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Faunal replacement and longitudinal zonation in an alpine stream

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With 2 figures and 2 tables in the text

Introduction

As one proceeds along an altitudinal gradient species replacements typically occur, so that the species list at one location may have little in common with the species list at another location some distance along the gradient. This observation is common to a wide variety of communities and has been well studied with plants (cf. WHITTAKER 1967) and birds (TERBORGH 1971) as well as in lotic environments. Perhaps because running water communities are so obviously environmental gradients a substantial number of biologists have studied longitudinal zonation in streams and proposed classifications schemes (see MACAN 1961; HYNES 1970 for reviews). I describe a new method for analysing faunal replacement originally proposed by TERBORGH (1971) and applied to an alpine stream community by ALLAN (1974). Finally I suggest the adoption of an index which utilizes the rate of faunal turnover to calculate the distance in vertical elevation to 50 % replacement of the community, and compare values calculated from a variety of running water environments.

Theoretical approaches to the analysis of faunal replacement

Past workers have utilized a variety of descriptive and classificatory approaches. These include attempts to describe types of watercourses, divisions into zones, and classification in accordance with the substratum (ILLIES & BOTOSANEANU 1963). DODDS & HISHAW (1925) attempted to relate the distributional patterns of aquatic insects to major vegetational zones, with some success. HUET (1959) has proposed fish zones with their dominants, and considered the relationship of these zones to river slope. The question remains, however, whether a gradation or continuum might better represent reality than the attempt to delineate biocoenoses, as considerable change may occur within a "zone" (MACAN 1961; HYNES 1970). A similar conundrum arises in plant gradient analysis (MCINTOSH 1967; WHITTAKER 1967). Nevertheless, species replacements do occur and the controlling mechanisms remain largely a mystery. Some workers have suggested gradual longitudinal changes in temperature, substratum, water chemistry and the like (MAITLAND 1966). Competitive replacement of similar species has been implicated (ALLAN 1974; BEAUCHAMP & ULLYOT 1932; BISHOP 1973; MAITLAND & PENNEY 1967), as well as the boundary between major habitat zones (DODDS & HISHAW 1925).

Most observations concerning the replacement of species along a gradient can be placed in one of three models (TERBORGH 1971). (1) Distributional limits of species on a gradient are determined by factors in the physical or biological habitat that vary continuously and in parallel with the gradient (gradient model). (2) Distributional limits are determined by competitive exclusion (competition model). (3) Distributional limits are determined by environmental discontinuities (ecotone model). Each model makes unique predictions when data are combined on the measures: population density curves, mutual exclusion, amplitude compression and faunal congruity curves. Population density curves are simply total numbers of each species plotted against altitude, distance or some other measure of the gradient. Mutual exclusion describes the event that where a pair of species meet their ranges may be sharply truncated, indicating a boundary maintained by competition. The evidence is particularly strong if the pair are congeners. Amplitude compression is where the mean range of closely related pairs which sequentially replace one another is less than the average range of the total collection. The mean range of replacing triplets should be less than the mean range of replacing pairs of congeners. Faunal congruity curves are calculated by determining the per cent of species found at a particular station which occur at higher and lower stations along the gradient. Tab. 1 indicates how the three models may be separated based on the above measures.

Tab. 1. A comparison of three models each predicting the pattern of faunal replacement along an environment gradient. Predictions unique to each model are in italics. After TERBORGH (1971).

Distributional feature	Model (1) Gradient	(2) Competition	(3) Ecotone
Population density curve	± normal	*repulsion interaction*	*truncation*
Mutual exclusion	none	*yes*	none
Amplitude compression	none	*yes*	none
Faunal congruity curve	smooth, symmetrical	smooth, symmetrical	*discontinuous*

It should be noted that the method of ILLIES (1953) in which he determined the number of species from each sampling station which were also represented in stations progressively further away from the reference station is essentially the same as a faunal congruity curve, except that ILLIES utilizes absolute numbers rather than percentages. THORUP (1966) criticized ILLIES' method as putting undue emphasis on the heights of the peaks (= absolute number of species), and BISHOP (1973) introduced per cent similarity measures to standardize comparisons in his study of the River Gombak.

Faunal replacement in an alpine stream

Cement Creek, Gunnison County, Colorado is a tributary of the East River watershed. Originating in snow melt at 3,600 m, Cement Creek receives no major tributaries and increases gradually in volume without changing substantially in stream type as it flows toward its confluence with East River at 2,602 m. The substratum is quite similar throughout the stream's length, consisting of pebbles, cobbles and boulders. Vegetation along its valley may be divided into three broad zones (following LANGENHEIM 1962): (1) upland herb above timberline at 3,475 m, composed of tall grasses, sedges and erect forbs; (2) spruce-fir coniferous forest from 3,475 m to about 3,200 m, composed primarily of Engelman spruce *(Picea engelmanni)* and sub-alpine fir *(Abies lasiocarpa)*; and (3) an aspen community type below 3,200 m, dominated by aspen *(Populus tremuloides)* but including a diverse mix of coniferous and deciduous vegetation. Scrub willows (*Salix* spp.) are the predominant river bank vegetation throughout.

