanski 1982).

4. Ecological appraisal

The present modification of Levins's model led to a radically different conclusion from the one originally drawn by Levins: assuming stochastic variation in the rate of local extinction and/or colonization, populations
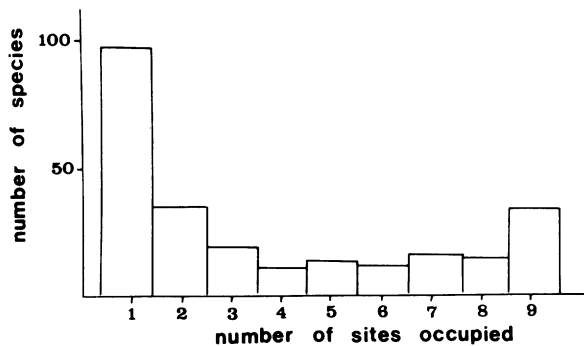
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Fig. 8. Frequency distribution of species' distributions in Simberloff's (1976) data on mangrove island insects. Maximum number of sites was nine.
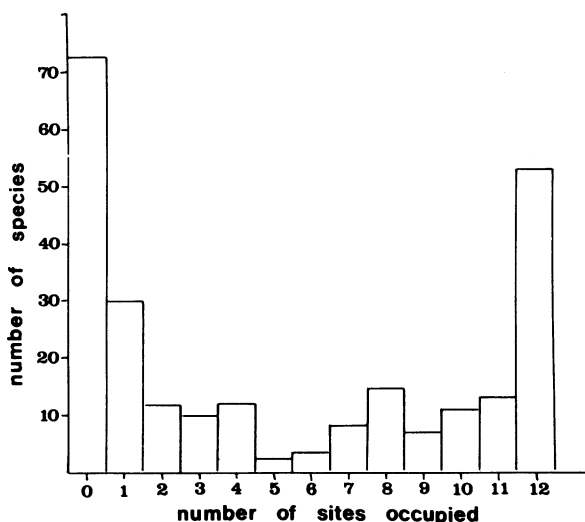

Fig. 10. Frequency distribution of species' distributions in Linkola's (1916) data on anthropochorous plants in Russian Karelia, U.S.S.R. The sites in question are isolated old houses and small villages, numbering 12 (sites 8 to 19 in Linkola 1916).

tend towards either one or the other of the (deterministic) boundary equilibria, $\hat{p} = 0$ and $\hat{p} = 1$, while in Levins's model p would hover around a stable internal equilibrium, $0 \leq \hat{p} \leq 1$. Which result more correctly reflects reality?

We recall that $\Phi(p)$ may be interpreted either as the distribution of p values in one species in a long period of time, or as the distribution of p values in many similar species at one moment of time (cf. Kimura 1964 for analogous interpretations in population genetics). To test the latter qualitatively, we require that all the species may establish local populations at the same sites, and that interspecific influences on model parameters are density- and frequency-independent. My model then predicts bimodality of p's, peaks close to unity and zero, while Levins's model predicts unimodality with the peak not very close to unity or zero.

Simberloff's (1976) data (cf. Fig. 5) support the present model; the distribution of the number of mangrove islands occupied by different species of insects appears bimodal (Fig. 8). To test this formally, we observe that

Fig. 9. Frequency distribution of species' distributions in Onthophagus in tropical lowland forest in Sarawak (Hanski unpubl.). Maximum number of sites was 12.

12 species were found from 6 islands, and 32 species from all 9 islands. The null hypothesis that the number of species is equal in these two classes is rejected: $\chi^2 = 9.09$, P < 0.01.

Onthophagus species in the lowland rain forest in Sarawak (cf. Fig. 4) also show a clear dichotomy into two sets of species (Fig. 9). I shall use the term "core" species for the locally abundant and regionally common species, and the term "satellite" species for locally and regionally rare species. In the case of mangrove island insects (Fig. 8), the same terms can be used, although "intermediate" species are now frequent.

