

Woody Plant Diversity, Evolution, and Ecology in the Tropics: Perspectives from Seasonally Dry Tropical Forests

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Annu. Rev. Ecol. Syst. 2009. 40:437–57

First published online as a Review in Advance on September 2, 2009

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev.ecolsys.110308.120327

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1543-592X/09/1201-0437\$20.00

Key Words

dispersal limitation, metacommunity, phylogenetic community structure, phylogenetic geographic structure, phylogenetic niche conservatism

Abstract

This review suggests that the ecology and patchy global distribution of seasonally dry tropical forest (SDTF) has distinctively structured the evolutionary history and biogeography of woody plant groups that are confined to it. SDTFs have few widespread woody plant species causing high β -diversity between separate areas of forests. These separate areas contain geologically old, monophyletic clades of endemic plant species that often have geographically structured intraspecific genetic variation. These patterns of diversity, endemism, and phylogeny indicate a stable, dispersal-limited SDTF system. SDTF species tend to belong to larger clades confined to this vegetation, exemplifying phylogenetic niche conservatism, and we argue that this is evidence that the SDTF is a metacommunity (biome) for woody plant clades. That phylogenetic, population genetic, biogeographic, and community ecological patterns differ in woody plants from tropical rain forests and savannas suggests a hypothesis that broad ecological settings strongly influence plant diversification in the tropics.

BACKGROUND: SEASONALLY DRY TROPICAL FOREST

The principal focus of this review is the seasonally dry tropical forest (SDTF) of the neotropics, the area that holds more than 60% of the remaining global stands of this vegetation (Miles et al. 2006). Several reviews (Gentry 1995; Murphy & Lugo 1986; Pennington et al. 2000, 2006a) discuss in detail the definition, ecology, and biology of neotropical SDTF, and here we provide only a brief summary and concentrate more upon the distinction of this vegetation as a biome apart from savannas.

Seasonally Dry Tropical Forest in the Neotropics

Our definition of neotropical SDTF is broad, including tall forest on moister sites to scrub rich in succulent plants on the driest sites. It occurs in frost-free regions where the rainfall is less than c. 1800 mm year⁻¹, with a period of at least 5–6 months receiving less than 100 mm (Gentry 1995, Murphy & Lugo 1986). The vegetation is mostly deciduous during the dry season, and the degree of deciduousness increases with declining rainfall, although the driest forests have more evergreen and succulent species (Mooney et al. 1995). SDTFs have a lower canopy and basal area than tropical rain forests (Murphy & Lugo 1986), and thorny and succulent species are often common (**Figure 1a**) especially in the drier formations. SDTF is tree dominated with a continuous canopy, which becomes increasingly broken with annual rainfall c. 500 mm or less.

Grasses are a minor element in the ground layer of SDTFs (Mooney et al. 1995), whereas savannas are defined by their abundant, xeromorphic, fire-tolerant grasses. Savannas are found under similar or slightly wetter climates than SDTFs, and these two biomes can coexist in close proximity. Savanna trees frequently have sclerophyllous, evergreen leaves owing to more nutrient-limited soils (Ratter et al. 1997), but SDTFs generally occur on fertile soils with a moderate to high pH. Succulent species are almost entirely absent from savannas, probably because they