The distributions of aquatic insects in Cement Creek were studied from 15 June to 10 July 1972 and 15 June to 10 August 1973. Sixteen sampling stations were located over the 24 km length of stream spanning 1,000 vertical meters. Benthic insects were collected with a kick net and SURBER sampler (mesh = 0.5 mm). All members of the

Ephemeroptera, Plecoptera, Trichoptera and Coleoptera were identified to species and enumerated. Of the 36 species collected, 27 were sufficiently common for analysis. Extremely rare species were not included as any statement concerning their distributions would be highly conjectural.

Results

If the ecotone model is correct, substantial faunal replacement should occur coincident with the boundaries between vegetational zones at 3,475 m and 3,200 m. Faunal congruity curves are presented for 6 of the 16 possible stations (Fig. 1), as the results were consistant for all. These curves do not exhibit any major discontinuities at the expected elevations, but appear to show rather gradual faunal replacement. The curves fall steeply at the upstream terminus (arrow A) as only a few species were able to survive at snow melt. A minor discontinuity or zone of rapid faunal replacement occurs ca. 2,800 m, corresponding to a canyon region of extreme turbulence (arrow C).

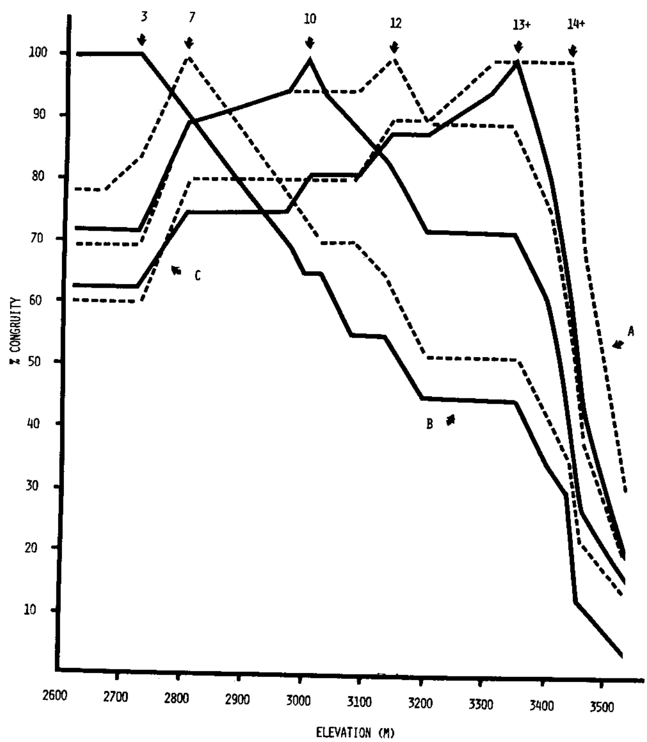

Fig. 1. Faunal congruity curves representing the degree of faunal replacement along the elevational gradient of Cement Creek. Each site is taken in turn as a reference point and the similarity of faunal lists at all other sites is expressed as a percentage of the faunal list at the reference site. Arrow A denotes rapid faunal depletion at the upper terminus, Arrow B the ecotone between aspen and spruce-fir, and Arrow C a steep canyon region.

To test the competition model, the population density curves were examined for evidence of mutual exclusion among congeners. Four species of *Ephemerella*, two species of *Rhithrogena* and seven species of *Rhyacophila*, or 13 out of the 27 species in the total analysis, were considered as potential competitors. Evidence of mutual exclusion was strongest in the two species of *Rhithrogena* (Fig. 2), but two each of *Ephemerella* and *Rhyacophila* also indicated exclusion. Thus between 2 and 6 out of 27, or 7—22 % of the community appeared to have their ranges determined by interspecific competition. The remainder must be attributed to the gradient model.

Fig. 2. Total numbers of the mayflies *Rhithrogena hageni* and *R. robusta* from 12 Surber samples and kick sample combined, 1973.

Terborgh's (1971) suggestion that altitudinally replacing species will possess ranges which are less than the average for the entire community (amplitude compression) was not borne out. Population abundance curves of many aquatic insects in Cement Creek were skewed in the downstream direction, presumably the result of immature drift. The upstream species of *Rhithrogena* maintained a presence throughout the range of the downstream species, but not the reverse. This pattern may prove to be common in replacing congeners of stream insects, and is explainable in terms of recent theory (Horn & MacArthur 1972) which utilizes high imigration rates to maintain the competitive coexistence of an inferior competitor in the habitat of its superior competitor. As a result the ranges of replacing congeners do not show amplitude compression.

