might imply that these traits are more important in terms of competitive interactions rather than habitat preferences. As evolutionary distance increases, species are likely to vary in an increasing number of traits, reducing the strength of competitive interactions. Therefore, competitive exclusion among close relatives would not preclude the possibility that habitat filtering influences community structure at broader taxonomic scales, but the important traits may differ.

How does this new study enhance our understanding of Cape diversity? Strong competition among closely related species in a region such as the Cape, where the species pool is composed of many close relatives, will place limits on species richness, as local richness is restricted by competitive exclusion. This same mechanism, by forcing spatial divergence of closely related species, will also result in high turnover of species along spatial gradients. As Slingsby and Verboom [7] observe, this rather neatly fits with the observation that the high diversity in the Cape is best characterised in terms of exceptional beta diversity (species turnover), whilst alpha diversity (local species richness) remains similar to that found in other Mediterranean-type biomes [9,10]. However, reasons for the rapid rates of diversification observed in Cape lineages, such as the sedges, remain a matter for speculation. Might the same processes responsible for structuring ecological communities also drive speciation rates [13]?

Slingsby and Verboom [7] present a convincing argument for phylogenetic structure in community membership, a likely product of competitive displacement of closely related species sharing similar functional traits. Measuring the maximum evolutionary distance between co-occurring species on a phylogenetic tree can therefore provide an estimate of limiting similarity. However, the web of competitive interactions is likely to be complex within any natural community. Considering only pair-wise interactions will tend to underestimate competitive load. For example, if the strength of competition scales with relatedness, a species co-occurring with a single close relative might experience the equivalent competitive pressure as a species co-occurring with two more-distant relatives, yet pair-wise comparisons will suggest the competitive load of the latter to be half that of the former. Generating a comprehensive model of species-co-occurrence will be challenging, requiring knowledge of phylogeny, biogeography, and ecomorphology for all species within a community.

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Evolutionary Biology: How Did the Human Species Form?

A recent analysis has shown that divergence between human and chimpanzee varies greatly across the genome. Although this is consistent with 'hybridisation' between the diverging human and chimp lineages, such observations can be explained more simply by the null model of allopatric speciation.

N.H. Barton

Neutral DNA sequences accumulate mutations at a roughly constant rate. Thus, by comparing sequences from different species, we can estimate how long ago these sequences diverged. The degree of divergence varies along the genome, primarily because the time when two lineages met in a common ancestor is a matter of chance [1,2]. In a recent paper, Patterson *et al.* [3] analyse a large dataset — almost 30 megabases of aligned sequence from several primate species — and confirm earlier findings (for example [4,5]) that the divergence time between human and chimpanzee varies widely across the genome. They argue that this variation implies that there was hybridisation between the diverging lineages that ultimately led to humans and chimpanzees, and that some genes were exchanged between them much more recently than were other genes. While this kind of analysis of divergence across the whole genome promises to tell us much about the process of

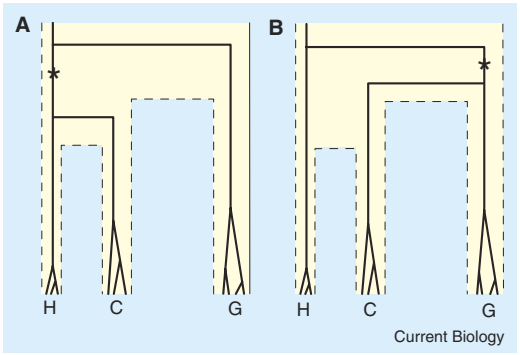

Figure 1. The relationship between genes is not necessarily the same as that between species.

(A) In this example, the genealogy (solid lines) that connects genes sampled from human, chimpanzee and gorilla corresponds to the phylogeny of these three species (dashed lines). The asterisk marks a mutation that is shared by human and chimpanzee, and so defines an HC site. (B) In this example, the genealogy is discordant with the phylogeny: C and G are most closely related. The asterisk marks a mutation that defines a CG site. On average, regions linked to CG and HG sites will show greater divergence between human and chimp than will regions linked to HC sites (see Figure 2).

speciation, in this case the data do not support the hypothesis of human–chimp hybridisation.

Inference of relationships amongst DNA sequences has been used most commonly to estimate phylogenetic trees. However, the genealogical relationships at any one locus in the genome do not necessarily correspond to the phylogeny of the species as a whole [1,2]. As we trace back the lineages of two genomic segments, sampled from two separate biological species, they may coalesce in a common ancestor at any time before those species became completely reproductively isolated (Figure 1A). In the simplest case of a single, well-mixed ancestral population, coalescence times are exponentially distributed, with a mean number of generations equal to twice the effective population size, 2 N_e. This distribution is highly variable, so that there is a 1% chance of coalescence more recently than 0.02 N_e generations before speciation, and a 1% chance of coalescence earlier than 9.2 N_e generations. Thus, if we have three species that diverged at closely similar times, it is quite likely that genealogies of individual genomic segments will not correspond to the overall phylogeny (Figure 1B). Patterson *et al.* [3] estimate that for human, chimp and gorilla, 18–29% of the genome shows such a discordant relationship.