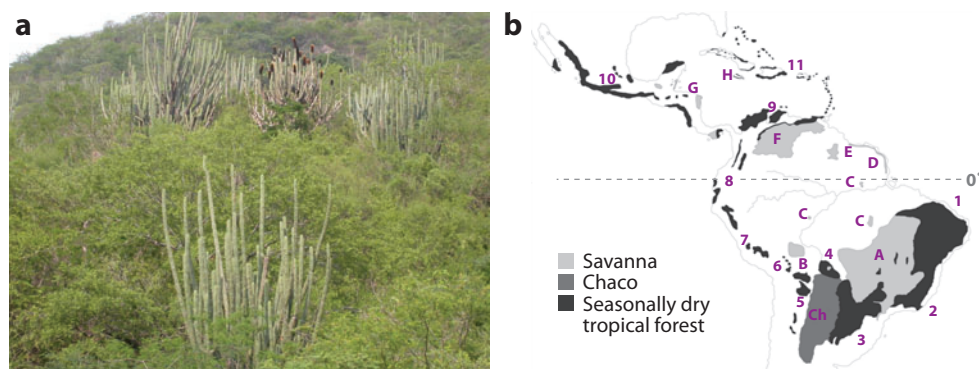


Figure 1

Geography and physiognomy of seasonally dry tropical forests (SDTFs). (a) Cacti and a low canopy are two of the hallmarks of much SDTF (near Playa Azul, Michoacán, Mexico). (b) Schematic geographical distribution of SDTF (dark gray) in the neotropics illustrating the patchy distribution, juxtaposition, and interdigitation with other forest types. 1, Caatingas; 2, southeast Brazilian seasonal forests; 3, Misiones Nucleus; 4, Chiquitano; 5, Piedmont Nucleus; 6, Bolivian inter-Andean valleys; 7, Peruvian and Ecuadorean inter-Andean valleys; 8, Pacific coastal Peru and Ecuador; 9, Caribbean coast of Colombia and Venezuela; 10, Mexico and Central America; 11, Caribbean islands (small islands colored dark gray are not necessarily entirely covered by seasonally dry forests). Savannas: A, Brazilian cerrado; B, Bolivian; C, Amazonian (smaller areas represented); D, coastal (Amapá, Brazil to Guyana); E, Rio Branco-Rupununi; F, Llanos; G, Mexico and Central America; H, Cuba. Ch, Chaco. From Pennington et al. (2006a) with permission.

lack adaptations to fire. The clear fire adaptations of savanna plants—such as thick, corky bark; the ability to root-sprout from substantial rhizomes; and protected buds—demonstrate that fire has been a key ecological and evolutionary force in savanna. The lack of such adaptations in SDTF plants suggests that fire has not been an evolutionary force in this biome, despite current vulnerability to dry-season fires set by humans.

SDTFs occur in disjunct patches (“nuclei”) scattered throughout the neotropics (**Figure 1b**), and we argue below that this fragmented distribution has persisted over long enough evolutionary timescales to have influenced the evolution and biogeography of component plant lineages. Wherever it occurs, SDTF is found within a complex of vegetation types depending on local climatic, soil, and topographic conditions. Major biomes that SDTFs contact include savanna woodland (e.g., the cerrado of Brazil), lowland tropical rain forest (e.g., in the Chiquitano region of Bolivia), and montane forest (e.g., in inter-Andean valleys). The ecotones can be broad to remarkably narrow, such as in certain inter-Andean valleys where precipitation can change radically over short distances.

Seasonally Dry Tropical Forest Around the World

Rain forests in the neotropics, Africa, and Asia are typically considered the same biome, despite differences in floristic composition. Physiognomic similarities such as the presence of large, often buttressed trees and leaves with drip tips are clear, and cross-continental comparisons of their biology are commonplace (e.g., Primack & Corlett 2005). In contrast, global comparisons of SDTFs (e.g., Richards 1996) are rare, which may reflect several factors. First, SDTF is physiognomically much more variable than rain forest, varying from low scrub to higher forests. Second, SDTFs generally exist in tiny fragments either naturally or because they have been so heavily fragmented by humans, and these often small remnants have not drawn as much attention from biologists in comparison with larger expanses of more pristine rain forest. Third, SDTF has numerous names, for example, “monsoon forest” in Asia, which has hindered comparisons. Even within the neotropics, it has a plethora of names from “caatinga” in northeast Brazil to “bosque tropical caducifolio” in Mexico and “cuabal” in Cuba.

