

# Dissecting Amazonian Biodiversity

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Biogeographical and biodiversity studies in lowland Amazonian rain forests typically refer to observed or postulated distribution barriers such as past unfavorable climates, mountains, rivers, and river floodplains that divide the uniform *tierra firme* (noninundated) forest. Present-day ecological heterogeneity within *tierra firme* has hardly been discussed in this context, although edaphic differences are known to affect species distribution patterns in both inundated areas and *tierra firme*. Quantification of landscape heterogeneity in Peruvian lowland Amazonia (500,000 kilometers squared), based on field studies and satellite image analysis, shows that Peruvian Amazonia is considerably more heterogeneous than previously reported. These observations have implications for the research, management, and conservation of Amazonian biodiversity.

Amazonian lowland rain forests are celebrated for their high  $\alpha$ -diversity or species richness within habitats (1–4), whereas  $\gamma$ - or regional diversity reported by floristic checklists (5) is surprisingly low. The recognition of only a few vegetation types (6) and the limited interest in  $\beta$ - or between-habitats diversity (1, 2, 4, 7, 8) have contributed to a general impression of wide-scale homogeneity. We surveyed the extent of habitat heterogeneity at different spatial scales in the tropical lowland rain forests of Peruvian Amazonia; the terms “habitat” and “biotope” are here used for units that seem reasonably uniform at the scale of observation without implying that they are homogeneous at more detailed scales.

Species distribution patterns of Pteri-

dophytes and Melastomataceae were studied in *tierra firme* along continuous transects at the local (10 to 10<sup>3</sup> m) and landscape (10<sup>3</sup> to 10<sup>5</sup> m) levels. At the local scale (Fig. 1), habitat differences correlated sometimes with canopy openings but more often and more clearly with topography. Within each transect in the field (0.25 to 0.65 ha), many species showed a distinct preference for either the moister valleys or the drier hills. Spatially separate, recurring species associations were hence found, with the greatest local diversity generally being found in the valleys. At the landscape level (Fig. 2), each transect represented a different biotope, as shown by the leveling-off of the species-area curves and the low percentage of species shared among transects (Fig. 2, B and C). Tree data collected along six of the transects (0.16 ha per site, minimum stem diameter 2.5 cm) showed the same floristic relationships (Fig. 2D); the correlation between the similarity matrices based on Pteridophytes and Melastomataceae on the one hand, and on trees on the

other, was 0.91 (Mantel test) (9). The observed floristic patterns could not be explained by geographical distances or geomorphology, but they correlated with topsoil properties (Fig. 2E). This suggests that the overall patterns in species composition are to a large extent edaphically controlled and therefore to some degree predictable.

The color patterns visible in satellite images are determined by the physical properties of the vegetation and soil and can therefore be used to identify different vegetation formations. Patterns shown by satellite imagery in the area we selected for detailed floristic studies were not especially pronounced as compared with patterns found elsewhere in Peruvian Amazonia (Fig. 3), but they nevertheless proved to reflect significant floristic differences. The transect on white sand soil (number 2) was expected to be floristically distinct, because the forest has a characteristic structure (6), but the differences among the structurally more similar forests of the other sites could only be anticipated because of their dissimilar spectral reflectances in satellite images (Landsat MSS and TM) (10) (Fig. 2). Also in other parts of Peruvian Amazonia, visual analysis of satellite images revealed numerous structurally and floristically distinct biotopes within the vegetation types already known. We have verified these patterns by field analysis throughout our study area (Fig. 3B); our most distant study sites were about 1200 km apart. Structural characteristics of the vegetation were documented along 2000 km of river, and during low-altitude flights over 4000 km of forest (10–12). Quantitative floristic data were obtained at 16 sites in *tierra firme* (46 square plots totaling 2.1 ha, 8 transects totaling 7.8 km) (2, 13) and along 8 river systems in inundated areas (17 transects totaling 6.5 km) (11, 14). No evidence of

