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# The individualistic and community-unit concepts as falsifiable hypotheses*

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## Abstract

This study reformulates the community-unit and individualistic concepts of plant communities as hypotheses concerning the distribution of species' boundaries along a gradient. These hypotheses are tested by an analysis of deviance on data derived from a direct-gradient analysis of a freshwater marsh plant community in Breckenridge, Quebec, Canada. Boundaries are clustered at certain intervals along the gradient ($p<0.001$), contradicting the individualistic hypothesis. Upper boundaries are not consistently clustered at the same intervals as lower boundaries ($p<0.001$), contradicting the community-unit hypothesis. Thus, neither of the two usual models of community structure explain the patterns found in Breckenridge Marsh, suggesting that the historical dichotomy is too limited. Hypotheses of pattern should be tested using inferential statistics. Hypotheses of mechanism should be tested by experimentation. The way out of the community-unit vs. individualistic community debate is to deny the dichotomy and to consider multiple working hypotheses of community structure.

## Introduction

The debate concerning of nature of community organization has continued sporadically for more than 70 years (see Whittaker, 1962 for a review of the controversy). The Clementsian interpretation (Clements, 1916), also called the 'community-unit concept' (Whittaker, 1975) was accepted by the majority of ecologists during the first part of this century. The works of Cain (1947), Egler (1947), Mason (1947), Whittaker (1951, 1956, 1967) and others quickly converted the majority of anglo-american community ecologists (McIntosh, 1967, 1975) to the 'individualistic concept' of community organization based primarily on the ideas of Gleason (1926, 1939). This transition to an individualistic viewpoint was due in part because, by using direct or indirect gradient analysis (Whittaker, 1967, the observed pattern of species replacements along a gradient was stated to be inconsistent with the patterns predicted by Clements.

In the context of testing between the two concepts mentioned above, direct gradient analysis still suffers from the problem of using subjective methods of analysing the observed patterns by failing to use inferential statistics to compare empirical data to the proposed models. In other uses of direct gradient analysis, Austin *et al.* (1984) have shown how Generalized Linear Modeling may be used to

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* Nomenclature as in Gleason & Cronquist (1963), Manual of vascular plants of northeastern United States and adjacent Canada, Boston, unless otherwise indicated except for the the grasses which are from Dore & McNeill (1980), Grassses of Ontario, Quebec.

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test between competing hypotheses concerning species ecological response curves, but their method cannot be used directly to test between the community-unit and individualistic concepts (see also Austin, 1987).

In this paper we use a direct gradient analysis (Whittaker, 1967) of the emergent vegetation of a freshwater marsh to obtain data on the distribution of species' boundaries relative to a gradient-complex of water depth. After stating falsifiable hypotheses based on the predicted patterns of the individualistic and community-unit concepts, the observed pattern of boundaries along the gradient is compared to these hypotheses using an analysis of deviance (McCullagh & Nelder, 1983).

## Hypotheses for the patterns implied by the two concepts

The community-unit concept claims that when species' distributions are plotted along some gradient or gradient-complex whose rate of change is constant, there exist groups of species. i.e. 'communities', which replace themselves along the chosen gradient (Whittaker, 1975). Within each grouping most species have similar distributions and the end of one group coincides with the beginning of another (Fig. 1).

The individualistic concept states that 'centers and boundaries of species' distributions are scattered along the environmental gradient' [Whittaker, 1975]. No distinct groups of species are predicted to exist therefore precluding the coincidence of one group with another.

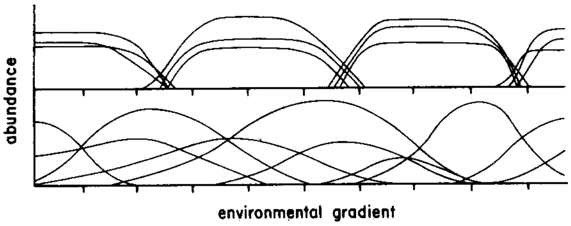


*Fig. 1.* Predicted distributions of species along an environmental gradient, according to the two concepts. Above: the community-unit concept; below: the individualistic concept (after Whittaker, 1975).