Another data set to test this prediction is due to a study by Linkola (1916) on the occurrence of anthropochorous vascular plants near houses and villages, isolated by natural forest, in Russian Karelia (then Finland, study area ca. 10 000 km²). There was a clear size effect, large villages having more species than small ones (Linkola 1916), and colonization of isolated houses and small villages was perhaps not random, because some species were lacking systematically from them (though some would do so by chance only). For these reasons, I have restricted the analysis to 12 similar sites in Linkola's (1916) material. The frequency distribution of occurrences at the 12 sites is clearly bimodal (Fig. 10), which strongly supports the present model (see Hanski 1982 for a full analysis of Linkola's material).

It suffices to mention here that Kontkanen's (1950) results on leafhoppers and Anasiewicz's (1971) results on bumblebees also support the present model. A full analysis of these two studies will be presented elsewhere (Hanski unpubl.).

5. More about testing the core-satellite hypothesis

The core-satellite species hypothesis is a simple null hypothesis to explain regional rarity. There are two important premises in the model: (1) regional population dynamics *is* important, and (2) stochasticity in regional population dynamics *is* important. Stochastic variation in the parameters of regional dynamics (extinction, colonization) may be due to either demographic or environmental stochasticity.

As the examples given in the previous section showed, testing the main prediction of the model is simple: Is the distribution of species' regional distributions bimodal? If the distribution is clearly bimodal, there are grounds for a dichotomy, and for the use of the concept in a strong sense. Otherwise, one is left with the option of labelling the opposite ends of a continuum, like the r-K species distinction (MacArthur and Wilson 1967) has been replaced by the r-K species continuum (Pianka 1970, 1972, 1974, Southwood 1977).

Other models than the present one may predict a bimodal distribution of regional distributions, and to more rigorously test this model necessitates intensive studies on the rates of local extinction and colonization. If data are available on the rate of change in distribution, validity of Eq. (6) may be tested directly. Alternatively, one may try to document changes in species' status from the core to the satellite class, or vice versa, between regions or in time. Such changes are predicted to occur even if the pattern of environmental stochasticity remains stationary. An alternative model, which we may call an "adaptation" hypothesis, states that core species are better adapted to the environment than are satellite species, and does not predict changes from core to satellite class, or vice versa. Note that also the present model allows for interspecific differences in $\bar{s}$ and σ_s^2 (Sections 3 and 8).

L. R. Taylor's work (1974, 1978, Taylor and Taylor 1977, Taylor et al. 1978, 1980, Taylor and Woiwod 1980) on insect abundance and distribution has demonstrated the ever-changing patterns of regional distributions, anticipated by Andrewartha and Birch (1954), and Taylor's work has shown the interdependence between abundance and distribution. His results imply that local extinctions and colonizations are frequent phenomena (see also Den Boer 1977, Ehrlich 1965, Ehrlich et al. 1980), and that spatial population dynamics is important in all species.

The gravest difficulty in testing the core-satellite species hypothesis in a multispecies context is habitat selection. How does one identify the "population sites" suitable for the species? The reason for insisting on "similar species" in testing the multispecies prediction is just this; if the species are so similar that they have similar habitat selection, there is no problem. Then the number of potentially inhabitable sites is the same and the denominator in calculating the p's is the same for all species. Identical species are, of course, an unattainable

abstraction, but in many groups of closely related species habitat selection may be sufficiently similar. An extension of the core-satellite hypothesis into analyses of niche relations (in Sect. 8) requires, in any case, a distinction between habitat and niche (Whittaker et al. 1973).

There is the danger that counter-evidence (unimodal distribution of p's) is dismissed on the basis that the species were not, after all, similar enough. This would be wrong; the question about habitat selection must be resolved before the test is performed. In any case it is safest to include only similar population sites (habitat patches) in the analysis, which, to some extent, removes this problem. These restrictions do not mean that this theory could not work on any species. Careful selection of the species and of the sampling sites is required only because of problems in testing the hypothesis.

To repeat, the core-satellite hypothesis should be tested only with sets of species which may establish populations at the same sites; or, if such data are available, with records for single species in the long course of time. I believe that the former requirement was fulfilled in the above examples. A counter-example is the distributional ecology of water-striders *(Gerris)*. Vepsäläinen has shown, in a series of papers (see especially 1973, 1974a, b, 1978, Järvinen and Vepsäläinen 1976), that *Gerris* species, nine of which occur in Finland, show significant ecological and morphological differences in their adaptations to living in different kinds of lakes, ponds, streams, etc., including wing dimorphism in many species. In this case habitat selection is clearly different in different species, and the core-satellite hypothesis should *not* be used for the whole set of species, though it could be used for each species separately. In the latter context, one could talk about core and satellite populations, and comparisons should be made between regions or times.