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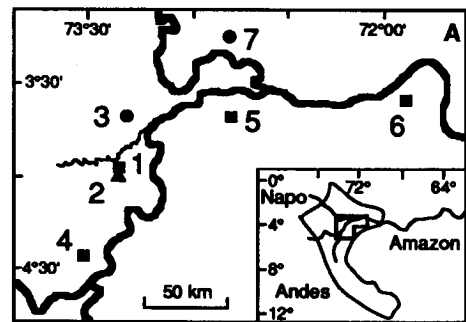
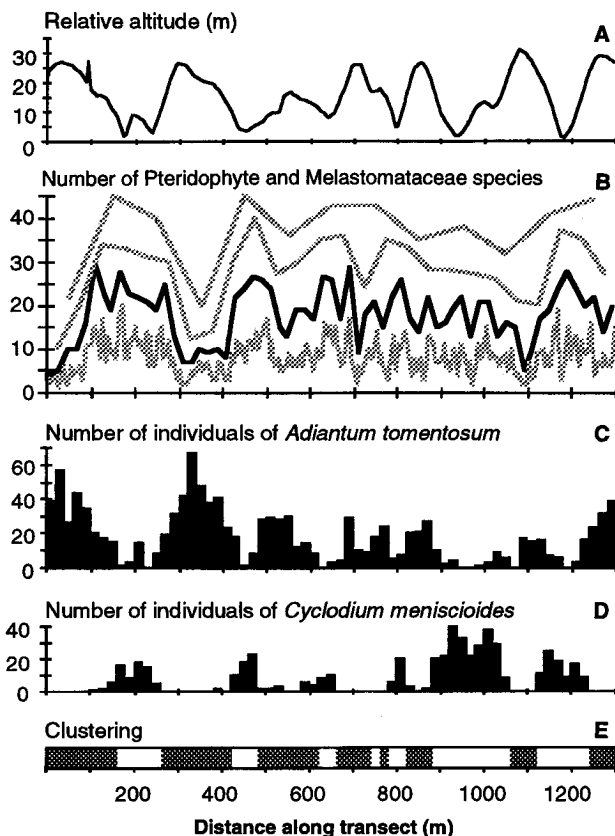
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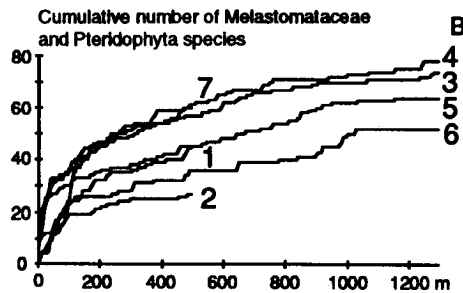
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**Fig. 1.** An example of a continuous 5-m-wide transect (1300 m in length) in Peruvian lowland Amazonia (transect 4 in Fig. 2; 4°28'S, 73°34'W). **(A)** Topography. **(B)** Local species diversity, measured as the number of Pteridophyte and Melastomataceae species within one sample. From bottom to top, the lines correspond to sample sizes of 25 m<sup>2</sup>, 100 m<sup>2</sup>, 250 m<sup>2</sup>, and 500 m<sup>2</sup>. In **(C)** to **(E)**, a sample size of 100 m<sup>2</sup> was used. Total number of species: 79. **(C)** Distribution of *Adiantum tomentosum* Klotzsch (fern), the most common species in the transect. Rank correlation of abundance with altitude: 0.62. Total number of individuals: 1150. **(D)** Distribution of *Cyclodium meniscioides* (Willd.) Presl (fern), the second most common species in the transect. Rank correlation of abundance with altitude: -0.75. Total number of individuals: 520. **(E)** Results of a cluster analysis with abundance data of Pteridophytes and Melastomataceae. A similarity matrix based on Chord distances was used to run an agglomerative hierarchical clustering, in which two groups of samples are clustered at a given similarity level if more than 50% of the possible among-cluster sample pairs have at least that similarity. All samples that were clustered together at a similarity level higher than 20% are shown with the same shading. The R-package (9) was used for the computations.



