Geographic variation and population systematics: distinguishing between ecogenetics and phylogenetics

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ABSTRACT

A series of quantitative procedures (1 - pattern of anagenesis in putative phylogentic trees; 2 - «correlation» based tests comparing observed and hypothesized patterns: 3 - congruence assessed by random re-sampling) are tested against a series of «known» cases of ecogenetically or phylogenetically caused geographic variation to establish whether they can distinguish between these two causes. The former two procedures can distinguish between these causes in some circumstances, but the last procedure is not particularly useful for this purpose because independent morphological character systems can have congruent patterns of geographic variation even when they are ecogenetically caused.

KEY WORDS: Geographic variation - Population systematics - Ecogenetics - Phylogenesis - Natural selection - Re-sampling - Congruence - Anagenesis - Causal hypotheses.

INTRODUCTION

Geographic variation within a species can be caused by factors that can be grouped under two main headings: ecogenetic and phylogenetic. Ecogenetic geographic variation has arisen as the result of current ecological conditions, that is, natural (and sexual) selection together with the influence of gene flow. Phylogenetically caused geographic variation does not relate to current conditions but is due to historical events, i.e., microphylogenesis over time. This can involve genetic drift after genetic isolation due to such things as vicariance events. Whilst much geographic variation will have been influenced by both factors some examples exist which appear to be predominantly due to one, or other, cause.

An example of ecogenetic variation free from phylogenetic effects comes from organisms which quickly develop geographic variation after being introduced into new territories. One such case is the geographic variation in the fruit fly, *Drosophila buzzatii*, introduced into Australia with *Opuntia* in the last century. Analysis of data supplied by Barker (Barker & Mulley, 1976; Sokal, 1983) reveals clear evidence of geographic variation in Australia. Frequencies of seven isozymes (EST1A, EST2A, EST2C, HEX-A, PGM-B, AO-A, ADH1C) from thirteen populations along a north-south climatic gradient (Fig. 1a) were subject to principal component analysis. The resulting PC1 shows distinct and significant latitudinal variation as illustrated in Figure 1b (correlation between PC1 scores and latitudine: $r = 0.8$, $P = 0.001$).

An example of geographic variation that appears to predominantly relate to historical events rather than current conditions is given by variation among the Philippine island populations of the Asiatic cobra, *Naja naja* species complex (Wuster & Thorpe, 1990). Canonical variate analysis of morphological characters reveals three main geographic groups of island populations: northern, south-eastern and south-western (Fig. 2). This does not relate to the latitudinal climatic variation but closely fits the historical (Pleistocene) distribution of land when sea levels were lower due to the expansion of the polar ice-caps (Fig. 2).

The aim of this paper is to investigate whether one can distinguish among the causes of geographic variation using quantitative procedures and to integrate cause with the choice of systematic approach and the formal use of subspecies. To this end the following propositions are considered.

