

THE USE OF CONVERGENCE AND DIVERGENCE IN THE  
INTERPRETATION OF ADAPTATIONS IN HIGH-MOUNTAIN BIOTA (\*)

Stéphan Halloy (\*\*)  
Fundación Miguel Lillo  
Miguel Lillo 251  
4000 Tucumán-ARGENTINA

Received September 27, 1982; July 5, 1983

RESUMEN: El uso de la convergencia y divergencia para la interpretación de las adaptaciones en biotas de alta montaña.

El método propuesto consiste en la comparación, correlación y análisis de regresión entre caracteres y factores en distintas localidades, donde las dimensiones de esos caracteres y factores se hagan cada vez más semejantes o más dispares. Como primera medida deben conocerse bien una serie de datos taxonómicos, históricos, físicos, etc., de los organismos y localidades en estudio. Para tal fin se proponen 20 premisas y se discuten algunos problemas básicos del proceso evolutivo. Luego se proponen cuatro modelos independientes con los cuales se pueden eliminar sucesivamente distintos tipos de factores, llegándose a corroborar la importancia de alguna relación carácter-factor; relación que se supone entonces debida a evolución por selección natural de los caracteres adecuados. El método es apto para ser usado en todo tipo de ambiente y puede someterse a tratamiento estadístico.

ABSTRACT: A method is proposed to determine presence of true adaptations originating by natural selection from characters of any other origin. Comparison, correlation and regression analysis between character and factor levels in different localities, seeking for increasing or decreasing distances between these levels, whether over a continuous gradient or not. A good amount of data from the localities and organisms studied are necessary (e.g. taxonomic, historic, physical, and so on). Twenty premises and a discussion of a few basic evolutionary processes considered problematical are proposed to facilitate the search for relevant data. Four independent working models are proposed, with which different types of factors can be successively eliminated so as to pinpoint and later corroborate a real evolutionary character-factor relationship. This causal relation is supposed to be due to natural selection of the adequate characters. The method can be used within any type of habitat and geographical region, and it is possible to use statistical treatment with good results.

\* \* \* \* \*

#### INTRODUCTION

Without convergence and divergence (evolution in short) we would have very little evidence to prove that organisms really adapt to their environment, or to interpret possible adaptations in fossil organisms.

When we see how a character "works" we can guess at what it was "made for". But only by investigating the same character in other contexts (organic or inorganic) may we be reasonably sure about conclusions. Otherwise we can not eliminate the mixture of historical, evolutionary

\* \* \* \* \*

(\*) A modified version of a talk given in August 1981 at the XIIIth International Botanical Congress at Sydney.

(\*\*) Fundación Miguel Lillo and Facultad de Ciencias Naturales, Tucumán.

Evolutionary Theory 6: 233-255 (August, 1983)

The editors thank P. Raven and W.D. Billings for help in evaluating this paper.

© 1983, The University of Chicago; rights owned by author.

and genetic limitations which could seriously modify our interpretation on natural selection forces (see for example Seddon 1974).

Organisms tend to react to any change in the environment by character change (fig.1). Also some characters could change randomly if selection is not acting upon them.

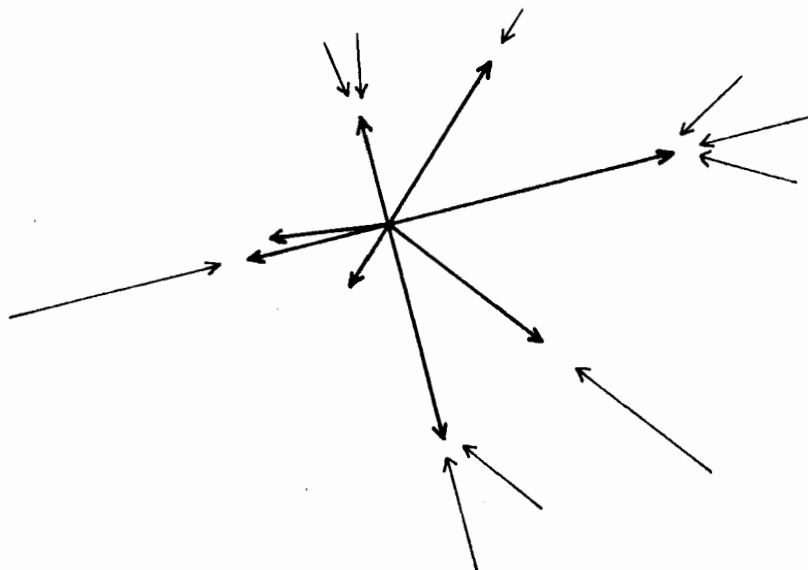


Figure 1: The principle of action-reaction: an organism will tend to react to any factor (either harmful or beneficial) by character change in evolutionary time. But characters also produce counteracting forces within the organism (arrows without complement). Thick arrows: characters and their consequences on the organismic budget. Some characters (non-adaptive) are in equilibrium within the organism but do not respond to a special external selective pressure. Thin arrows: selective pressure due to diverse factors.

\* \* \* \* \*

If selection is brought about by the action of diverse factors, then it should become manifest through the appearance of similar forms of organisms where factors are similar. This actually happens, and so the use of convergence and divergence is merely a combination of ecological data with evolutionary principles and data.

The method here proposed is hardly new in general conception. The general principles applied have been at the base (albeit not very systematically) of most interpretations of adaptations. Examples of the results are common rules of ecology (Bergman's rule, Allen's rule, and so on).

The purpose here is to make explicit a few necessary conditions to make the method work, and to propose some mechanisms (such as step by step models) for its useful application. A description of some examples makes the whole method more understandable.

Since this is based on universal evolutionary-ecological principles it should be applicable to almost any situation on earth (except for errors in the method itself). If high mountain biota is cited in the title it is because most examples given belong to this area, with which the author is more familiar.

The original idea for this method appeared while doing a comparative study on the high mountains of Ecuador and northwestern Argentina, financed thanks to an OAS fellowship. The rest was worked out while working for the Fundación Miguel Lillo and Facultad de Ciencias Naturales

in Tucumán, Argentina. Dr.R.F.Laurent kindly read the manuscript and discussed many problems. The abstract for the XIII I.B.C. was read and corrected by Dr.P.Seeligmann and typed by Mrs.A.Colombres. M.Halloy kindly typed the final version, and A.Dupuy drew the final figures.

#### Some Previous Works

It is not my intention to review papers using in some way or another (usually unsystematically) this method to study adaptations. Only a few papers are mentioned here as examples of a very ample literature.

The search for correlation of characters and factors in different environments, either with or without the use of statistical instruments, is quite old. In fact it is just as old as the search for causes and effects.

A very good basic work is D'Arcy Thompson's "On Growth and Form" where the idea is to relate organismic form and function to simple physical and chemical limits.

Raunkiaer (1934, see also Warming 1909 and Du Rietz 1931), related the life-forms of plants to the climatic conditions where they live, obtaining a classification of life-forms of individual species and life-form spectra for each locality. These spectra introduced a predictive attribute: without knowing the climate one should be able to infer it from a life-form spectrum. Ellenberg and Mueller-Dombois (1965-66) greatly expanded this classification scheme and Bocher (1977) discussed some of the theoretical problems inherent to life-form evolution and classification. Many other systems for classification have been proposed, usually keeping in mind the ecological predictive attributes of such systems. Grime (1979:76) followed these views, hoping that "future methods of vegetation analysis and description will rely increasingly upon criteria which are functional (i.e. concerned with characteristics of life-history and physiology) rather than taxonomic." If the views exposed here are correct, then such classification should enormously help in the interpretation of adaptations (since necessarily all similar, or converging, cases are brought together) and thence transform studies of organismic characters into potentially predictive studies as to the selective factors responsible.

