

Chapter 5

The Evolutionary Ecology of Linguistic Diversity in Human Populations

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It is probably fair to say that Colin Renfrew has not been entirely sympathetic to an evolutionary and biological approach to prehistory. To quote from his Huxley Lecture of 1991: 'I have always thought that the attempt to draw too close an analogy between biological (or Darwinian) evolution and the evolutionary process of human cultural development was a vain one'. Or from the same lecture "'Social evolution" is a misleading term when it kindles hope of some analogy with the processes ubiquitous in the living world of mutation, natural selection, and speciation' (Renfrew 1992). Even in his massively influential *Archaeology and Language*, he cannot resist a small sideswipe at the role of biology, or at least physical anthropology. 'I personally remain to be convinced that any clear historical conclusions can be drawn from such work [the study of human skeletal material], although it is theoretically possible that they might' (Renfrew 1987).

Given this scepticism for things biological, it is perhaps ironic that, in his recent work in collaboration with geneticists, he has been at the forefront of inter-disciplinary research with one of the central disciplines of evolution and biology (Renfrew & Boyle 2000). By exploring the link between the genetic traces of population diversification and the phylogeny of languages, especially that of Indo-European, he has stimulated a whole new field of archaeological research which is now tackling these issues on a broader scale (Bellwood 2001). The fecundity and success of this paradigm, which Renfrew has named 'archaeogenetics' (Renfrew & Boyle 2000), seems a far cry from his earlier distancing from things evolutionary. Not quite, would no doubt be his typically robust response to such an accusation. Genetics, he would argue, provides an invaluable tool with which to explore aspects of prehistory, but the actual approach to which remains truly archaeological. In archaeo-

genetics, archaeology is the bride, not the bridesmaid. Genetics is just doing the catering. And it is true, that the models that Renfrew has developed for explaining the patterns of linguistic diversity are resolutely archaeological and anthropological, and little is drawn from the theories of the biological sciences. Genetics is an empirical, not a theoretical, stimulant.

This, of course, is a bit like saying that some of my best friends are geneticists, but I would not want my daughter to marry one of them; empirical collaboration is one thing, but theoretical fusion is another. Such things, however, as many have found out, are difficult to stop once the contact is there. Such is the spirit of this paper — to consider briefly the relationship between Renfrew's theory of language change and replacement, and cognate ideas in evolutionary biology. I will suggest here that Colin Renfrew's model of change can be a stimulus to considerations in evolutionary ecology more generally, and that evolutionary theory can provide an important basis for this field.

Language, speciation and evolution

Leaving aside the question of the origin of language itself, there are a number of reasons why various evolutionary models might be applicable to the pattern of language change. Language changes, and in that process languages diversify, forming new units. This is analogous to the way in which populations diverge, and in the process become reproductively isolated. There have been many models of speciation developed, exploring whether it occurs sympatrically or allopatrically, is related to adaptation, or occurs stochastically, and whether there is any ecological basis to its patterning (Mayr 1963; White 1978; Templeton 1980). Certain ecological conditions, it

has been argued, are more likely to promote speciation than others — mosaic habitats, for example, resource rich environments, etc. It has also been argued that certain adaptive and behavioural traits are also more likely to lead to reproductive isolation, and hence the formation of new taxa at a higher rate — for example, ecological specialists rather than generalists (Vrba 1984; 1992).

There is thus a similarity between the process of speciation and language diversification that would merit considering whether it is possible to look at the ecological conditions under which new languages form. In addition, languages, like species, also become extinct, and are replaced one by another — a central element in much of Renfrew's recent work. Extinction of both languages and species can benefit from an examination of its ecological context.

We should, of course be aware that there are important differences between languages and species, and that the processes may be different. These are not homologies, but our approach is one of analogy. The key differences are the fact that languages can be transmitted horizontally as well as vertically, and that clearly an individual is capable of speaking more than one language and adopting new ones. Nonetheless, there remain important parallels: one is that languages are generally defined as being a system of spoken communication that is intelligible to speakers of that language, but not to others. This is, in effect, the equivalent of the genetic boundaries that occur between species, and allows us to treat both as lineages. Both language and species, however, share an intermediate level in which the process of divergence actually occurs — that of dialect formation in language, and sub-species in biology. It is at this level, often associated in both cases with geographical separation, that the mechanisms of change occur most actively. Thus, although we talk here of language divergence and formation, much of it will actually be occurring in the formation of dialects, in the same way as much of the action in evolutionary biology is really taking place in sub-species (Foley 1999).

Renfrew's models of language change and replacement

Renfrew's ideas about the processes and types of language change and replacement, as opposed to his specific reconstructions of the history of Indo-European, have been outlined in various publications (Renfrew 1987; 1992; 1994; 1998; 2000). His models comprise a number of inter-locking elements, relat-

ing partly to the processes of language change and diversification (essentially language evolution), partly to language replacement, partly to do with the economic, social and demographic processes underlying change and replacement, and partly the identification of a particular set of major historical events. Figure 5.1 is an attempt to summarize the main components of Renfrew's thinking on this subject.