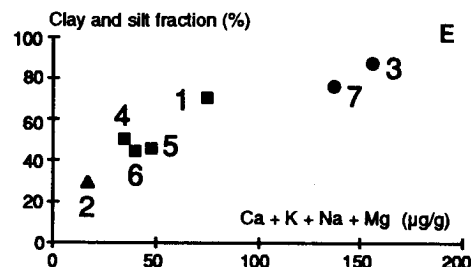
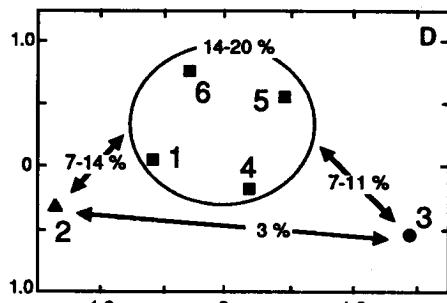
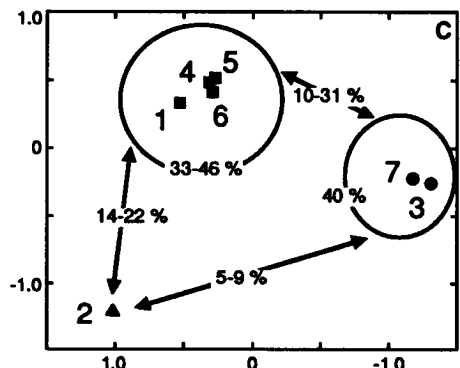
**Fig. 2.** **(A)** Sites where patterns in satellite imagery were documented by quantitative floristic and soil studies in noninundated forests of Peruvian lowland Amazonia. The symbols reflect roughly the color of the sites in the satellite images: triangles, dark; squares, intermediate; circles, light. **(Inset)** Location within Peruvian Amazonia; for location within South America, see Fig. 3A. **(B)** Species-area curves for Pteridophytes and Melastomataceae in the transects. **(C)** Ordination of the transects based on floristic similarity of Pteridophytes and Melastomataceae (Jaccard index); floristically similar transects plot close to each other, dissimilar transects far apart. The percentage of shared species between transect pairs is indicated within and between each transect group. Nonmetric multidimensional scaling; computed for two dimensions with SYSTAT 5.2 (27). **(D)** Ordination based on floristic similarity of trees. Otherwise as in **(C)**. **(E)** Topsoil characteristics of the transects. Means of several samples taken at 5- to 10-cm depth. The bases were extracted from bulk samples (1 M ammonium acetate, pH 7), and the clay and silt (<0.06 mm) fraction was determined by wet sieving after ultrasonic dispersion of the suspended sample.



disagreement between satellite imagery and the actual landscape was found.

On the basis of these data, stratified random sampling of satellite images was used to estimate landscape heterogeneity in Peruvian Amazonia through 448 transects totaling 13,400 km (Fig. 3). Both vegetation (revealed by colors) and geomorphology (revealed by shades) contributed to macropatterns that involved differences in the shape, size, abruptness, orientation, and repetitiveness of biotope patches. Within each satellite image (185 km by 185 km), between 21 and 54 different biotopes were visible, and a 30-km-long transect typically crossed 4 biotopes (Fig. 3D). Although we were conservative in distinguishing biotopes, the heterogeneity of terra firme areas nevertheless exceeds that of previously reported data by more than an order of magnitude. Furthermore, relatively homogeneous biotope patches are small: Their mean length was 4.6 km in terra firme and 1.7 km in inundated terrain, whereas only 8 transects (1.8%) showed a patch diameter more than 30 km (Fig. 3E). The average abruptness of the ecotones between different biotopes varied among regions, but practically no difference in this respect was found between terra firme and inundated areas (Fig. 3F). The terra firme biotopes were in 49% of the cases limited by another kind of terra firme biotope, and in 13% by open water.