Within the field of high elevation studies, many notes on convergence between tropical high mountain ecosystems have been made (Hedberg 1964, Troll 1968, Hedberg & Hedberg 1979, etc.). But a more methodical study has been realized by Scott and Billings (1964) who searched for the correlations between different ecological factors and one adaptive characteristic (productivity) within one mountain area. This led to interesting conclusions on the possible importance of certain factors usually considered unimportant in high mountain ecology (ex: partial pressure of carbon dioxide and/or oxygen).

Oceanic islands are of course perfect study areas for cases of convergence and divergence (adaptive radiation), and as such have long attracted attention (Carlquist 1974).

The predictive attribute of character-factor relationships are much used in paleontology. Organisms, or relatives of organisms actually living in certain conditions of temperature and precipitation are used as possible indicators that such conditions existed in the past, where fossils of these organisms are found (Braun-Blanquet 1979: 673). Ex: thick cuticle in a fossil plant leaf is taken to indicate certain conditions of aridity or water stress.

Although the basic idea behind this is correct, many errors are committed because even living organisms are only partly understood as to the causal factors influencing their characters.

The same predictive attributes are used by botanists when using

such terms as xerophilous, rain forest, and so on, which are based on convergent adaptive characteristics of individuals or communities. As soon as these characters are "seen" (often including unconscious perceptions of sight, smell, physical sensations of sound etc.), some general deductions on the climate and other environmental factors can reasonably be made by sufficiently trained persons.

The search for environmental limiting factors has also led towards the search for character-factor causal relationships (see for example Dajoz 1978: 15-16).

DEFINITIONS

To avoid misunderstandings, the meanings given to the main words used here are listed below.

Convergence is taken here as any decrease of the distance between the values of two or more characters in time (fig. 2, b-c; 3, b-d and c-e). Factors may also converge in time, but usually it is enough to find similar values of a factor (without knowing its past development) to investigate its adaptive result.

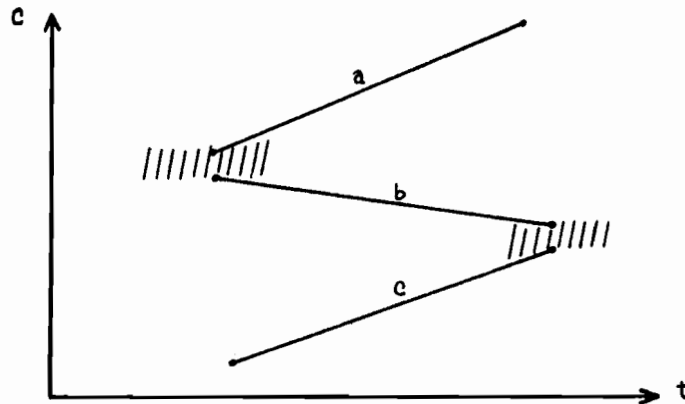


Figure 2: Evolutionary divergence (species a and b) and convergence (species b and c). C: character dimension; t: time; hatched zone: zone of competitive exclusions (see point 7) if living at the same place.

\* \* \* \* \*

Divergence is taken as the appearance and/or increase of the distance between the values of two or more characters in time (fig. 2, a-b; 3, a-b, b-c, d-e). Again, factors may diverge, but without knowing their history, it is enough to know that a factor has progressively greater (or smaller) values over a geographical area (gradient) to relate these changes to biological characters.

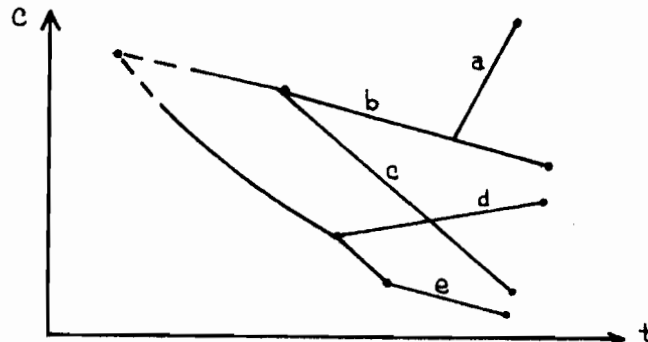


Figure 3: Divergence (species a-b-c and d-e) and convergence (b-d and c-e) in complex phylogenies. C: character dimension. t: time.

\* \* \* \* \*

Parallelism occurs when character distance remains constant in time (as defined by Dobzhansky et al 1977:265). As defined it is probably a rare or even non-existent event, being rather a theoretical concept which has been often misunderstood. The usual example of parallelism between marsupials and placentals is a clear misunderstanding, as certainly this (and most other cases of supposed parallelism) has implied divergence followed by convergence (as for example in fig. 3, b-d and c-e). See also DISCUSSION.

Character is used here as any feature of an organism. Most characters are considered adaptive, which implies that they are ultimately dependent on environmental factors via natural selection. This dependence is either direct, through ontogenetic time, (so-called phenotypic characters, although their capacity to vary is ultimately dependent on genes selected by natural selection) or indirect through evolutionary time (fixed genotypic characters). For residents of a given habitat, both phenotypic and genotypic characters may be equally adapted. Characters include not only morphological, anatomical and physiological, but also behavioural, cultural and genetic features (or any other group of characters subject to natural selection).

Factors are all features of the environment which can or not influence in some way the organisms living in a certain place and time. This includes not only physical, chemical and biotic factors, but also internal "limitations" due to evolutionary history or other temporal factors (thus characters may also be factors).

Except if explicitly said otherwise, convergence and divergence will be used here for functional (= of adaptive value) convergence and functional divergence (see following PROBLEMS).

#### PROBLEMS

Both characters and factors present serious drawbacks to the study of character-factor relations. Although some of these are treated here, others are particular to each case, and different methods must be adapted to particular instances. The models proposed in this paper are based on the assumption that the character and factor dimensions have been adequately studied, and thus that they have been screened or modified in order to be apt for further analysis. This means that it must be estimated what parameters are really the most adequate to study a character or factor, what are their behaviour (fluctuations in time, random or directional), how they can best be measured quantitatively or estimated qualitatively, etc.

Convergence or divergence could be divided into two categories: functional (adaptive) and non-functional (non-adaptive). Since function is often hard to determine, it is just as often hard to say to what category a character belongs. In an absolute sense, it is questionable whether non-functional characters exist at all, but here we mean only the relative importance with respect to one particular factor. Thus a character may be non-functional with respect to a great series of factors, yet functional with respect to another factor.

Sufficient convergence between characters probably means that there is also functional convergence (see point 12).

Non-functional convergence probably may occur; which means that different factors may be tolerated by similar adaptations. Yet it seems that this similitude will never be as deep (how deep depends on the character studied) as in functional convergence, since it is possibly due mostly to fortuitous combinations.

What is sometimes interpreted as non-functional convergence are

garoos, but many differences persist (and probably can not be eliminated except through evolutionary sidelines) because the initial form on which selection acted already had limitations (ex. wings in the ostrich could possibly not develop into walking limbs). The apparent impossibility of Hymenophyllaceae ferns to live in dry habitats is evidently related to some physiological or morphological limitation which can not be modified within the actual genetic constitution of the family. This "limitation" is of course not absolute, as it permits this family to be quite successful in humid environments.

In fact, all life on earth apparently has a basic genetic similarity which limits evolution of characters to those possible under such a genetic and chemical system. These wider limits are, at least from our point of view, hard to determine, since we have no different system to compare with.

4. Other internal limits. All the characters of an organism must reach a sort of equilibrium where an imperfect adaptation may be justified by the extra cost that would be implied by further perfection. On the contrary, a character may also exist to balance some other internal character, but would have no value by itself (see fig. 1).

