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Pleistocene forest refuges in the Amazon: evaluation of the biostratigraphical, lithostratigraphical and geomorphological data

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The theory of Pleistocene forest refuges states that during the arid cycles of the Pleistocene the Amazon lowland forest was reduced to a number of isolated patches. According to the theory, this isolation period contributed to the present subspecies–species level of biological differentiation of the forest biota via allopatric differentiation. The theory is mainly supported by the present vicariant distribution patterns of the lowland biota, especially birds and woody Angiosperms. The patterns are thought to reflect the past locations of the forest refugia. The question approached in this paper is whether there are also independent biostratigraphical, lithostratigraphical or geomorphological data which could show that the forest refuges have been isolated by savannas. Recent findings in the fluvial geomorphology of the Amazon basin, reviewed here, reveal geomorphological barriers which could explain the observed distribution patterns on the basis of present and past edaphic differences, rendering the Pleistocene forest refuge theory implausible and unnecessary.

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1. Introduction

Until recently, the dominant theory accounting for the high species diversity of the tropics has been the time stability hypothesis (Fischer 1960). This theory, mainly supported by the high within-habitat species diversity of the marine infauna (Sanders 1968, Sanders & Hessler 1969), suggests that environments free of unpredictable perturbance will have high species richness due to the reduced rate of extinction. Furthermore, a long and stable climatic and geologic history imagined for these environments would provide sufficient time for evolutionary differentiation. The tropical broad-leaved rainforests have been recorded as areas of high potential for the application of the stability theory.

However, the geological and biostratigraphical data obtained from northern tropical South America (Van der Hammen 1974, 1982, 1985, Van der Hammen & Wijmstra 1974, Hooghiemstra 1984) show the late-Pleistocene (Wisconsin-Würm glaciation) aridity to have also affected the areas which are at present covered by broad-leaved or other types of tropical forest. Besides the Americas, the Last Glacial Maximum (LGM) and the early Holocene altitudinal movement of vegetation is also documented for several sites in South-East Asia (Walker 1970, Hope 1980, Walker 1982). A reduction in size, but not fragmentation, of the lowland Congo (Zaire) basin rainforest in Africa during the late Pleistocene is demonstrated by the presence of stabilized sand dunes both north and south of the present forest (Livingstone 1982).

The Amazon basin has repeatedly been referred to as an area without apparent geomorphic isolation barriers or large-scale areal edaphic differences which would cause differentiation of populations (Croizat 1958, 1976, Emsley 1965). Nevertheless when Haffer (1969, 1978) presented the first distribution maps of the lowland birds covering most of the basin area, it became clear that there are distinct centres of endemism. Haffer introduced the idea of species dynamics based on Pleistocene forest refuges to explain this patchy distribution pattern. The Amazon Pleistocene refuge theory has gained wide acceptance, as in addition to forest birds, several other groups show a

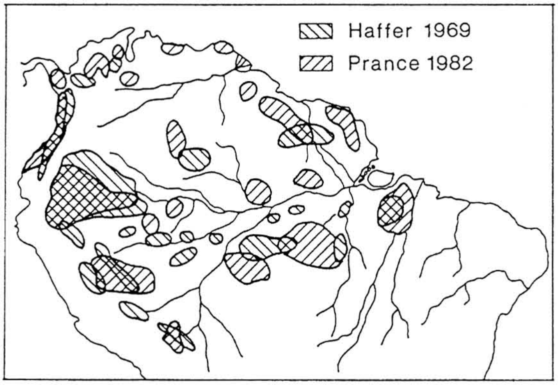

Fig. 1. The proposed refuge areas during the late Pleistocene. Data from Haffer (1969) and Prance (1982).

tendency towards patchy distribution patterns within the apparently continuous lowland forest (Fig. 1).

In this survey, I examine the major non-biological studies used by biogeographers as supporting evidence for the evolution of the late Pleistocene landscape in the Amazon lowlands, and I evaluate their applicability in explaining the present distribution patterns of the forest biota.

I furthermore question the concept of the absence of geomorphic or edaphic barriers within the Amazon forest. New evidence shows that the forests of the western Amazon are much younger than has been believed (Campbell & Frailey 1984). The dynamics of floodplains in the late Quaternary have disturbed sites previously considered to be stable Pleistocene refuges (Salo et al. 1986, Räsänen et al. 1987) and have diversified the structure of the forest beds.