The starting point for his models is that they attempt to describe and explain language change as experienced or pin-pointed at a particular geographical place — be that place a small valley or region, or a whole continent (Fig. 5.1A). The models are thus specifically concerned with change in historical and geographical context — an interesting convergence, of course, with many evolutionary models in general. Following initial colonization, language change can be seen as a process of divergence, of convergence, and will ultimately end up with the extinction of languages and their replacement if the process of dispersal is sufficiently powerful.

In terms of what is observed linguistically, each of these processes of change will be observable — in theory at least — in the languages themselves (Fig. 5.1B). Divergence, for example, will be measurable in terms of increased diversity within a language family; convergence observable in shared words, and perhaps a shift in some grammatical structures (e.g. word order). As linguistic history must generally be inferred from extant languages, in effect the evidence for such changes will be in the form of linguistic signals that have left traces in descendent languages.

As Renfrew makes clear, however, the language is not the main driver of these changes, but is carried along by larger social, economic and demographic processes (Fig. 5.1C). The same is true, of course, for genes, the distribution and frequency of most of which are simply a reflection of the history of the population (the exception are those genes that are under strong selection, such as those which act in relation to malaria which can confound historical signals: Tishkoff & Williams 2002). His models therefore identify a number of factors which can contribute to whether languages change, are replaced, or remain the same. There are many such processes, of which perhaps the significant and general is that of population dispersal; however, the one most closely associated with Renfrew is that of elite dominance, where a small population can impose their language on a larger one through a process of social coercion, power and influence (Renfrew 1992). English, as it

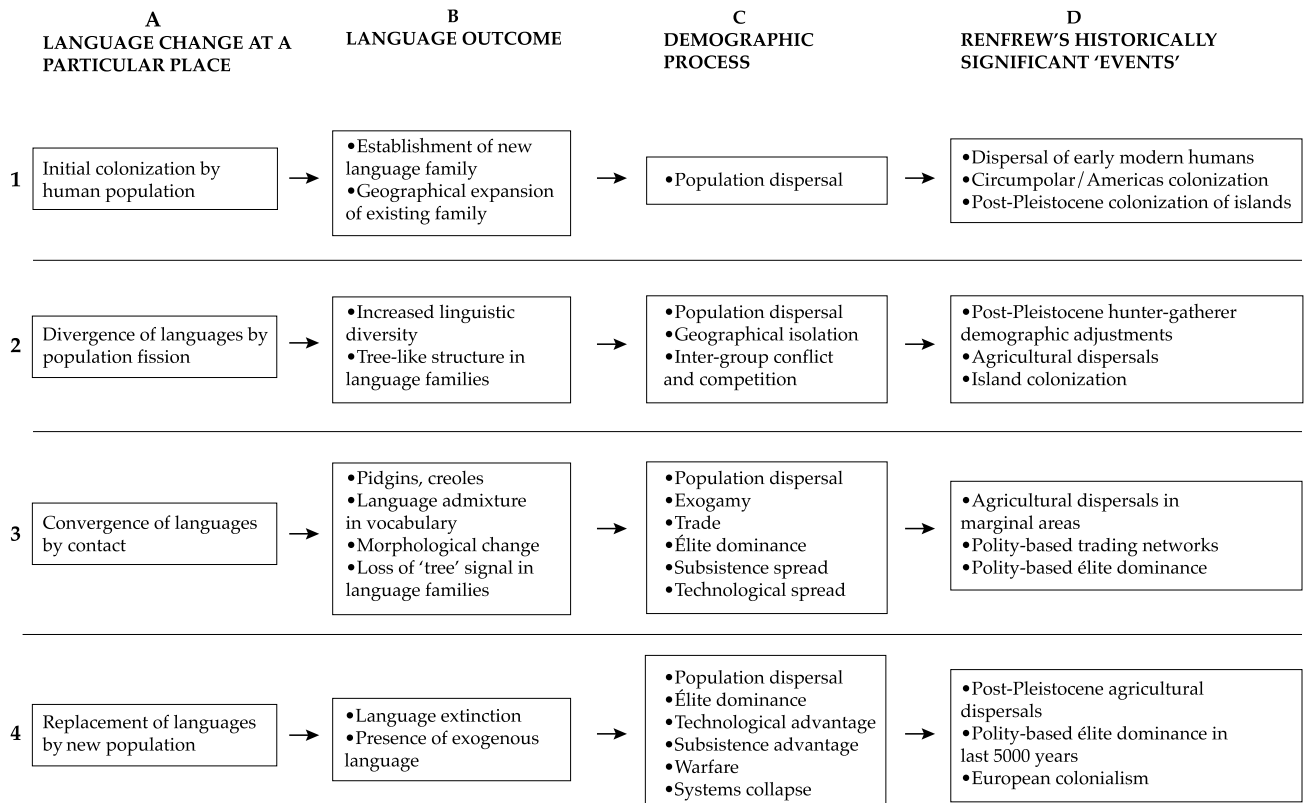


Figure 5.1. Renfrew's language change model: his model is focused on the language history of a particular geographical area (region or continent), which will occur over time (A). On the basis of the demographic history certain linguistic signals will be observable (B), which are in turn the product of demographic processes (including social, technological and economic) factors (C). These in turn have shaped and been shaped by the particular historical events since the emergence of a language-bearing hominin (D).

has spread around the world, is perhaps the best example.

