HABITAT DIVERSITY AND THE DISTRIBUTION OF SPECIES IN THE RAIN FORESTS OF PERUVIAN AMAZONIA

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Résumé : L'Amazonie est constituée d'une mosaïque complexe d'aires avec différentes histoires géologiques. Par conséquent, plusieurs types de sols sont présents dans les différentes aires, la nature tout comme l'activité du processus géologique actuel présentent de larges variations. Dans les dernières années, les recherches botaniques en Amazonie ont donné de plus en plus d'importance aux effets des conditions géologiques et géomorphologiques dans la distribution et l'écologie des espèces végétales et des types de végétaux. La présente étude résume ces résultats à propos de l'Amazonie péruvienne.

Mots-clés : Histoire géologique, conditions édaphiques, écologie du paysage, végétation de la forêt pluvieuse, modèles de distibution des espèces

Abstract: Amazonia consists of a complex mosaic of areas with different geological histories. Consequently, different kinds of soils are found in different areas, and both the nature and activity of present-day geological processes show wide variation. In recent years, botanical research in Amazonia has paid increasing attention to the effects of the geological and geomorphological conditions on the distribution of plant species and vegetation types. The present paper summarizes such results from Peruvian Amazonia.

Keywords: Geological history, edaphic conditions, landscape ecology, rain forest vegetation, species distribution patterns

Introduction

The Amazon basin can be roughly divided in three regions, each of which is characterized by its special geochemical conditions (FITTKAU et al., 1975). The Guayanan and Brazilian shields are characterized by old crystalline rocks, Central Amazonia by nutrient-poor recycled sands, and Western Amazonia by relatively young sediments of Andean origin. At a more detailed scale within this general framework, each of the major regions is geologically heterogeneous.

The western periphery includes the entire Amazonian Peru, within which several smaller regions can be distinguished on the basis of such characteristics as geological history and topography. As these factors largely determine the local edaphic conditions, each region provides very different growth conditions for plants. Consequently, if edaphic preferences are found among Amazonian plant species, it can be expected that their distribution patterns reflect the regional and local geochemical differences.

Landscapes in Peruvian Amazonia

Peruvian Amazonia is situated in the geologically active foreland basin of the uplifting Andes. During its history, a variety of geological processes have taken place, and as a result the sediments that at present cover the land surface have widely different origins and ages (RÄSÄNEN et al. 1987, 1990). A recent geoecological map has distinguished four major groups of landscapes in lowland Peruvian Amazonia (PAUT, 1993; RÄSÄNEN et al., 1993): 1) areas of modern (Holocene) fluvial deposition, 2) areas of Pleistocene deposition, 3) old dissected terrain, and 4) uplifted mountains.

Areas of modern fluvial deposition cover 29% of Peruvian Amazonia, and they include the present meander belts of rivers, seasonally or permanently inundated floodbasins, and recent fan formations (RÄSÄNEN et al., 1993). All these environments are characterized by some degree of environmental liability due to the effects of sediment accumulation, erosion and river channel migration. Especially dynamic are the meander belts of actively migrating white-water rivers, and they are usually covered by vegetation in different stages of succession. The structure and floristic composition of the vegetation vary locally according to the severity of the flood stress and the age of the soil underneath (LAMOTTE; 1990; LAMOTTE-PEZO, 1992; PUHAKKA et al., 1993).

Floodbasins are found along the larger rivers but further from them, beyond natural levees. They are not much influenced by direct fluvial dynamics, and therefore the changes in their vegetation are more related to such gradual processes as changes in ground water level. Consequently, the vegetation patches are relatively large in area and more diffuse than in the meander belt. Floodbasins are characterized by extensive swamps that may be covered by trees, palms, shrubs or open vegetation depending on the degree of waterlogging of the soil (KALLIOLA et al., 1991). The largest of these basins extends over 47,000 km² between the rivers Ucayali, Marañon and Huallaga (RÄSÄNEN et al., 1992).

Fan formations occur all along the Andes where rivers enter the Amazonian plains and rapidly deposit a large part of their sediment load. Most of the fans are rather small, but between the rivers Morona and Tigre in northern Peru a fan of the river Pastaza covers 54,000 km². This fan is special not only because of its huge size, but because its sediments have a volcanic origin and are therefore geochemically very different from the sediments elsewhere in Amazonia (RÄSÄNEN et al., 1992). The Pastaza fan is covered by a complex mosaic of swamps and forests, but since not many botanical studies have been conducted there, it is not known whether the area is floristically as distinct as geologically.