Trout populations were surveyed by electrofishing to determine if their distribution affected insect distribution. Trout zonation occurred with *Salmo clarki*, *Salvelinus fontinalis* and *Salmo trutta* replacing one another downstream. Some overlap occurred and typically included the largest individuals of the downstream replacing species. The replacement of one trout species by another did not appear to influence faunal replacement of the insect community. Nor did the boundary between regions with trout and an upper trout-free zone. However, a pronounced effect on total abundances was indicated, as numbers of benthic insects were 2 to 6 times higher in the trout-free headwaters.

A comparison of faunal replacement patterns

The above analysis incorporates the assumption that faunal replacement is strongly influenced by biotic interactions among the stream inhabitants. We may then ask whether these interactions are of similar intensities under different conditions, latitudes and altitudes. For example, the contention that the tropics are richer in species might suggest more biotic interactions and more rapid replacement. Thus an index suitable for comparing faunal replacement is needed.

I suggest utilizing the slope of faunal congruity curves plotted against vertical elevation as a rate of faunal replacement. This may be calculated as % faunal replacement per vertical meter, or inversely, as the distance to 50 % replacement of the fauna of a particular station. At least two potential biases should be recognized. Failure to separate similar species which altitudinally replace one another will underestimate faunal replacement and result in too large an estimate of the distance to 50 % replacement. The exclusion of rare species from analysis may have the same effect, as rare species will often be quite restricted in their range.

Tab. 2. Distance to 50 % faunal replacement in vertical meters, calculated from the slope of faunal congruity curves. All data are for aquatic insect communities unless otherwise designated.

River	Distance to 50 % faunal replacement (vertical meters)	Highest elevation in study (m)	Locale	Reference
Ariba R.	~ 550	550	Trinidad, W. I.	Hynes 1971
Cement Creek	~ 500—1,000	3,500	Colorado, U.S.A.	Allan 1974
Fulda R.	~ 125	700	Germany	Illies & Botosaneanu 1963
Gombak R.	~ 125	250	Malaysia	Bishop 1973
Gombak R. (algae)	~ 30			
Gombak R. (pisces)	~ 100			

I have calculated the distance to 50 % faunal replacement for several rivers (Tab. 2). The alpine stream exhibited much larger values, with distances to 50 % replacement in the order of 500 m in the upstream direction, and 1,000 m downstream. The lower values were simply the result of the upstream terminus of Cement Creek at snow melt, and the values of 1,000 m should be more representative. I have argued elsewhere (Allan 1974) that this aquatic insect community was "loosely packed" (MacArthur 1972); that is, the level of biotic interactions was low. Most species clearly differed in trophic role, substratum preference, body size or altitudinal range. A low rate of faunal replacement may be characteristic of loosely-packed communities of alpine regions.

The Ariba river also suggests a low rate of faunal replacement while the Fulda and Gombak are similarly high. In the absence of more complete data any interpretation must be highly speculative. Conceivably the lower rate of faunal replacement for the Trinidadian river may be a case of "ecological release" typical of islands where species richness is reduced relative to mainlands (MacArthur 1972).

As Bishop (1973) presents faunal congruity curves for different trophic levels it is possible to compare their replacement rates. Bishop's data indicate that algae exhibit a greater degree of uniqueness to a particular station than do other components of the community. The flora is 50 % replaced in only 30 vertical meters of elevation (Tab. 2). Fish are intermediate but show 50 % replacement in a distance more similar to that of the insect fauna. It would be interesting to compare herbivorous and piscivorous fish in this regard.

Conclusions

Whether one chooses to view the longitudinal distribution of organisms in streams as a collection of discrete communities (biocoenoses) or as a gradual gradation, the phenomenon of species replacement remains. The methods described herein for evaluating species replacement shift emphasis from a community-continuum debate to quantitative comparisons of the roles of ecotones, competition and subtle gradient effects, and provide a basis for comparing the rate of species replacement in different streams.

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Discussion

CHUTTER: What mesh net was used on your SURBER sampler?

ALLAN: .50 mm mesh. The kick net was .65 mm mesh.

MARGALIT: What sampling techniques were used in your experiments?

ALLAN: 12 SURBER samples and a kick sample at each site. The species list was further supplemented by colonization experiments reported elsewhere.

POTTER: The 36 species you report seems low even for that elevation.

ALLAN: Addition of dipterans, which I excluded, and sampling in seasons other than summer, would both increase the faunal list.