The limits imposed on character modification depend to a certain degree on a combination of the actions of different factors, as well as the multiple interactions of different adaptations. Characters can thus become factors (see point 5).

For example some disadvantageous characters (example sickle-cell anemia, due to the presence of hemoglobin S) may present some strong advantage (resistance to malaria) which selects in favour of the character. Nonetheless, in time it is probable that better solutions will appear (ex. hemoglobin C, see Ricklefs 1973: 70) and replace the first. Thus disadvantageous compromises seem to be only temporary solutions waiting for better innovations (see points 10 and 11). See also the limiting effect of epigenetic factors as viewed by Alberch (1980).

5. Biotic limits. The causal relationships sought for in the convergence-divergence method are not only related to abiotic factors, but also to all biotic factors.

What for one species is an adaptive character (ability to eat hard leaves for example) can be a negative factor in the evolution of another species (the plant preyed upon for example). Most biotic characters are in some way factors affecting the evolution of contemporaneous and contiguous species.

We must then include, in the search for selective forces, those which may produce mimicry, escape characters in general, comensalistic relations, toxic substances either against predators or of possible use in competition, more complex factors which generally depend on evolutionary history (example: presence of placental versus marsupial herbivores), and so on.

6. Different strategies coexisting may seem like different character values equally well adapted to the same factors, but this in part responds to the fact that environment is diverse, and thus values of factors differ considerably in space and time. This permits different, equally successful strategies to coexist (ex. five radically different plant life-forms in tropicalpine environments, Hedberg 1973), and consequently leads to a better community utilization of the environment.

For another part, these different strategies respond to phylogenetic and genetic limitations of the biota available for evolution in the



area considered and represent a balance between these limitations and the best possible use of the environment (see point 3 and 10).

7. The combination of the former limits with limitations to geographical dispersal seen on a time scale means that at a given time and place are available for evolution only a very small sample of genomes, with only limited evolutionary perspectives. Further evolution will typically need successive entries of new migrants with completely different genomes. The biogeographically related species living in one place can adapt to a new environment only at a speed dependent on their previous history of selection; and also on external conditions in the new environment, such as limitations to speed of growth, length of generations or size of populations.

High elevation biotas may be only beginning to colonize the elevations at which we find them (e.g. Billings 1974:137; Halloy 1982: chap. 38), and thus may not completely reflect good adaptations to the greatest altitudes. Most of them reflect numerous inherited characters from lower elevations (example spines in plants "climbing" from the dry puna to wet high-andean regions).

8. Cultural characters are selected through particular ways only indirectly related to genetics (Ricklefs 1973: 74). These mechanisms promote a greater speed of apparent change (see for example the spread of opening milk bottles in the Great Tit, Fisher and Hinde 1949, Hinde and Fischer 1952), but cultural characters are in the long run also subject to a series of limitations, including environmental and genetic ones. Most cultural characters are also subject to natural selection, leading to clear convergences between human cultures living in similar environments (ex. high andine and himalayan cultures).

As in genetic evolution, cultural traits may appear as random exploratory behaviour, somewhat analogous to mutations (Ricklefs 1973:75). Some appearance of directional (voluntary) cultural evolution does exist in some animals including man, but it is not certain how much this apparent directionality is really free from the random appearance of certain "intelligent" choices like in the case of the Great Tit (above). An illustration of this is given by convergence between man made machines and different animals which they seem to mimic.

9. The characters considered should belong to resident species within the habitat whose factors are being investigated. A certain percentage of species in most habitats are "temporary" or strays from some other habitat. They live and persist there because of the proximity of a source of abundant diaspores coming from organisms living in different conditions (see for example Van Steenis 1961) and because minimum physiological requirements do exist in the alien environment.

This group of species can be considered, since they at least survive, but the adaptive value of their characteristics must be considered of a different weight (usually less) than those of resident species. These strays usually reproduce rather badly or not at all, and thus can have little or no genetic exchange with the main population. In this case they are hardly involved at all in the natural selection of characters suited for the habitat being considered.

If reproduction is efficient, in time a resident population will result. In this case, reproductive isolation can ensue, and characters are bound to adapt normally to local factors, becoming one more resident species. If not, some characters at least will remain selected by extra-habitat pressures on the original population via gene flow. These situa-

tions, in time, lead to the inherited characters of different biogeographical elements (see point 7).

10. Convergence of species living in a different place or time can theoretically be unlimited if the same niche is to be occupied and given enough evolutionary time (see fig.4). In fact, this is limited by pre-existing genetic constitutions (see point 3). On the contrary, species living at the same time and place have a limit to convergence (limiting similarity of MacArthur and Levins 1967) in those characters subject to competition, as for example a material resource such as food (see fig.2).

Not so for other non-competing characters. Coexisting species can conceivably converge indefinitely towards certain ideal characters as long as this does not imply niche overlap in some crucial necessity (a possible example could be hairs on leaves), and as long as other limitations (points 3, 4, 5) can be eliminated in time.

Of course the model of figure 4 is valid for one or a few characters, rarely or never for all simply because niche dimensions themselves vary through time.

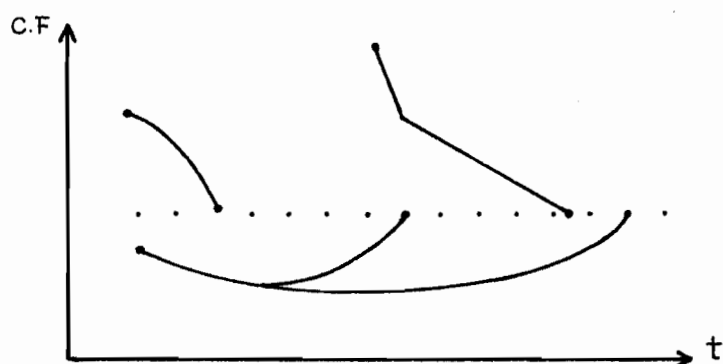


Figure 4: Convergence at different times is not subject to competitive exclusion (see point 10). C, F: character or factor dimension. t: time.

\* \* \* \* \*

11. Nearly perfect convergence has rarely occurred, probably because not enough evolutionary time was available with sufficiently constant conditions. Since selection works on random mutations occurring at a definite rate, greater length of time increases the possibility of "finding" the ideal mutation and later the ideal combination of mutant genes (see point 4). A changing abiotic environment means new adaptations must constantly be sought, before old ones become sufficiently perfect. In some cases an organism can prolong the constancy of its environment by migrating together with fluctuating climatic zones. But even then, many abiotic factors change while biotic factors all around are constantly changing.

12. The same character has a high probability of having the same meaning wherever it may be found (e.g. having been selected for by the presence of the same values of one or more factors). If more than one species converge simultaneously in the values of one or more characters at the same places, the probability becomes even higher (see Method). This means that, for example, caulirosulate plants (occurring in tropical mountains but also tropical lowlands, subtropical deserts, and cool wet forests) must be explained by something else than temperature or water relations (Hedberg 1964, Smith 1974 and 1979). For example the possibility of "inherited" characters (or primitive characters, Mabberley 1974). One explanation commonly aduced (protection of apex) is pos-



sible in all these cases, but protection may be from cold, drying or better still from herbivores (Smith 1980).

On the other hand the character "caulirosula" is accompanied by quite different characters in different places (e.g. type and density of leaves, thickness of stem, prefoliation, hairs, scales, gels, etc.). Thus if the "same" character seems to have different meanings in different circumstances, it is either because not enough factors have been investigated, or because the "character" is actually part (or all) of a complex of characters which are dependent on different factors. This complex varies from place to place according to the independent evolution of the constituent characters. In this case we should divide the complex into its constituent parts, and look for the meaning of each of these as they converge or diverge (see also system 3).