Recent global definitions of biomes in seasonally dry tropical regions fail to delimit biologically meaningful units. For example, Olson et al.’s (2001) “tropical and subtropical broadleaf forest” combines SDTF and the Chaco vegetation from central South America. The Chaco, which receives regular frost, has temperate not SDTF floristic affinities (Pennington et al. 2000). Various tropical, woody, seasonal formations are found around the world under the broad climatic parameters suggested for neotropical SDTF above (500–1800 mm annual rainfall; 5–6 month dry season). In the final section of this review, we indicate approaches that might identify the kinds of seasonal forest that compose the same biome (global metacommunity) as neotropical SDTF.

FLORISTIC COMPOSITION OF NEOTROPICAL SEASONALLY DRY TROPICAL FOREST

The emerging picture of neotropical SDTF is one of large changes in taxonomic composition with distance—high β diversity—from the species to family level (e.g., Castillo-Campos et al. 2008, Gillespie et al. 2000, Linares-Palomino et al. 2009, Trejo & Dirzo 2002). Although Gentry’s (1995) influential review emphasized a floristic similarity at the family level, a more heterogeneous pattern of diversity is detected even at this high taxonomic level for neotropical SDTF (e.g., Linares-Palomino 2006, Lott & Atkinson 2006, Queiroz 2006; also discussed by Pennington et al. 2006a, p. 9). Despite high levels of β diversity, there is perhaps a phylogenetic integrity to the SDTF floristic elements. Leguminosae is the most species-rich family everywhere with the exception of

the Caribbean (Lugo et al. 2006) and Florida (Gillespie 2006), where Myrtaceae dominate. Some woody families are more abundant in SDTF than elsewhere and characterize this vegetation. These include Capparaceae, Zygophyllaceae (especially in Central America), Malvaceae subfamily Bombacoideae, and Cactaceae, which often is one of the most species-rich and abundant families. Erythroxylaceae are abundant (though also characteristic of the Brazilian savannas), and *Bursera* (Burseraceae) is common in Mexican SDTF. The sparse ground cover often contains Bromeliaceae, Asteraceae, Malvaceae subfamily Malvoideae, Araceae, Portulacaceae, and Marantaceae, but few grasses.

Gentry's (1995) article also contained an influential discussion of α diversity—diversity within a single area of a certain habitat—in SDTF. He noted that his most species-rich transects were distant from the equator, thereby contradicting the latitudinal gradient in species diversity. In Gentry's dataset, the SDTF of Chamela in western Mexico at c. 19°N and of Quiapaca in Bolivia at c. 15°S were most species rich. This led Gentry to a “reverse latitudinal gradient” hypothesis of species richness to contrast the pattern found in rain forests. Later studies now suggest that Mexican SDTFs to the south of Chamela are at least as species rich (e.g., Trejo & Dirzo 2002, Williams 2008). However, the lack of a conventional latitudinal diversity gradient in SDTF in comparison to tropical rain forest underscores one of the main points of this review—that distinct biomes with differing biogeographies (e.g., large equatorial expanses of rain forest versus highly fragmented and more broadly north-south distributed patches of SDTF) should be considered separately in studies of macroecology and evolution.