PROPOSITIONS

Determining cause

Ecogenetically and phylogenetically caused variation can differ in nature so that they may sometimes be
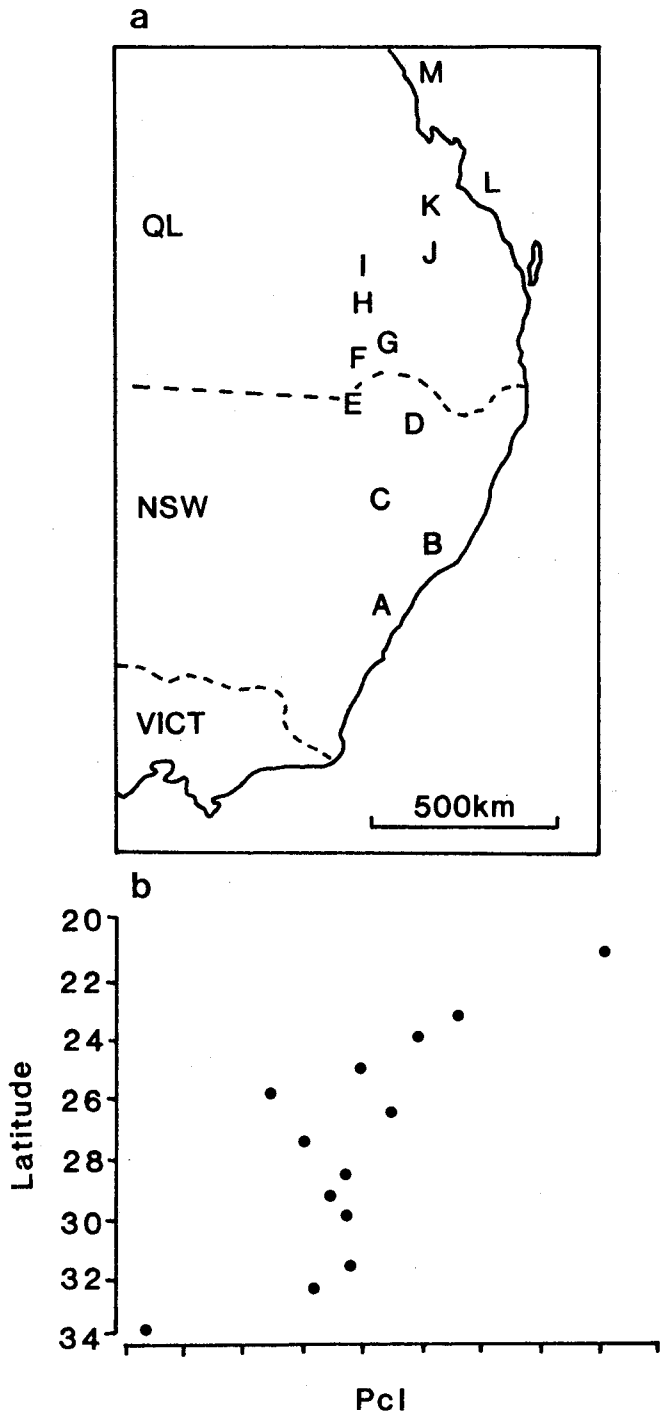
Fig. 1 - Ecogenetic geographic variation in the fruit fly, *Drosophila buzzatii*, introduced into Australia. Localities of samples A to M arranged along a latitudinal climatic gradient. Overall isozyme differentiation of samples A to M (PC1 from a principal component analysis of 7 isozyme frequencies) plotted against latitude.

distinguished by the appropriate quantitative procedures.

Phylogenetically caused variation

As all character systems are subject to the same phylogenesis there should generally be broad congruence among various character systems, such that the pat-

tern in one system should be broadly predictive of the pattern in other systems. Consequently, it may be possible to define «natural» groups and formal subspecies may be useful. The generalized pattern of variation can be described by phenetic methods and the ancestral-descendant sequences can be hypothesized by phylogenetic methods.