13. Characters resulting from random genetic drift (without selective importance) can be disclosed by comparing other species groups living in the places under study (system 1 and 2). If the character has selective value it should appear in different species with similar life styles. In some impoverished biotas (or when working with strongly aberrant species) no similar example can be found. In these cases, pairs of similar localities differing in the same way could give clues to the meaning of the character studied (or also see system 4).

14. Relatively fixed phylogenetic characters serve as "markers" to indicate the direction of evolution (see fig. 5 and 6). These characters are of course variable from one group to another, and are the constant preoccupation of taxonomists. Some of them do vary under selective pressure, but only very slowly. The least affected by selection may appear from the fact that no other organisms in the same environment present the character (or character dimension). This is typical of strategies: different ways of life which, within evolutionary time available, do not seem to differ fundamentally in selective advantage (but see also point 6).

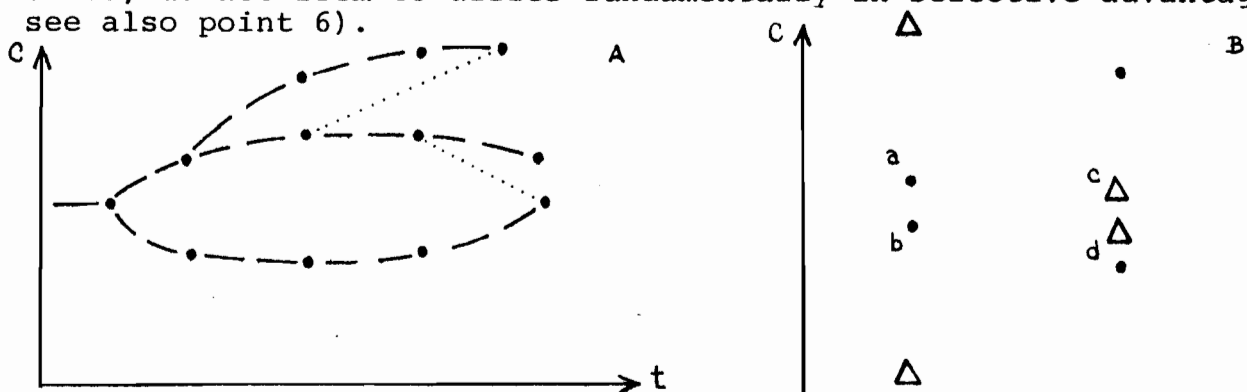


Figure 5: Phylogeny in general is only visible thanks to series of fossils through time (A) or to "marker-characteristics" (B and fig. 6). C: character dimension.

in A: points: known fossils; t: time; dashed lines: supposed phylogenies; pointed lines: other possible phylogenies.

in B: triangles: marker-character; points: character affected by selection; a-b: species converging in one character but phylogenetically separate; c-d: close relatives diverging at different speeds.

\* \* \* \* \*

Some of the best marker-characters seem to be some macromolecules such as proteins and nucleic acids which according to Dobzhansky et al (1977:313) "contain significant information about phylogeny". As in ta-

xonomy, the best "marker" is usually given by the combination of several different characters, all of which must supposedly be as little influenced by selection as possible. Marker-characters either do not change in time, or change at near stochastical rates.

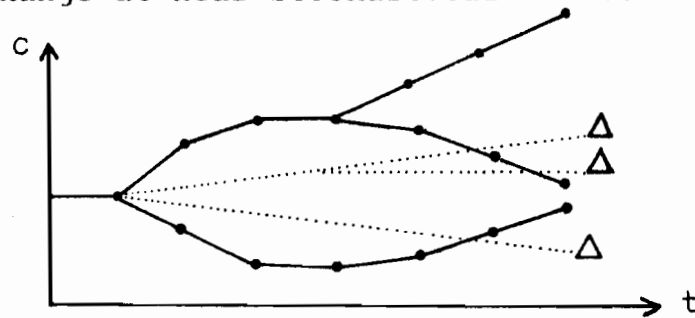


Figure 6: Thanks to fossils and "marker-characters" evolutionary history may be reconstructed. Points: character affected by selection, visible in fossils. Triangles: "marker-character" (visible or not in fossils) "drifting" at a nearly constant stochastical rate.

\* \* \* \* \*

15. The decrease of distance between character dimensions in space (over a geographical area) can be a representation of convergence in time if adequate marker-characters (see point 14) or fossils can prove it (see fig. 12). If one species of an otherwise different genus or family converges with the characters of another family it can be taken as strong support for the existence of a character-factor relation between that species and the second family with some factor of their common environment.

The same is valid for the increase of character dimension in space and divergence in time.

16. Convergence of characters is the more significant the more distantly related are the species which exhibit it. In a similar way, similar values of a factor are more instructive in environments generally differing in many factors.

17. Divergence of characters is the more significant the more closely related are the species which exhibit it. For this reason, divergence must especially be looked for in neighboring communities of a same macroenvironment, or in neighboring systems isolated by geographical barriers and exhibiting vicariant taxa (see system 1 and 2).

In the same way, increase of the distance between dimensions of one or a few factors is the most significant when found in otherwise similar environments.

18. Factor-character relations are not necessarily the same in short term laboratory or field experiments as in long term evolutionary events. Two types of factor-character relation apparently do not influence character selection.

a) A factor with direct physiological influence on some trait (ex. temperature on leaf size and form) will not necessarily produce the same reaction in the organism through natural selection (although apparently it often does, as for example the shortening of internodes in high mountains, see Hedberg 1964).

b) Another kind of influence does depend on a mutual adaptation of a character to a factor dimension; but the factor is here used by the organism as a signal, and implies no limitation in the sense of point 2.

These include all sorts of phenological signals (temperature, day-length, etc.) which produce a reaction in an organism which is actually an adaptation to some other factor (ex. flowers open as an evolutionary response to the presence of pollinators at a certain time of the year, but may be using temperature as a signal to know the right time).

19. The presence of a certain phylogenetic group, usually indicator of certain factor levels, is the more significant the least is its normal dispersal ability, since it indicates the optimum factors have probably been present for a long time, and thus have been acting selectively on the local biota.

The absence of a certain phylogenetic group is the more significant the greater is its usual dispersal capability (ex. ferns) and is less significant for low capability groups since they may not have arrived due to this reason rather than due to below optimum conditions on arrival.

20. The proportion of species of the biota presenting a certain character, as compared to the proportion of individuals (or biomass, cover, etc.) within the biota presenting the same character, gives good clues as to selective pressure (Halloy, 1982, Chap.43).

If the first is high and the second is low we may suppose the character is common in the biota due to biogeographical or temporal reasons implying different selective pressures at the source.

If the species presenting the character are few but very common, we may suppose selective forces are highly favorable to this character in spite of a poor genetic basis in the region studied. Care must be taken to prove if the character studied is really the one selected for (e.g. conferring the possibility to be common), or if it is common simply because the other characters of the species make it highly efficient in spite of the one we are studying.

#### THE METHOD

The method of using the distance between character and factor values to interpret adaptive relations is based on usual experimental procedure. Factors and characters are eliminated or compared one at a time to discover causal relationships. Contrarily to usual experiments, this method uses mainly "natural" experiments (Ricklefs, 1973:726), that is, pre-existing ecosystems in which as many relevant factors as possible are measured and correlated with observed characters. Quite apart from other advantages and disadvantages, "natural" experiments are a great advantage for conservation, as effects on the environment are usually minimized.

For extremely minute or simple characters one could theoretically find a direct one to one relationship to a factor. In reality, due to all the external and internal interactions (see premises) it seems evident that we can find a series of factors. Nonetheless, if we can order these factors in a hierarchical way, one factor will probably appear as more important (somewhat as in the principle of limiting factors). In the case of complex characters (e.g. productivity) a certain (limited) number of factors with similar hierarchical values may apparently be expected (see Scott and Billings 1964).