Following Pielou (1975, 1977), explicit hypotheses of these two concepts are formulated using the following terms: define *'upper boundary'* as that point on the gradient where the distribution of a species (*not* a group) begins relative to an arbitrary direction on the gradient. Define *'lower boundary'* of a species as that point on the gradient where its distribution ends.

The individualistic hypothesis states that:

(i) the average number of boundaries (both upper and lower) in each interval of the gradient should be equal except for random variation about the mean;

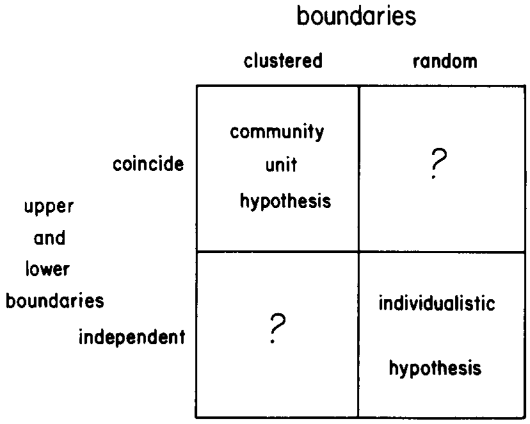
(ii) the number of upper boundaries per interval of the gradient should be independent of the number of lower boundaries.

The community-unit hypothesis states that:

(i) there should be significantly more boundaries (both upper and lower) in some intervals of the gradient than in others, i.e. boundaries are clustered;

(ii) the number of upper and lower boundaries per interval should increase and decrease together along the gradient.

The patterns predicted by these hypotheses are shown in Fig. 2. Note that the 2×2 table suggests at least two other possibilities for patterns along a gradient, as pointed out by Whittaker (1975).



| | | boundaries | |
|---|---|---|---|
| | | clustered | random |
| upper and lower boundaries | coincide | community unit hypothesis | ? |
| | independent | ? | individualistic hypothesis |

*Fig. 2.* The number of community patterns which could be obtained from species whose boundaries are either (a) randomly distributed or clustered and whose upper and lower boundaries are either (b) coincident or independent. Note that the two historical community concepts do not exhaust the possibilities shown.

## Methods

The study site is near Breckenridge, Quebec, which is approximately 40 km northeast of Ottawa, Ontario, Canada (45°48′00′′N, 45°57′30′′W). This marsh occurs on a very gently sloping shoreline. On the highest ground is a forest dominated by *Acer saccharinum* which is flooded during the high water period each spring. The study site itself consists only of herbaceous emergent species (see Fig. 4); this portion of the marsh extends for ca 200 m although not all of this section of marsh was actually sampled. Beyond 200 m from the edge of the tree canopy, floating leaved species such as *Nuphar variegatum* and *Potamogeton* spp. are found, giving way finally to submerged vegetation. There are no obvious vegetational discontinuities in this marsh; it is not at all like stepping off a bank and into the river bed. Furthermore, the section of the marsh actually studied was well within the average annual upper and lower water levels for this section of the river. Since many abiotic environmental factors are correlated with water depth (e.g., Hutchinson, 1975; Spence, 1982; Keddy, 1985) there are no obvious abiotic discontinuities either.

To obtain a random sample of the emergent community a 200 m line was established running along the edge of the tree canopy and divided into 5 m segments. Thirteen of these segments were chosen using a random number table to be the locations of belt transects running down into the marsh. Each transect was therefore at least 5 m distant from any other transect.