Assuming the reality of core and satellite species, one may rephrase Hutchinson's (1959) question and ask: Why, in a given community, are there n core and m satellite species? Constraints on core and satellite species diversity are entirely different, which warrants two questions (n and m) instead of one ($n+m$). Nevertheless, satellite species may become, besides regionally extinct, also core species, and a core species can move to regional extinction only through a stage as a satellite species. Therefore the numbers of species in the two kinds are not independent of each other.

A specific prediction may be derived for the most universal trend in species diversity, namely that the number of species tends to increase with area, whether the region in question is an island or part of the mainland. Because satellite species survive as a set of small populations, their regional existence should hinge on the size of the region (e.g. Hanski 1981a). Therefore, as regions – e.g. islands – become smaller, the proportion of satellite species should decline. If Diamond's (1975, see also 1971, 1973, and others) series of species from

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D-tramps to High-S species is matched with the continuum from core to satellite species, the proportion of satellite species indeed decreases with decreasing island size. Diamond (1975: 358), however, considers his D-tramps to be "r-selected", and High-S species to be "K-selected", which is in contrast with the present conceptualization – core species are certainly not "r-selected".

6. The core-satellite hypothesis and r-K theory

There exists a common basis for the core-satellite hypothesis and the by now well established r-K species theory (MacArthur and Wilson 1967, Gadgil and Bossert 1970, Pianka 1970, 1972; but see Wilbur et al. 1974, Southwood 1977, Christiansen and Fenchel 1977, Schaffer 1979). Both hypotheses stem from the same model – the logistic equation – which has been applied at the level of local abundance in the r-K model, and at the level of regional distribution in the core-satellite model.

Nonetheless, the r-K species concept is used in a deterministic fashion to predict properties of species from the properties of their environment (e.g. Pianka 1970, 1974, Southwood 1977, Vepsäläinen 1978), while the core-satellite distinction is caused in the model by stochastic variation in spatial population dynamics. Unlike the satellite species, r-species are thought to be frequently locally abundant in comparison with K-species, but this does not follow from the mathematical model (logistic equation).

Although the two concepts are fundamentally different, core species are related to K-species, and, less obviously, satellite species are related to r-species.

7. A historical perspective

It is common in ecology that authors – or their readers – find "new" ideas preceded by earlier workers (Hutchinson 1978, McIntosh 1980), and nowadays preferable by Darwin. This may be viewed as a mark of soundness in the argument – or is McIntosh (1962) correct in claiming that "certain ideas seem to be invulnerable to attack and persist although subjected to multiple executions"? The core-satellite hypothesis is not an exception to the rule. The irony here is that the idea McIntosh was executing in 1962 was nothing else but bimodality of the distribution of spatial occurrences – the very prediction from the models in Sect. 3.

G. F. Gause (1936a: 323, see also 1936b) wrote: "The most important structural property of biocoenosis is the existence of definite quantitative relations between the abundant species and the rarer ones." One such relation, which Gause (1936a) discussed at length, is Raunkiaer's "law of frequency" (Raunkiaer 1913, 1918, 1934; a pioneering work by Jaccard in 1902),

which has been much used especially in plant ecology until the 1960's (e.g. Oosting 1956, Hanson and Churchill 1961, Mueller-Dombois and Ellenberg 1974), and which is of special relevance here. To see this, divide p into 5 segments of equal length (–0.2, 0.21–0.4, etc.), and denote by A to E the numbers of species falling into the 5 classes. Raunkiaer's "law of frequency" states that $A > B > C \gtreqless F < E$. Quite unexpectedly, the simple theory suggested in Sect. 3 predicted Raunkiaer's "law of frequency".