These demographic processes are general ones underlying all human adaptation, but in the way in which Renfrew developed his language change models, they are in turn associated with a particular set of historical events, and thus return to the context emphasized at the beginning of the models described here: namely, that as well as being specific to a particular geographical location, they are also linked with specific phases of prehistory (Fig. 5.1D). The one most associated with Renfrew is that of agricultural dispersals (Renfrew 1998). Starting initially with his hypothesis that the distribution of the Indo-European family was the result of the Eurasian agricultural dispersals, he later extended this to other agricultural expansions, such as those of Africa and eastern Asia (Bellwood & Renfrew 2002).

Overall, therefore, Renfrew's models are designed to take the universe of language change, characterize what might happen, ascribe some underlying

social and demographic causes, and then associate these with particular prehistoric contexts.

The ecology of language diversity

Renfrew's models have drawn on one branch of evolutionary biology — that of molecular genetics. This has happened in two ways. Firstly, as the model described above shows, there is an underlying sense of the tree-like structure of language diversification. This is implicit in both Greenberg/Ruhlen style approaches based on comparative wordlists (Greenberg 1963; Ruhlen 1994), and the classical morphological approach to linguistic reconstruction. Although what biologists would refer to as horizontal transmission — i.e. the movement of words or grammatical structures from one language to another in which there is no ancestral relationship — does occur, it is probably less important as a mechanism in the actual formation of new languages. It may play a role, however, in shaping the direction in which a language

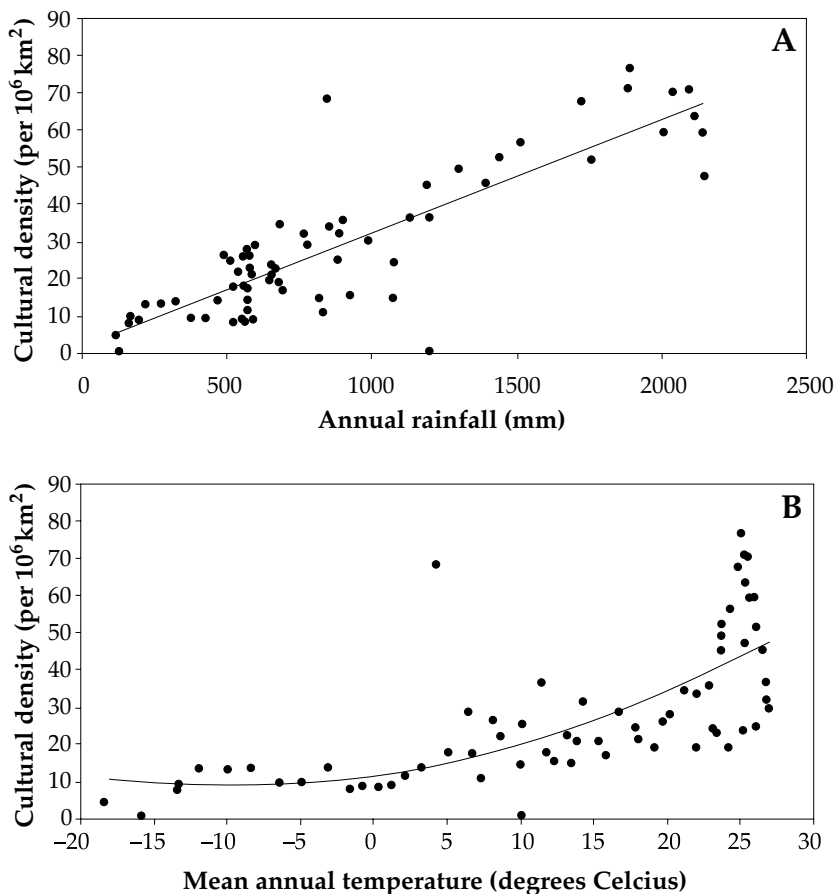


Figure 5.2. Linguistic diversity is strongly related to environmental variables. Here cultural density (the relative number of identifiable groups sharing such traits as: language/dialect; political system; descent group) is positively correlated at a global scale with mean annual rainfall (A), and negatively correlated with temperature (B). Although this plot is global, similar relationships can be shown for longitudinal slices of the world with very different histories, suggesting that this is not simply a historical artefact. (Source: Collard & Foley 2002.)

changes (for example, loan French words in English, or clicks in some Bantu languages). Thus languages show a signal of descent with modification, much as biological organisms do.

This inherent tree structure (i.e. phylogeny) provides the basis for the second linkage between Renfrew's model and genetics — namely that as both genes and languages exhibit this structure, and both are carried by people and populations, there should be a concordance in the trees of each. Luca Cavalli-Sforza and colleagues made the first such formal comparison (Cavalli-Sforza *et al.* 1988), but others, including Renfrew and co-workers (Renfrew 1992), have pursued this concern with regard to molecular data (Barbujani 1997). There have thus been a number

of direct comparisons of the languages and genetic histories of various human populations (Bellwood 2001; Bellwood & Renfrew 2002).

This comparison of linguistic and genetic distributions, however, does not offer directly an insight into the heart of the relationship between what is an evolutionary process — the diversification of populations, and a cultural one — the diversification of languages. Both elements are the product of fundamental biological processes, namely the growth, contraction and interaction of populations. As with most evolutionary problems, therefore, the problem is ecological. The question we need to address is thus that of the ecological basis for population differentiation, which will be the conditions under which language change will or will not occur.

