fied selection pressures, probably a prevalent infection other than malaria. The high frequency of CD36 deficiency in other races[4,5] may have a similar explanation.

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Taxonomy

Species status of hybridizing oaks

The two widespread species of oak tree in Europe, *Quercus robur* L. and *Q. petraea* (Matt.) Liebl., hybridize extensively, calling their taxonomic status into question. Here we use microsatellite DNA, a highly informative genetic marker, to show that *Q. robur* and *Q. petraea* are discrete taxonomic units despite this intensive hybridization. Furthermore, individual oaks can be assigned to separate species.

Oaks are a classic example of a taxonomic group that has significantly challenged existing species concepts[1], of which the 'biological species concept' is the most popular. Two European species, *Q. robur* and *Q. petraea*, hybridize without any significant mating barriers[2]. Despite the high gene flow between them, the two species show clear differences in leaf and fruiting structures[3]. The two species are largely sympatric, but there are some habitat differences: *Q. robur* grows in wetter and more alkaline habitats, whereas *Q. petraea* is more drought resistant.

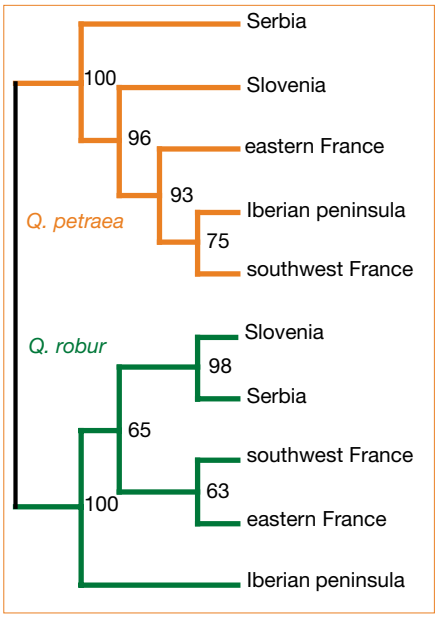

Figure 1 Dendrogram of 10 European *Quercus robur* and *Q. petraea* populations (162 individuals) based on the proportion of shared alleles at 20 microsatellite loci. One population from each species was sampled at five locations. The dendrogram was computed using a UPGMA approach in PHYLIP[12]. Numbers are bootstrap support values.

In contrast to morphological characters and ecological preferences, it is difficult to find any interspecific differences using molecular markers. Chloroplast markers were found to be polymorphic, but could not discriminate between *Q. robur* and *Q. petraea*[4,5]. Similarly, the two species show very similar RAPD and allozyme frequencies[6–8]; nor did ITS sequences, a popular marker for species determination, reveal any interspecific differences (G.M., C.C.F. and C.S., manuscript submitted).

The taxonomic status of oaks has implications for forest management. Given the two species' different habitat preferences, the European Community, seeking to avoid the use of maladapted seed, has established guidelines for the trade of oak seed material (71/161/EWG, 30.3.1971). According to these, each seed lot must not contain more than 0.1% of seeds from another species. But without unambiguous criteria for taxonomic classification, this guideline cannot be put into practice.

We used microsatellite analysis, which has been shown to discriminate between closely related species[9], to address the question of species status in *Q. robur* and *Q. petraea*. To account for geographic differences, we sampled one population (approximately 16 individuals) from each species at five locations that covered almost all the species' European range. If *Q. robur* and *Q. petraea* are good taxonomic units, then populations should cluster according to species rather than geographic origin. Figure 1 shows a dendrogram based on the proportion of shared alleles[10] at 20 microsatellite loci. In accordance with the assumption that *Q. robur* and *Q. petraea* are separate taxonomic units, all populations of the same species group together. This separation between the two species has very strong bootstrap support (100%). *F*-statistics also indicate a significant difference between the two species ($P < 0.01$), although there is also a significant component of variation due to the geographic origin of the population ($P < 0.01$).

In the light of the EC's requirement for unmixed seed lots, we tested whether the genotypic information from the 20 loci typed for both species is sufficient to identify the species of an individual. Eighty-one oak samples from Ireland, which were not included in the previous analysis, were typed using the same set of microsatellites. Using an assignment test based on allele frequencies[11], we determined the species status of those 46 samples that had either a clear *Q. robur* or *Q. petraea* phenotype, based on three characters of leaf morphology (petiole length/lamina length, auricle development and mid-rib pubescence). For no individual was the incorrect species assigned. Morphological and molecular evidence agreed in 78% of cases. In 22% of the cases, the molecular analysis was either not informative (7%) or indicated a hybrid status (15%).

Our molecular analysis demonstrates that *Q. robur* and *Q. petraea* are separate taxonomic units, which can be designated by the use of microsatellites. The important question remains as to how the species differences are maintained despite the high levels of interspecific gene flow.

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