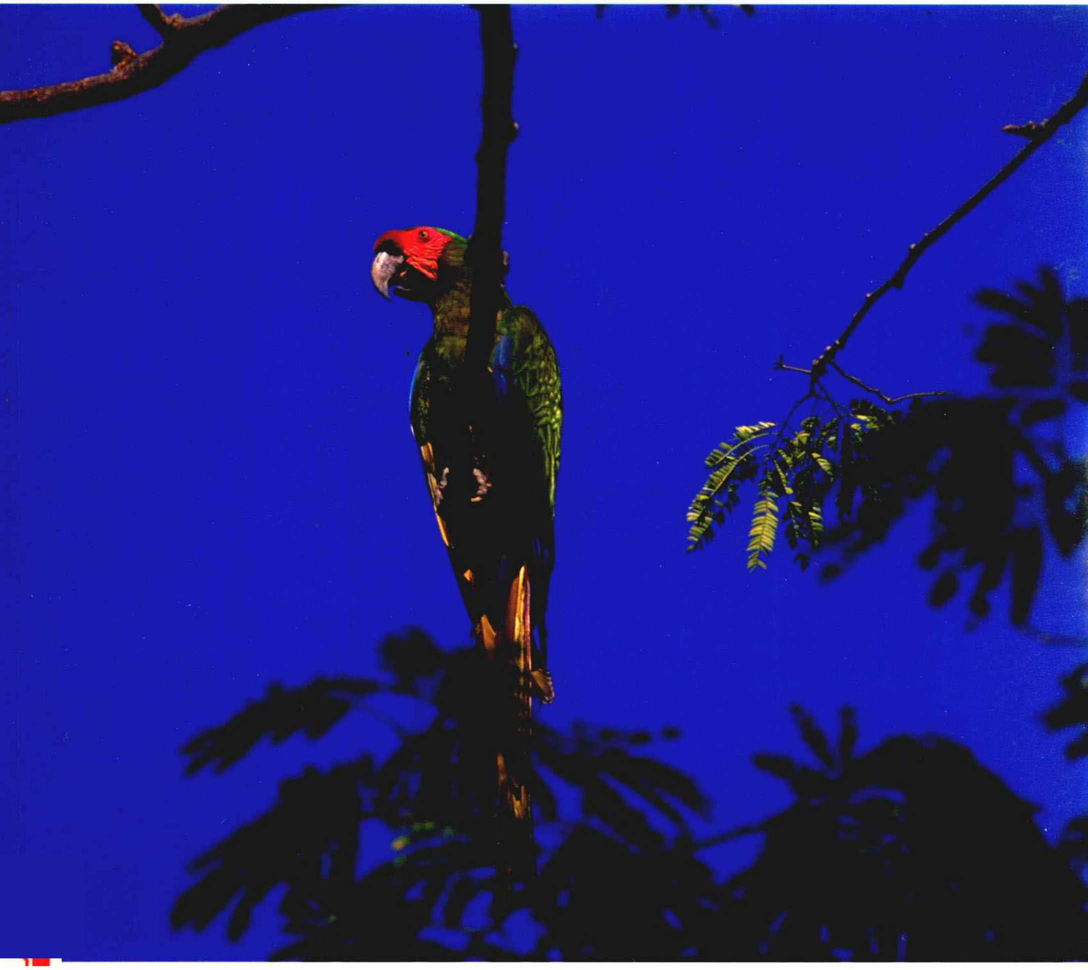
Seasonally Dry Tropical Forests

Ecology and Conservation



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SEASONALLY DRY TROPICAL FORESTS