SPECIES DISTRIBUTION PATTERNS: β DIVERSITY AND ENDEMISM

Studies of β diversity in neotropical rain forest (e.g., Pitman et al. 1999, 2001; Condit et al. 2002) are facilitated by standard inventory plot methodology. In contrast, the different methodologies used in inventory studies in neotropical SDTF hinder the comparison of both α and β diversity. Some workers use plots, others transects, and the qualifying sizes for stem diameters vary. Despite these heterogeneous data, a recent study reveals that β diversity of woody plants is high among neotropical SDTF nuclei. Linares-Palomino et al. (2010) have assembled a database of 3839 species from 806 inventories (sometimes supplemented by herbarium records from outside the plots) and floristic lists across the entire range of neotropical SDTF. It seems unlikely that this approach would underestimate floristic similarity because a thorough floristic list captures more species than a single inventory plot. Despite this, floristic similarity is low between the major nuclei of SDTF. It is perhaps unsurprising that areas as widely separate as the Caribbean islands and the Brazilian caatinga show low Sørensen index (a commonly used index of floristic similarity) similarities of 0.07 (Linares-Palomino et al. 2010). More startling are Sørensen similarities of only 0.14 for the woody floras of the SDTF of the Mantaro and Marañon inter-Andean valleys in Peru, which are separated by only c. 400 km (Linares-Palomino 2006). In the analysis of Linares-Palomino et al. (2010), of 253 possible pairwise comparisons of SDTF regions, 203 pairs had low Sørensen similarities of less than 0.30, which corroborates a transect study of 20 SDTF sites across Mexico, whose average Sørensen similarity was only 0.09 (Trejo & Dirzo 2002). In contrast, Sørensen similarity between rain forest plots in Ecuador and Peru separated by c. 1400 km is c. 0.35 (Condit et al. 2002).

The high β diversity among SDTF nuclei or sample sites stands in contrast to the original emphasis placed on widespread SDTF species by researchers originally circumscribing this forest type (Gentry 1995, Pennington et al. 2000, Prado & Gibbs 1993). A particularly influential article by Prado & Gibbs (1993) used distributions of widespread species, such as *Anadenanthera colubrina*, to propose a continuous SDTF, the “Pleistocenic Arc,” during glacial periods in southern South

America that included the caatinga, piedmont forests in Argentina and Bolivia, and the Paraná. Prado & Gibbs (1993) and Pennington et al. (2000) speculated further that a widespread glacial SDTF may have spread into Amazonia, the Andean region, and even to the Caribbean coast of Colombia and Venezuela. Linares-Palomino et al. (2010), however, demonstrate that widespread species in neotropical SDTFs are an exception. Of the 3839 species in their database, only 55 (1.43% of the total) have been recorded from 10 or more of the 23 SDTF nuclei defined by these researchers. Of these 55, only 9 are ecological specialists confined to SDTFs. The paucity of more widespread SDTF species argues strongly against a widespread Pleistocene SDTF formation throughout the neotropics or across the whole of tropical South America (Linares-Palomino et al. 2009), but SDTF may have indeed been more widespread across the more restricted area of northeast Brazil to Paraguay and Argentina (Caetano et al. 2008, Linares-Palomino et al. 2009, Prado 2000).

