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The Role of Pleistocene Forest Refugia in the Evolution and Biogeography of Tropical Biotas

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Refuge theory postulates that repeated oscillation of dry and moist climatic periods during the Pleistocene caused an alternating fragmentation and coalescence of areas of lowland tropical rainforest vegetation, leading to genetic differentiation and speciation in isolated populations of rainforest organisms and hence accounting for much of the high diversity now apparent in these habitats. The theory, which became widely accepted during the 1970s, is still based largely on inferences from modern species distribution patterns and on selected palaeoclimatic and geomorphic data. However, much of this evidence has multiple interpretations; indeed, modern population genetic theory argues against many of the tenets of refuge theory. Moreover, there is no palynological evidence against which refuge theory might be tested. Although large-scale dynamic processes have undoubtedly played many parts in promoting diversity in tropical rainforest, refuge theory must be seriously questioned on many counts.

The view, once widely held, that moist lowland tropical rainforest in its present geographical distribution is a vegetation formation of considerable antiquity began to change in the 1960s. Initially, the evidence motivating this change consisted of data from lake sediment cores, which showed increases in the abundance of pollen from grasses and other savanna vegetation, and decreases in forest tree pollen, during several periods in the Pleistocene[1,2]. Other geological and pedological data also appeared to be inconsistent with the notion of stasis in the distribution of tropical rainforest. Subsequent attempts to estimate the effect of the Pleistocene glaciations on global climate suggested that some equatorial regions experienced as much as a 3°C lowering of mean sea-surface temperature[3]. These results implied that regions now covered by moist tropical rainforest were once cooler and drier, and possibly covered by vegetation more characteristic of this altered climate.

From this new view arose the notion that climatic change during the Pleistocene may have been severe enough to cause areas of continuous tropical forest to fragment and contract into small pockets or 'refugia'[4,5]. For ecologists and evolutionary biologists, who have long puzzled over the tremendous diversity of tropical rainforest organisms, this seemed to provide a physical mechanism (climatically driven splitting of geographic ranges) that promoted speciation, and therefore explained the great diversity of species in the tropics. In fact, the view that the geographical distribution of tropical rainforest has been very dynamic has spawned a minor cottage industry, concerned with interpreting the apparent patterns of speciation and biogeography of tropical forest organisms in its light[6].

This theory, linking Pleistocene climate change to apparent patterns in the biogeography and speciation of tropical forest organisms, has been called variously the 'biological model for diversification in the tropics' or, more simply, 'refuge theory'. It has been invoked to explain the biogeography and patterns of speciation of birds, butterflies, lizards, frogs, mammals and plants, in Central and South America, Africa and Australia[5–11]. In substance and in method, this is not unlike earlier attempts to explain patterns of speciation and biogeography of plants and animals in temperate and boreal regions in North America and Europe[12–15]. Refuge theory is a combination of theory, assumption and interpretation that can be viewed most productively on several levels, proceeding from general to more specific tenets.

In the most general sense, refuge theory suggests merely that (1) climatic change can alter the geographical distributions of species, isolating conspecific populations, and (2) that this may lead to genetic differentiation and ultimately speciation. The first of these claims has been corroborated by physical evidence of Pleistocene climatic change and simultaneous changes in tree species distributions in temperate North America and Europe[16–18]. The second claim rests on the widely held view that through genetic drift and different regimes of natural selection, isolated conspecific populations may become sufficiently different genetically to merit classification as distinct species (the allopatric model of speciation). However, the view that physical or geographical isolation is a necessary prerequisite to genetic differentiation has been questioned[19].

