ON THE EXPLANATION OF THE ELEVATION EFFECT BY A DYNAMIC INTERPRETATION OF SPECIES DISTRIBUTION ALONG ALTITUDINAL GRADIENTS

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SUMMARY

In this paper I analyse Backhuys' (1968) data on altitudinal distributions of 23 plant species on 108 mountain tops in the Swiss alps with which he shows the existence of the elevation effect in that area. However, when using the whole distribution of the frequency of occurrence at different elevations instead of the one value of the lower range limit only, I come to the conclusion that the proposed explanation for the elevation effect cannot be shown by the data assembled by him. Yet, the ideas behind this approach lead to the interesting perspective of the possibility to define these kind of distributions partly in static terms, and partly in dynamic ones. Thus far they have been looked at from a static point of view only.

INTRODUCTION

This paper briefly considers the same data from which Backhuys (1968) concluded that Van Steenis' (1961) elevation effect can be shown to exist in a number of alpine plant species in Switzerland. This effect implies that plant species — and probably animal species as well — are absent from mountains below a certain minimum elevation, but that on mountains higher than this minimum elevation they also occur, quite unexpectedly, at altitudes below this minimum elevation. Van Steenis (1961) explained this phenomenon by a dispersal of propagules from a high-elevation zone of permanent establishment downhill into a zone containing temporary populations. Backhuys (1968) showed the elevation effect for 23 alpine species represented by 6976 records from herbarium sheets and from the literature. As to its causation he assumed the operation of the same downhill diffusion process of plant propagules from permanent habitats into temporary ones.

Here, I shall show that Backhuys' (1968) assumed explanation of the elevation effect cannot be substantiated from his data. Moreover, the nature of this data set is such that the question of whether or not the causation of the effect can be explained by it remains open.

Table 1. Values of the mean altitude ($\bar{x}$) of each species, together with the measure of skewness (g) of the altitudinal frequency distribution; the statistic t expresses the value of g divided by its standard error (cf. Snedecor, 1956, p. 200). The first column contains the number of records per species (N), and the fifth column contains the percentage of records falling below the critical level. Asterisks indicate significant values of g at the 5% probability level.

Species	N	$\bar{x}$	g	t	%
Achillea nana L.	397	2345	0.08	0.64	76.8
Alchemilla pentaphyllea L.	241	2287	0.01	0.07	34.4
Androsace helvetica (L.) All.	265	2342	0.12	0.83	8.3
Arabis coerulea (All.) Hänke	321	2632	−0.27*	−2.01	43.9
Campanula cenisia L.	313	2499	1.02*	7.40	89.5
Cardamine alpina Willd.	278	2335	−0.12	−0.79	21.6
Carex curvula All.	370	2410	−0.29*	−2.25	17.6
Chamorchis alpinus (L.) Rich.	196	2171	−0.38*	−2.21	6.1
Chrysanthemum alpinum L.	400	2289	0.19	1.57	16.3
Eritrichium nanum (Vill.) Schrad.	318	2705	−0.22	−1.64	1.6
Gentiana brachyphylla Vill.	368	2414	0.23	1.78	4.3
Lloydia serotina (L.) Rchb.	254	2298	−0.32*	−2.11	11.4
Loiseleuria procumbens (L.) Desv.	307	2183	0.07	0.51	20.2
Minuartia sedoides (L.) Hiern	260	2451	0.97*	6.41	13.5
Poa laxa Hänke	322	2500	−0.07	−0.51	7.8
Ranunculus glacialis L.	504	2517	−0.04	−0.34	27.2
Salix reticulata L.	319	2048	0.18	1.34	3.4
Saxifraga biflora All.	199	2540	0.27	1.57	68.8
Saxifraga seguieiri Spreng.	359	2527	−0.54*	−4.18	3.9
Sesleria disticha (Wulf.) Pers.	262	2503	−0.68*	−4.52	75.2
Sieversia reptans (L.) R. Br.	270	2468	0.08	0.50	47.8
Soldanella pusilla Baumg.	198	2104	−0.06	−0.33	40.4
Trisetum spicatum (L.) Richt.	255	2531	−0.20	−1.30	35.3