The water level on 24 July 1984 was marked and will be called the 'standard zero' water level; this corresponds to a Geodetic height (Water Survey of Canada) of 58.40 m based on water level records from the Brittania Bay, Ontario measuring station (number 02KF005) located in the same drainage basin. Using a surveying level, each transect was divided into 5 cm height intervals based on the standard zero mark. Each transect was surveyed down to a height of -40 cm and up to, but not including, the edge of the tree canopy. Transects were not extended into the forested region to avoid the confonding affect of an animal runway. Because the edge of the tree canopy varied along the marsh, the upper limit of each transect corresponded to a height of from 30 cm to 15 cm above the standard zero mark.

Transects were censused in the order in which they had been randomly chosen and in each 5 cm height interval of all transects the presence or absence of all species was recorded. All species found in the section of the marsh actually surveyed were herbaceous emergent plants; no transects penetrated into the region of the marsh containing floating-leaved or submerged vegetation.

Voucher specimens for all species were collected and sent to the Systematics Division of Agriculture Canada for verification and deposited in their herbarium (DAO). Note that two species, *Lysimachia terrestris* and *Lysimachia thyrsiflora*, could not be separated in their vegetative state and were therefore grouped together as *Lysimachia* spp.

In order to determine the location of boundaries it had to be assumed (Pielou, 1977; Underwood, 1978; Keddy, 1983) that a gap in the distribution of a species along a transect did not represent a true disjunction. In reality, only species that were uncommon in the marsh showed such gaps and so it seems reasonable to accept such an assumption. If the highest height interval censused contained a species then the upper boundary for that species could not be determined, nor could the lower boundary be found if the species was present in the lowest height interval censused. Finally, if a species had both its upper and lower boundary in the same height interval it was excluded from the analysis to avoid a bias in part (ii) of the two hypotheses.

The procedure described above yields a contingency table consisting of the number of upper and lower boundaries found in each relative height interval of each transect. These data were analysed by an analysis of deviance (Karson, 1982; McCullogh & Nelder, 1983).

An analysis of deviance is analogous to an analysis of variance but is not restricted to assumptions of normality in the error structure of the model. To test for significant systematic components of the data, one looks at the difference between the deviance of the data from a model not incorporating the factor of interest and the deviance of the data from a model in which the factor is included. The deviance is measured using the log-likelihood ratio, or $G^2$, which is asymptotically distributed as a chi-squared variate. Since the contingency table is three-dimensional, all but the third order interaction term is tested using marginal totals [Sokal & Rohlf, 1981]. In this study, all marginal totals were larger than five and so the (null) assumption of a chi-squared distribution for $G^2$ is reasonable. See Austin *et al.* (1984) for a brief description of analysis of deviance and Generalized Linear Models in general.

Part (i) of the two hypotheses can be evaluated by testing for a main effect of relative height along the gradient; if this effect exists then there are significantly more boundaries in some height intervals than in others. The interaction term between the type of boundary (upper or lower) and relative height is used to evaluate part (ii) of the two hypotheses. If this interaction term exists then the number of upper and lower boundaries per height interval does not increase and decrease together.

Since we collected data using relative neight intervals, the actual distance of marsh included within an interval may vary depending on the slope of the shore; for instance, in Breckenridge Marsh the height intervals had distances from a minimum of 0.8 m to a maximum of 19.1 m. If boundaries are randomly distributed along the relative height gradient but some intervals are correlated with longer distances, then a spurious clustering of boundaries would be found. To solve this problem the distance occupied by each height interval was included as a covariate and its effects removed.

Finally, it should be noted that only one marsh was studied and so no inferences should be made concerning between-marsh patterns.

The Genstat V statistical package was used and the data were analysed on the Agriculture Canada computer network.

## Results

Both upper and lower boundaries are clustered ($p < 0.001$; Fig. 3). The individualistic hypothesis is therefore rejected. As well, there was a significant interaction between the type of boundary (upper or lower) and the main effect of relative height on the gradient, indicating that the pattern of clustering with respect to upper boundaries differed from the pattern of clustering amongst lower boundaries along the gradient ($p < 0.001$, Table 1). In fact, there was no correlation between the number of upper and lower boundaries per relative height interval ($r = 0.009$, $p > 0.38$). We must therefore reject the community-unit hypothesis as well.