PHYLOGENETIC PATTERNS OF SEASONALLY DRY TROPICAL FOREST SPECIES

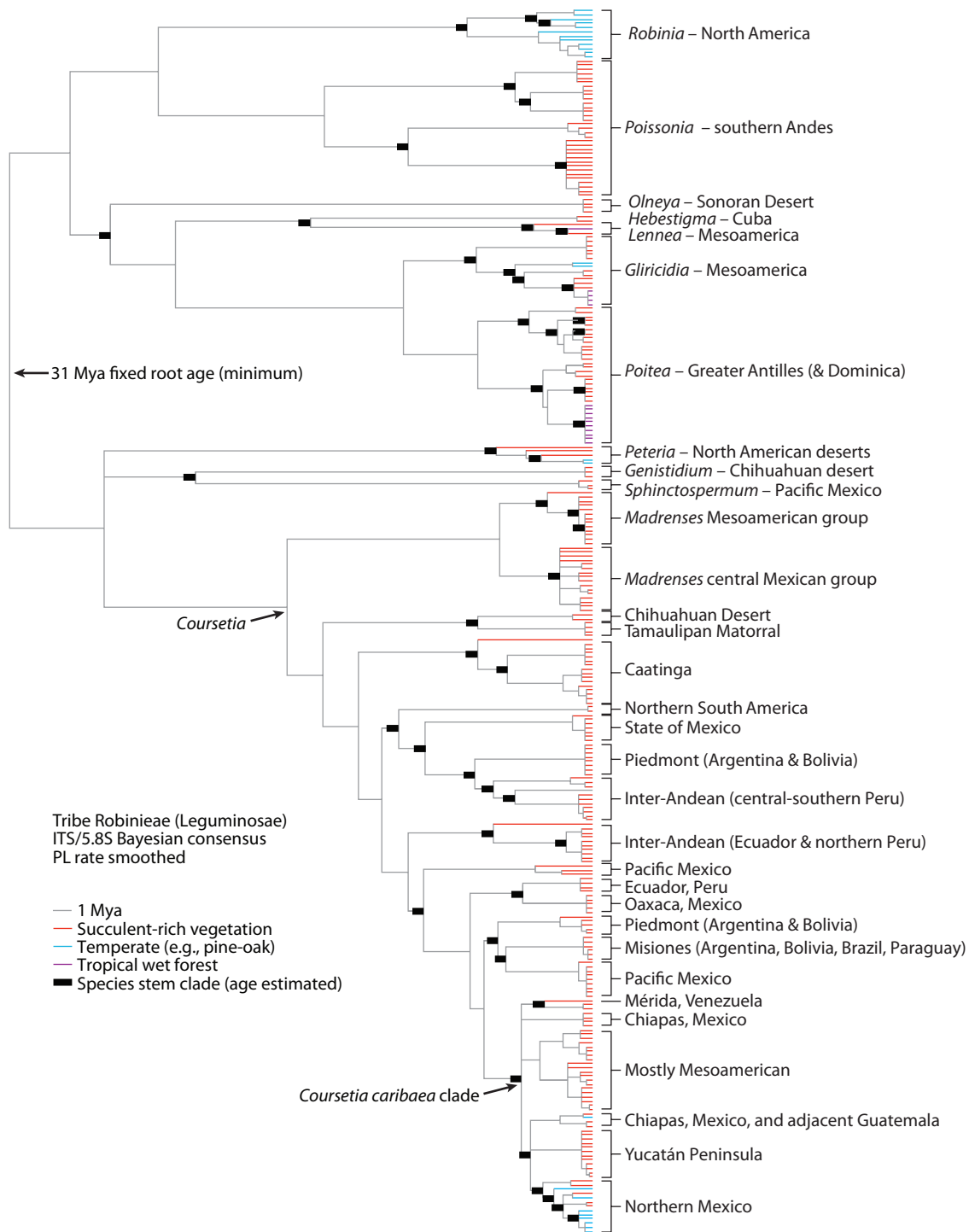
Over the past ten years, at least 15 molecular phylogenetic studies have accumulated that include clades with many of their species confined to neotropical SDTF biome (Becerra 2003, 2005; Becerra & Venable 2008; Edwards et al. 2005; Lavin et al. 2000, 2003, 2004; Pennington et al. 2004; Pirie et al. 2009; Schrire et al. 2009; Tripp 2008). Three features emerge from these phylogenetic studies: (a) Many of these clades are confined to or concentrated in SDTF, which is evidence of phylogenetic niche conservatism (e.g., Donoghue 2008, Harvey & Pagel 1991); (b) endemic species confined to a single SDTF nucleus are monophyletic and relatively old, commonly predating the Pleistocene, based upon molecular age estimates; and (c) sister species often occupy the same nucleus of SDTF, indicating a high degree of phylogenetic geographic structure.

