Biogeographical affinities among Neotropical cloud forests

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Abstract. Biogeographical affinities among cloud forests in the Neotropical region were studied through a track approach, by constructing generalised tracks based on the results of a parsimony analysis of endemicity (PAE). Distributional data on 946 genera and 1,266 species of vascular plants (Pteridophyta, angiosperms, and gymnosperms) from 26 cloud forest patches from Colombia, Costa Rica, Cuba, Honduras, Jamaica, Mexico, Peru, Puerto Rico, and Venezuela were analysed; and four localities from eastern and western United States were also included as outgroups. The track analysis identified six generalised tracks: a first one that includes the majority of the cloud forests of Mexico, Central America, the Antilles, and northern Colombia; a second one that includes southern Mexico and northern Central America; a third one that includes the mountains in northwestern South America; a fourth one that includes the mountains in southwestern South America; and two others in western and eastern United States. It is concluded that the Neotropical cloud forests are closely related and that those of the Caribbean subregion exhibit complex relationships, which could be due to the complex tectonic history of the area.

Key words: Neotropics, cloud forests, vascular plants, panbiogeography, track analysis, parsimony analysis of endemicity.

Introduction

The Neotropical region ranges in the Americas, from central Mexico to central Argentina (Morrone 1999, Morrone et al. 1999). This biogeographic region is characterised by its great diversity of ecosystems, which include among others, steppes, grasslands, savannas, moorlands, and dry, moist, and cloud forests (Cabrera and Willink 1973, Dinerstein et al. 1995). Within the Neotropical ecosystems, cloud forests are particularly interesting from a biogeographic viewpoint (Luna et al. 1999). The northernmost stand of cloud forest is found in the Sierra de San Carlos and Gómez Farias (Tamaulipas), in the Mexican Sierra Madre Oriental, between 1,300 and 1,400 m (Briones 1991). The southernmost cloud forest is found in northeastern Argentina, at approximately 27–28° S (Webster 1995). Neotropical cloud forests are characterised by their archipelagic distribution, the presence of endemic taxa, and their high biodiversity, which highlight their biogeographic and biological importance. They have been considered also as one of the main world centres of domestication of certain plants such as corn, beans, peppers and tobacco, which have been
clues to the flourishing of Pre-Columbian civilizations.

Neotropical mountains harbour ca. 45,000 species of flowering plants, which when compared to the 250,000 species worldwide, show that they constitute one of the world’s great centres of biological diversity (Churchill et al. 1995). Recently, attention has been placed in the study of these Neotropical montane forests, including principally their conservation (Churchill et al. 1995; Hamilton et al. 1995). Notwithstanding, their biodiversity is relatively poorly studied.

Graham (1995) recently argued that the close affinity between the forests of Mexico-Central America and northern South America are due to the arrival of elements by different routes and at various times across the Panamanian land bridge and the North Atlantic. He suggested that the montane vegetation is composed of four biogeographic components, three basically Gondwanic and one Laurasic.

It is becoming increasingly recognised that the Neotropical cloud forests rank high within the world’s most threatened ecosystems (Hamilton et al. 1995), and that the damage done to them is far more likely to be irreversible, because they have low resilience to disturbance. These communities have been severely disturbed for centuries by human activities such as forestry, road building, agriculture, farming, colonization, pasture, and fires. The increasing human population has placed pressure on these forests, so that the disturbance is so extensive in several areas that the original vegetation is disappearing quickly (Luna et al. 1988). Many of these forests are today restricted to the most inaccessible slopes and have been partially replaced by grasslands and croplands. It has been proposed that biogeographic analyses can help identify priority areas for biodiversity conservation (Grehan 1993, Morrone and Crisci 1995, Morrone and Espinosa 1998, Espinosa and Morrone 1998).

If taxon-area cladograms for a cladistic biogeographic analysis are not available, Parsimony Analysis of Endemicity or PAE (Rosen 1988; Morrone 1994, 1998) can be used to recognize patterns of biogeographical homology, equivalent to generalised tracks (Craw et al. 1999).

Our main objective is to analyse the main biogeographical patterns among several Neotropical cloud forests, by applying a track approach using PAE.

Material and methods

Taxa. From a data set composed of 1,727 genera and 7,307 species of vascular plants (gymnosperms, angiosperms, and pteridophytes), the taxa present in a single locality were deleted, obtaining a list composed of 946 genera and 1,266 species. These were obtained from field work from 1982 to 2001; published floristic surveys (Shreve 1914; Seifriz 1943; Whittaker 1956; Whittaker and Niering 1965; Howard 1968; Frye 1976; Alvarez del Castillo 1977; Cruz and Eraza 1977; Gutiérrez 1980; Sugden 1982; Luna et al. 1989, 1994; Puig 1989; Haber 1991; Long and Heath 1991; Meave et al. 1992; Kelly et al. 1994; López et al. 1994; Campos and Villaseñor 1995; Ruiz 1995; Silverstone-Sopkin and Ramos-Pérez 1995; Téllez 1995; Michener-Foote and Hogan 1999); Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio) projects (Flores 1992–1994, Santana 1993, Santiago and Jardel 1993); and internet on the www (Dillon 2001). The complete list is available through e-mail upon request to the senior author (ilv@hp.fcien-
cias.unam.mx). This list was carefully checked in order to assess the plant diversity and detect synonyms by consulting the relevant literature or communication with specialists. The units of analysis were 26 Neotropical cloud forest patches from Colombia, Costa Rica, Cuba, Honduras, Jamaica, Mexico, Peru, Puerto Rico, and Venezuela. In addition, four localities from eastern and western United States were included as outgroups (Fig. 1; see Table 1).

Track analysis. The panbiogeographic method was originally developed by Croizat (1958, 1964) and consists basically of plotting distributions of organisms on maps and connecting their discontinuous distributions together with lines named individual tracks, according to their minimal geographical proximity. The summary lines resulting from the coincidence of different individual tracks are considered generalised tracks, which indicate the preexistence of ancestral biotas that