Due to the growing possibilities of error related to numerous factors changing at different rates at the same time, observations must be multiplied whenever possible, and comparisons should constantly be brought forth even when data are scarce.

Different localities studied may be either separate in space (in most cases of present studies) or in time if sufficiently good paleontological reconstructions are at hand. The spatial gradient in factor and character dimensions simulates the temporal gradient and is adequate for analysis (see point 15).

Multiple regression is apparently a good way to analyse all the data obtained by any of the four systems proposed below (see, for example, method used by Scott and Billings 1964).

Attention can be focused either on characters or factors. In most cases, although the examples given below are the simplest possible, the same procedure can easily be applied (and will be more significant) to groups of species. For example, in system 1, instead of studying only Geranium in a number of communities, we can study all the species of these communities for the presence of one or numerous characters. Character values can then be expressed as percent of total number of species, percent of species presenting different values of the character (as plant height in a Raunkiaer life-form spectrum), or better still as percent cover of the species presenting the character against total cover (or percent biomass, etc.).

In the first two cases I have found that floristic and faunistic keys can be powerful tools to start with. This is especially true for keys to floras or faunas of regions of ten to a hundred square kilometers, although other sizes are also good. Especially in floral keys, characters of adaptive value are frequently used, being the most visible, and thus the key lumps together phylogenetically distant groups which converge in one or more characters.

Cuatrecasas (1968) gave interesting "biotipological" spectra for plant associations of the páramos of Colombia, where character dimensions have served to separate character classes, and the percentage of species in each class has been calculated. A regression analysis between these type of data and numerous factors measured with the greatest detail possible should give very interesting results.

These same complex procedures can be followed in each of the four models below.

Four different models are proposed to elaborate data, depending on the nature of the problem. Each of these may in turn be worked out at any desired level, from the analysis of a single character to that of composite characters depending on community interactions. Figures 7 to 11 show some features of these models as used in one particular case.

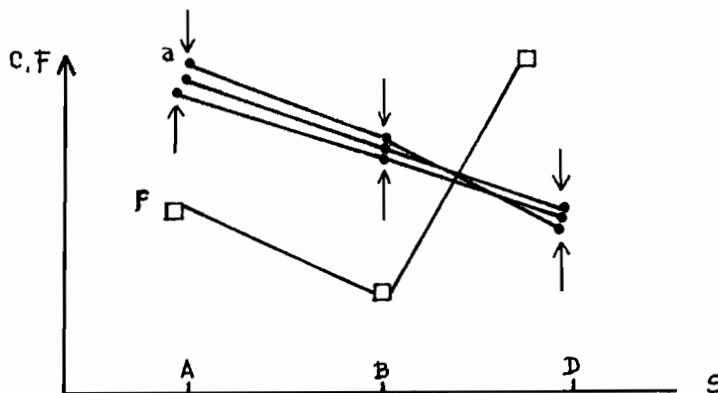


Figure 7: Species groups (a) presenting the same character should be studied in as many localities as possible. Apparent correlation between the character dimension and one factor (f) between two localities (A-B) may prove false between another pair (B-D). C, F: character or factor level. S: space. Arrows: selective pressure due to one or more unknown

factors.

\* \* \* \* \*

The four models imply the same basic comparison method, only with some differences in the material studied. Intermediate categories could probably be added with a mixture of functional details (for example comparison of distant localities with different conditions and diverging characters). They can be used alone or combined.

Systems one to three give progressively less importance to possible historical and phylogenetic similitudes, while system 4 eliminates as far as possible the presence of common factors, present or past. A step by step analysis through the four systems will give strong corroboration to conclusions obtained through only one system.

As we go from System 1 to 4 the importance of divergence decreases, while that of convergence increases. In other words, divergence in System 1 and 2 is significant (more so in 1), while convergence in these same cases may be due to common historical factors (biogeographical).

In this case consideration of a character which converges between species a and b of families A and B may become more significant if those character values are rare or extreme both in family A and B, thus showing that the character is diverging from that usual in those families but converging toward a common point. This means that it has probably been selected for.

In systems 3 and 4 convergence becomes the most important focus point. Yet at the same time, as above, corroboration of causal relationships are always better if data of divergence within the phylogenetic groups considered can be obtained.

System 1: Comparison between communities inside one small biogeographical unit. The adaptive differences between these (divergence) may be explained mostly by differences in the environment (soils, microclimates, etc.) as long as groups of related species are used. Only a few characters and a few factors will vary. Many factors of the environment remain constant. Most genetic characters (using groups of related species) are constant. Effects of genetic drift or phylogenetic stability (both independent of natural selection) may be eliminated by seeing if the character gradient present in one group of species reappears in different groups of related and unrelated species (see fig. 8).

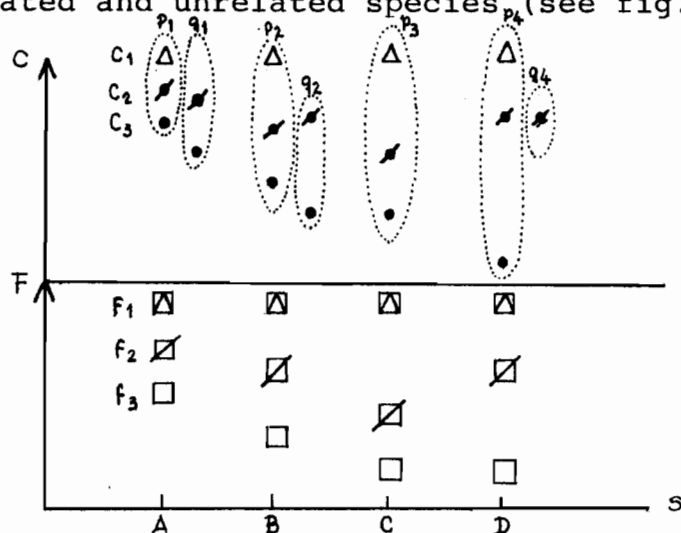


Figure 8: Comparison of different character dimensions ( $c_1$  to 3) in different populations or related species (e.g. one genus as p or q) living in different communities (A to D) of a same area with the factor

values measured in the same area ( $f_1$  to 3).  $c_2$  and  $c_3$  seem to correlate with  $f_2$  and  $f_3$ .  $c_1$  is a relatively constant character which may "pre-adapt" group  $p$  to areas where certain conditions exist (like factor  $f_1$ ), but is not essential to another strategy as used by  $q$ .  $c_3$  and  $f_3$  correspond to examples of figures 9 and 10.

$p_{1-4}$  and  $q_{1-4}$ : different populations or closely related species within two different phylogenetic groups.  $q_3$  does not exist.

$c_{1-3}$ : characters differing in level of expression from one population or species to another.  $c_1$  does not exist in  $q$ , and  $c_3$  disappears in  $q_4$ , which is in accordance with its very low level in  $p_4$ .

C: character dimensions.

F: factor dimensions.

S: space.

\* \* \* \* \*

Example 1: Scott and Billings (1964) made an analysis of productivity (a complex character) in relation to a good series of environmental factors by multiple regression. They obtained data on the relative importance of different factors to this one character. The results could now be compared as in system 2 to obtain possible evolutionary trends.

Example 2: Geranium presents at least four sympatric species in the Páramo del Angel (Ecuador), each living in different associations and differing in some quantifiable characteristics (as hair length and density for example). Comparison can then be made between the gradient presented by Geranium and those presented for the same character in other genera or unrelated species.

Example 3: Different tribes of people have often coexisted (example, in the Andes with complex integration of cultures and commerce, F. Salomon, XII-1979, MAB course, Quito) and yet evolved different cultures. Some at least of these cultural characters may be dependent on a different ecological relation with the environment; others ("cultural drift") may be analogous to genetic drift.