Ecogenetically caused variation

As different characters may be responding to different selection gradients there may be incongruence among character systems and the variation in one system may not predict the variation in other systems. Consequently, subspecies are inappropriate as they may not be predictive. Phenetic methods can be used to describe generalized patterns, whereas phylogenetic methods
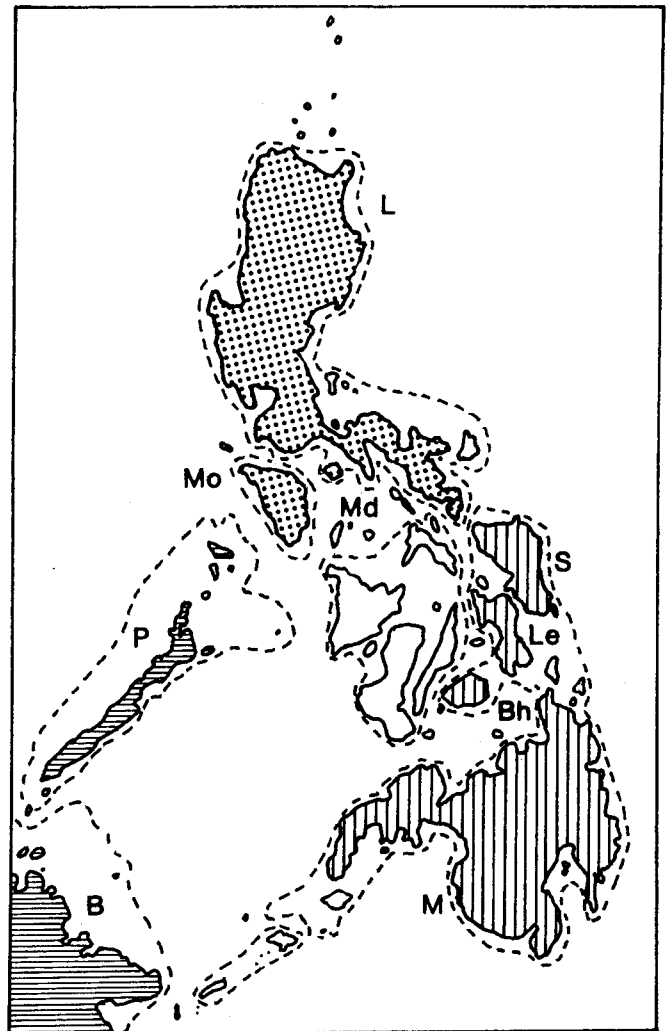
Fig. 2 - The relationship between past islands based on Pleistocene sea levels (dotted line) and current geographic forms of the Asiatic cobra in the Philippines and adjacent islands. B, Borneo; Bh, Bohol; L, Luzon; Le, Leyte; M, Mindanao; Md, Marinduque; Mo, Mindoro; P, Palawan; S, Samar. The dotted area is the distribution of «philippinensis», the vertical hatching is the distribution of «samarensis» and the horizontal hatching is the distribution of «sumatrana».

should not be used as the putative tree may reflect current selection gradients and gene flow, but not an ancestral-descendant sequence.

MODELS

Testing prospective procedures for discriminating between ecogenetic and phylogenetic geographic variation requires them to be tried on «known» cases of both. Of course, strictly speaking, one cannot know the cause of geographic variation in any case study, but one can be sufficiently sure of the broad nature of the cause in several cases to make it worthwhile using them in an attempt to test the procedures. Similarly, whatever the procedure, it will have expectations that the data fulfill certain requirements. In reality, it is not likely that a given case (or model) will fulfill all the ideal requirements for all procedures, but, even so, much can be learnt from these cases.

The phylogentic model is the east-west categorical differentiation of the grass snake, *Natrix natrix*, in mainland Europe. The eastern and western forms meet along a sharp transition zone running north-south in central Europe. This zone does not relate to any ecological change, but is orientated in the same way as those of other pairs of races/species (White, 1978; Thorpe, 1979) in similar, but not identical, positions in central Europe. It is thought that this set of transition zones is the product of ice-cap induced vicariance in the Pleistocene (Thorpe 1979, 1984a).

There are several ecogenetic models, but not all are suitable for all procedures. One of the ecogenetic models is the latitudinal geographic variation in Australian *Drosophila buzzatii* as discussed above. Another set of models is supplied by the Canary Island lizards. There is one widespread lacertid, gecko and skink on each island. Two of the high altitude islands, Tenerife and Gran Canaria, have very distinct parallel latitudinal variation in climate (the north is warm, moist with lush vegetation whilst the south is hot, arid and barren), but independent «histories». All lizard species on the two islands (except the Gran Canaria gecko which is yet to be fully studied) show parallel latitudinal geographic variation in relation to the climatic gradients. It is possible, but unlikely, that the parallel variation within an individual island could be due to common historical events (such as lava flow induced vicariance), but only ecogenetic variation in response to similar climatic variation can explain why it is common to the species in both islands. A similar situation exists in Lesser Antillean anoles. The Dominican anole (*Anolis oculatus*) shows altitudinal and longitudinal variation in response to climate changes (Malhotra & Thorpe, 1991), some of which are paralleled in the sister species (*A. marmoratus*) on the adjacent island of Guadeloupe. Once again, such parallel variation on different islands with parallel climatic changes points to the cause being ecogenetic rather than phylogenetic.