Most recently, refuge theory has been applied largely to the Pleistocene and early Holocene history of tropical biotas. In its original statement, refuge theory postulated a succession of climatically induced effects on the geographical distributions of plants and animals, paralleling the successive glacial and interglacial periods during the Pleistocene. As regards the nature of these effects on the geographical distribution of biotas, the theory proposed that during periods of increased aridity (associated with widespread glaciation) the geographical ranges of species were fragmented so that identifiable community units (e.g. rainforest) were preserved in isolated pockets or 'refugia'; it also proposed that during warmer and more moist interglacial periods the geographical ranges of species once restricted to refugia would have tended to coalesce again. Furthermore, this sequence of range contractions and expansions was postulated to have occurred repeatedly, in concert with each Pleistocene glaciation.

Palynology

Palynological and plant macrofossil data documenting major changes in the distribution of lowland tropical rainforest are quite scarce; only for Africa, Australia and one site in South America are data available for such regions[2,20,21]. Even though palynological data from higher elevations[21,22] and from drier habitats[23,24] point to shifts in the distribution of forest and savanna vegetation, the nature and extent of these changes in lowland regions are poorly known throughout the tropics[25]. Furthermore, most of the palynological data from South America date from the Holocene (since 10 000 years BP) rather than the Pleistocene[26]. Much of the geomorphic evidence, consisting of large areas of dune fields, alluvial fans and river terraces in the Amazon and Orinoco catchments (which could not have been deposited in forest vegetation) is also Holocene[21]. However, since these features represent fluctuations in levels of runoff

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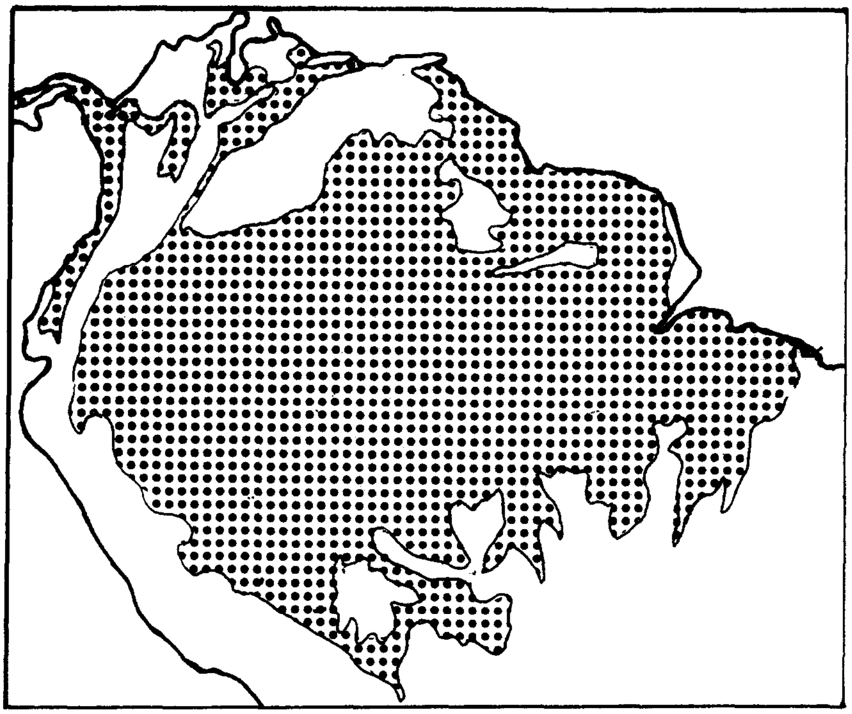


Above: the approximate present natural extent of lowland rainforest (shaded) in northern South America. **Opposite**: refuge areas that have been suggested to have existed at the end of the Pleistocene.

and in sea levels, it is difficult to infer what changes, if any, occurred in forests not directly underlain by these geomorphic features. A comprehensive and geographically widespread assessment of the palynology of the lowland tropics, similar to that undertaken to describe the biogeographic dynamics of north temperate trees, will be necessary before refuge theory can be viewed as probable. For many areas of the tropics, this will be very difficult because the environments suitable for pollen deposition and preservation are extremely rare.