Areas of Pleistocene deposition cover 7% of Peruvian Amazonia (RÄSÄNEN et al., 1993). They consist of old river terraces and other formations of fluvial origin, such as river channels and floodplains that have become abandoned because of tectonical uplifting or other reasons. These forma-

tions are especially found along the Ucayali river and in eastern Madre de Dios. Abandoned river channels seem often to be covered by swamp forests and palm swamps, although open swamp vegetation also occurs. The terrain over vast areas in Madre de Dios is very flat and covered by tall forest.

The most extensive landscape is old dissected terrain, which covers 62% of Peruvian Amazonia (RÄSÄNEN *et al.,* 1993). In PAUT (1993), this landscape group was divided in five smaller ones on the basis of their appearance in satellite imagery. The northeastern area is the largest one, and it presents an undulating topography with few striking features. The most notable exception is formed by some white sand areas, supporting forests that are both structurally and floristically distinct from the surrounding rain forest on clay soil.

In the more southern areas, the topography of the terrain becomes much steeper and the color patterns more distinct. Especially striking are the patterns found in the Fitzcarrald watershed area, which correspond with the alternating of structurally complex rain forest with bamboo forest. Bamboo forest was described by HUBER already in 1906, and has since then been mentioned in several articles dealing with the vegetation of Acre and adjacent areas of Peru (RADAMBRASIL, 1976; SOARES BRAGA, 1979; ONERN, 1980; PRANCE, 1989). The most common bamboo species seem to belong to *Bambusa* subgenera *Guadua* and *Merostachys,* but not much more can be said of these forests because of lack of botanical research.

Uplifting mountains are found scattered at Serra do Divisor and around the city of Pucallpa, and they cover 2% of Peruvian Amazonia (RÄSÄNEN *et al.,* 1993). In some places, the uplifted sediments may be as old as Cretaceous in origin. No botanical work has apparently been done in these mountains, but their isolated position and geological distinctness may have given rise to special floras.

Distribution of plant species

It is widely recognized that extreme edaphic conditions, such as prevail in for example white sand areas, rock outcrops, and inundated areas, exert a strong influence on the vegetation. The vegetation in such areas is often both structurally and floristically less complex than is the surrounding rain forest. Generally, the overall floristic similarity between inundated and non-inundated areas is low, and the vegetation in non-inundated areas is on average richer in species (cf. DUMONT *et al.,* 1990). It has also been reported that in some plant groups the species are specialized in one or the other of the edaphically different environments. For example, the *Passiflora vitifolia* complex can be divided into four species, each of which is restricted to one of the following substrates: seasonally inundated soils, non-inundated alluvial soils, non-inundated lateritic soils, and non-inundated white sands (GENTRY, 1981). The regional differences in the landscape and geology described above suggest that this kind of distribution patterns may be more widespread than has hitherto been realized. Not only can edaphic specialization be expected in other plant groups, but also the edaphic factors that determine it may turn out to be more subtle than the ones recognized before.

In inundated areas, the striking difference in the color of white-water, clear-water and black-water rivers is known to correlate with nutrient content and acidity of the water, which together with the predictability and severity of the floods is reflected in the structure and floristical composition of the vegetation (PRANCE, 1979; JUNK, 1989; KUBITZKI, 1989; KLINGE *et al.,* 1990; LÓPEZ PARODI & FREITAS, 1990; PUHAKKA *et al.,* 1992, 1993). However, these river types are not clear-cut, and the chemical characteristics of the sediments of different rivers in Peruvian Amazonia show wide variation between the extremes (KALLIOLA *et al.,* 1993). Regional studies have shown that the species composition of young successional vegetation along different rivers can be very different, which may partly be due to differences in sediment chemistry and partly due to differences in river channel dynamics (PUHAKKA *et al.,* 1992, 1993). More extensive floristic work is needed to clarify how distinct the floras of chemically different rivers actually are, and whether there are general biogeographical patterns to be found in the distribution of the species growing in flooded habitats.

Within the non-inundated rain forest, DUCKE and BLACK (1953) noted that sites with unusually fertile, alkaline or sandy soils are found in several parts of Brazilian Amazonia, and that each of these

soil types supports a number of endemic plant species. The most well-known of these special soils are the extremely nutrient-poor white sands, because the vegetation that grows on them is structurally distinct and has attracted repeated scientific attention (ANDERSON, 1981; ENCARNACIÒN, 1985; VAN DER WERFF, 1992; GENTRY & ORTIZ, 1993; RUOKOLAINEN & TUOMISTO, 1993; TUOMISTO & RUOKOLAINEN, 1994; RUOKOLAINEN et al., in press).