PROCEDURES

Three quantitative procedures are used in an attempt to distinguish between ecogenetic and phylogenetic variation and to investigate this proposition: 1) testing for a direction of evolution by considering the pattern of anagenesis in putative phylogenetic trees; 2) testing causal hypotheses by using «correlation/regression» procedures to compare observed and hypothesized patterns of variation; and 3) investigating congruence by random re-sampling.

Pattern of anagenesis and direction of evolution

In a phylogenetic tree based on a well buffered data set the extent of divergence should be related to the order of divergence, i.e., the branches nearer the root should tend to be longer (show greater anagenesis) than the more recent branches. The pattern of anagenesis can therefore be used to test for a significant direction of evolution (Thorpe, 1982, 1983, 1984a) in a putative phylogenetic tree. Phylogenetically caused variation should result in a tree that is related to geography and which has a significant direction of evolution, whilst ecogenetically caused variation should result in a putative tree that may be related to geography, but without a significant direction of evolution (Thorpe, 1982, 1983, 1984a).

The phylogenetic model, the grass snake, has a statistically significant direction of evolution in both western and eastern lineages of Wagner trees constructed from numerous morphological characters (Thorpe, 1982, 1983, 1984a, b). The various lineages of the tree can be interpreted in terms of range expansion (Thorpe, 1982, 1983, 1984a, b) showing the east-west and Balkan zones to be secondary and the Pyrenean zone to be primary. Reticulate evolution between the Italian and Iberian lineages is also revealed (1982, 1984a). Consequently, this phylogenetic model conforms to the expectation that historically/phylogenetically caused geographic variation results in a distinct pattern of anagenesis. The positive result is recorded in Table I.

The ecogenetic models, the Tenerife gecko and the Australian fruit fly were also subjected to this procedure. A Wagner tree was constructed for the 13 Australian fruit fly populations based on the frequencies of seven isozymes. The tree is clearly related to geography (Fig. 3), with northern and southern «lineages». However, there is clearly no tendency for the branches near the root to have greater anagenesis from those near the terminal sections of the lineages. When the tree is tested for a significant direction of evolution, using the rank correlation tests in Thorpe (1984a, b, 1991) to correlate position and extent of divergence in a putative «lineage», then there is no section of the tree that gives a significant direction of evolution. For example, if one takes a midpoint root, the rank correlation between extent and position of divergence in the northern «lineage» is $r_s = -0.16$, $P > 0.05$). Consequently, this putative «tree» relates

TABLE I - *Conformation (+) or non-conformation (–) of the proposition that ecogenetic and phylogenetic causation can be determined by the quantitative procedures. NC represents no comparison and ? represents equivocal results.*

Cause: Model	Procedure		
	1-Anagenesis	2-Correlation	3-Resampling
Phylogenetic:grass snake	+	NC	+
Ecogenetic:Australian fruit fly	+	NC	NC
Ecogentic:Tenerife gecko	+	+	-?
Ecogenetic:Tenerife lacertid	NC	+	NC
Ecogenetic:Gran Canaria skink	NC	+	NC
Ecogenetic:Dominican anole	NC	+	NC

to the geoclimatic ecological gradient, but does not give ancestral-descendent sequences. It may be a Wagner tree, but it is not a phylogenetic tree in a biological sense.

This model conforms to the expectation that ecogenetically caused geographic variation does not result in a distinct pattern of anagenesis with greater divergence near the root. The positive result is recorded in Table I.

The second ecogenetic example, the Tenerife gecko, is the subject of a detailed study (Thorpe, 1991). Thirty-five characters from three morphological systems (colour, scalation, body-dimensions) are used to construct a Wagner tree joining 14 populations (Thorpe, 1991). Once again the north-south geoclimatic gradient (the latitudinal climatic differences within Tenerife in this case) is reflected in the Wagner tree, which has northern and southern «lineages». However, there is no tendency for the branches nearer the root to have greater divergence, so when the tree is tested for a significant direction of evolution it can be seen that there is none, no matter what section of the tree is considered (Thorpe, 1991). This model also conforms to the expectation that ecogenetically caused geographic variation does not result in a distinct pattern of anagenesis with greater divergence near the root. The positive result is recorded in Table I.