If the results obtained thus far from the study of how glaciation affected the geographical distribution of temperate and boreal tree species can serve as an indication of what might be expected for tropical biotas, then doubt is cast upon refuge theory. The overwhelming evidence is that species' geographical distributions were altered individually, not in community units, and that range disjunctions arose infrequently[27,28]. Nevertheless, it is conceivable that tropical biotas behaved differently to temperate ones, and it would be possible to reject or corroborate this aspect of refuge theory with palynological data of sufficient detail and geographic coverage.

Paleoclimatology

Paleoclimatic aspects of refuge theory are also issues for debate. The temporal and mechanistic relationship between the onset, buildup and recession of glaciers in polar regions and pluvial and arid periods in the tropics is more complex than imagined under refuge theory. Glacial periods do not appear to correspond to times of aridity in the tropics, and pluvial periods have been observed to occur during the period of glacial buildup and during interglacial periods.

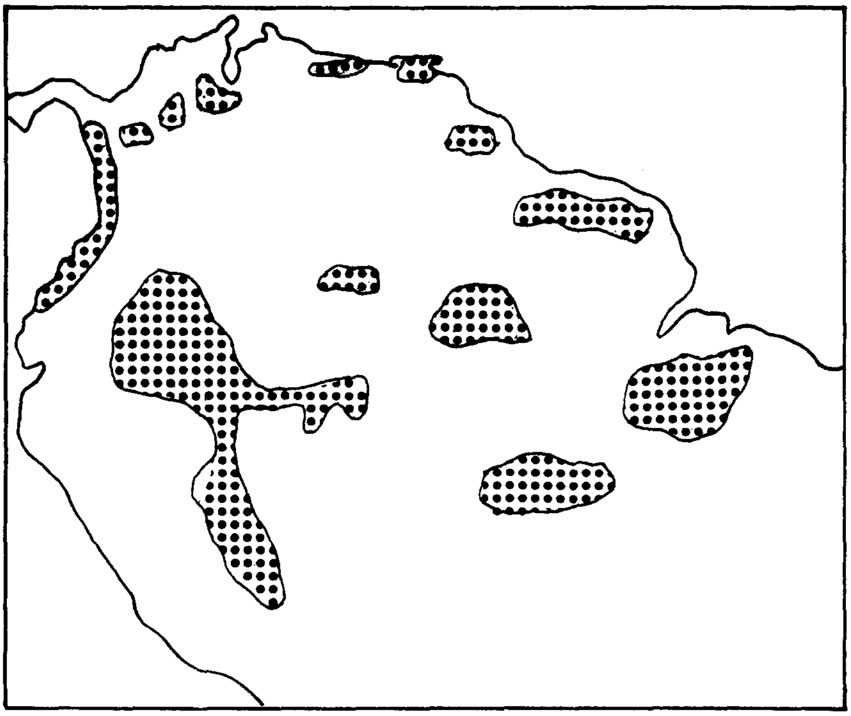
It is also difficult to imagine how increases in the extent of glaciation in polar regions could give rise to the highly insular climates necessary to generate patchily distributed warm and moist lowland tropical rainforest[29]. The climate of the intertropics is determined by a complex interaction of land–sea geography and topography (which did not change radically during the Pleistocene) with the major components of atmospheric circulation.

One such component, important in determining tropical climates, is the Walker circulation; this has three major zones of upward air motion (hence rain prone) and three major zones of downward air motion (hence arid). The rain prone areas are currently located in the Amazon Basin and Northern Andean region, the Congo Basin (Zaire), and on the Maritime Continent of New Guinea and surrounding areas. These three regions include most of the area naturally covered by moist lowland tropical rainforest. The Intertropical Convergence Zone (ITCZ, the meteorological equator) is a circumglobal circulation. The wet regions generated by the Walker circulation may have varied somewhat in location or extent during the Pleistocene, but there is no reason to expect glaciation to have caused further fragmentation and isolation of these wet areas. The extent of the seasonal excursions of the ITCZ may also have varied, but again it is highly unlikely that this circulation shifted greatly or broke down. It is not surprising to find that areas peripheral to the rain prone regions, such as eastern Brazil, eastern Africa, India and Australia, show major changes in vegetation during the Pleistocene; this is probably due to contraction, expansion or shifts in location of the wet regions. But it is unlikely that the climate and vegetation of the wet tropical lowlands themselves changed substantially.