INTRODUCTION

RODOLFO DIRZO, HILLARY S. YOUNG, HAROLD A. MOONEY,
AND GERARDO CEBALLOS

The usual perception that the term *tropical forests* refers to evergreen tropical rain or moist forests is inaccurate. The tropical forest biome is, in reality, a mosaic of different vegetation entities including, at mid elevations of the tropics, the patchy and biogeographically restricted tropical cloud forests and, in the lowlands, the rain forest per se and the seasonally dry tropical forests (SDTFs). At least part of the biased perception of the term *tropical forest* stems from the fact that, by far, tropical rain forests are the most studied and, indeed, most popularized among the general public. SDTFs, in contrast, have been seriously neglected. For example, only 14 percent of articles published on tropical environments between 1950 and 2005 focus on dry forests (Sánchez-Azofeifa et al. 2005). Such scientific bias, however, determines that our understanding of the planet's biodiversity, the ecosystem services it provides, and the anthropogenic threats to it in general, and to the tropical forest biome in particular, is in turn biased and will remain grossly incomplete if we do not pay attention to the SDTFs still present in the different parts of the world. The present volume is an attempt to fill part of this lacuna in our knowledge on tropical ecology by analyzing the ecology and conservation of SDTFs in Latin America. This volume represents, also, a sequel to the first and only other global synthesis, (Bullock et al. 1995) and provides a complement to some recent efforts conducted at a more local level (e.g., Ceballos et al. 2010).

SDTFs are forests with a mean annual temperature typically greater than 17 degrees Celsius, rainfall ranging from 250 to 2000 millimeters annually, and an annual ratio of potential evapotranspiration to precipitation of less than 1.0. However, by far the most distinctive character of this forest type is its seasonality, with 4 to 6 dry months (rainfall less than 100 millimeters), which in turn determines the distinctive phenology of the plants and the forest as a whole: an alternating deciduousness during the dry season, followed by an evergreen physiognomy during the rainy season. Such environmental seasonality represents a unique combination of challenges for the living biota contained within SDTFs and, accordingly, results in a series of special morphological, physiological, and behavioral adaptations of plants (chap. 8), animals (chap. 5, 6), fungi and soil organisms (chap. 4), and probably microorganisms. The climatic seasonality and the coupled seasonality of organisms and their ecological roles determine in turn the ecosystem processes (productivity, water and nutrient cycling, etc.) that characterize SDTFs (chap. 7–10).

Beyond their phenology and seasonality, three "macroscopic" features define the importance of SDTFs. The first is their wide coverage, encompassing 42 percent of tropical ecosystems worldwide, globally representing the second largest type of tropical forest (Miles et al. 2006; chap. 3). Second is their high biological diversity, which, although not comparable with the species richness of tropical rain forests, is nevertheless considerable (chap. 1, 4, 5, 6, 12). SDTF biodiversity includes other facets of great significance, in particular SDTFs' remarkable concentration of endemic species, their diversity of life-forms and functional groups of plants and animals (Dirzo and Raven 2003), and their incomparable beta diversity, or spatial species turnover (chap. 1). SDTF beta diversity is underscored by the high plant species dissimilarity (or floristic distance values) among sites, both within a relatively restricted region (e.g., Mexico, with a mean dissimilarity of 91 percent among all possible pair-wise comparisons of 20 study sites; Trejo and Dirzo 2002) and among the 21 major geographic nuclei that encompass the SDTF in the Latin American region (with 203 out of 253 possible pairs having dissimilarity values of more than 70 percent; chap. 1). The unusual SDTF beta diversity, combined with the impressive concentration of endemic taxa (e.g., 60 percent of plant species in Mexican SDTF), is an aspect that has important biogeographic (chap. 2) and conservation (e.g., chap. 12–16) implications. Finally, a third distinctive feature of SDTFs is their uneven distribution across the tropical regions of the world. Such forests have a greater distribution in the Neotropical and Caribbean region, encompassing approximately 700,000 square kilometers of land covered by SDTFs, representing 67 percent of the global coverage of this ecosystem.