Nonetheless, with papers by Gleason (1920, 1929) and Romell (1930), criticism of the "law of frequency" started to accumulate (Gause 1936a, Preston 1948, Williams 1950), culminating in the above-mentioned "execution" by McIntosh (1962). It had been shown that the frequency distribution of species' frequencies depends, in Williams's (1950) words, on "the number of quadrats, the size of the quadrats, and on the Index of Diversity of the population." This criticism is justified. In view of the connection to the core-satellite hypothesis, one significant difference between the "laws" should be pointed out (see also Hanski 1982).

Frequency is the fraction of (usually small) samples, typically quadrats, in which the species occurs, all samples having been taken from the same homogeneous community. *Distribution,* as it was defined in the introduction and used in the models (Sect. 3), is a measure of occurrence on the between-site scale. Although the "true" population level may be difficult to specify (for an extreme example see Brussard and Ehrlich 1970a, b), the distinction between distribution and frequency is an important one whenever regional population dynamics are important, i.e. whenever many local populations are studied. It has been pointed out that the highest (E) of Raunkiaer's frequency classes is more inclusive than the lower ones, because the frequency classes include unequal density classes (Gleason 1929, Ashby 1935, McIntosh 1962). But unlike between density (abundance) and frequency classes in homogeneous communities, there is no simple statistical relationship between distribution and local abundance, the correlations in Figs 1 to 4 (Sect. 2) being due to ecological processes (notwithstanding problems of sampling; Sect. 2). In fact, the purpose of using the "law of frequency" was to determine the homogeneity of a stand of vegetation (or a community of animals; see e.g. Kontkanen 1950); bimodality (D < E) was namely expected only in homogeneous stands, which is an interesting convergence to my independently thought requirement of similar habitat selection in the species to be analysed (Sect. 5).

8. Concluding remarks: visiting Hutchinson's niche space

After these observations and theorizing, the reader may ask: What is gained by calling regionally common and

locally abundant species core species, and rare species satellite species?

My answer is twofold. If the frequency distribution of species' regional distributions is indeed bimodal, this is interesting for its own sake, because it appears not to be the null hypothesis for many ecologists, who rather expect the kind of unimodality predicted by Levins's model. Secondly, and more importantly, if such a dichotomy exists in many natural communities, this should help us to provide a functional explanation for patterns of abundance and distribution. To take an example, if the core-satellite hypothesis is upheld, one may proceed by restricting the application of the equilibrium theory (MacArthur 1972, May 1973, 1976) to the core species, and employing appropriate non-equilibrium models for the satellite species. Caswell (1978) presumably had a similar idea in mind when he, after discussing the virtues of equilibrium and non-equilibrium models in ecology, conjectured: "Perhaps a community consists of a core of dominant species, which interact strongly enough among themselves to arrive at equilibrium, surrounded by a larger set of non-equilibrium species playing their roles against the background of the equilibrium species."

In the introduction I referred to a third structural property of communities besides abundance relations (Engen 1978) and spatial distributions (Simberloff 1978): distribution of species, or strictly speaking their "niches", in Hutchinson's (1957) niche space. The perennial question is how well spaced-out niches are in niche space. Intuition says and theory (e.g. MacArthur 1972, Lawlor and Maynard Smith 1976) predicts that interspecific competition causes better spacing-out, and ultimately and ideally leads to a uniform distribution of niches in niche space. In view of the controversy about the importance of competition in structuring communities (Paine 1966, Harper 1969, Janzen 1970, Dayton 1971, Connell 1975, 1978, Caswell 1976, Glasser 1979), this is an important question. The problem is that, in practice, other factors besides competition come into the play, making any "test" difficult. It is not surprising, therefore, that this kind of argument has led to widely varying conclusions (MacArthur 1972, Schoener 1974, Sale 1974, Inger and Colwell 1977, Southwood 1978, Strong et al. 1979, Pianka et al. 1979, Hanski 1979a, Lawlor 1980). The difficulty is in the formulation of a proper null hypothesis (see especially Lawlor 1980; the null hypothesis is *not* necessarily a random distribution of niches in niche space, Hanski 1979a, Grant and Abbott 1980), and in the multitude of factors potentially – and in practice – causing changes in niche position.