Phylogenetic Niche Conservatism

The study of robinoid legumes (Lavin 2006, Lavin et al. 2003, 2004) best illustrates the three general phylogenetic patterns of clades with many species largely confined to SDTFs. The studies by Lavin and colleagues show an abundance of SDTF lineages highlighted in red (**Figure 2**). Altogether, 61 of the 78 sampled robinoid legume species show phylogenetic conservatism to SDTF. On three separate occasions, involving a total of five species, robinoid legumes have evolved relatively recently into tropical wet forest (*purple terminals* in **Figure 2**). On perhaps seven different occasions (involving 12 taxa), robinoid legumes evolved into montane or northern latitude forests with a frost period (indicated in *blue*). The high degree of phylogenetic niche conservatism to SDTF suggests that the probability of SDTF lineages dispersing to a more distant SDTF site is greater than the probability of species from adjacent biomes evolving the adaptations necessary to enter the SDTF, similar to the findings of phylogenetic niche conservatism at the biome level for diverse angiosperm lineages in Southern Hemisphere temperate and subtropical biomes (Crisp et al. 2009).

Age of Seasonally Dry Tropical Forest Lineages

Fossil and climatic evidence indicates SDTF to be a relatively old biome dating from perhaps the Middle Eocene in North America (Graham 1999), which means that it is perhaps unsurprising that molecular phylogenies indicate ancient SDTF lineages. Evidence for geologically old, geographically confined species clades comes from phylogenies in which species are represented by multiple DNA accessions that are resolved as monophyletic assemblages (e.g., Schrire et al. 2009; robinoid



legumes in **Figure 2**). These phylogenies are often reconstructed using nuclear ribosomal internal transcribed spacer (ITS) and 5.8S DNA sequences, which may bias against finding monophyletic species because nuclear loci have longer expected times to coalescence than do plastid loci (e.g., Zink & Barrowclough 2008). We predict that this pattern of coalescence of nuclear DNA loci sampled from accessions of single species confined to isolated SDTF areas will be characteristic of SDTF clades and suggest that woody plant lineages adapted to SDTF tend to persist in a localized area over evolutionary time. This prediction is bolstered by macrofossil evidence that suggests some SDTF nuclei in the Andes may have persistence times measuring several million years or more (Burnham 1995, Burnham & Carranco 2004). Such persistent, dispersal-limited SDTF nuclei would result in small effective population sizes of old constituent species and the coalescence of even nuclear genetic variation.

Geographic Phylogenetic Structure

Regardless of age, a high degree of phylogenetic geographic structure with sister species tending to occupy the same nucleus of SDTF (e.g., **Figure 2**) is indicative of highly limited historical dispersal between SDTF nuclei (Pennington et al. 2006c). Reasons for dispersal limitation could include island biogeographic rules such as the large distances between source and founder areas, their small sizes, and the evolutionarily persistent nature of SDTF species. SDTF species are drought tolerant, and immigrants into SDTF nuclei therefore have to contend not only with such ecological hurdles as erratic moisture availability, but also with the resident woody plant community that is hardy and persistent. These island biogeographic and ecological factors predict that phylogenetic relatedness should be highly geographically structured at all levels, from within species to among sister species and perhaps even to the entirety of a SDTF-confined clade (Lavin 2006).

Detecting phylogenetic structure to test this prediction can be accomplished by randomization tests (e.g., as implemented in MacClade; see Maddison & Maddison 2005) or by adapting analyses of phylogenetic community structure (Webb et al. 2002). These approaches were used by Lavin (2006) to compare the geographic phylogenetic structure of phylogenies of clades of species largely confined to rain forests and SDTF. An alternative method is the isolation by distance approach taken from population genetics (e.g., Grefen et al. 2004) but applied to clades of species. The isolation by distance hypothesis predicts a positive relationship between geographic and phylogenetic distances when other ecological determinants are not structuring genetic variation. In the case of the genera of robinoid legumes, *Coursetia* and *Poissonia*, there is a positive relationship between geographic and phylogenetic distance for pairwise distances among SDTF taxa sorted by genus and continent (**Figure 3**). This positive relationship is stronger among clades distributed in the more widespread and patchy South American SDTF. Schrire et al. (2009) found this positive relationship to be stronger in SDTF than savanna inhabiting clades of Indigofereae. Lavin (unpublished data) found this relationship to be stronger in SDTF than in wet-site inhabiting clades of the genus *Aeschynomene*. All of this points to greater levels of dispersal limitation in SDTF than in other lowland tropical vegetation, caused at least in part by the widespread and patchy distribution of this biome and its persistence over evolutionary timescales.