Evolution and Biogeography

The tenets of refuge theory discussed above focus on the effects of climatic change on biogeographic dynamics, not on the component of the theory dealing with its consequences for the genetic structure, evolution and speciation of tropical forest organisms. Refuge theory makes no specific predictions about how the envisioned repeated sequences of range contraction and reexpansion should affect a species' genetic structure and evolution, other than to say that they *might* lead to differentiation between populations isolated in refugia. To refuge theorists, this has implied that regions where morphological or genetic differentiation between populations is observed probably represent areas of contact between populations formerly isolated in their respective refugia. This assumes that after the climate ameliorated, tropical rainforest refugia coalesced and provided the opportunity for isolated populations to come into secondary contact. So-called 'zones of secondary contact', defined by the presence of parapatric distributional boundaries of species and members of superspecies groups, areas of hybridization, and geographic variation in species' morphology, would thus fall most often *between* putative refugia. Hence, the locations and extent of refugia could be defined by mapping zones of secondary contact. Therefore, evidence from the *modern* distributions of species could be used to infer the locations of Pleistocene refugia. Also, consistency across taxa in the location of regions of differentiation would serve as evidence in support of refuge theory in general, and of a specific set of postulated refugia in particular.

More recently, the locations of refugia have been inferred using maps of the diversity of endemic species. Regions with high numbers of endemic species are considered to have been refugia[30]. The rationale for this inference is not clear, but must involve viewing refugia or so-called 'centers-of-endemism' as centers-of-dispersal or centers-of-origin from which these relict endemic taxa have not dispersed.



Problems of interpretation

The inference of the existence and role of rainforest refugia based on extant patterns of differentiation between populations and species of forest organisms can be criticized in three respects.

As illustrated by Endler[19,31,32], Vuilleumier[33], Benson[34] and Barton and Charlesworth[35], there are no logical or theoretical reasons for assuming that all regions of morphological or genetic differentiation between populations have arisen during isolation and are therefore 'secondary contacts'. It is possible or even likely that extant barriers (e.g. rivers and uplands) to gene flow and dispersal, as well as geographical gradients in regimes of natural selection, could give rise to primary zones of genetic and morphological differentiation. It is also difficult to distinguish clearly between primary and secondary zones of differentiation, although Thorpe[36] suggests that phylogenetic analyses may be sufficient to do so.

Even if one grants that instances of near or full isolation between populations are more likely to lead to speciation, why must one postulate an event some 18 000 or more years ago as the cause of isolation? Are geographical distributions so static that glaciations are necessary to isolate populations? Could not some event in the intervening 18 000 years, such as sea-level change, fire, a change in the geographical range of a predator, or short-term climatic variation, cause populations to be isolated temporarily? Sanford *et al.*[37] have shown that, at least in some parts of the Amazon basin, rainforest fires have been common during the last 6000 years. Salo *et al.*[38] provide evidence that more than one fourth of the lowland rainforest in the western Amazon has been affected by the erosional and depositional activity of rivers. Twelve per cent of these forests are successional.

One might also examine the geographical distribution of putative secondary contacts and ask if, as suggested by refuge theory, they fall to a statistically unusual degree *between* the postulated refugia. Beven *et al.*[39] did just that for over 400 species and subspecies of birds in the Amazon basin, as well as for superspecies groups and species with disjunct distributions. They found that the largest data set used so far to infer the existence of refugia does not provide support for such an inference. They also found that contrary to refuge theory, refugia postulated for different taxa (birds, plants and lizards) are not particularly concordant.