Although extensive in the northwestern parts of Brazilian Amazonia, in Peruvian Amazonia white sand soils are found only as restricted patches. The most extensive of these are situated along the valley of the Nanay river, and minor areas are found close to the lower Ucayali river. At least ferns and the Melastomataceae react strongly to the change in soil texture; there is an almost complete turnover of species at the sand-clay transition (TUOMISTO & RUOKOLAINEN, 1994). In some genera of ferns, the species form two groups: those that grow only on clayey soil, and those that grow only on sandy soil. For example, Lindsaea lancea (L.) Bedd. var. lancea is only found on clay, while Lindsaea divaricata Kl. is typically found on sand. The genus Trichomanes has at least three species that are restricted to sand, namely T. bicorne Hook., T. cf. crispum L., and T. martiusii Presl, while T. elegans Rich. and T. pinnatum Hedwig grow in the immediate vicinity but only where the soil is clayey (TUOMISTO & RUOKOLAINEN, 1994). Among sandy soil sites, there are differences in drainage, with the waterlogged sand areas supporting vegetation that is both structurally and floristically distinct from vegetation on well-drained sand (KAHN & de GRANVILLE, 1992; RUOKOLAINEN & TUOMISTO, 1993; TUOMISTO et al., in press). In some sandy sites, the forest is reduced to low scrub with very low species diversity (ENCARNACIÓN, 1985; RUOKOLAINEN & TUOMISTO, 1993). The change from clay soil to sand soil may be abrupt or gradual, and intermediate soils are frequently found. There seems to be a gradation of different soil types between the extremes, and a corresponding gradation of intermediate vegetation types. Also less extreme differences in soil texture, such as between clay and sandy loam, have been reported to correspond with species composition of fern communities (YOUNG & LEÓN, 1989).

In clay soil areas it has been observed that fern species react strongly to local differences in drainage that are caused by the undulating topography (POULSEN & BALSLEV, 1991; RUOKOLAINEN & TUOMISTO, 1993). Different species of the same genera may be found in different parts of the moisture gradient. Of the tree ferns, for example, Cyathea lasiosora (Mett. ex Kuhn) Domin is found mainly on the relatively dry hill tops and slopes, while C. pungens (Willd.) Domin is exclusively found in waterlogged valleys and may there form almost monospecific stands. Similarly, Polybotrya caudata Kze. is only found on waterlogged soils, while P. pubens Mart. and P. osmundacea Willd. are mainly found in drier sites (pers. obs.). Similar observations have been made with trees in French Guiana (LESCURE & BOULET, 1985) and Colombia (DUIVENVOORDEN & LIPS, 1993). Amazonian palms have been well studied in this respect: it has been found that the species growing on well-drained soil are different from those on waterlogged soil, and that the degree and seasonality of waterlogging promote further floristic differences among swamp communities (KAHN & CASTRO, 1985; KAHN & MEJIA, 1990; KAHN & MEJIA, 1991; KAHN & de GRANVILLE, 1992).

Conclusion

Whenever edaphic gradients in Amazonia have been floristically studied, the distribution patterns of many plant species have been strongly skewed, suggesting that the species in question have marked edaphic preferences. It seems therefore a reasonable working hypothesis that if edaphic differences are found among rain forest sites, floristic differences can also be expected. In those cases that have been studied until now, this has indeed been the result. However, many of the different geoecological units that PAUT (1993) distinguished in Peruvian Amazonia on the basis of satellite imagery have never been visited by a botanist, and the overwhelming majority of all plant collections have been obtained from rather restricted areas and often without reference to edaphic conditions. Therefore the current phytogeographic data are seriously biased and incomplete, and much field work is still needed if even the most basic questions are to be answered. Furthermore, new

approaches need to be adopted to make most use of the field work efforts. As satellite images make it possible to monitor large areas and to estimate the spatial representativeness of field results, they have proved especially useful in geological and vegetation studies in Amazonia (e.g. KALLIOLA *et al.,* 1991; RÄSÄNEN *et al.,* 1993; TUOMISTO *et al.,* in press). Hence, phytogeographical research can bene-fit immensely from the use of satellite images in combination with data from other sources to explain the present distribution patterns of the rain forest species.

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