MATERIAL AND METHODS

The material I used consisted of Backhuys' (1968) data only. These data comprise records of 23 species from 108 Swiss mountains of over 2000 meters high. As mentioned, Backhuys collected these data from both herbarium sheets in Swiss collections, as well as from the literature. Backhuys was very careful in his choice of plant species; he included species with different ecological requirements, though all species were confined to the alpine zone. The number of records of each of the species investigated varied between 200 and 500 (table 1). The altitudinal level of occurrence of plants on the mountains chosen was classified into intervals of 100 m.

In the present paper I applied techniques different and extended relative to those of Backhuys; instead of characterizing the altitudinal frequency distribution of the recorded occurrences by one single statistic only – the lower range limit – I used the mean and skewness as characteristics of the whole frequency distribution. I also calculated the proportions of records found on high mountains that are below the minimum elevation for the species. (In the following I refer to this minimum elevation, that is, the height of the lowest mountain with permanent establishment of a species as the critical level for this species.) This number, together with the skewness (cf. Snedecor, 1956) of the altitudinal distribution of the data is taken to indicate a possible over-representation of the species at altitudes below the zone of optimal occurrence. If the proposed explanation of the effect is correct, then the skewness of the distribution is expected to be negative in the majority of species (fig. 1). Also, the number of records below the critical level should comprise a reasonable proportion of the total number of records for the species concerned, and not just a few records, nor the majority of them.
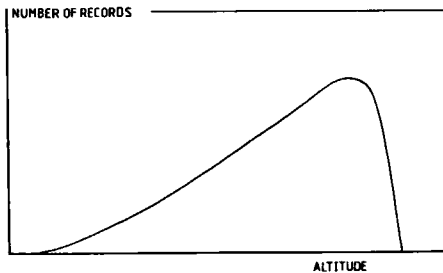

Fig. 1. Hypothetical skew frequency distribution of records as expected when individuals diffuse downhill from their preferred biotopes at higher altitudes. The coefficient expressing skewness (g) is in this case negative.