2. The Amazon refuge theory

The Amazon Pleistocene refuge theory, or the biological model for diversification in the tropics (Haffer 1969, 1979, 1981, 1982, Simpson & Haffer 1978, Prance 1982), states that in tropical South America, Pleistocene climatic cycles caused reduction and fragmentation of the forest cover and partial replacement of the rain forest by savanna, caatinga and cerrado vegetation.

According to the theory, "plant and animal populations isolated in the more-or-less restricted forest and nonforest refuges during adverse climatic phases either became extinct, survived without much change, or differentiated to the taxonomic level of subspecies or species before they came into secondary contact with previously conspecific populations or other refuges during the following favorable expansive phase" (Haffer 1982). The present biota of the Amazon basin is rich due to the large number of vicariant recently differentiated animal and plant species with delimited distributions.

The concept of the climatically induced former isolation of the Amazon lowland biota has increasingly influenced biogeographic reasoning concerning the area, and the time stability hypothesis has quietly vanished as more evidence for arid cycles in the Americas during the Pleistocene has become available. The refuge theory is also strongly affecting research in other fields, especially linguistics and anthropology (e.g. Meggers 1975, 1982, Migliazza 1982).

The concept of the splitting of populations due to climatic cycles is not new in tropical biogeography. The isolation effects of arid periods have been postulated in Australia (Gentilli 1949, Keast 1961) and Africa (Moreau 1963, 1966, Carcasson 1964). Actually, the refuge theory as formulated by Haffer is not far from general vicariance biogeography (Nelson 1979, Weitzman & Weitzman 1982). The theory merely offers a specific factor for the isolation dynamics (climatic cycles), and it confines the scene mainly to the Amazon basin. The importance of the theory, however, is in the fact that it postulates specific areas, refuges, by locating their past sites in the Amazon area.

While the literature on the Quaternary climate of extra-Amazonian tropical South America is expanding rapidly, there are no undisputed data on the basin area itself. Hence, it is impossible to confidently project where tropical forest may have persisted during this period. Past refuges have been delimited by using in the main two criteria: (1) areas within the basin which are of higher altitude than most of the present forest (e.g. >300 metres) are supposed to have received constant rainfall also during the arid phases; (2) areas with high present rainfall are thought to have also had this character in the past (Haffer 1978). However, by far the most widely used criterion has been the delimitation of areas with high endemism as former refuges. The major works locating and delimiting the refuges (Haffer 1969, Brown & Ab'Saber 1979, Prance 1981, 1982, Brown 1982) have basically used the latter method.

Although the refuge theory is at present widely accepted, there has been increasing criticism of the circularity of the concept (Benson 1982, Endler 1982, Beven et al. 1984). The "evidence" supporting the theory largely relies on present distribution patterns rather than on independent geologic, geomorphic or biostratigraphical data (Connor 1987). Moreover, different refuge sets do not coincide too well (for an example, see Fig. 1).

3. Biostratigraphy

The northern Cordillera of the Andes and the Guianas dominate the Quaternary palynological studies of the tropical South America (Van der Hammen 1982). The north Andean areas, in particular, exhibit a downward shift of vegetation zones, lowering of the temperature and reduced precipitation, contemporary with the glacial maxima of the northern latitudes (Van der Hammen et al. 1973, Van der Hammen & Van Geel 1973, Van der Hammen 1974). Summing up the data, Van der Hammen (1982) concludes that during the LGM, the altitudinal forest limit was 1200–1500 metres lower than today (below 2000 meters). The Holocene data, derived mainly from the coastal range of Venezuela and the Andes (reviewed in Schubert 1987) and studies of Lake Valencia in Venezuela (Salgado-Labouriau 1980), clearly show oscillation between cooler and warmer phases, as well as between drier and more humid ones.

Although some data is available from the coastal lowlands of Guinea and Surinam (Van der Hammen 1974, Livingstone & Van der Hammen 1978), the Magdalena Valley (Wijmstra 1967, Jungerius 1976), and Llanos Orientales and Rupununi savannas in Guiana (Van der Hammen 1974, Livingstone & Van der Hammen 1978), they are mainly Holocene or provide no ^{14}C or other dating. These data strongly suggest that in these northern areas the Holocene climate too has been subject to short periods of dryness.