On the other hand, among the region's tropical forests, SDTFs are regarded as the most threatened, with an estimated conversion of at least 48 percent of its extent into other land uses (Miles et al. 2006), an estimate similar to that of chapter 3, suggesting that only 44 percent of SDTF remains in the region (see also chap. 12, which cites an estimate of only 30 percent). Furthermore, a significant proportion of the remaining area of SDTF is fragmented to a varying degree, with important negative consequences on species and genetic diversity (chap. 11), as well as on several ecological processes, including species interactions crucial to plant reproduction, plant recruitment, and forest regeneration (chap. 11). In addition to land use change, other global environmental changes, in particular climatic change (chap. 16), have the potential to affect the structure, diversity, and functioning of SDTFs as well as the delivery of crucial ecosystem services they provide to human societies (chap. 15).

Given the dramatic magnitude of forest conversion and the persisting high rate of SDTF deforestation, coupled with the fact that protected areas including SDTF are extremely limited (e.g., only about 6 percent of SDTF in Central America has protected-area status; Miles et al. 2006), conservation of such vegetation and its biodiversity, ecosystem processes, and services will depend on how much SDTF biodiversity can be preserved in the mosaic of forest remnants and human-occupied areas—the agroscape (chap. 12). Conservation of SDTFs into the future will depend also on the extent to which such landscape mosaics can be used as biotic sources for restoration of degraded areas (chap. 12, 13) and the extent to which such agroscape can be valued for its biodiversity and maintenance of ecosystem services (chap. 15). Recent research suggests that SDTF biodiversity conservation in the agroscape, although quite challenging, holds high promise (chap. 12). Such hope is enhanced by isolated examples that show that the useful flora of seasonally dry Neotropical forests is of considerable cultural and economic importance (chap. 14). This combination of facts coupled with an appreciation of the traditional knowledge of the rural inhabitants of SDTF areas suggest that forest management, involving local communities, has potential to become sustainable (chap. 14).

The exuberant biodiversity of SDTFs and the ecosystem processes that characterize them represent an ecological resource we are just beginning to learn how to interpret. This is a task we urgently need to confront. We hope this volume will contribute to such an endeavor.

We are grateful to the Center for Latin American Studies of Stanford University for the support to hold a conference on the ecology and conservation of SDTFs, from which the present volume is derived. We also thank Fundación Telmex and Fundación Telcel, from Mexico, for partly sponsoring the production of this volume.

CONTENTS

PART I

Seasonally Dry Tropical Forests as a Natural System

Chapter 1

Neotropical Seasonally Dry Forests: Diversity, Endemism, and Biogeography of Woody Plants

Reynaldo Linares-Palomino,
Ary T. Oliveira-Filho, and R. Toby Pennington

Neotropical seasonally dry forests are found from northwestern Mexico to northern Argentina and southwestern Brazil in separate areas of varying size (fig. 1-1). Their different variants have not always been considered the same vegetation type (e.g., Hueck 1978) or biogeographic unit (e.g., Cabrera and Willink 1980), but recent work has helped to define the extent, distribution, and phytogeography of seasonally dry tropical forest (SDTF) as a coherent biome with a wide Neotropical distribution (Prado and Gibbs 1993; Pennington et al. 2000; Pennington, Lewis et al. 2006). This unified interpretation is important both for biogeographic inference and for setting conservation priorities in Neotropical SDTF, which is the most threatened tropical forest type in the world (Miles et al. 2006).

Pleistocene climatic changes have been proposed as a possible force influencing the overall distribution of SDTF in the Neotropics (Prado and Gibbs 1993) and in driving evolution in SDTF plants (Pennington et al. 2000). Prado and Gibbs (1993) and Pennington et al. (2000) proposed a hypothesis in which during glacial times of cooler and drier climate, SDTFs were much more extensive than at present, perhaps forming contiguous forests across wide areas of the Neotropics. This view of current more-restricted areas of SDTF as "refugia" has been challenged by palynological studies that suggest the rain forests of Amazonia occupied hardly any less area than today and that the SDTFs of the Bolivian Chiquitano have been assembled recently (reviewed by Mayle 2004, 2006).