Figure 1 illustrates the simplest possible model, of abrupt allopatric speciation, in which a single randomly mating population splits into two overnight. In reality, physical barriers may arise gradually, and populations are more or less subdivided geographically. These factors will tend to increase random heterogeneity in divergence times across the genome [6]. Moreover, genetic differences that define biological species will accumulate gradually, and regions of genome that are linked to such 'speciation genes' will show greater divergence. In the extreme, we might have a situation in which two distinct populations 'hybridise'. However, this is only one extreme of a continuum, in which various physical and genetic factors inflate the heterogeneity across the genome.

The best understood example of such phenomena involves *Drosophila pseudoobscura* and *D. persimilis*. These are clearly distinct species, but do very rarely hybridise in nature. Remarkably, most loci show a scrambled genealogy, in which the relation between genes bears little relation to the species from which they are sampled. (That is, a gene is often more closely related to one sampled from another species than it is to any gene sampled from its own species.) Some loci, however, do show a relationship that matches the true species phylogeny, and these lie in or near chromosomal inversions that are known to be responsible for reproductive isolation [7,8]. More generally, there are many examples of discordance between genealogies at different loci. The most striking involve mitochondrial DNA, which often introgresses across species boundaries, for reasons that remain unclear [2]. Such patterns are not surprising, because exchange of around one individual per generation will scramble genealogies based on neutral genes, and favourable alleles can spread with even lower levels of successful hybridisation [2,8,9]. A substantial proportion of present-day species are divided by hybrid zones between divergent populations [9], indicating that speciation is a protracted and complex process.

Patterson *et al.* [3] analysed variation in divergence time in an ingenious way. They identifed 30,461 sites carrying a mutation that is shared by human and chimp, but not other apes, which they termed HC sites. These correspond to the species' true phylogeny (Figure 1A). Some sites (12,348 in total), however, were found to carry mutations shared by human and gorilla, or by chimp and gorilla — termed HG and CG sites, respectively — implying a genealogy that differs from the phylogeny (Figure 1B). (Many more sites (306,757 in all) carry variants in a single species, human, chimp or gorilla; these are more abundant because the time back to the two speciation events — one between human and chimp, and the other between the joint human-chimp ancestral lineage and gorilla — is long compared to both that between the two speciation events, and to the typical time for coalescence within the ancestral population.)

Patterson *et al.* [3] then determined the average divergence between human and chimp sequences that are linked to the different classes of sites. Regions closely linked to HC sites differ by only 86% of the overall average, whereas those linked to CG or HG sites differ by about 147% of the average (Figure 2). (Multiple mutations can generate CG or HG sites even if human and chimp are most closely related in the true genealogy; however,

there are straightforward and well-established ways to correct for multiple hits, and the figures given here were corrected accordingly).

This variation in divergence across the genome is not as large as that seen in other species, for example the *Drosophila* example cited above, but it is nevertheless highly statistically significant in this very large dataset. Patterson *et al.* [3] argue that it implies that the human and chimpanzee lineages began to diverge, but later hybridised. The notion that the human lineage hybridised with the chimp lineage has attracted widespread attention for obvious reasons. Such a scenario — or a range of kinds of population subdivision — can indeed account for diversity among loci in divergence, but Patterson *et al.* [3] do not test whether their data are consistent with the simple null model of abrupt allopatric speciation of a single well-mixed population. A simple calculation (H. Innan, personal communication) shows that their data are consistent with an ancestral effective population size of N_e ~45,000, which does not seem unreasonable, and is consistent with previous studies [4,5]. Thus, there is no statistical evidence for hybridisation.

There is of course much more information in the data than the variance in divergence times among genomic segments. The degree of correlation between genealogies along the genome is reflected in the rate of decay of the graph in Figure 2, which occurs over ~1 kilobase or $\sim 10^{-3}$ centiMorgans. This decay is expected to be over a length of genetic map of order $1/2N_e$ [10], which is consistent with the N_e estimated independently (see above). Several methods for detecting deviations from this null model have been proposed (for example [10–13]); in particular, Innan and Watanabe [13] found that there is no significant support for a model of human–chimp speciation in which gene flow decreases gradually, rather than halting abruptly. The data would be consistent with a smaller ancestral N_e, plus a variety of factors that would inflate variation in divergence time, but there is no indication as yet that such models are required.

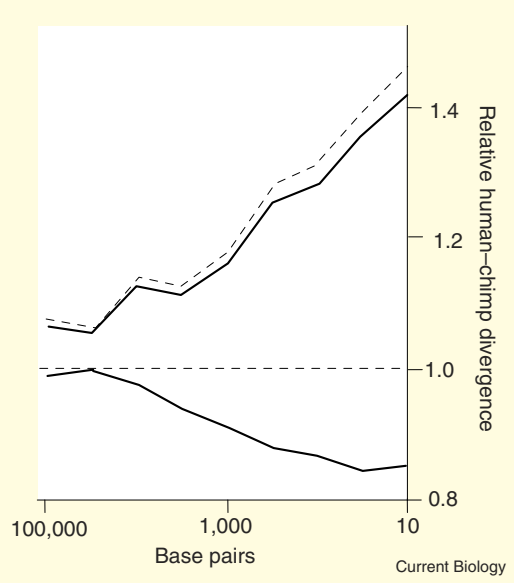

Figure 2. Mean divergence between human and chimpanzee sequence, for regions linked to different classes of focal site.