For the Amazon lowlands, palynological data are available from only three sites. This lack of data is largely due to the absence of permanent lakes in the lowlands and to the poor development of peat layers.

3.1. Rondônia

The Rondônia material (Absy & Van der Hammen 1976) was obtained from three sites (Katira, Capoeira and Rio Preto) between the rivers Jamari and Machado supposedly representative of pre-Holocene sediments. The sediment cores were collected from dissected valleys created by surface erosion (denudation) and are partly composed of sediments derived from colluvial processes of the valleys. They are considered to be younger Pleistocene (Van der Hammen 1982), though no radiometric dating is presented. The area is at present covered by rich broad-leaved forest. Cerrados-type savannas are at some 300 km distance from the site; minor isolated savannas are also distributed close to the area. The pollen analyses of the cores reflect an early forest period, followed by a period of grass savannas, then by a forest cover corresponding to the present Holocene situation (Van der Hammen 1982). As the site is outside the refuges suggested by Haffer (1969) and Prance (1981), the data gives support at least to the shrinkage of the forest areas during some epoch of the Pleistocene. However, due to the marginal situation of the Rondônia site, it does not implicate forest fragmentation.

3.2. Holocene floodplain lakes

The only available Holocene pollen materials, backed by ^{14}C-dating, are from the central Brazilian Amazonia and the territory of Roraima (Absy 1979, 1982). The cores have been collected from five floodplain lakes. During the period surveyed, major changes in the dominant pollen types *Alchornea, Symmeria*, Myrtaceae, *Miconia, Cecropia* and Poaceae have been observed. The explanation for these fluctuations, given by Absy, is that they reflect Holocene changes of local vegetation cover following the local fluctuation of the ground-water table and river-water level. This would indicate changes in the local climate. In the discussion, Absy merely describes the dynamics of the floodplain depressions. She does not mention the possibility of channel migration as an explanation for the oscillation observed. The data suggest to Absy that during the Holocene, 4000 B.P. (Before Present) and 2700–2000 B.P. there were major drier phases in the climate. Minor drier phases have been observed at 1500, 1200 and 700 B.P. However, the increase in pollen, indicating the drier phase of 4000 B.P., is only documented in one of the cores. The 2700–2000 B.P. phase is documented in 3–4 cases.

Irion (1976) suggested that Absy's (1979, 1982) result may be interpreted in terms of the fluctuation of the floating meadows, abundant along whitewater rivers. The floating meadows consist of several Poaceae, such as *Paspalum repens, Echinocloa polystachya* and *Hymenachne amplexicauli*. The expansion in the area of floating meadows in the floodplain environment could be triggered by several factors in addition to local climatic cycles.

The presence of *Cecropia* spp. and *Alchornea* pollen in the cores suggests an additional explanation for the fluctuations observed. Since the lakes are all situated within the present floodplain, they are affected by active channel migration (Salo et al. 1986, but see Sternberg 1960). Channel migration is largely unaffected by the local pattern of rainfall, especially along the large Andean-origin whitewater rivers. The successional development, following channel migration and the formation of backwater depressions, chutes and oxbow lakes, creates the same series of pollen stratigraphy changes as the proposed climatic oscillations. The Rondônia material is also subject to such an interpretation, although to a lesser extent. The successional series following deposition of the point-bars include trees, such as *Cecropia* spp. and *Alchornea castaneifolia*, and various grasses. The observed oscillation cycles of a few hundred years fit the channel migration rates reported from some Western Amazon floodplains (Lathrap 1968, Salo & Kalliola 1987).

Colinvaux et al. (1985) have collected Holocene sediment cores from six floodplain lakes and two crater explosion (maar) lakes from the floodplains of the Rivers Aquarico and Napo, Ecuadorean lowlands (<700 m a.s.l.). The data include ^{14}C datings of different core levels from most of the lakes. No pollen data from these cores have so far been published. The authors report increased flooding activity between 1300 and 800 B.P. This is evidenced by a gyttja deposition during the uppermost 800 radiocarbon years, indicating little or no flooding from the parent river. Under this gyttja, in four lakes there is a deposit of clay and fine sand similar to the sediments in modern rivers. ^{14}C ages were obtained for the bottom of this unit in two of the lakes (Añangucocha, Limoncocha) indicating an age of 1300 years in both cases. In Añangucocha, this level is underlain by organic deposits dating from 3040±80 B.P.