The ecology of linguistic diversity has been addressed most notably by Nettle (1998; 1999). In his early paper on global linguistic diversity, he showed that there was a strong statistical relationship between the number of languages in a given area and the type of environment. In particular, he argued that where risk (in terms of environmental variability such as seasonality or annual fluctuations) was high, then language diversity would be low. The underlying mechanism he proposed was that social networks

would remain large as a means of dampening the risk in one particular area, thus inhibiting language differentiation. Others have also shown that there is a strong environmental component to language diversity at both regional and global scales (Mace & Pagel 1995; Collard & Foley 2002; Moore *et al.* 2002) (Fig. 5.2).

These analyses essentially use equilibrium models to explore the relationship between environmental variables and language distribution — that is, the aerial diversity of languages. Elsewhere, Nettle (1999) makes the distinction between language diversity and phylogenetic diversity — i.e. not the number of languages, but the number of identifiable linguistic stocks or lineages. The biological comparison would

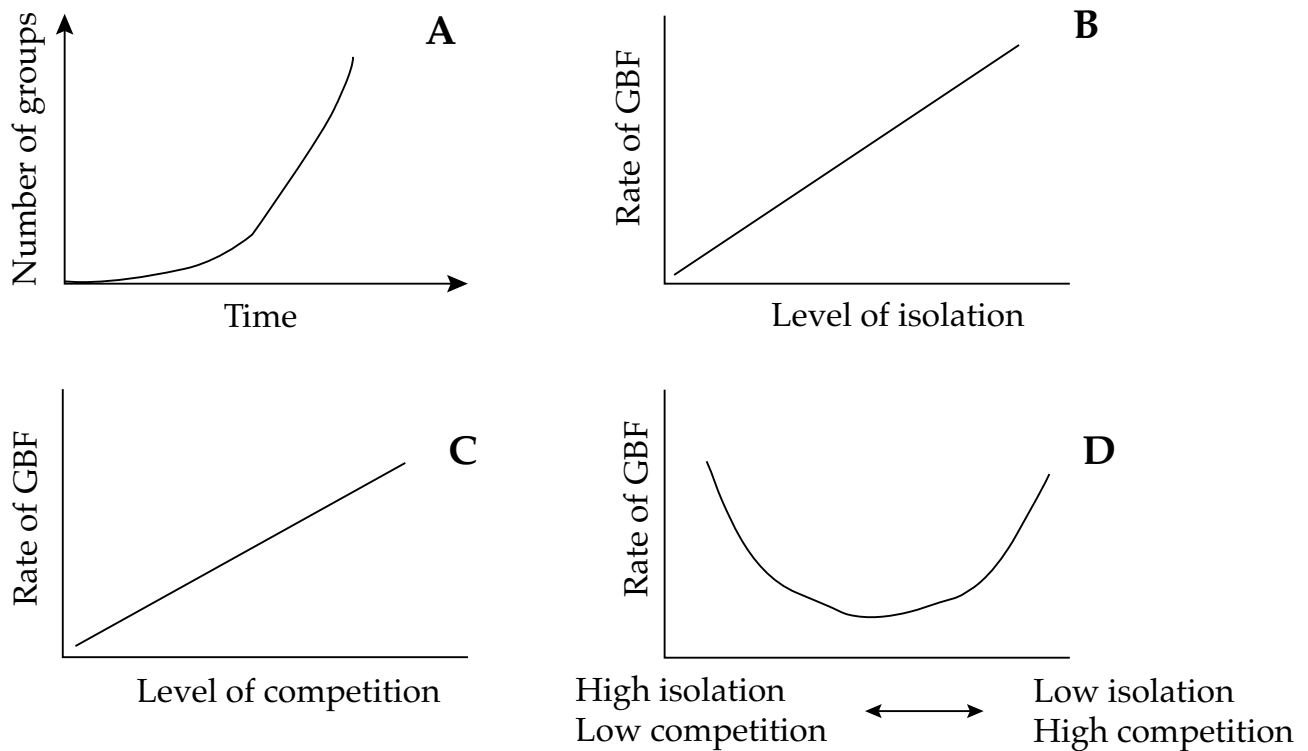


Figure 5.3. Simple one population model of the rate of group boundary formation (GBF). Under a process of fission groups will tend to diversify (A). The rate will be a function of the level of isolation in which fissioned groups find themselves (B), and the degree of competition between and within groups (C). However, as the degree of isolation and the level of inter-group competition will be inversely related to each other, then the rates of GBF will be described by a U-shaped function. Thus the ecological conditions shaping isolation and competition can be used to specify language diversification rates.

be the difference between the number of species in an area compared to the number of higher taxonomic units, genera, families, and so on. Where language diversity is a product of ecology, according to most of the analyses carried out so far, phylogenetic diversity reflects history since colonization. Nettle, in particular, has argued that in the early days of colonization stock density will be relatively high and increase, and then will decline as extinction and replacement takes place.