RESULTS

The numbers of records of each species in each altitudinal interval were taken from Backhuys' table 1, and from these data the skewness of the various distributions was calculated. Table 1 in this paper shows that these values are significant in only one third of the cases (8 out of 23 species were significant at the 5% probability level), of these 2 species were positive, and 6 were negative. This means that in those species the greatest number of records was either below or above the average altitudinal level of the species concerned. Therefore, these data do not support the idea of a diffusion of propagules from optimal biotopes higher up the mountains, where the species occurs permanently, into habitats of temporary occurrence mainly at lower elevations.
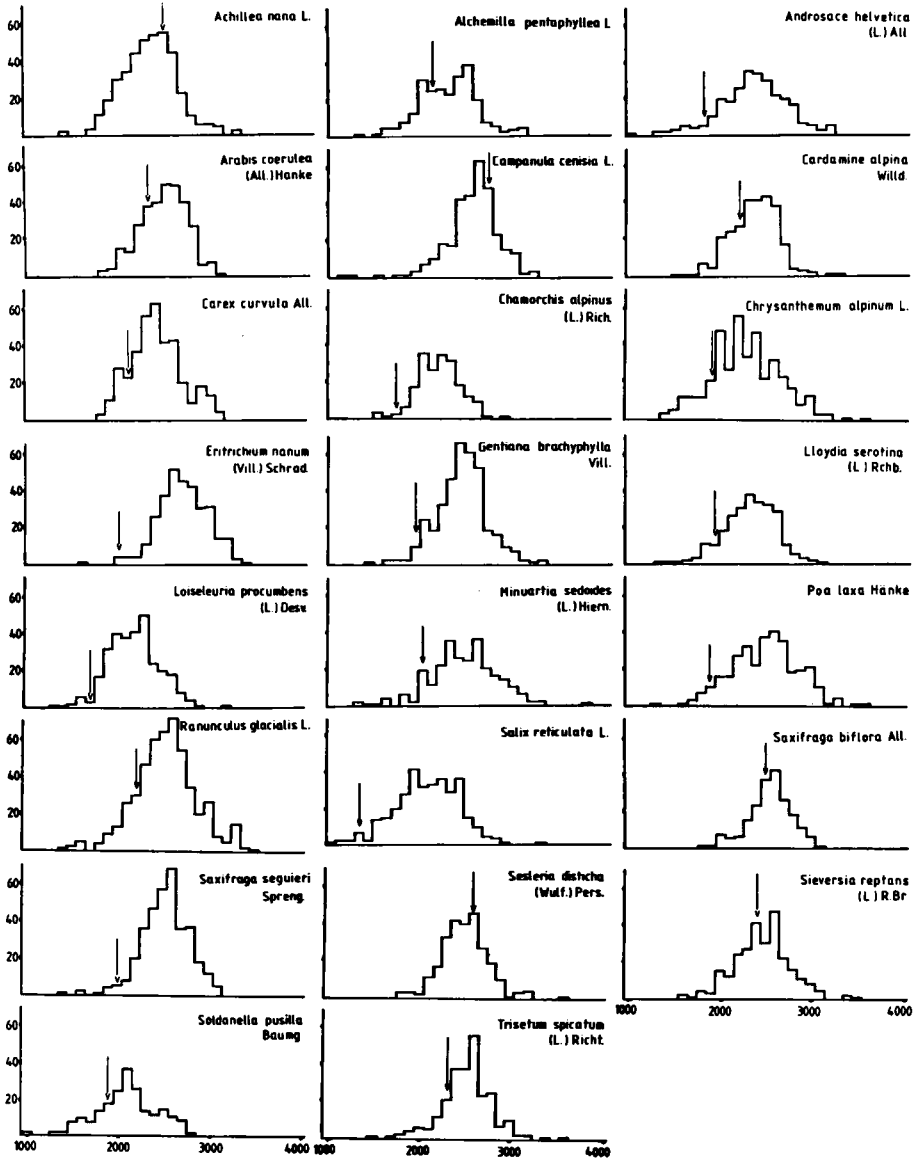
Fig. 2. Frequency distribution of records of all 23 species along the same altitudinal gradient. The arrows indicate the critical level. Data from Backhuys' tables 1 and 2.

Apart from parameters as the mean and the skewness of the distribution, a third measure that could indicate the occurrence of a diffusion process mainly downhill from the permanent habitats is the location of the critical level relative to the location of the total frequency distribution of the species (fig. 2). As mentioned, one

would not expect a negligibly small proportion of all records below the critical level. Yet, very small proportions happen to occur in 10 of the 23 species, that is, in nearly half of the cases (*Androsace helvetica:* 8.3%; *Chamorchis alpinus:* 6.1%; *Eritrichium nanum:* 1.6%; *Gentiana brachyphylla:* 4.3%; *Lloydia serotina:* 11.4%; *Loiseleuria procumbens:* 20.2%; *Minuartia sedoides:* 13.5%; *Poa laxa:* 7.8%; *Salix reticulata:* 3.4%; *Saxifraga seguieri:* 3.9%). These proportions are, in my opinion, too low to indicate a process of any significance, particularly in those cases where they entail just the tail of a symmetric frequency distribution. But, of course, this opinion may be a matter of taste; one can disagree about which proportion may be large enough to indicate the supposed elevation effect in these cases.