«Correlation» between observed and hypothesized patterns

An observed pattern of geographic variation can be «correlated» and/or regressed against a pattern(s) hypothesized by a given cause(s) (Dietz, 1983; Dillon, 1984; Manly, 1986; Thorpe & Brown, 1989a, b, 1991; Brown & Thorpe, in press, a, b). There are many problems with this procedure (discussed in Thorpe & Brown, 1989a, b), but when the patterns are unidimensional, several problems can be overcome by simultaneously considering the hypothesized patterns

(independent variables) in relation to the observed pattern (dependent variable) using partial correlation analysis. Alternatively, Mantel tests may be used to compare patterns of geographic variation and potential causative hypotheses when they are represented by similarity matrices.

One of the problems with this procedure is hypothesizing realistic, precise patterns without resort to circular logic. This cannot readily be done with the historical (ice-cap induced vicariance) hypothesis for the grass snake, because although one can hypothesize the orientation and general position of the post-Pleistocene contact zone one cannot hypothesize its exact position. Consequently a «no comparison» is recorded in Table I.

This procedure has been applied to several ecogenetic models, selected from the Canary Island lizards, i.e., Tenerife lacertid, Tenerife gecko and Gran Canaria skink as well as to the Dominican anole.

For the Tenerife lacertid Thorpe & Brown (1989a, b) investigated six colour pattern characters, both univariately and simultaneously with canonical variate analysis, to give the observed pattern among 67 localities. Patterns were derived from seven different
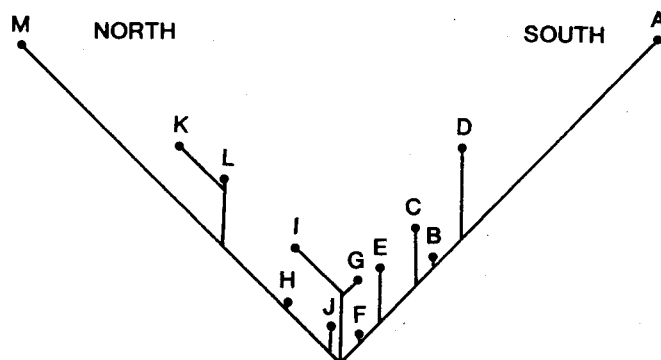

Fig. 3 - Wagner tree of *Drosophila buzzatii* populations (Fig. 1a) showing the presence of geographic «lineages», but the absence of a pattern in the anagenesis.

feasible, or previously suggested, ecogenetic and phylognetic hypotheses. Using partial correlations, these were simultaneously compared to the observed patterns and a specific ecogenetic hypothesis accepted, i.e., topographically determined climatic conditions with the possibility of some gene flow. As expected, this procedure has indicated an ecogenetic cause for this model so a positive result is recorded in Table I.

In the study of the Tenerife gecko canonical analysis was used to summarize the observed geographic variation among the 14 localities in each of three morphological systems. i.e., scalation, colour pattern and body dimensions. Four hypothesized patterns (two phylogenetic, two ecogenetic) were simultaneously compared with the observed patterns by partial correlation. A specific ecogenetic hypothesis (selection for climatic conditions plus gene flow) was accepted by this procedure so a positive result is recorded in Table I. These tests were repeated using simultaneous Mantel tests which gave supporting results (Thorpe, 1991).

Brown & Thorpe (in press, a, b) investigated the colour pattern, scalation and body dimensions of the Gran Canaria skink both univariately and simultaneously (using canonical variate analysis), to give the observed patterns among 47 localities. Four hypothesized patterns (three ecogenetic, one phylogenetic) were tested against the observed patterns by partial correlation and simultaneous Mantel tests. Various ecogenetic hypotheses were accepted (primarily, selection for latitudinal and altitudinal climatic effects), but the phylogenetic hypothesis was rejected (Brown & Thorpe, in press, a, b). This conforms to expectations so a positive result is recorded in Table I.