System 2: Once a first idea is obtained as to the possible relations between characters and factors, one can search for other localities isolated from the first by barriers to see if the same type of divergence occurs when the same factor gradients are present. These localities can be rather close (conditioned by the same macroclimatic and geological environment) but separated by barriers to biological dispersal. Biogeographical affinity is great because of proximity and similar conditions in the localities considered. It is especially useful to compare pairs of equivalent communities (like lake shores, south facing slopes, rock outcrops, etc.).

Again, genetic and physical factors are purposefully kept relatively constant, although genetic factors may be varied (combination of biogeographical elements of diverse origins, see fig. 9).

Example 1: Oceanic archipelagoes are the most typical cases to study in this way and have been used precisely so in a comparative mind (Carlquist 1974). Other insular systems can be analysed in the same way (such as high mountains for example, Hedberg 1961, Simpson 1979, etc.).

Example 2: Geranium species exist all along the Andes often with more than one species per region. Thus the four species of the Páramo del Angel can be compared with two from Antisana (Ecuador), three from Cotopaxi (Ecuador), one from Chimborazo (Ecuador), four from Cumbres Calchaquies (Argentina) and many more. All these species can be classified first according to the type of community they occupy. Further groups of species of other genera with similar distributions can also be compared; for example Perezia, Werneria, Plantago, and so on.



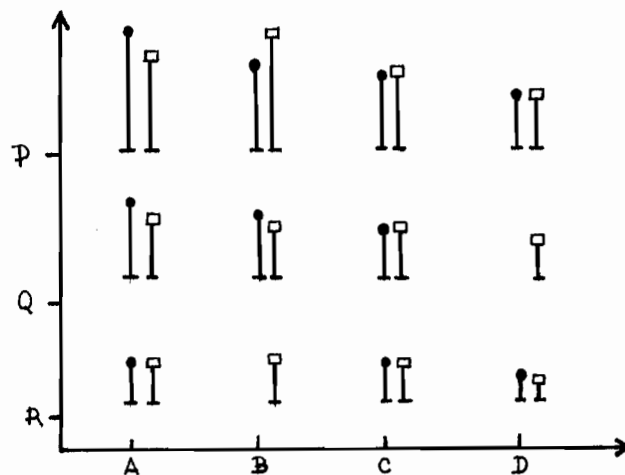


Figure 9: If instead of one locality we now use the same type of associations in geographically isolated but relatively close localities, we can eliminate certain historical and geographical factors (System 2). In this case, supposing  $c_3$  and  $f_3$  of figure 8 are again being studied, their apparent relation is corroborated (the same character and factor are being investigated in all twelve cases). A, B, C, D: different types of communities (ex. lake shore, swamp, grassland). P, Q, R: different localities. Length of lines represents character (points) or factor (squares) levels. In QD and RB the phylogenetic group studied is not present. Instead of each line representing the average character level in one population it can express the percentage representation of species (or individuals, biomass, coverage) of the whole biota or taxocenosis (ex.: birds, angiosperms) presenting a certain level of the character considered. This would give a value for every locality regardless of phylogenetic groups present.

\* \* \* \* \*

System 3: (fig.10). Around the world, localities with very similar general physical conditions may be found which are sufficiently distant (and/or separate by barriers) so that phylogenetic groups are for the most part unrelated. Now, instead of searching for divergence within a phylogeny, we must search for convergence between unrelated species. If possible, groups of converging organisms of one place are compared with their counterparts at the other localities. Most biogeographical, historical (inherited) and phylogenetic common factors are now eliminated (see point 16). Most biological factors are also different in essence, but some biological interactions may recur by convergence.

Example 1: Equatorial mountain systems such as the Espeletia páramos of South America have numerous converging life-forms when compared with volcanoes of East Africa and the mountains of New Guinea (Hedberg and Hedberg 1979; R.Gradstein 1981, pers.comm.).

Example 2: Cactaceae are replaced in Africa by Euphorbiaceae and Asclepiadaceae living in similar desert conditions and converging in numerous characters.

Example 3: A remarkable example is the great climatic similitude between the Cumbres Calchaquíes (Argentina) and Central Otago (New Zealand) mountains (Bliss and Mark 1974, Halloy 1981, 1982). Although there are some important differences the similarities go into a lot of details. A comparison of the vegetation characteristics of these two areas would certainly be very interesting to interpret the meaning of adaptations.

Example 4: Human cultures in the Andes and Tibet-Nepal show some

remarkable similarities evidently due to some limitations of the environment (since they have appeared independently). Characters due to drift must be eliminated to study character-factor relations. Some notable physiological divergences in their adaptations to high altitude show phylogenetic relations are not so close (Heath and Williams, 1979: 54-55).

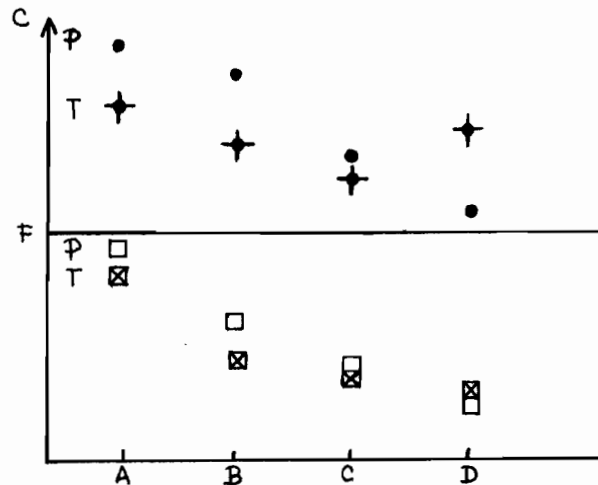


Figure 10: Unrelated (or slightly related) species from different communities (A to D) of one locality, as in figure 8, are now compared with those of similar communities, as to factors in general, in faraway localities. This eliminates phylogeographical, historical and most biological interaction factors (System 3). P and T are separate localities where the same character and factor (ex.  $c_3$  and  $f_3$  of figure 8) are investigated as to their levels either in one species group at each locality, or (much better) as a percentage of the total taxocenosis studied (see text). Points and crosses: character level in each community of the two localities. Squares: same for factors.

\* \* \* \* \*

System 4: In this case, instead of looking for similar factors in general, we look for as many localities as possible (both geographically and temporally separate), no matter how different, where a certain character exists. As these localities often differ considerably, we must then find what they may have in common (see point 12 and fig. 11). It is often useful to look for factor gradients inverse to character gradients supposedly affected (if they exist) in which case the relationship is not as supposed (falsification of hypothesis according to Popper's principle).

This system eliminates possible unknown factors related to the one we are studying and most phylogenetic and historical factors (see fig. 11).

Example 1: Productivity values were compared in completely different mountains and was found to be sometimes inversely related to temperature and length of the growing season (Halloy, 1981), thus contradicting some common ideas. In this case, altitude (low pressure) seemed to be more important than the previous two factors. It does not mean that these are unimportant. Since the whole method is relativistic, elevation appeared here as the primary factor. Afterwards different localities with the same elevation should be compared to see the second factor at work, and so on.

Example 2: The rosette trees (caulirosula) of equatorial high mountains of Africa and South America have counterparts in the subtropical mountains of Hawaii, but also (with notable divergences in the complex

of characters) in islands (Dracaena, Lobelioids of Hawaiian forests), in cloud forests (tree ferns), palms, cold temperate rain forests of southern Chile, deserts, and so on (plus fossil forms). Although some characters of mountain caulirosulas are possibly exclusive to them, many are shared with quite different environments. A good search would possibly reveal some common factor, as for example evolutionary stages and history, relative insularity and possibly low predation; see also point 12.