The evolutionary ecology of human populations: driving linguistic change

The analyses described above show that there is an ecological basis to linguistic diversity. While a case can be made that there is a direct role of language in this process — for example Nettle’s argument concerning the relationship between linguistic inter-communicability and risk avoidance — most would recognize that language is in fact a proxy for some-

thing more closely associated with the demography and behaviour of populations. Language as a phenomenon does not lead to diversity: instead, linguistic diversity is a product of the way in which populations form boundaries, merge, and become extinct. Thus, it should be possible to consider the extent to which a more general evolutionary ecological model can be developed as a framework for Renfrew’s processes of linguistic change. The advantage of this approach is that it will help us to establish the conditions under which different outcomes may occur.

Language is what can be described as a ‘whole group character’ (Pepper 2000) — namely all members of a particular group possess that particular trait (e.g. all members of the Maasai speak Maa; other traits may be possessed by only some members of the group (e.g. blue eyes). Other groups will possess different values (i.e. another language) for this whole group trait. As such language can be considered primarily as a group-boundary marker (albeit a rather special one). Language diversifica-

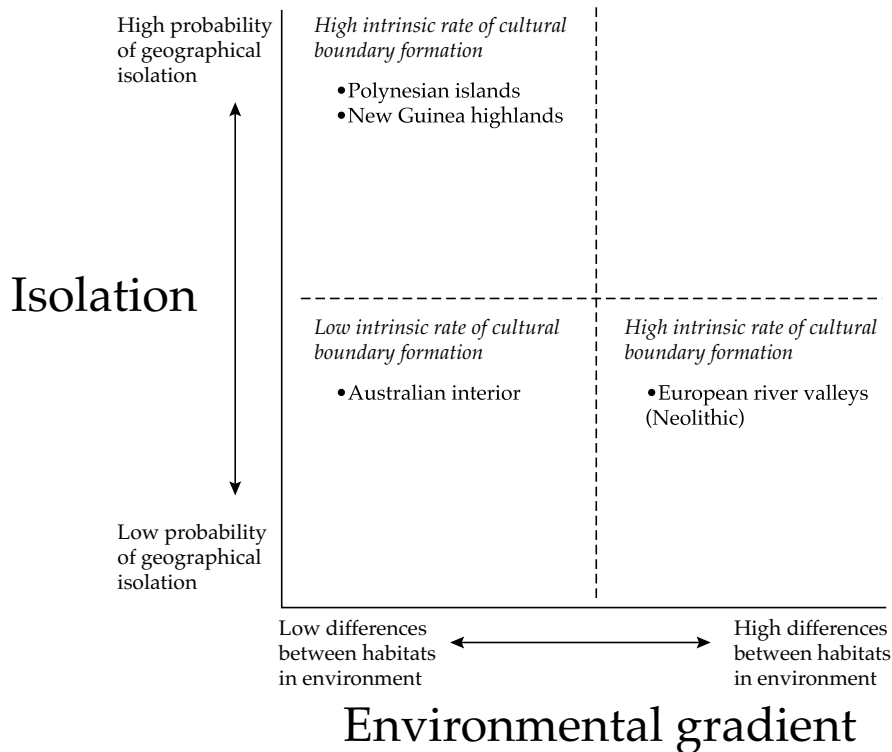


Figure 5.4. Relationship between environmental isolation and resource gradients in rates of group-boundary formation. Environments may have either high or low probabilities of forcing populations to become isolated, and they may also be either relatively lacking in major differences in resource richness or else have marked gradients from resource poor to resource rich. The former will determine the rate of boundary formation due to drift and isolation; the latter the rate of boundary formation due to competitive fissioning.

tion is, therefore, fundamentally a process of inter-group boundary formation.

So we are concerned here with the ecology of group-boundary formation — under what conditions will it occur or be inhibited, and what will determine its rate. We can start with a simple single population model — for example a new population in a previously uninhabited territory (cf. Renfrew’s initial conditions in Fig. 5.1). Groups will diversify as fission occurs through growth; the rate of fission will be dependent upon two parameters — degree of isolation and degree of competition. Where geographical isolation is high, then allopatric drift will result in the separation of groups, and therefore separate linguistic markers of this group. Equally, competition may also lead to an increase in the rate of group-boundary formation, as each group attempts to monopolize resources. Interestingly, there is an inverse relationship between isolation and competition, such that these two processes will work in opposition to each other. This is a common component of evolu-

tionary models, where selection and drift are seen as complementary mechanisms. Thus, as isolation decreases between groups, then levels of inter-group competition will increase. The resulting pattern of the *rate* of group-boundary formation will therefore be U-shaped (Fig. 5.3). There is a further implication of the relationship between isolation and competition in that as an area is increasingly occupied, then it will move through the U-shaped curve.

This is a very simple model, which implies a set of conditions under which high or low rate of group fission will occur, and hence in which a single language lineage will diversify. Those conditions are the ones that would apply for a simple hunter-gatherer dispersal into areas without previous occupation — in other words, most of the Upper Pleistocene dispersals. Environmental conditions, however,

could produce different outcomes. Where environmental resource gradients are high, then intense competition may start to operate very early in colonization, producing a high rate of differentiation; where they are low, language diversity may build up more slowly. Where there is a low gradient of resource differences, but high geographical isolation, then diversity will grow relatively rapidly. As early agriculture in Europe is very much river valley-centred, then one would expect the competitive model to apply; the same may be the case in certain parts of Europe in the later Pleistocene (the Dordogne, for example). The colonization of the Australian interior, or the occupation of the highlands of New Guinea, might be examples of low environmental gradient and high isolation respectively. The settlement of the islands of Polynesia are clearly a classic example where there is a low environmental gradient (one island is much the same as another), but there is a high level of isolation, producing a high rate of differentiation.