*Table 1.* Analysis of deviance of the boundary distributions in Breckenridge Marsh, Quebec, Canada. The 'change of deviance' column tests the significance of each term in improving the goodness-of-fit in each successive model. **: $p < 0.001$; n.s. $p > 0.05$.

| Terms | d.f. | residual deviance | d.f. | change of deviance |
|---|---|---|---|---|
| Constant | 297 | 433.4 | - | - |
| Interval length (covariate) | 296 | 420.5 | 1 | 12.8** |
| Height interval | 283 | 365.0 | 13 | 55.6** |
| Boundary type | 282 | 364.0 | 1 | $1.0^{\text{n.s.}}$ |
| Height interval × Boundary type | 269 | 293.7 | 13 | 70.3** |

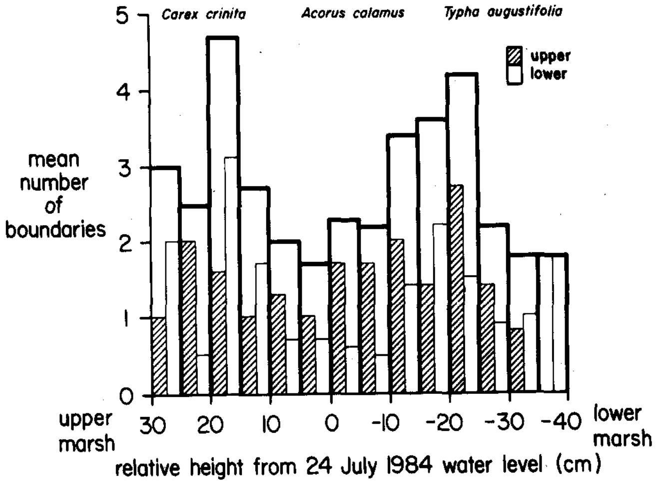


*Fig. 3.* The mean number of species boundaries in each 5 cm height interval plotted against relative height. Within each rectangle the mean number of upper boundaries (hatched) and lower boundaries (clear) are shown.

Although the covariate, the actual distance of marsh included in each interval, was significant (Table 1), the effect was to increase the importance of clustering along the gradient since when the covariate was excluded from the analysis, the change of deviance due to relative height was decreased from 55.6 to 43.5. This is because some of the longest relative height intervals contained very few boundaries. In any case, the amount of deviance explained by the covariate was small.

In order to better visualize these results, Fig. 4 shows the distribution of each species plotted against relative height in the marsh, averaged over the 13 transects. It can be seen that there exists one group of species (from *Lycopus uniflorus* to *Lysimachia nummularia*) which all reach their lower distributional limits in the interval from 10 to 20 cm. Equally important is the absence of any species whose distribution begins at this part of the gradient. In the interval from -10 to -25 cm there occurs another group of species (from *Iris versicolor* to *Carex vesicaria*) who all reach their lower distributional limits. Here there also exists a group of species simultaneously beginning their distribution (from *Sparganium eurycarpum* to *Penthorum*