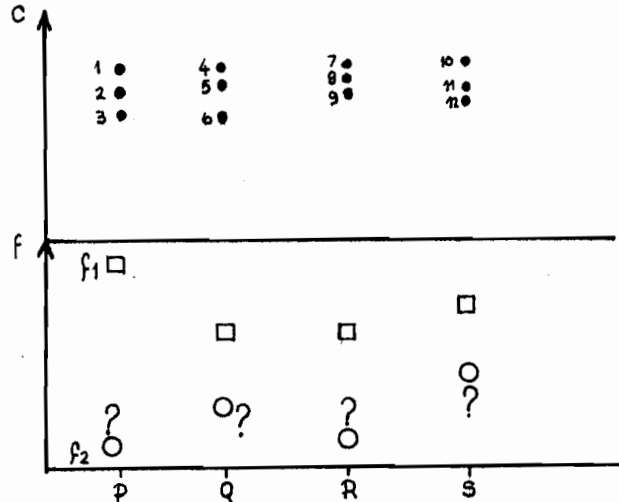


Figure 11: One character present in unrelated species (1 to 12) of a same locality (in this case by sets of three) will probably also be found in distant localities very similar (figure 7 A, B) or sometimes very dissimilar in most factor dimensions ( $f_1, f_2$ ). In this case, if a common factor (?) can be found it has added weight thanks to elimination of series of factors usually occurring together (especially phylogenetic and physical) since most factors are divergent (System 4). Points: character level in different species within and between localities. Squares, circles and ?: factors. P, Q, R, S: distant localities.

\* \* \* \* \*

### DISCUSSION

Convergence between characters, if coincident with nearing of distance between factors (fig. 12) may be a good way to prove causal evolutionary relations between factors and adaptations; or to determine the relation between form, function and natural selection. This must be corroborated by finding as many cases as possible where the relation exists while other characters and factors are changed as much as possible (divergence, see Method).

The other way is to prove experimentally that a character does function in a certain way (for example insulation of trunks of caulirosulas by dead leaves, Smith 1979). This does not prove that natural selection has acted in that direction (in other words that the character was "wanted") although some studies of this type tend to imply it. The character may be the result of other evolutionary pressures on a complex of characters (see Halloy 1982, chap. 39, and premise 12). Another confusion can appear due to "signal" factors (see premise 18).

Convergence proves that options available to an evolving organism are limited. The niche hyperspace of Hutchinson includes limitations to form, physiology and other characters. For organisms adopting very similar niches, natural selection acts in trimming characters to similar aspects. Even man-made machines submit to these general laws and have thus

some notable convergences with certain animals.

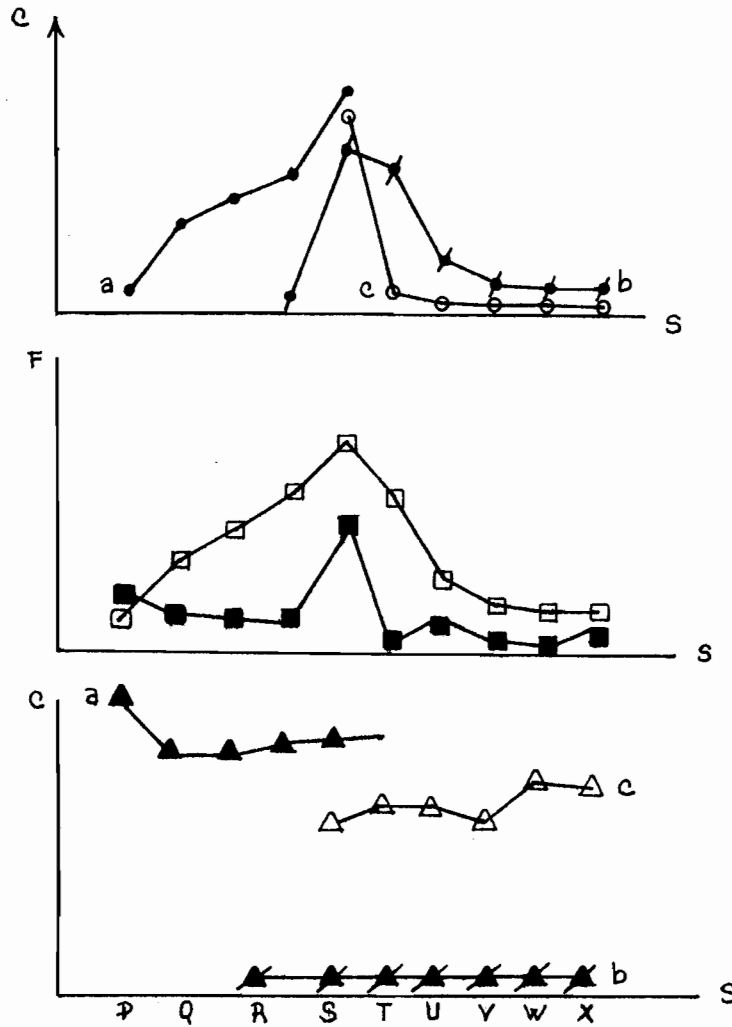


Figure 12: "Convergence", or nearing of distance between character levels over a spatial gradient may permit visualization of convergence in time if adequate marker-characters or fossils can prove it happened in a similar way. Thus the study of convergence in time can be correlated with "convergence" of factors in space to give a good idea of evolutionary pressures. The same, but inverted, is true for divergence. C: character dimensions. F: factor dimensions. S: space. Circles: adaptive character of three phylogenetic groups converging for most localities (P to X) but most especially (and for most species) in S, where some factor becomes crucial. Triangles: character level typical of the phylogenetic group involved (a to c) either adaptive to a factor constant in all localities or non-adaptive. Squares: two different factors whose levels are found to correlate with character levels investigated (circles). To distinguish the most important implies verifying premises, and if possible obtaining data as in Systems 1 to 4.

\* \* \* \* \*

In different localities or times convergence can reach the point of producing taxonomic confusions (also sometimes in the same locality at the same time). Plants belonging to different orders or classes can resemble each other more in certain characters than other species of the same genera (ex. certain species of Blechnum subgen. Lomaria with Cycas and fossil Bennettitales). In animals, tree frogs of different continents

were until recently considered as a same family (or even genus) while now being considered separate (Laurent 1979). These independent families have evolved convergent adaptations to a similar mode of life (and thus similar niche dimensions).

In these cases only the presence of marker characters (ex. in plants cited reproductive organs, anatomy, etc.; in tree frogs osteology, caryotypes, proteins, etc.) will show real phylogenetic affinities.

In some cases convergence may occur to a rather detailed degree (ex. leaf form, petiole, cuticle aspect, venation) in certain organs belonging to organisms whose other parts are otherwise different (ex. leaves of certain species of Ficus, Philodendron, Anthurium, Glossop-teris and Elaphoglossum (and probably others).

Although convergence between distantly related groups is more spectacular, it may happen at the lowest levels of genetically separate groups (recently evolved species). This has been called parallelism (Simpson 1961) implying it is a different phenomenon, yet it is simply convergence between more closely related groups. Since in any case of convergence the principal working agent is natural selection, there seems no reason to distinguish convergence between families or orders from that occurring between species. Both are qualitatively equivalent phenomena, differing quantitatively due to a different degree of genetic limitations (see premise 3 and DEFINITIONS).

The method proposed here has been used very few times and only through use will it be possible to find some of its limitations or the necessity to add more conditions or premises. An evident limitation already visible is the necessity to use a great number of data from distant localities, which is not always possible. Also basic phylogenetic and climatic data are often inexistent or incomplete for many regions. Finally, data from different authors are hard to compare because of the use of different criteria and methods, or even different units. Thus a great help would come from a generalized format of factor and character analysis applicable to any locality.