Figure 2

A chronogram of the robinoid legumes (adapted from Lavin 2003, 2004, 2006) derived from DNA sequence data from the nuclear ribosomal internal transcribed spacer region. Thickened branches indicate where an age estimate was made for the stem clade of a species represented by multiple DNA accessions. This illustrates that many extant species have an estimated age of origination around 4–6 Mya. Of the 81 species in this tribe, 78 were sampled. These 78 species are represented by 293 individuals sampled and sequenced throughout the geographical range of each species.

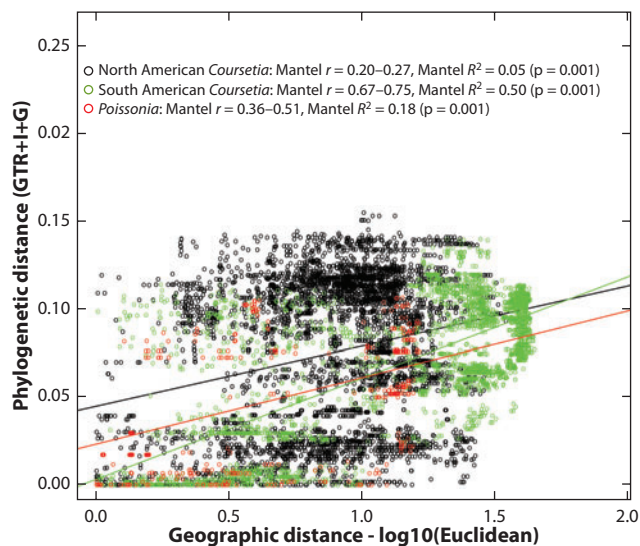


Figure 3

The relationship between geographical and phylogenetic distance for 244 samples of 41 *Coursetia* and *Poissonia* seasonally dry tropical forest (SDTF) species is found over broad geographical scales (modified from Lavin 2006). Of the total 48 species in these two genera, 47 were sampled for intraspecific variation and 41 species are nearly confined to SDTF vegetation. A model selection approach (e.g., Burnham & Anderson 2002) reveals that geographic distance is the most important explanatory variable of phylogenetic distance (note the Mantel r 95% confidence intervals). The response variable of phylogenetic distance was measured by the GTR+I+G nucleotide substitution model. Other ecological variables (e.g., elevation) often perform little better than an intercept-only model. This positive relationship is detected regardless of data transformations (e.g., box-cox or principal coordinates analysis) and has also been detected for other SDTF legume subclades of the tribe Indigofereae (Schrire et al. 2009) and *Aeschynomene* (M. Lavin, unpublished data).

POPULATION GENETIC PATTERNS IN SEASONALLY DRY TROPICAL FOREST SPECIES

Intraspecific genetic variation that is highly geographically structured has been found in two SDTF species in South America and two in Mesoamerica. Such high geographic structuring within small geographical areas is consistent with the phylogenetic studies and is suggestive of dispersal limitation and long persistence of isolated SDTF populations.

Caetano et al. (2008) studied *Astronium urundeuwa* (syn. *Myracrodruon urundeuwa*; Anacardiaceae) across its full distribution from northeast Brazil to Bolivia using chloroplast DNA (cpDNA) and nuclear microsatellites. Their results showed deep, probably pre-Pleistocene, divergence between northern and southern populations. Furthermore, fixation indices (F_{st} , a measure of population differentiation) for cpDNA averaging 0.97 are suggestive of lack of seed flow between three major geographical groups of populations in northeast Brazil, Central Brazil, and Argentina-Bolivia-Paraguay. Caetano & Naciri (2009) studied *Geoffroea spinosa* populations from areas of its disjunct distribution across South America. Multiple cpDNA substitutions separate the western South American populations in the Galapagos, Peru, and Ecuador, and all remaining populations further east in South America, which are indicative of a deep divergence, probably predating the Pleistocene. Within the eastern group, separated geographical groups of *G. spinosa* populations have F_{st} values averaging 0.99, indicating limited dispersal.