In their study of the Dominican anole Malhotra & Thorpe (1991) used seven characters from the colour pattern, scalation and body dimensions recorded from 33 samples distributed throughout Dominica. They use Mantel tests to show that the morphology is related to current ecological conditions and they use partial correlations to show that various character constellations are related to specific ecogenetic causes. That is, colour pattern and visual aspects of the body shape are related to vegetation, scalation to rainfall, and body size to altitude. This conforms to expectations of ecological causation so a positive result is recorded in Table I.

Random re-sampling/congruence

If the geographic variation is caused by historical phylogenetic processes then all characters systems would, in general, be subjected to the same processes and should be broadly congruent. On the other hand ecogenetic variation in one character or character system can be quite independent of that in another system where different selection pressure pertain. For example, characters in the Tenerife lacertid and Gran Canaria skink can be adapted either for predominantly altitudinal, or predominantly latitudinal, differentiation (Thorpe &

Baez, 1987; Thorpe & Brown, 1991; Brown & Thorpe, in press, a, b).

Congruence among characters and character systems cannot readily be separated from the influence of character number (Thorpe, 1985, 1987a) so the following procedure (Thorpe, 1985) is used to investigate congruence. Completely non-overlapping subsets, of a given number of characters, can be randomly selected from a large set of significant, independent characters (with a low within-locality correlation to avoid genetic correlations) drawn from a range of independent systems. The congruence between the ordinations (first two principal components) depicted by these subsets can be measured by rotational fit, R^2, (Gower, 1971) and the mean congruence computed for the given size of subset. The mean R^2 is then plotted against the number of characters in a subset. Such random re-sampling procedures are being used increasingly in quantitative research (Efron, 1982; Thorpe, 1987a, and references therein).

High congruence should lead to a rapid increase in R^2 values with character number and then a high asymptote, whilst no congruence should result in low R^2 values that do not increase with character number (Fig. 4). According to the proposition phylogenetically caused variation should tend to conform to the high congruence case, whilst the ecogenetically caused variation may tend to conform to the low congruence case.

In the phylogenetic model, the grass snake, 71 characters from six morphological systems were studied across 14 populations (Thorpe, 1985). Early analyses of this data set used product-moment correlations to measure congruence (Thorpe, 1985), but these have been repeated using R^2 to compare 2D ordinations so that they are more directly comparable to the results derived from the ecogenetic model. Congruence increases rapidly to a high asymptote (Fig. 4b) as expected for historical/phylogenetic variation so a positive result is recorded in Table I.

In the ecogenetic model, the Tenerife gecko, 35 characters from three morphological systems were studied across 14 populations (Thorpe, 1991). The procedure used was identical to that used for the above phylogenetic model. Congruence starts lower than in the phylogenetic model and does not increase as rapidly (Fig. 4b). Nevertheless, it does increase indicating some congruence among morphological systems in this ecogenetically caused variation. Consequently, a questionable/negative (-?) result is indicated in Table I.

DISCUSSION

As the ecogenetic and phylogenetic models were based on «real» data they, almost inevitable, had limitations. The first procedure, the pattern of anagenesis in putative phylogenetic trees, appears to be capable of distinguishing between ecogenetic and phylogenetic
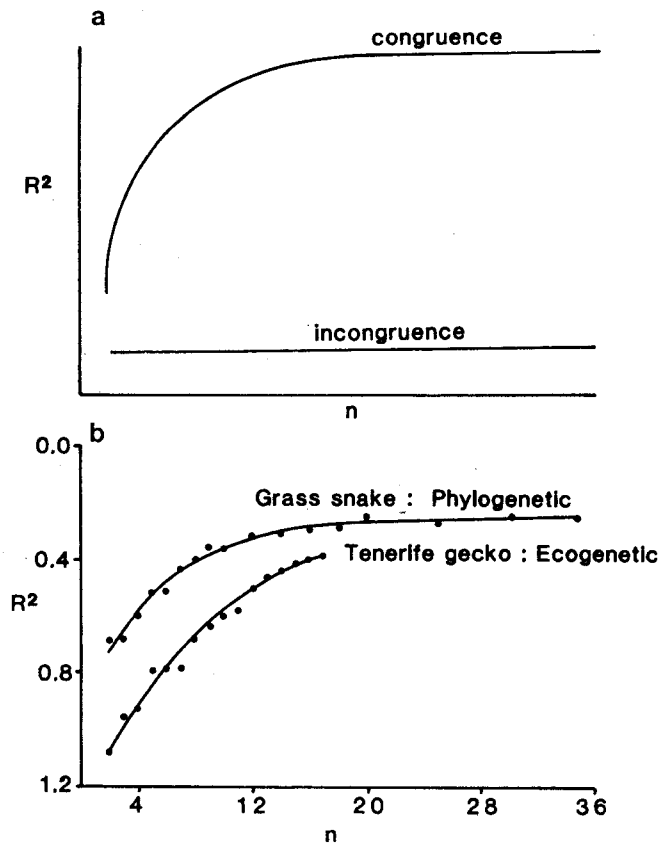
Fig. 4 - Plots of mean congruence (R^2) against character number (n) derived from random re-sampling. Fig. 4a. The type of relationship expected from congruent and incongruent patterns of geographic variation. Fig. 4b. The observerd relationship (line statistically fitted through means, Thorpe, 1991) between congruence and character number for the phylogenetic model (grass snake) and the ecogenetic model (Tenerife gecko).