In summary, ecological heterogeneity in Peruvian Amazonia ranges from plant asso-



ciations a few hundred meters or less in length (Fig. 1) through landscape patches several kilometers in diameter to regional patterns hundreds of kilometers in size (Fig. 3). An important part of this heterogeneity is linked with variation in soils (1, 2, 4, 8, 15, 16), which is determined by geological processes and climate. Sediments of different provenances and chemical compositions have been deposited in a wide array of environments ranging from fresh-water fluvial to marine or brackish tidal systems, and exposed surfaces have been subject to erosion and soil formation for different periods of time (17, 18). A variety of edaphic conditions and ecotones are hence found, but both their characteristics and their effects on the forest biota are practically unexplored. For example, the heterogeneity and patchiness of biotopes may create geographically separate subpopulations of plants and

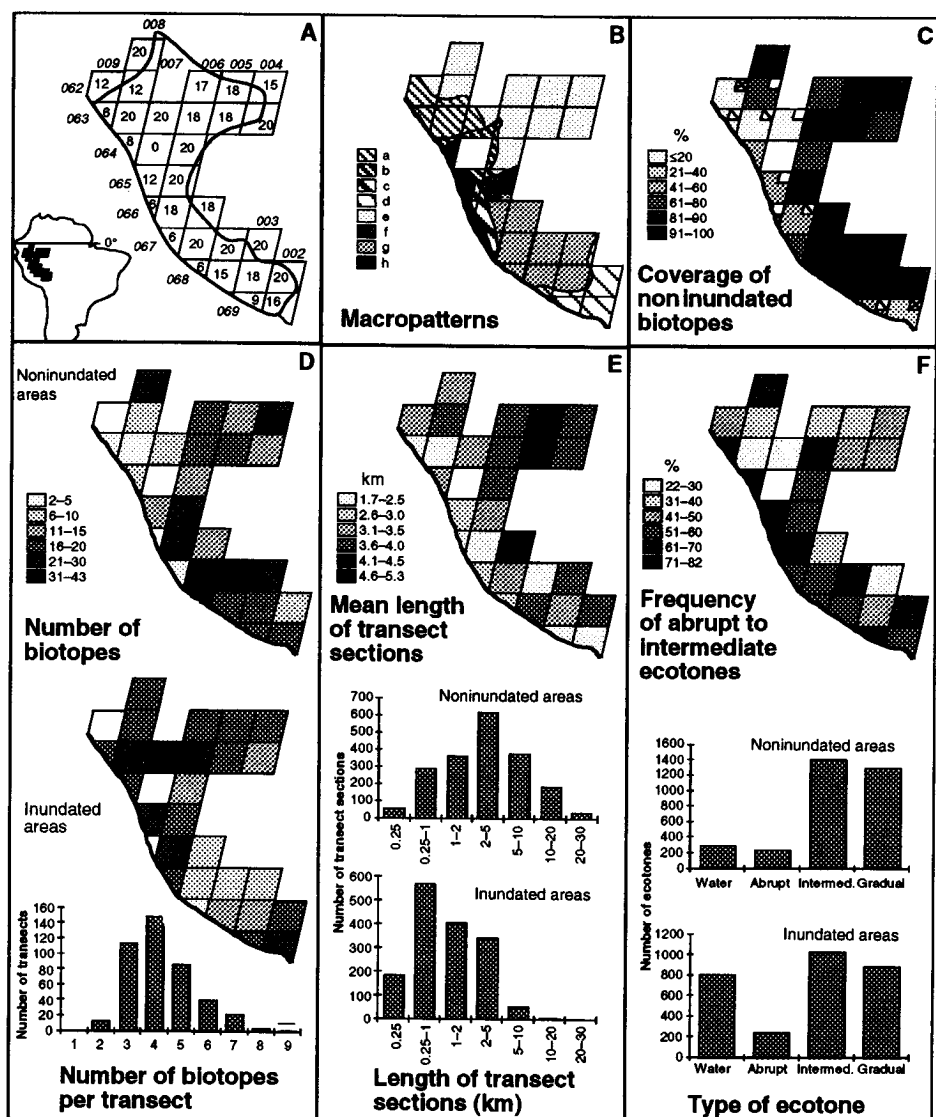
animals and lead to metapopulation dynamics with ecological and evolutionary implications (19). The influence of present-day environmental conditions on species distribution patterns can be effectively studied through use of the same principles as in temperate areas, and in spite of the great species richness it therefore becomes possible to define which species are ecologically capable of colonizing a given rain forest site. Thereafter, the relative importance of factors that cannot be directly measured can be inferred. Chance and biotic interactions (20), as well as the existence of dispersal barriers and active processes during the geological or climatological history (17, 21–23), may have caused differences in species composition to accumulate between ecologically similar sites, or lessened differences among dissimilar sites at all spatial scales.