Lower curve, HC sites; upper curve, HG and CG sites. The upper dashed curve includes a correction for multiple hits. The horizontal dashed line indicates the genome-wide average, defined as 1. (Adapted from [3]; data are for alignments where five primate species are available.)

Patterson *et al.* [3] also found that the whole X chromosome shows significantly less divergence between human and chimpanzee than any other chromosome. This pattern can partly be explained because there are fewer copies of the X than of the autosomes, and because its mutation rate may be lower, because the X spends relatively more time in females than in males and the female germline involves fewer cell divisions. However, such factors can account for only a small part of the discrepancy. Moreover, the X chromosome shows the expected pattern in human–gorilla comparisons, which implies that its unusually low divergence between human and chimp is due to factors that acted during the relatively short time between the two speciation events shown in Figure 1.

Patterson *et al.* [3] propose that the X was involved in hybrid incompatibility — a pattern which is found in speciation in general, and which arises because incompatibilities due to recessive alleles are expressed in males that carry one copy of the X [14]. However, incompatibilities associated with the X should *reduce* gene flow and hence increase divergence times, as is the case for the *Mus* example cited by Patterson *et al.* [3,15]. The difference between X and autosomes remains puzzling — like similar differences observed in the pattern of divergence between rearranged and non-rearranged, and coding versus non-coding regions [16,17].

The heterogeneity in divergence between human and chimpanzee genomes is consistent with abrupt speciation from a large ancestral population, or with a complex and protracted speciation process from a smaller ancestral population, or with a wide variety of complex population structures. Additional information can be gleaned from the detailed pattern of divergence across the genome, but it seems unlikely that we will be able to say much more even when the complete gorilla genome sequence becomes available. One difficulty is that because the effective population size of humans and other primates has been quite small in the recent past, almost all lineages within each species will have coalesced more recently than the speciation events (Figure 1). Thus, we cannot get much extra information from polymorphism within species. However, the approach attempted by Patterson *et al.* [3] has proved much more successful in other groups, in which speciation was more recent, or is still in progress: genetic loci

that are likely to be responsible for speciation have been identified, and patterns of gene flow and ancestral demography have been inferred (for example [15,18,19]). As the extensive data that we have now for primate genomes become available for other, more tractable groups, we will gain a much better understanding of the genetic basis of speciation.

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Neandertal Genetic Diversity: A Fresh Look from Old Samples

The recent publication of three old Neandertal mitochondrial sequences shows that the genetic diversity of the Neandertals has been largely underestimated. It suggests that the Neandertal population was extensively subdivided geographically, and that its genetic diversity changed markedly over time.

Laurent Excoffier

The place of Neandertals on the human family tree is still a highly controversial subject. The analysis of the non-coding control region of the mitochondrial DNA (mtDNA) in a few Neandertal specimens has revealed that their sequences are very similar to each other, but clearly different from those found in modern and early humans [1–6], suggesting that modern humans did not interbreed with Neandertals when they colonized Europe [1,7]. However, this interpretation has been criticized. Hybridization events could have occurred, but would not have been detected if there had, for instance, been a recent selective sweep in the modern human lineage [8] or if the Neandertal genes that passed into the modern human gene pool had been lost by genetic drift in the last 30,000 years [9]. As only a small portion of the geographic range of the Neandertals has been explored genetically (Figure 1) and only relatively young fossils have been examined (<45,000 years old), the analysis of additional individuals should yield more precise information on the genetic diversity of the Neandertals and their relationship with modern humans.

The recent publication of three additional Neandertal mtDNA sequences in *Current Biology* [10–12], two of them in this issue, has indeed revealed new and interesting features. A sequence from El Sidrón (Northern Spain) [10] was found very similar to those found in Croatia (Vindija) and Germany (Feldhofer) (Figure 1B). This suggests a common origin for all these individuals, who lived up to 2000 km apart, and the most recent common ancestor of these five sequences has indeed been dated to 130 ky ago [10] — very close to the end of the so-called Riss glaciation. Thus, these individuals could have originated from a range expansion following this glacial maximum [10].

The analysis of a 50 ky old Italian Neandertal from Monti Lessini in Italy [11] has shown that the mtDNA sequence of this individual was very divergent from the other Neandertals and closer to that of modern humans. When considering the overall extent of Neandertal variability, the divergence of this Italian lineage is compatible with a geographic subdivision of the Neandertal population into three clades some 40–50 ky ago. Neandertals from Italy and the Caucasus (Mezmaiskaya) are both clearly distinct from the other Neandertals at that time (Figure 1B) and from each other. Additional sampling