From these data, the authors conclude that the area was subjected to increased flooding during the period 1300 and 800 B.P. This would further suggest that floods like this might maintain high floodplain forest diversity by preventing competitive exclusion within the forest communities. The authors note that the suggested flooding period comes close to the wet period postulated by Absy (1982) for her Holocene floodplain lake material.

The irregular flood periods of the basinal forelands of the Andes are a very probable occurrence. However, in the light of the fact that there are only four lakes, situated along two rivers, which give the 800 year mark as the beginning of isolation from the parent river, and only one which gives evidence of an organic layer *below* the deposit of riverine sediments, the conclusion may be immature.

It is possible that the presence of riverine sand merely marks the date of river channel cutting and formation of the oxbow lakes. The stratigraphy described may also have its explanation in channel migration towards the oxbow lakes, increasing the sedimentation of river suspension sediments during the annual high water period. More cores are badly needed from the western Amazon basin for exploring the possibility of climate oscillations affecting large areas.

3.3. Interstadial pollen from the Napo refuge

The first two last glacial ^{14}C dates (33 520 ± 1010 B.P. and 26 530 ± 270 B.P., indicating the Mid-Wisconsin interstade) obtained from the Amazon basin, together with a description of the forest bed of the same age have recently been published by Liu & Colinvaux (1985). The sample site is located in Mera, Equador, at an altitude of 1100 m a.s.l., representing a marginal area of the lowland basin. The area is important because it is located within the limits of the proposed Napo refuge, which has achieved undisputed concordance among the mappers of centres of endemism (e.g. Haffer 1969, Prance 1982).

The sample is composed of both fossil wood, which provided material for the dating, and pollen. The wood is apparently *Podocarpus*, suggesting a lowering of the Andean montane forest by some 700 metres. The pollen assemblage also suggests Andean montane forest dominance. These data indicate that at least part of the proposed Napo refuge territory was not covered by modern type broad-leaved rainforest during the time it should have been according to the refuge theory and published distribution maps.

To summarize the biostratigraphical evidence of the basin area, it is clear that no direct evidence can be found to support anything other than shrinkage of the forest area.

4. Lithostratigraphy and geomorphology

Sites offering potential in the search for Quaternary paleoclimatological indicators in the Amazonian basin are scarce. With the exception of the maar lakes recently found in Ecuador (Colinvaux et al. 1985), all the other lakes so far studied are floodplain lakes with rapid floodplain sedimentation. Peatbogs, which are the major sources for biostratigraphical analyses in the temperate latitudes, are virtually lacking from the Amazon, with the exception of *Mauritia*-litter accumulation in the permanently waterlogged floodplain depressions of the upper Amazon (Malleux 1982). Hence the mineralogical and geochemical study of the Amazonian sediments will be invaluable to the reconstruction of past climatic fluctuations.

4.1. Marine delta sediments

Sedimentological cores have been obtained from the prodelta of the Amazon (Damuth & Fairbridge 1970, Damuth & Kumar 1975). The prodelta stratigraphy contains feldspar, originating from erosional processes during an arid climate: this suggests arid phases during the Pleistocene (Damuth & Fairbridge 1970). However, the feldspar particles may have their origin in the headwaters of the northern tributaries of the Amazon draining the Guianan shield aeas. Milliman & Barretto (1975) have also questioned the aridity hypothesis and attribute the increase in feldspar content to the increase in the erosion depth at a lower sea level during the last glacial maximum .

4.2. "Stone lines"

The presence of "stone lines" in the Amazonian lowlands is considered to be among the most important pieces of evidence, outside of biogeographical distribution data, supporting the refuge theory (Simpson 1982). The presence of Fe-oxide and hydroxide conglomerites, especially in the area of the Barreiras Formation (Sombroek 1966, Irion 1984), has demanded explanations and it is suggested that these stone lines are homologous with those evolved under a strictly arid savanna climate (Journeaux 1975, Brown & Ab'Saber 1979, Ab'Saber 1982). Under an arid climate type, the savanna stone lines are formed when wind erosion in the absence of covering vegetation removes the clay, silt and sand, causing the accumulation of coarser-grained material on the surface. This process leads to the stone pavement presently evidenced widely e.g. in the areas of the Orinoco Mesa-formation.