However, matters become more tricky when we apply the opposite argument; often too large a proportion of the records happens to lie below the critical level. In my view this is the case in *Achillea nana* (76.8%), *Campanula cenisia* (89.5%), *Saxifraga biflora* (68.8%), *Sesleria disticha* (75.2%), and *Sieversia reptans* (47.8%). I think that these very large proportions of populations, lying below the critical level, expose a critical problem: here we are inclined to interpret the zone with the highest or modal frequency as the ecologically optimal zone, although this need not be the case. As Backhuys stated correctly, the survival of populations away from the ecological optimum may be increasingly dependent on diffusion the greater the distance to this optimum. But when, due to gravity, the propagules tend to disperse more downhill than uphill, this optimum may, of course, itself be displaced downhill as well. And we actually have no measure to indicate how far this optimum may be dispersed. In other words, to some extent not just the tails, but the whole frequency distribution may be a mixture of both the responses to ecological conditions and the diffusion process that we want to estimate. According to its altitudinal distribution *Achillea nana*, for example, may not be the best choice for illustrating the elevation effect, as it may preferably occur below the critical level estimated from the 108 mountains investigated (fig. 2). Without independent information on the species' ecological responses, in observations like these, it is impossible to distinguish these two processes from each other. Stating that the species chosen are all alpine species, and using the lowest range limit as the only characteristic of the whole frequency distribution hides this problem.

DISCUSSION

It will be clear that it is quite hazardous to estimate a process of downslope diffusion from a comparison of two points only instead of from the shape and location of the whole frequency distribution, or, even better, from a comparison of an observed distribution with a potential one without diffusion occurring. In the present case these difficulties may be even greater because of the choice of mountains over 2000 m high. This difficulty becomes clear when we realize that only half of the 108 mountains studied reach more than 200 m above this minimum elevation. The resulting shortage of high-elevation biotopes, as shown by figure 3, may affect the shape and location of the frequency distributions along an altitudinal gradient. And even
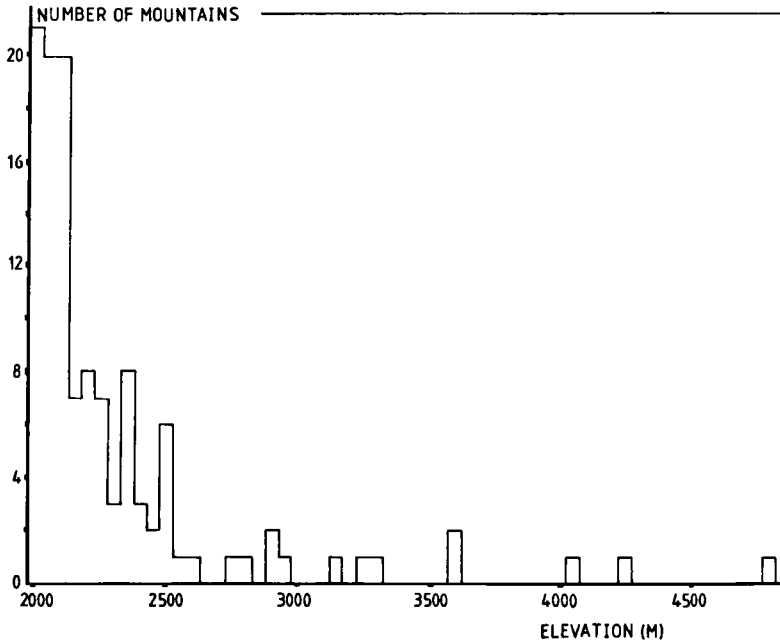
Fig. 3. Frequency distribution of altitudes of the 108 mountains in Backhuys' (1968) investigation.

when the number of mountains higher than 2200 m would have been greater than it in fact is, we could account for a relative shortage of high-altitude biotopes because of the conical shape of most mountains. Both facts, the relative shortage of high peaks and the relative shortage of high-altitude biotopes on the existing peaks, make it difficult to evaluate and to compare the location and shape of frequency distributions along altitudinal gradients. It is actually surprising to find symmetrical distributions anyway! Yet, surprising as it may seem, symmetrical distributions appear to be rather common, as no mention of asymmetrical distributions has been made so far in a growing list of literature on tree species found along altitudinal transects on various mountains in North America (cf. Kessell, 1979; Whittaker, 1952, 1956, 1960; and others).