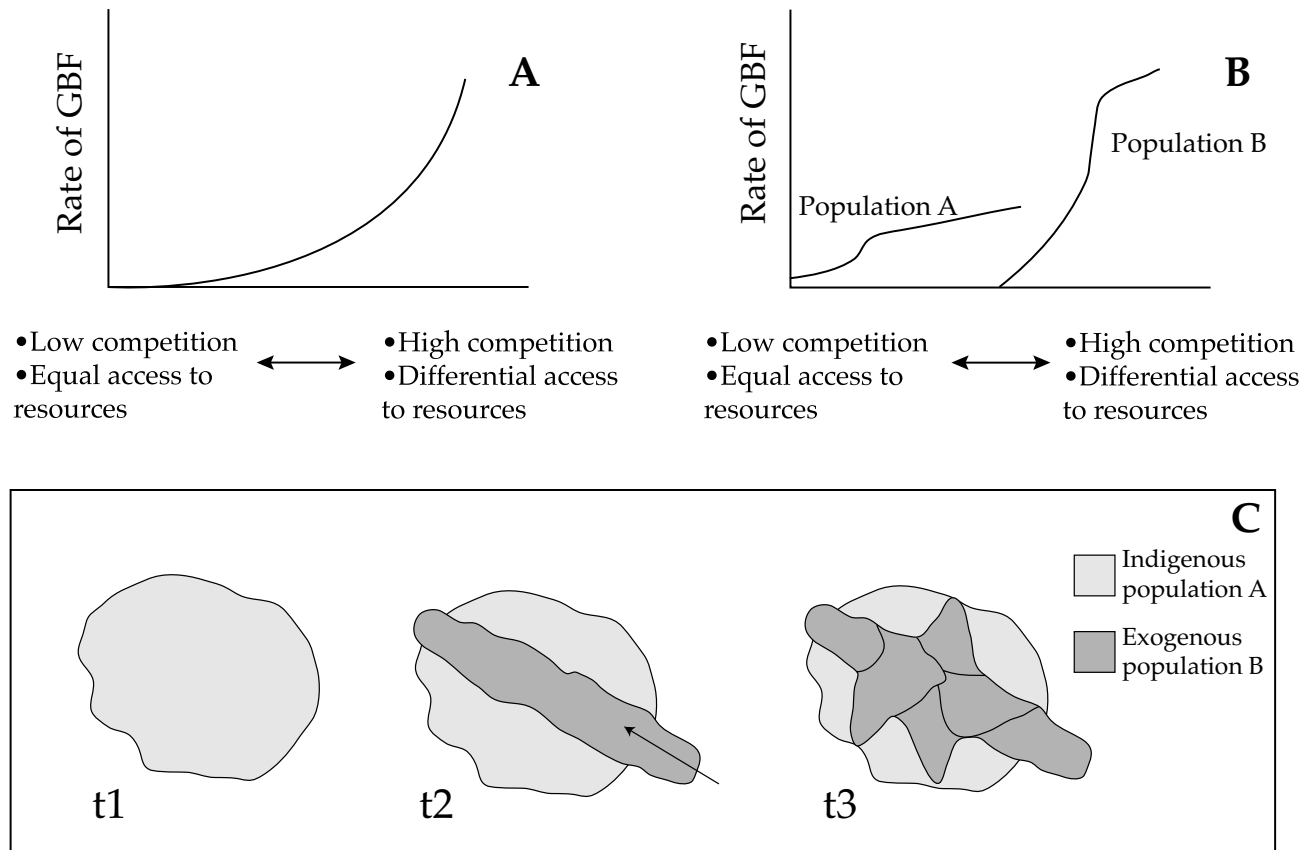


Figure 5.5. One- and two-population models of the rate of group-boundary formation (GBF) under conditions of differential access to resources. Where all groups have a more or less equal access to resources the rate of boundary formation will be low, increasing as competitive differentials increase (liable to be associated with territoriality, resource storage, patchy resource distribution, etc.) (A). These effects would be enhanced where two populations are involved, one of which may have a greater competitive edge (B). If the interactive effects of the two populations are taken into account, then the rate of group-boundary formation is likely to be enhanced as the presence of the highly competitive population will increase the geographical isolation of the less competitive one, increasing the rate of fragmentation.

It is necessary to qualify this model in one important way. Isolation and competition are no more mutually exclusive than 'r' and 'K' are in the ecological models; they are on a continuum, and are elements of any situation (MacArthur & Wilson 1967; Pianka 1970). What is being described here is the way in which they contribute to the growth of diversity, their relative importance (Fig. 5.4).