There is a clear inconsistency in the dating of the "stone line" horizon. Journeaux (1975), following Sombroek (1966), places the stone lines of the Belterra clays in the Barreiras Formation in the Calabrium (>2.5 Ma). Ab'Saber & Brown (1979) suggest that the stone lines, as well as paleosols (laterites, paleopavements and other concretions in the subsoil) are predominantly of late Pleistocene age. The discrepancy further reflects the lack of radiometric dating from this horizon.

The present discussion of the nature and origin of the Belterra clays is also relevant in the case of the Amazon stone lines. The general explanation for the Belterra clay formation by Sombroek (1966), suggesting that the area was formed by a Tertiary lake, has recently been amply criticized by Irion (1978, 1984, see also Sombroek 1984:524). Two major points from this criticism can also be lodged against the refuge theory.

First, the presence of lake sediment deposits like the Belterra clays would suggest a highly homogenous sediment structure through wide areas in central Amazonia. This homogeneity would make it difficult to postulate edaphic differences in the forest bed. The interpretation of Irion with regard to the origin of the Belterra clays is that they were formed on continental sediments affected by lateritic weathering and the formation of pisolithic layers. The grain size distribution of the Belterra clays is predominantly bimodal (Irion 1982), with up to 20% of the quartz in the uppermost horizons being 1 mm or more in size, and below this, 70% of the kaolinite in a fraction of less than 0.2 µm which strongly suggests weathering.

Furthermore, for the "stone lines" there is an alternative explanation to that given by Ab'Saber because of the weathered nature of the Barreiras sediments. The Belterra clays and the pisolithic layer from a single weathering unit. Fe oxide and hydroxide minerals characterizing the "stone lines" are formed as the lowermost pisolithic unit in the weathering series of the Barreiras sediments. The precipitation permitting the formation of the pisolithic layer must have been the same as it is at present. For this reason, the presence of pisolithic layers does not favour the hypothesis of aridity but, on the contrary, implies that the climate remained humid during the process (Irion 1982).

4.3. Denudation pattern

During the RADAM-project, full SLAR-imagery cover of the Brasilian Amazon was developed. Material is also available from the lowlands of Perú. The imagery has been analyzed by various authors. The relevant works for the reconstruction of paleoclimates in the Amazon basin are those interpreting the denudation pattern of the pediplanes. Tricart (1974, 1975) analyzed areas along the lower Amazon river west of Santarém. He points out that the pediplanes in the Santarém area are deeply dissected, and suggests that this dissection may have taken place during an arid phase without dense forest cover.

This area is characterized by old weathered deposits (the Barreiras Formation). Irion (1984) concluded that the sedimentological history of the area was continental fluvial, not lacustrine. This suggests that the differences observed in the dissection (denudation) pattern at the pediplanes merely reflect the age heterogeneity and sedimentological variation characterizing large fluvial basins. As there are few works describing the evolution of the dissection pattern under the present humid conditions and forest cover, there is no basis for interpreting the present dissection pattern as reflecting locations of Quaternary savannas (caatinga-cerrados) vegetation. It should also be noted that the absence of radiometric datings from the erosional reliefs leaves the question of erosional epochs unanswered.

5. Present geomorphical barriers in the Amazon basin

It is clear that the observed fragmentation of the Amazon biota into "core areas" or "centres of endemism" has formed the basis for reasoning along the lines of the refuge theory. Locations of former refuges have been suggested for birds (Haffer 1969, 1978), lizards of the genus *Anolis* (Vanzolini & Williams 1970), Nymphalid butterflies (Brown 1982) and several woody Angiosperm plants (Prance 1981, 1982).

Most biogeographers supporting the refuge theory repeatedly stress that in addition to the isolation induced by climatic cycles, there are other plausible reasons for the existence of centres of high endemism (Brown & Ab'Saber 1979, Prance 1981, Brown 1982, Haffer 1982). However, there is little documentation of these barriers or discontinuities. Haffer (1982) surveys two alternative frameworks, the Tertiary orogeny of the Andes, and the isolating effect of river channels. While the Andean orogeny is largely accepted as the major splitting agent of the Tertiary biota into the Pacific and Amazonian components (Croizat 1958, 1976), Haffer considers the orogeny to be of minor importance in explaining the subspecies–species level differentiation of the modern Amazonian biota.