If there have been connections between some or all of the seasonal forests in the Neotropics during recent geological time, we would expect to find high floristic similarity among them. Prado and Gibbs (1993) and Pennington et al. (2000) highlighted a number of unrelated SDTF tree species that are widespread and found in several of the disjunct areas of Neotropical SDTF. They argued that these repeated distribution patterns were evidence of a once more widespread and perhaps continuous seasonal forest formation. These authors failed, however, to place these widespread species in the context of the entire woody flora of these areas, and no analyses of overall floristic similarity were presented.

In this chapter, we present a quantitative analysis of floristic similarity of the flora of the major areas of seasonal forests (SFs) in the Neotropics, including those of the floristically and ecologically unrelated but geographically adjacent vegetation of the Cerrados (savannas) and Chaco woodlands (fig. 1-1). This is the first quantitative analysis of the floras of these forests since Sarmiento (1975), who considered genera, and not species. Our species-level analysis provides a more fine-grained view of floristic variation. We use an ordination approach to analyze inventory data of woody plants from sites throughout Neotropical SDTF and examine the implications of the results for (1) patterns of diversity and endemism, (2) patterns of floristic relationships, (3) beta diversity, (4) biogeographic history, and (5) conservation prioritization.

Quantitative Analyses of Neotropical Seasonally Dry Tropical Floristic Nuclei

We define SDTFs following the broad concepts of Beard (1955) and Murphy and Lugo (1995), including tall evergreen SFs on moister sites, at one extreme of the series, to thorn woodland and cactus scrub at the other. We delimited 21 floristic nuclei of Neotropical SDTF, plus the Cerrado and Chaco areas (fig. 1-1). When nuclei are geographically isolated, this definition was straightforward, and in other cases we used previous phytogeographical studies that have revealed high affinities between some areas (e.g., Gentry 1995) for the equatorial Pacific SDTF in Peru and Ecuador. Published and unpublished but reliable tree inventory data from plots and sites for each of these regions were then aggregated to produce an initial species list for each of the floristic nuclei. Each nucleus' species list was enriched,