An element of this model is that there is no competitive differential either within or between groups. Although groups may compete with each other, the model would see the outcome as largely stochastic. We can add a further dimension by considering what happens when there is a difference in the competitive abilities of groups or individuals. Where that difference comes from may not, at this

level, matter very much: it could be a technological superiority (the Upper Palaeolithic), and subsistence advantage (agricultural dispersals), or a combination of the two. It could also relate to social behaviour, such as the ability to amass military groups (important for Renfrew's ideas relating to elite dominance).

We can characterize two types of situation — one where there is relatively little competitive differential, or, put another way, there is relatively little variance in the ecological efficiency of groups or individuals; and one where competitive differential or variance is high. To flesh these out, we might envisage the former being what Binford has termed collectors in the hunter-gatherer foraging spectrum (Binford 1980), while the latter might be hunter-gatherers with more patchy, high-quality resources (that

can be monopolized); a further example might also be the difference between forest swidden agriculturists and pastoralists.

Figure 5.5 considers how this differential might influence group-boundary formation, and hence language diversity. Where resource access differentials are low, then in effect the difference between one group and another will be fairly minimal; people and resources are therefore likely to flow across boundaries, and reduce such boundary formation. As the differentials increase, then such flow will either be reduced or will become increasingly in one direction. In either case boundary formation will be enhanced. Thus we can posit that high levels of differential access to resources will enhance the formation of group boundaries, and thus language as well.

This model essentially posits a single metapopulation in which some groups are 'better' than others — or indeed it could work at the level of individuals or families who are more prone to set-up independent communities. A further level of complexity can be added by considering this same model in terms of two populations, where one has a competitive edge over the other. An example of this would be Renfrew's classic agricultural dispersals. In this case, it would be a situation where one population is more prone to boundary formation than the other.

Of course, this allows for no interactive effects between the two populations. We can consider one simple model of such interactions by adding a spatial component. One effect of the more competitive population would be to expand and fragment within the range of the less competitive one; this will lead to a fragmentation on the peripheries of the less competitive one, thus raising their intrinsic rate of group-boundary formation through isolation — in effect producing a situation in which the two processes that enhance the rate of group-boundary formation will occur simultaneously (Fig. 5.5). These models would predict that, in the case of agricultural dispersals into areas occupied by hunter-gatherers, there would be an increase in the rate of differentiation of groups and languages in both subsistence systems.

Thus far we have considered in theoretical terms how particular ecological conditions can promote or inhibit the formation of cultural group boundaries, and hence the diversification of languages — in other words, the facts that condition the different levels of linguistic diversity that Renfrew has addressed from an archaeological standpoint. Key factors in considering divergence within a single related founder population are the level of geographical isolation,

the degree of inter-group competition, and the extent to which there is a gradient of inequality of access to resources between groups. When two population models were considered, these effects could be seen to be interactive.

The ecology of language replacement

What has been described above is a model for how different ecological conditions might affect the generation of new languages. There is, however, another element, which is central to Renfrew's models, that of language replacement. The ecological and evolutionary equivalent of this is the extinction of populations or species, and more specifically, where such extinction occurs in the context of competitive exclusion.

Languages, of course, can become extinct in two ways: either all the speakers may die, or else they may survive but adopt another language. These are probably parallel to genuine species extinction (the loss of a gene pool, including all its adaptive traits; the loss of a people and its adaptive traits including its language) and pseudo-extinction (the loss of particular traits as a species evolves into something else; the loss of a particular language as its speakers acquire another one). We can consider models for when these might operate.

Leaving aside catastrophic events, extinction among animal populations seems to be predicated upon two major factors — habitat loss and competitive exclusion (Lawton & May 1995). As human populations are essentially able to live in all habitats, the former of these is less significant, at least in the sense that habitat loss is almost always related to other human populations occupying the same geographical areas as habitats change.

Competitive exclusion can lead to both real extinction and pseudo-extinction. An example of the former would be the cultures of Tierra del Fuego, where, through a process of displacement and active interference, the populations actually died out, and their languages with them. An example of the latter would be the disappearance of the various Celtic languages from Britain as English replaced them. What is the difference between these two processes? One answer can be found in the mechanisms identified in Renfrew's language-replacement models — namely agricultural dispersals versus elite dominance. In the case of agricultural dispersals, although there is considerable controversy on this subject (Richards *et al.* 1996; Chikhi *et al.* 1998), it is clear that in some parts of Europe, such as the Danube, there

was actual replacement of populations (Lahr *et al.* 2000; Pinhasi *et al.* 2000). The same was probably the case with the agricultural dispersals of East Asia (Bellwood 2001; Ke *et al.* 2001). In contrast, where *élite* dominance has occurred the indigenous population has persisted, but has changed its language — in parts of Melanesia, among the tribal populations of Southeast Asia, and among Pygmies.

The distinction between agricultural dispersals and *élite* dominance is one of degree, however, not quality. Any competitive replacement is in a sense a process by which a group with some advantage (subsistence, political power, technology, etc.) displaces another. The quantitative element lies in the demography involved, and it is this that explains the difference between pseudo-extinction and actual population extinction. As is illustrated in Figure 5.6, where the indigenous population is at a low density (for example hunter-gatherers), and the exogenous one is at a high density (Lahr *et al.* 2000), then the outcome will be actual population extinction, and language extinction. At the other extreme, where the exogenous population is at a low density and the indigenous one at a high density, then the outcome will depend upon the degree of adaptive difference; a high degree of adaptive difference, which is essentially what *élite* dominance means, will result in pseudo-extinction; where the difference is less marked, then it would be expected that the indigenous language may persist. Language persistence in the context of some genetic change is thought to have been the case with Finnish (Sajantila *et al.* 1995; Sajantila & Pääbo 1995) although this has been disputed (Bandelt *et al.* 2002). Where the two populations are more closely matched in terms of population density, then the outcome will depend upon the degree of competitive difference, and can in turn lead to either greater or lesser degrees of language diversification.