The major river channels are a potential splitting factor in the apparently continuous lowlands. The development of the Amazon river system during the early Quaternary may have caused the isolation and differentiation of previously continuous and uniform populations on opposite river banks (Haffer 1978). In fact, this idea has repeatedly occurred to Amazon biogeographers (Wallace 1853, Bates 1862, Sclater & Salvin 1867, Hellmayr 1910, 1912, Mayr 1942).

Haffer (1978) reviews the available data on bird distribution in relation to the River Amazon and the main tributaries. The conclusion is that the numbers of species range borders tend to increase downstream along the Amazon and also along the Rio Negro, the Rio Madeira and the lower Rio Tocantis. However, as detailed information on present species interaction is virtually nonexistent, there is little opportunity for distinguishing the separating effect of the channels *per se* from the competitive interaction between species occupying opposite banks. In any case, most of the works which analyze the possible effect of the river fail to realize that Amazonia is a complex of wide floodplains and interfluvial areas. The opposite channel banks are in most cases part of the same recent geologic formation, the present floodplain, and few edaphic differences are expected to occur between them.

Hershkovitz (1968, 1969, 1977, see also Kinzey 1982), after analyzing distribution data for several lowland primates (mainly Callitrichidae), has the merit of being the first author to clearly distinguish floodplain dynamics from the isolation effects of the river channels alone. He states that the "shifting of river courses and to a minor degree, waifing, where unoccupied territory was involved, was probably more effective in promoting speciation among Amazonian callitrichids during any one climatic regime than shifting climates during the entire Pleistocene" (Hershkovitz 1977:413).

The evidence for large-scale river system alterations has been scarce until recently. The analysis of the Western Amazon basinal forelands, where the present floodplain dynamics are probably most active, has revealed a complex network of both modern and previous floodplains (Klammer 1984, Salo et al. 1986, Räsänen et al. 1987). In addition to the present flooded várzea, the non-flooded *tierra firme* relief shows well preserved marks of terraces and abandoned floodplains. These observations imply that the proposed Western Amazon refuges have been subjected to recent fluvial perturbance and sedimentation. Campbell & Frailey (1984) showed the present *tierra firme*-forest along the river Acre, Bolivia, to grow on top of an up to 35 m thick Holocene, not Pleistocene, alluvium bed. The ^{14}C age of these sediments varied between 10 085 ± 150 and 5 575 ± 105 years (three sites). While more radiocarbon samples are needed to examine the age-heterogeneity of the Western Amazon floodplain deposits, the unstable geologic nature of the area is evident.

Erwin (1982), after analyzing the between-floodplain differences in canopy beetles (Curculionidae and Chrysomelidae) and other insects in the Manaus area, revealed an unexpectedly low similarity between the floodplain faunas. Based on the floodplain dynamics processes driven by eustatic sea-level alterations, Erwin & Adis (1982) have proposed that both the short and long-term fluvial mosaicism of the Amazon basin may have had similar isolation effects to the climatic cycles.

6. Conclusions

It seems clear that the evidence describing habitat fragmentation in the extra-Amazonian areas of South America is strong enough to support the refuge concept in these areas (Schubert 1987). However, it is equally clear that the geological or biostratigraphical evidence compiled from the basin itself is hardly sufficient to give any support for the theory. Two main deficiencies are apparent. First, the fragmentation of the forest has not been documented, while there is some indication that shrinkage of the area has taken place, at least during the LGM (Liu & Colinvaux 1985, Absy & Van der Hammen 1976). Secondly, the fact that no LGM radiometric dates from the Amazon lowland area (<500 m) are yet available means that there is little chance of reconstructing the late Pleistocene history of this area.

Furthermore, the major body of works favouring past climatic fluctuations as a key mechanism for past biological differentiation neglect the edaphic mosaicism of floodplains in Amazonia. While Holocene floodplain dynamics most probably merely maintain the high level of species divesity through site-turnover, the Quaternary changes in the extension of the molasse basins and the dividing denudating areas may cause biological differentiation between areas (Räsänen et al. 1987).

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