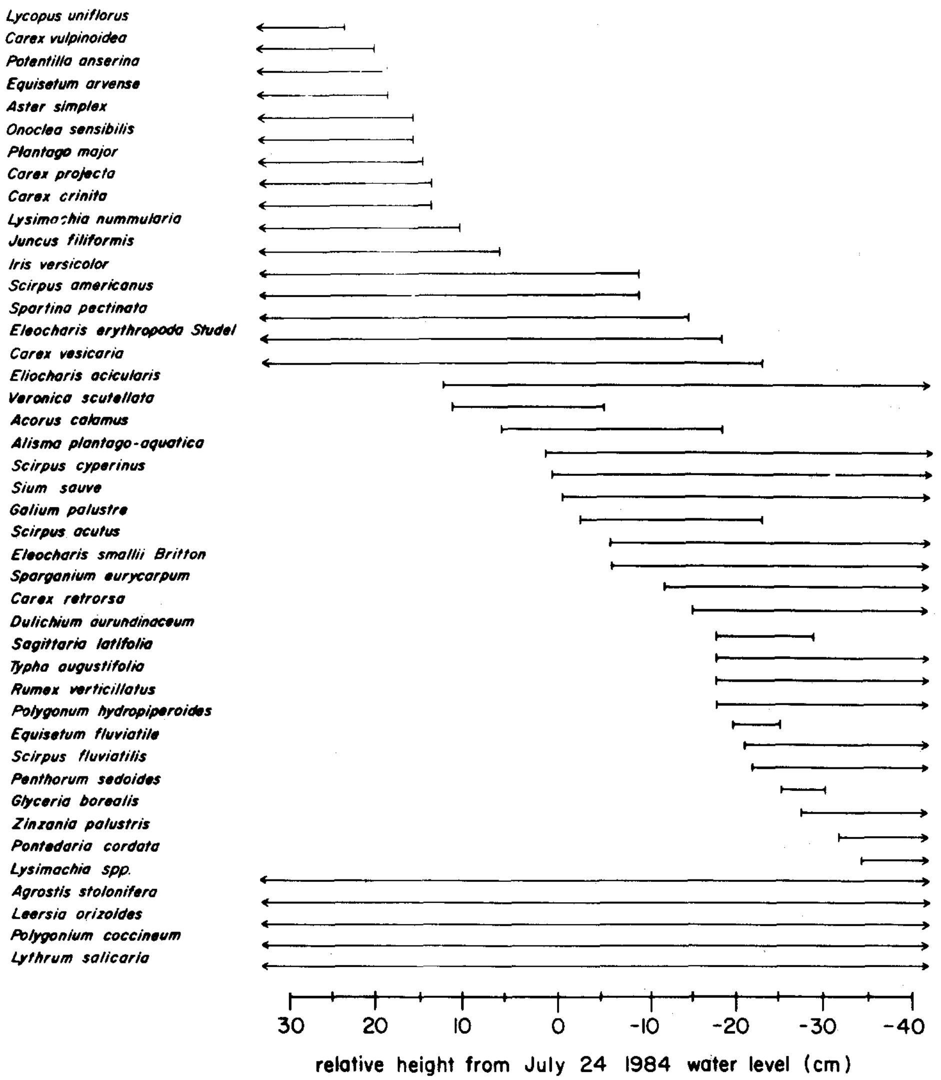


*Fig. 4.* The distribution of all plant species occurring in at least two transects, relative to the height gradient (upper marsh to the left, lower marsh to the right). These distributions are determined by calculating the average position of each species' upper and lower boundaries over the thirteen transects.

*sedoides*). It is this disconcordant pattern of upper and lower boundaries that causes the interaction term in Table 1.

In order to compare these results with those of other studies, we have computed Underwood's (1978) statistic. Using that test, lower boundaries are again found to be clustered ($p < 0.01$) but upper boundaries appear to be randomly distributed ($0.1 > p > 0.05$). Underwood's test is conservative in that it often fails to detect non-random patterns, which explains the differences between the results of the two tests.

## Discussion

In order to relate the results of this study to the debate concerning the individualistic and community-unit concepts it is necessary to consider the argument both from the perspective of pattern and from the perspective of the mechanism (see Austin, 1985, 1987).

### Hypotheses of pattern

The debate concerning pattern has usually been structured as a dichotomous choice between the predicted patterns of the community-unit and individualistic concepts (Curtis, 1955; Gleason, 1926; McIntosh, 1967; Whittaker, 1951; but see Whittaker 1975 for an exception). Such a dichotomy is misleading however, because it implies that evidence contradicting one expected pattern can be interpreted as evidence supporting the other. Such reasoning has been used to support the individualistic concept (Curtis, 1955; Whittaker, 1951, 1967). If we recognize that the two predicted patterns do not exhaust the number of possible patterns available (Whittaker, 1975) then one can no longer rely on negative evidence to support either of the two usual concepts of community organization along a gradient.