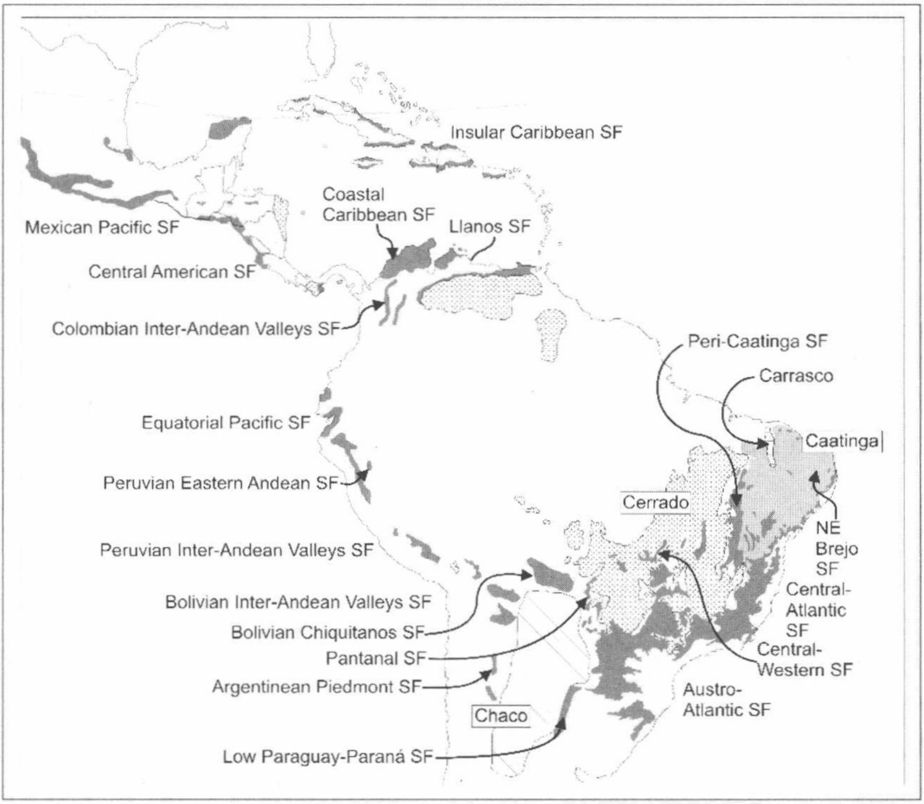

FIGURE 1-1. Floristic nuclei of Neotropical seasonally dry vegetation used in the analyses (SF = seasonal forests).

whenever possible, with additional information of plants reported for the area (e.g., herbarium collections, checklists, and our own field experience). We considered plants that are woody and reach at least 3 meters during some stage of their life cycle, excluding woody lianas and climbers. Main sources of data were Ratter et al. (2003), Linares-Palomino et al. (2003), and Oliveira-Filho (unpublished data). The data were homogenized using relevant taxonomic literature and online databases (W3Tropicos, IPNI, ILDIS) by checking for synonyms and misspellings. Doubtful identifications and records were excluded. The taxonomic treatment of families follows the Angiosperm Phylogeny Group II classification (APG 2003).

The final dataset included 3839 species from 806 floristic lists (table 1-1). Classification (UPGMA using group average and TWINSPAN) and ordination (nonmetric multidimensional scaling, MDS) analyses using standard settings in PC-ORD (McCune and Mefford 1999) were performed on a subset of 1901 species present in two or more floristic nuclei.

The MDS ordination and the UPGMA cluster analysis were performed using the Sørensen distance. The same index was used to assess beta diversity among floristic nuclei, allowing comparison of our results with beta diversity studies of the Cerrado (Bridgewater et al. 2004).

Each species found in 10 or more floristic nuclei (i.e., widespread species) was then annotated as ecologically versatile if it occurred in several forest types, including SDTF (e.g., *Maclura tinctoria*, *Trema micrantha*; table 1-2). We also annotated SDTF specialists (e.g., *Anadenathera colubrina*, *Sideroxylon obtusifolium*) and SDTF generalists—species that generally grow in SDTF but are occasionally found in other vegetation (e.g., *Guazuma ulmifolia*, *Tabebuia impetiginosa*). Annotation was based on bibliographic sources (e.g., Flora Neotropica Monographs) and our own field experience.

Patterns of Plant Species Diversity

Diversity and Endemism

The number of floristic lists per nucleus ranged from 2 to 376 (table 1-1). While this does not represent even geographic coverage of inventories, we do not believe our results are excessively biased, because nuclei covered by few studies often have many species and vice versa. For example, the Peruvian Eastern Andean SF nucleus has 101 species from just 2 lists, whereas 358 species are recorded from 376 lists in the Cerrado. This pattern of nuclei with more lists but lower overall species numbers (e.g., Coastal Caribbean SF, 19 lists, 135 species) and nuclei with a low number of lists but high numbers of species (e.g., Bolivian Chiquitanos SF) may reflect several historical and ecological factors, including the relative size of the nuclei and different rainfall regimes.

Species numbers ranged from 45 to 1602 per nucleus (table 1-1). The percentage of unique species present in each nucleus ranged from 1.9 percent in the Paraguay-Paraná SF to 77.5 percent in the Insular Caribbean SF (table 1-1). While these unique species are not strictly endemics (they may be present in other areas outside our nuclei), their numbers offer a reasonable proxy for levels of endemism.

Of the 3839 species, 457 were present in 5 or more nuclei, and only 55 (1.43 percent of the total; table 1-2, fig. 1-2A) have been recorded in 10 or more nuclei. Of the latter, 24 are ecologically versatile species, 22 are SDTF generalists, and only 9 are SDTF specialists (table 1-2).

The uneven geographic coverage and heterogeneous nature (from plots,