Language replacement, in this comparative evo-

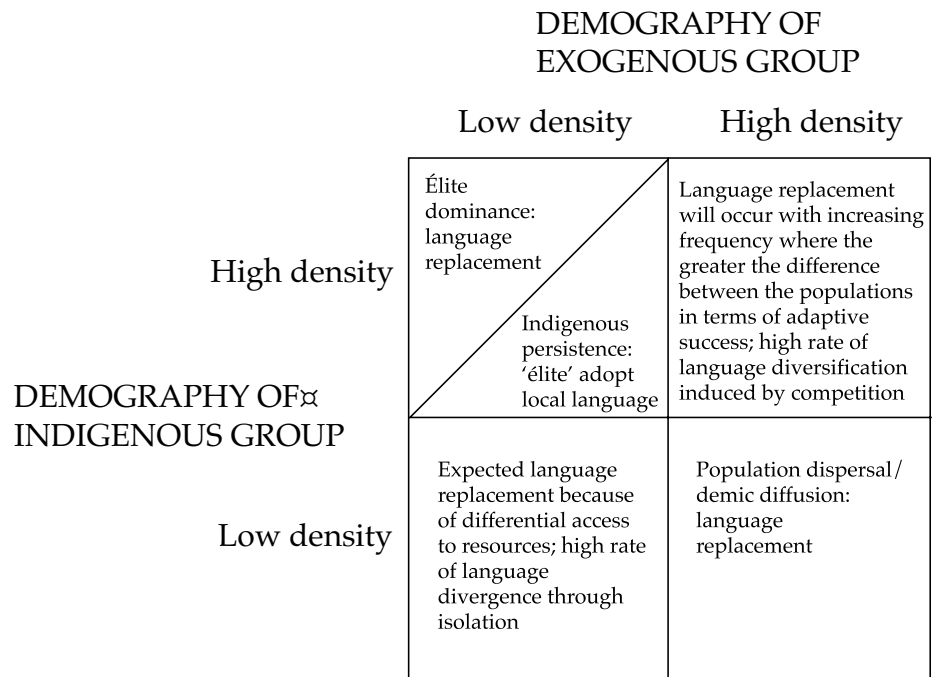


Figure 5.6. *The role of demography in language replacement, shown here in terms of a hypothetical indigenous population, and an incoming one. The outcome for languages will depend upon the relationship between the two, and could result in either local persistence, replacement of language but genetic persistence (pseudo-extinction), or language replacement with genetic replacement (actual extinction).*

lutionary framework drawn from a consideration of extinction processes, appears to be dependent upon two major factors — the relative demographies of the populations, and the degree of difference between their adaptive efficiency. Depending upon these there can be persistence or replacement, and either real extinction of populations, or else pseudo-extinction with the genes persisting but the languages disappearing. Finding more precise estimates for these parameters will be an important part of future research in this field.

Conclusion: evolution, ecology and social processes in linguistic prehistory

The prehistory of languages has until recently not been fashionable in archaeology. Two reasons can be posited for this state of affairs: the lack of direct evidence about the languages spoken by pre-literate societies, and the fact that archaeologists have often abandoned a concern with the 'who's who' of prehistory in favour of questions about process (and indeed, post-process). Renfrew's work in this field has been one of the main stimulants to its development. Furthermore, by incorporating new techniques

drawn from molecular biology, both for reconstructing genetic history and applying directly to linguistic history (Forster & Toth 2003), there is also a closer relationship between questions in archaeology and those in evolutionary anthropology. Here we have attempted to build a further bridge by exploring the ecological conditions that may underlie Renfrew's models of linguistic diversification and language replacement. There are good grounds for doing this: firstly, because it has been shown that patterns or linguistic and cultural diversity are strongly related to environmental factors; and secondly, because language diversity and replacement are driven by the processes of group-boundary formation, which are themselves sensitive to environmental and ecological factors.

How, though, does this square with Renfrew's scepticism about biology and evolution in the pursuit of prehistory? One answer, of course, might be that, with the time on his hands that retirement will allow, he will vigorously pursue an evolutionary approach in the next phase of his work. More likely, however, he will remain deeply sceptical, and look instead for the political, social and cognitive factors that have played a greater role in the many models of cultural and linguistic change that he has developed. There is, though, perhaps one further insight from evolutionary biology that might be worth emphasizing: namely the distinction between ultimate and proximate causation. Most evolutionary explanations emphasize that the ultimate cause of evolutionary change lies in the nature of resource distribution that provides the selective environment; however, for complex social mammals at least, the actual proximate causation is more likely to be the social — and in the human case the political — arena in which evolutionary games are played out. As has been suggested by many before (Renfrew 1973), social and ecological factors are complementary elements in the explanations of culture change.

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