variation based on the results obtained from the grass snake (phylogenetic), Tenerife gecko (ecogenetic) and Australian fruit fly (ecogenetic) models. Ideally one would prefer more populations in both the ecogenetic models and more characters in the Australian fruit fly case.

The second procedure, «correlation» based comparison of observed and hypothesized patterns tests, could not be employed with the phylogenetic model (as explained above), but «correctly» selected ecogenetic hypotheses from among several ecogenetic and phylogenetic hypotheses proposed for the within-island variation in lizards, i.e., Tenerife gecko, Tenerife lacertid, Gran Canaria skink and Dominican anole. This procedure has not been used for the Australian fruit fly. Consequently, in some circumstances, this procedure can be used to distinguish between ecogenetic and phylogenetic variation.

The third procedure, random re-sampling to assess congruence, gave the expected curve for the phylognetic model, but did not indicate the «expected» very low congruence for the ecogenetic model (Tenerife gecko). This procedure requires numerous characters from

several independent systems, including, preferably, biochemical characters. Consequently, this procedure cannot easily be used to distinguish between ecogenetic and phylogenetic causes when only morphological systems are used.

In conclusion, one can see that ecogenetically caused variation may be distinguished by testing for a direction of evolution using the pattern of anagenesis, and by testing causal hypotheses using «correlations» to compare observed and hypothesized patterns, but not by using random re-sampling to assess congruence, except perhaps if biochemical data are included.

Prior to considering the implications for populations systematics it is appropriate to recall that, apart from conventional «subspecies naming», one can conveniently partition the various approaches to intraspecific systematics into two schools: 1) the multivariate (phenetic) approach which aims to describe the pattern of geographic variation and/or relative similarity of the populations using quantitative analysis of several characters and; 2) the phylogenetic approach which aims to hypothesize ancestral-descendent lineages (Thorpe, 1987b).

Irrespective of whether one uses a phylogenetic or phenetic approach direct «correlation» tests of causative factors may be useful in establishing cause, and random re-sampling (Felsenstein, 1985; Thorpe, 1985, 1987a, and references therein; Wuster & Thorpe, 1989) may be useful in establishing the reliability of the patterns (whether ordinations or trees).

Multivariate ordination analysis makes no assumptions about cause and can be used to investigate both ecogenetically and phylogenetically caused geographic variation. On the other hand, phylogenetic methods do assume a cause and therefore should not be used on intraspecific morphological data without testing for cause (e.g., by anagenesis), and should not be used at all if the cause is ecogenetic.

A part of the original proposition was that subspecies could not be used with ecogenetically caused variation due to low congruence. However, random re-sampling has shown a fairly high level of congruence among characters from three morphological systems in the Tenerife gecko. Nevertheless, I maintain that this is insufficient congruence to allow for subspecies as it is unlikely to predict the variation in other systems, e.g. isozymes, DNA and mtDNA.

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