Recognizing ecological heterogeneity

makes it possible to put biological research in Amazonia into perspective. The interpretation and extrapolation of point data, such as floristic and faunistic inventories in a given locality (3, 4, 13), depend on spatial environmental patterns. Therefore, it is important that biodiversity research use methods that carefully distinguish in which biotope, and at which spatial scale, the study is performed.

Recommendations for nature conservation in Amazonia have been based on identified centers of biodiversity or endemism (24). Because these centers are mainly artifacts of inadequate and biased biogeographic data (25), this approach is misleading and should not be used as the basis for important decisions. For example, few detailed floristic inventories have been published for Peruvian Amazonia (4, 11, 26), and our results show that these have sampled only a tiny

**Fig. 3.** Analyses of Landsat Thematic Mapper (TM) satellite images covering most of Peruvian Amazonia below 500 m altitude. Images from the years 1984 to 1991 were processed by INPE (Brazil) with data from bands 3 (0.63 to 0.69  $\mu\text{m}$ ), 4 (0.76 to 0.90  $\mu\text{m}$ ), and 5 (1.55 to 1.75  $\mu\text{m}$ ). Hard copies of the color composites were produced at 1:250,000. **(A)** The study area; location in South America as shown in inset. Rows and paths of the images and the number of transects analyzed in each image are indicated. Each transect corresponds to 30 km in the field; their coordinates and orientation were assigned at random, and out of a maximum of 20 transects per satellite image, those that covered mountains or clouds were excluded. Within the transects, sections that were sufficiently distinct in texture or color to represent different biotopes were characterized by their length, type of environment (water or inundated, noninundated or unspecified biotopes) and type of the ecotones between sections (abrupt, intermediate, or gradual). Only sections longer than 250 m were recognized, except for open water which was recognized whenever identifiable (for example, small rivers). All images were analyzed twice, in random order, and by one person (R.K.); time of observation had no detectable effect on the results. **(B)** Macropatterns showing characteristic geomorphology or vegetation in satellite images (11). Hatched regions are predominantly inundated biotopes, stippled predominantly noninundated. a, Pastaza fan; b, Ucayali basin; c, Ucayali basin; d, Madre de Dios basin; e, Iquitos arch region; f, Contamana–Serra do Divisor; g, Fitzcarrald arch region; h, Andean foothills. **(C)** Percentage of noninundated biotopes of the total length of the transects. Small squares indicate the abundance of unspecified biotopes: none, <10%; white, 10 to 20%; slash, 21 to 30%; cross, 31 to 55%. **(D)** Total number of biotopes (spectrally clearly different, spatially coherent patches) in each satellite image; inundated biotopes include also the unspecified ones. Histogram: frequency distribution of the number of different biotopes within a transect. Open water and constructed ground cover types (towns, roads, cultivations, young secondary forests) were ignored. **(E)** Mean diameter of biotope patches, measured as length of transect sections. Histograms: frequency distribution of patch diameters. **(F)** Proportion of abrupt and intermediate ecotones within transects, excluding limits with open water. Histograms: frequency distribution of different ecotones.



fraction of the area's biotopes, the total number of which by far exceeds 100. Inadequate sampling of different biotopes leads to erroneous conclusions on the distribution of species and the conservation value of different areas. Furthermore, underrepresentation of  $\beta$ -diversity may explain the relatively low  $\gamma$ -diversity reported for the area (5). Therefore, in studies like national biodiversity assessments it is imperative to take the limits of ecologically comparable patches into account when planning biological field research and extrapolating the results. Reliable spatial data, such as maps of vegetation and soil properties, are urgently needed for precise hypothesis formulation and testing in ecology and biogeography and for directing conservation efforts to preserve representative environments from different regions.

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