In this paper we have shown that the distribution of the species in Breckenridge Marsh are non-random, but do not correspond to the patterns predicted by the community-unit hypothesis. This demonstrates that the historical dichotomy is too limited, but might also be taken to suggest that Breckenridge Marsh is exceptional, since the results disagree with a large body of evidence apparently demonstrating individualistic distribution patterns (for example: McIntosh, 1975; Whittaker, 1962, 1975). Although this may be true, there are two reasons to believe that such a conclusion should be questioned.

First, the only other study in which both direct-gradient analysis and inferential statistics was used (Keddy, 1983) found boundary clustering in a lakeshore plant community. Three other studies have used inferential statistics to test boundary distributions, although the species ranges were not obtained using direct gradient analysis. Of these, Pielou & Routledge (1976) found clustering, Underwood (1978) found a random distribution, and Dale (1984) found a contiguity of upper and lower boundaries.

Second, the studies supporting the individualistic concept did not use inferential statistics to compare observed patterns with those predicted by the observed patterns with those predicted by the individualistic hypothesis and therefore may have failed to detect true non-random patterns. By subjectively scanning the distributions of many species along a gradient by eye, all but the most pronounced structure of such data would appear random, therefore biasing conclusions in favour of the individualistic concept.

### Using pattern to deduce mechanism

In this paper we study the pattern of species' ranges relative to an obvious environmental gradient, but make no attempt to interpret our results as a test of any causal hypotheses. In the context of this debate however, pattern has generally been used to prove or disprove proposed mechanisms of community organization (Clements, 1916; Gleason, 1926; Whittaker, 1951, 1975). Certain assumptions are combined to produce a model of community organization, predicted patterns are derived as logical consequences of the model, and then the observed patterns of natural communities are compared with those predicted by the model. If the observed and predicted patterns are different then the underlaying mechanistic model is assumed to be wrong. If the observed and predicted patterns are similar then the underlaying mechanistic model is assumed to be correct (Whittaker, 1951). The problem with such an approach is that, given the large number of abiotic, biotic, and interactive factors to choose from, there are so many degrees of freedom that many different causal mechanisms could all 'explain' the same empirical pattern.

Consider our demonstration of boundary clustering in Breckenridge Marsh. This can be made consistent with the individualistic hypothesis by assuming that there are one or more abiotic factors which change rapidly at those points on the gradient where boundaries are clustered. There exists in Breckenridge Marsh, as in all natural communities, many abiotic factors which could possibly explain such a pattern: the degree of anoxia due to flooding or to ice cover, the degree of moisture stress when the water level falls, changes in any one of many mineral nutrients or ratios of nutrients, disturbance due to ice damage or wave action in the spring, and so on. If it is possible to find a correlation of boundary clustering with a rapid change in any one of the large number of abiotic factors to choose from, should this correlation be interpreted as agreement with the individualistic concept? If some other abiotic factor is shown to change rapidly in a section of the marsh where there are relatively few boundaries, should we then conclude that the individualistic concept is still correct but that the factor in question plays no causal role? By arguing in such a way we render the individualistic concept unfalsifiable at the level of pattern analysis.

The problem is not solved by choosing strong environmental gradients such as the altitudinal gradient up mountainsides (Whittaker, 1951, 1956) or the gradient of relative water depth in a lake (Keddy, 1983) or in a marsh, in which many abiotic gradients are correlated to produce a gradient-complex. This is shown in Fig. 5 where the distributions of various species are plotted along a hypothetical gradient, together with the values of two abiotic factors. If one were to do two different direct-gradient analyses of this 'gradient', then relative to factor A the boundaries would be clustered but relative to factor B the boundaries are regularly spaced. These two different results are obtained even though the two factors are positively correlated. Thus, the problem remains: the individualistic hypothesis is unfalsifiable when using pattern to deduce mechanism.