Another problem with the tradition of inferring refugia from data on extant patterns of differentiation between populations and species is that the same data have been used in both the generation and the corroboration of specific refugia hypotheses. This problem could be readily eliminated if independent data were used to test each putative refuge. This could be accomplished by splitting data sets; using part to generate and part to test a specific refuge hypothesis, or by using one taxon to generate and another to test a refuge hypothesis.

Conclusions

On balance, it still appears that Pleistocene and Holocene climatic change affected the geographical distribution of tropical biotas and may have led to genetic differentiation and speciation. However, this is unlikely to have occurred as pictured by refuge theory. The palynological and plant macrofossil data necessary to determine if and where forest refugia existed are not yet available. Geophysical evidence describing how the climate changed in the lowland tropics is also lacking. Data on the geographical distribution of extant zones of morphological and genetic differentiation between populations and species are consistent with several evolutionary interpretations, with or without deviating from the allopatric model of speciation. Finally, even if we had well corroborated phylogenetic reconstructions of the history of each population and species, and even if these all indicated the same evolutionary and biogeographic pattern, there would be no reason to attribute this striking evolutionary congruence to Pleistocene glaciations and forest refugia. One could as plausibly postulate some more recent (or older) barriers to dispersal and gene flow as causing the observed pattern of evolution. Forest fires and river dynamics[37,38] may be just as important as determinants of patterns of speciation and biogeography as the effects of Pleistocene climatic changes on the distribution of rainforest vegetation.

On the other hand, if after detailed palynological and macrofossil study, the distribution of forest in lowland tropical regions can be shown to have been patchy during the Pleistocene glaciations, it would at least provide some factual basis for forest refugia. However, demonstrating that the isolation of populations in those forest patches is the cause of extant zones of morphological and genetic differentiation will remain problematic. Although cladistic analysis and other methods of phylogenetic inference may provide a means of reconstructing the pattern of evolution, this pattern can only be firmly linked to historical hypotheses concerning climatic and biogeographic dynamics by the use of fossil evidence. Neontological data are insufficient to infer paleoecological phenomena.

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When Does Grazing Benefit Plants?

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Many recent studies have attempted to support the hypothesis that grazing can have positive effects on plant growth and fitness. However, a recent critical survey has shown that many of these studies suffer from poor experimental design, and consequently that the hypothesis may only be tenable under very particular circumstances.

Over the last decade many authors have investigated the coevolution of plants and their grazers, and some years ago it was postulated that a certain degree of consumption or clipping of plant parts may benefit plant growth or even plant fitness[1–4]. Recently Belsky[5] discussed the evidence of more than 40 different studies that might support this hypothesis. First of all, she categorized the prevailing definitions of the responses of growth to herbivory and clipping (see Box 1), and then discussed the effects of herbivory on total dry weight, shoot dry weight, tiller production, seed size and longevity of plants.

Belsky's survey showed that almost all the studies that might provide evidence for 'overcompensation' had serious imperfections. Of 20 papers that are frequently cited to support the hypothesis of increased plant growth or even fitness after herbivory, the great majority either lacks sufficient experimental evidence, shows many errors in methodology and experimental design, or was not confirmed in later studies.

Furthermore, the scope of most studies of compensatory growth or fitness has been limited to above-ground production, expressed as standing crop from an agricultural viewpoint or seen as edible food from the viewpoint of a biologist studying animal intake. In general, however, defoliation strongly affects root performance and root growth; root reserves can become depleted and part of the root system may die off[6]. Such reductions in root performance after defoliation may result in considerable mortality despite a higher relative shoot growth rate[7]. Although the term 'compensatory growth' is very often used to refer to above-ground biomass alone or to numbers of shoots, leaves, seeds, etc., it is generally more relevant to refer to the total dry weight production and the seed production.

One of the few examples that definitely demonstrates overcompensation is that of early defloration of two cotton varieties[8]. If all flowers are removed during the first 25 days of the flowering period, secondary

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