This is where the core-satellite hypothesis may prove useful. The following heuristic argument shows that there exists, after all, at least one unequivocal null hypothesis: if interspecific competition is important in structuring communities, core species should be better spaced-out in niche space than satellite species.
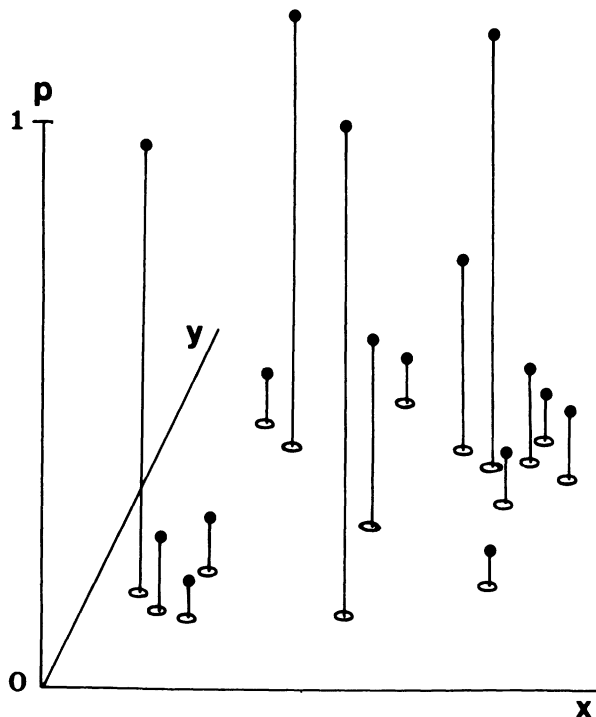

Fig. 11. A schematic representation of the hypothesis, explained in Sect. 8, that core species are better spaced-out in niche space than a random sub-set of the same size of all species, and better spaced-out than satellite species. x and y are two niche dimensions, and p denotes distribution, as in the rest of the paper, which varies from 0 to 1. Open circles represent niche positions, and the black dots give the position of species in the 3-dimensional space. It should be recalled that the argument is stochastic (see text), and the situation depicted in this figure is a static picture of a dynamic process.

Recall that the model is:

$$\frac{dp}{dt} = s_i p_i (1-p^i), \quad i = 1, \ldots, n \qquad \text{(Eq. 6)}$$

where n is the number of species, and s_i is a random variable with mean $\bar{s}_i$ and variance $\sigma_{s_i}^2$. The probability that species i is a core species at a given time is an increasing function of $\bar{s}_s/\sigma_{s_i}^2$. How does interspecific competition influence this ratio? Competition should increase the rate of extinction, it should decrease the rate of colonization – hence competition will decrease $\bar{s}_i$ – and it will probably increase $\sigma_{s_i}^2$. Consequently, $\bar{s}_i/\sigma_{s_i}^2$ will decrease, and the probability of species i staying/becoming a satellite species increases. The closer the competitor(s), the stronger the effect. Naturally, if there are two close competitors, both of which are core species, this model only predicts that one of them is likely to become a satellite species. The stochastic nature of the single species model is preserved in the multispecies context.

We may visualize species in a space constructed of Hutchinson's (1957) niche space and of one extra axis,

giving the extent of spatial distribution, p, which correlates, as we saw in Sect. 2, with abundance (Fig. 11). The greater the density of other species in the neighbourhood of any species in niche space, the smaller the probability that this species is, at a given time, a core species. Hence, core species are not expected to be a random sub-set of all the species with respect to niche position; we expect core species to comprise such a sub-set within which species are better spaced-out from each other than species are within a truly random sub-set. It follows that core species are also better spaced-out than satellite species.

A within-community analysis, such as suggested here, provides a concrete point of reference to test null hypotheses about community structure. Still, the present model cannot be but one step towards better understanding of community structure and its evolution. For instance, one could argue that even if core species are better spaced-out than satellite species in a community, this is perhaps not due to competition but to predation. Other studies are necessary to establish which explanation is correct. Theoretical work is also needed to clarify the expectations in multispecies communities. The value of the present approach can only be judged after several ecologists have tried it independently on their own data. Tests on dung beetles (Hanski 1980a) and bumblebees (Hanski unpubl.) have given encouraging results (see also Hanski 1979b, 1980b).

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