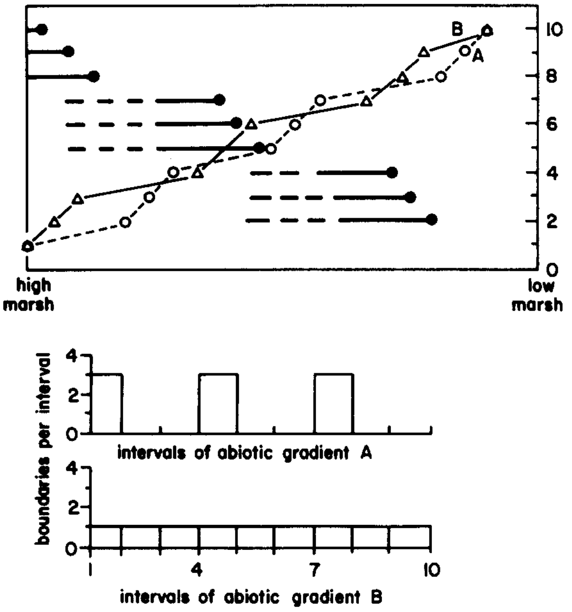


*Fig. 5.* (a) Field distributions of nine species plotted in a hypothetical gradient along with the values of two correlated abiotic factors. (b) Distribution of species' boundaries obtained from direct-gradient analyses of this marsh relative to the two abiotic factors.

### *Hypotheses of mechanism*

Whereas hypotheses regarding pattern can be tested using inferential statistics, hypotheses regarding mechanisms must be tested with experiments. Levins & Lewontin (1982) and Simberloff (1982b) restate the assumed mechanisms producing individualistic communities in an experimentally testable form. In Simberloff's words: 'species are individually distributed according to their interactions with their physical surroundings and ... only upon falsification of this hypothesis ought one to move on to more complex (physical environment × other-species interaction) ones'. Such a hypothesis has the advantage of not only being falsifiable but, contrary to Simberloff (1982a, b), has actually been falsified in many field experiments. These experiments test the assumed mechanism and not the predicted patterns which may arise as logical consequences from the mechanisms.

Sharitz & McCormick (1973) have demonstrated that the distribution of *Sedum smallii* on granite outcrops in the southeastern United States is controlled by a complex interaction of abiotic factors and competition with *Minuartia uniflora.* One boundary of *S. smallii* on these outcrops is determined by moisture stress and shallowness of the soil. The other end of its distribution is controlled through competitive exclusion from *M. uniflora.* Studies on the rocky intertidal zone (Connell, 1972; Lubchenco, 1980; Paine, 1984) have also demonstrated the importance of both biotic factors as well as interactions between biotic and abiotic factors in determining the structure of such communities.

Grace & Whetzel (1981) give evidence that the distribution of *Typha angustifolia* is partly determined by competition with *Typha latifolia* in the ponds which they studied. Silander & Antonovics (1982), in a series of removal experiments, showed that the distributions of most of the plant species in a coastal plant community were profoundly affected by the types of neighbours that were removed. Snow & Vince (1984) and Vince & Snow (1984) used transplant experiments in an Alaskan salt marsh to demonstrate the interaction of biotic and abiotic factors in determining the structure of that community. Other papers reaching similar conclusions were reviewed by Connell (1983) and Schoener (1983). Finally, Turkington & Aarssen (1984 and references therein) present evidence that biotic interactions can produce coevolutionary differences between local genotypes, depending on the types of species which each interacts with, therefore biotic interactions may affect community structure on an evolutionary timescale as well.

There is therefore a large body of evidence which falsifies the causal assumptions of the individualistic concept and demonstrates integrated, that is causally dependent, responses of species within a community.

Hypotheses of pattern should be tested using inferential statistics. Hypotheses of mechanism should be tested by experimental manipulations, making sure not to equate correlation with causation (Levins & Lewontin, 1982). The way out of the community-unit vs. individualistic community debate is to deny the dichotomy and to consider multiple working hypotheses of community structure.

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