### CONCLUSIONS

The character-factor relation brought about by natural selection is conditioned by a series of limitations whose relative effects could ideally be determined.

The method proposed above gives a possibility of separating most causal factors and determining their relative evolutionary importance. It distinguishes signal factors and other non-adaptive factors from selective factors producing functional characters as a response of the organism. It also allows for clarification of the relative importance of historical, phylogenetic, geographic and other factors.

The four models give four independent pathways to corroborate hypotheses on evolutionary character-factor relations. In the best of cases all four systems may be used successively, each one adding to the corroboration or modification of initial hypothesis. Each model studies the relative weight of the factor, character, evolutionary history, geographical, genetic and other limits.

All of the relations obtained in this way, if sufficiently tested, have a good predictive value. So that the characters of an organism can give us a good idea of its adaptations, or inversely the factors of the environment can give us a good idea of what kind of adaptations we could plausibly encounter.

## LITERATURE CITED

- Alberch, P., 1980. Ontogenesis and Morphological Diversification.- Amer.Zool. 20: 653-667.
- Billings, W.D., 1974. Adaptations and Origins of Alpine Plants.- Arct. Alp.Res. 6 (2):129-142.
- Bliss, L.C., and Mark, A.F., 1974. High alpine environments and primary production on the Rock and Pillar range, Central Otago, New Zealand.- N.Z.Journ.Botany 12: 445-483.
- Böcher, T.W., 1977. Convergence as an evolutionary process.- Bot.Journ. Linn.Society London 75: 1-19, 2 plates.
- Braun-Blanquet, J., 1979. Fitosociología.- H.Blume Ediciones, Madrid, 820 pp.
- Carlquist, S., 1970. Hawaii -A Natural History.- The Natural History Press, Garden City, New York, 463 pp.
- , 1974. Island Biology.- Columbia University Press, New York, 660 pp.
- Cuatrecasas, J., 1968, Paramo vegetation and its life forms.- Colloquium Geographicum 9: 163-186.
- Dajoz, R., 1978 (3<sup>eme</sup> ed.). Précis d'écologie.- Gauthier-Villars, Paris, 549 pp.
- Dobzhansky, T., Ayala, F.J., Stebbins, G.L. and Valentine, J.W., 1977. Evolution.- W.H.Freeman and Company, San Francisco, 572 pp.
- DuRietz, G.E., 1931. Life forms of Terrestrial Flowering Plants. I.- Acta Phytogeographica Suecica III (1): 1-95.
- Ellenberg, H. and Mueller-Dombois, D., 1965-66. A key to Raunkiaer plant life forms with revised subdivisions.- Ber.geobot.Inst.ETH, Stifg Rübel, Zürich, 37: 56-73.
- Fisher, J. and Hinde, R.A., 1949. The opening of milk bottles by birds.- Brit.Birds 42: 347-357. (apud Ricklefs 1973).
- Grime, J.P., 1979. Plant Strategies and Vegetation Processes.- John Wiley & Sons, Chichester-New York-Brisbane-Toronto, 222 pp.
- Halloy, S., 1981. La presión de anhídrido carbónico como limitante altitudinal de las plantas.- Lilloa 35 (3): 159-167.
- , 1982. Contribución al estudio de la zona de Huaca-Huasi, Cumbres Calchaquíes (Tucumán, Argentina). II.- Climatología y Edafología en relación con la Composición y Adaptación de las Comunidades Bióticas. Thesis, Fac.Cs.Nat., Un.Nac.Tucumán. 839 pp.
- Heath, D. and Williams, D.R., 1979. Life at High Altitudes.- Studies in Biology n°112: 60 pp, Edward Arnold Ltd., London.
- Hedberg, I. and Hedberg, O., 1979. Tropical-alpine life-forms of vascular plants.- Oikos 33: 297-307.
- Hedberg, O., 1961. The phytogeographical position of the afroalpine flora.- Rec.Advances Bot. 1: 914-919.
- , 1964. Features of afroalpine plant ecology.- Acta Phytogeographica Suecica 49: 1-144.
- , 1973. Adaptive evolution in a tropical-alpine environment.- in V.H.Heywood (ed.) "Taxonomy and Ecology": 71-92. Academic Press, London-New York.
- Hinde, R.H., and Fisher, J., 1952. Further observation on the opening of milk bottles by birds.- Brit.Birds 44: 393-396. (apud Ricklefs 1973: 74).
- Hinton, H.E., 1977. Enabling Mechanisms.- in J.S.Packer and D.White (eds), "Proceedings of XV International Congress of Entomology": 71-83. The Entomological Society of America, College Park, Md.20740.
- Laurent, R.F., 1979. Esquisse d'une Phylogenese des Anoures.- Bull. Soc. zool.France 104 (4): 397-422.



- Mabberley, D.J., 1974. Pachycauly, vessel-elements, islands and the evolution of arborescence in "herbaceous" families.- *New Phytol.* 73: 977-984.
- MacArthur, R.H., and Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species.- *Amer.Nat.* 101: 377-385.
- Parsons, R.F., 1968. The significance of growth-rate comparisons for plant ecology.- *Amer.Nat.* 102: 595-597.
- Pirlot, P., 1976. *Morfología evolutiva de los Cordados*.- Ed.Omega, Barcelona, 966 pp. (transl. from French).
- Raunkiaer, C., 1934. *The life forms of plants and statistical plant geography; being the collected papers of C.Raunkiaer, translated into English by H.G.Carter, A.G.Tansley and Miss Fansboll*, Clarendon, Oxford. (apud Grime 1979).
- Ricklefs, R.E., 1973. *Ecology*.- Chiron Press Inc., Newton, Mass. 861pp.
- Scott, D., and Billings, W.D., 1964. Effects of environmental factors on standing crop and productivity of an alpine tundra.- *Ecol. Monogr.* 34: 243-270.
- Seddon, G., 1974. Xerophytes, xeromorphs and sclerophylls: The history of some concepts in ecology.- *Biological Journal of the Linnean Society* 6: 65-87 (apud Böcher 1977).
- Simpson, B.B., 1979. Quaternary biogeography of the high montane regions of South America.- in W.E.Duellman(ed.) "The South American Herpetofauna...": 157-188. Monograph of the Mus.Nat.Hist., The University of Kansas, n°7, 485 pp.
- Smith, A.P., 1979. The function of dead leaves in *Espeletia schultzii* (Compositae), an Andean Caulescent rosette species.- *Biotropica* 11: 43-47.
- , 1980. The paradox of plant height in an Andean Giant Rosette species.- *Journ.Ecology* 68: 63-73.
- Van Steenis, C.G.G.J., 1961. An attempt towards an explanation of mountain mass elevation.- *Proc.Kon.Akad.Wet.A'dam C* 64: 435-442, 1 fig.
- Thompson, D'Arcy, 1942 (new edition). *On Growth and Form*.- Cambridge University Press, Cambridge. 1116 pp.
- Troll, C. (ed.), 1968. *Geo-ecología de las regiones montañosas de las américas tropicales*.- Proc. UNESCO Symposium, Colloquium Geographicum 9, Ferd.Dümmlers Verlag, Bonn.
- Walter, H., 1977. *Zonas de Vegetación y Clima*.- Ed.Omega, Barcelona. 245 pp. (transl. from German).
- Warming, E., 1909. *Oecology of Plants. An Introduction to the study of Plant communities*.- Oxford Univ. Press, London. 422 pp.
- Wiley, R.H. and Richards, D.G., 1978. Physical Constraints on acoustic communications in the Atmosphere: implications for the evolution of animal vocalizations.- *Behav.Ecol.Sociobiol.* 3: 69-94.