On the other hand, the concept of an elevation effect is important, as it adds a dynamic aspect to the study of optimum responses along environmental gradients. Gradient analysis, as developed by Whittaker (1967, 1975) in vegetation analysis and Gause (1931) in animal ecology, is still static in outlook. In the present approach distributions of the frequency of occurrence of some species along an environmental gradient are seen as ecological expressions of basic physiological traits. Thus, species distributions are viewed as numerical expressions of a physiological response to differences in temperature, humidity, some chemical condition of the soil, etc., which

is sometimes modified by competition (e.g. Beals, 1969; Ernst, 1978; Whittaker, 1975). This latter process, competition, can be thought to affect the value of K, representing the asymptote of the logistic growth curve of a population, particular to a certain environmental condition (Gause, 1932, 1934).

Contrary to this approach, the elevation effect particularly draws attention to dispersal of propagules along a gradient. As Backhuys (1968) suggested, the impact of dispersal will become greater the smaller the chances of independent survival under suboptimal conditions. Near the margins of the distribution, populations may even consist entirely of sterile individuals, and they may therefore be completely dependent on a permanent flow of propagules from other populations nearer to the optimal zone. Therefore, observed distributions may partly result from responses to local conditions, and partly from a diffusion process of plant propagules.

Yet, when Van Steenis (1961) distinguished between a zone of permanent occurrence and a zone of temporary occurrence, he clearly had another dynamic process in mind; these distributions are not instantaneous, but they are defined over a certain period of time. This view was also held by Backhuys (1968). Survival chances never remain the same, but they fluctuate in time. In the central parts of the distribution conditions are thought to be optimal and to fluctuate least, and they may become less and less favourable and stable the farther away from these central conditions. This implies that the population's extinction probabilities gradually increase towards the margin of the distribution. Central populations may fluctuate only a little from year to year, but they can always be found and hardly run the risk of extinction. This may differ in marginal populations, showing more violent fluctuations (cf. Klages, 1942), and they may die out more frequently.

To obtain a more complete picture of these two dynamic processes of diffusion and the probability of extinction, one can think of an extension of Carter & Prince's (1981) epidemic model, that in their case explains processes at range margins only. In their paper they distinguished a number of sites from which seeds are disseminated (y), the dissemination rate (β) from these sites to a number of new, unoccupied sites (x), and the rate of extinction (γ) at each occupied site. In a more general application of their model, covering the whole distribution range instead of the margins only, one can think that in the centre y is great and x low, whereas the reverse holds for marginal locations. The dissemination rate β may be constant over the whole range, although it may be less effective near the margin, where there are less populations, lying at greater distances from each other. Finally, the rate of extinction may increase from the central areas to the margins of the distribution range because of a gradual decrease in natality and an increase in mortality. All parameters determining these processes may either be more or less constant, fluctuating only within narrow limits, or they may fluctuate widely, being subjected to chance. In the first case, when they are more or less constant, there is little difference between Van Steenis' (1961) zone of permanent occurrence and the zone of temporary occurrence, all populations being more or less permanent. But when the aspect of chance fluctuations gradually increases, the less constant the parameter values become, and the wider the zone of temporary occurrence becomes. The extreme case, though not

at all exceptional or unlikely, is that all populations are more or less temporary, the central ones included.

I think this extension of Carter & Price's (1981) epidemic model may give the best mathematical picture of the processes Van Steenis (1961) had in mind when formulating his idea about the causal mechanism of the elevation effect, although this effect itself was not borne out by Backhuys' (1968) data.

CONCLUSIONS

These considerations lead us to conclude that Backhuys' (1968) data demonstrate the existence of the elevation effect, but they do not sufficiently show the supposed explanation, or the biological reason, given by Van Steenis and by Backhuys in Swiss plant species. However, the ideas explaining the elevation effect add considerably to the concept of altitudinal distributions of the frequency of occurrence of plant (and animal) species in terms of dynamic responses to environmental conditions in space. This dynamic situation can be formulated in a model that separates the static aspects of the physiological response from the dynamic ones of the spatial distribution among various locations. As such, these different components of the whole process generating these frequency distributions can now be tested in the field.

ACKNOWLEDGEMENTS

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