Highly structured intraspecific variation was detected for the Mesoamerican SDTF populations of *Gliricidia sepium* (Dawson et al. 1995, Lavin et al. 1991) and *Spondias purpurea* (Miller & Schaal 2005). In *S. purpurea*, a species distributed in the Pacific coastal SDTFs of Mesoamerica, cpDNA *trnG-trnS* alleles fall in two clear groups from southern Mexico and Central America and western-central Mexico (Miller & Schaal 2005). In *G. sepium*, SDTF populations from Yucatán, Mexico, were fixed for a cpDNA haplotype that was distinctly different from that found in SDTF populations elsewhere in Central America. The few nuclear ITS sequences so far analyzed from across the range of *G. sepium* (Lavin et al. 2003, 2004) suggest that intraspecific nuclear variation in this species could be several million years old. Nuclear (RAPD) and mtDNA genetic variation of *G. sepium* showed a strong isolation by distance signature from a localized area in Guatemala (Dawson et al. 1995), thus suggesting that genetic variation from these genomes would validate the cpDNA findings at larger geographical scales.

ARE SEASONALLY DRY TROPICAL FOREST PATTERNS OF DIVERSITY, ENDEMISM, AND PHYLOGENY FOUND IN OTHER TROPICAL BIOMES?

We have argued that a hypothesis of biome stability and dispersal limitation explains the patterns of species distributions, population genetic structure, and phylogenetic geographic structure found in the woody plants of neotropical SDTF. This begs the question whether patterns of diversity, endemism, and phylogeny are different in other major biomes in the neotropics that have different distribution and ecology. Two such biomes are tropical woody savanna (**Figure 1b**) and tropical rain forest. The largest areas of these biomes in the neotropics are the tree savannas (“cerrados”) occupying 2 million km² of central Brazil, and the rain forests of Amazonia and the Guianas, occupying 5.5 million km². In contrast to SDTFs, these comprise larger, more continuous areas.

Owing to the high diversity and inadequate taxonomy of the Amazonian flora, there is no comprehensive database of the distributions of its tree species. However, remarkable databases of the distribution of the woody species of the Brazilian cerrado savannas have been assembled by Ratter et al. (1996) and Oliveira-Filho et al. (2006). Using these databases, Bridgewater et al. (2004) described an oligarchy of c. 120 widespread, woody species that tend to dominate the entire area of the cerrado biome. Pitman et al. (1999, 2001) described a similar oligarchy of widespread tree species dominating the rain forest of western Amazonian Peru and Ecuador. However, it seems that no such oligarchy of tree species dominates the different nuclei of SDTFs (Pennington et al. 2006a, Williams 2008).

The possibility of a greater proportion of widespread species in the cerrados and Amazonian rain forests than in SDTFs could reflect two nonmutually exclusive hypotheses. First, these widespread species may be superior competitors, perhaps with stronger adaptations to fire in the cerrado. Second, the disturbance of the cerrado biome by fire and the rain forest biome by drought may cause local extinctions and, therefore, permit establishment of the most abundant immigrant propagules. This second hypothesis is one that suggests weaker dispersal limitation in savannas and rain forests than in SDTF. The degree of dispersal limitation might be expected to influence the relative abundance of species through ecological drift (Hubbell 2001). In isolated patches of SDTF that experience little effective immigration, drift may lead to endemic species becoming locally common, whereas in rain forests and savannas, fewer species would drift to higher abundance because of high immigration rates. These patterns are manifest in herbarium collections cited in monographs of the tribe Robinieae that is confined mostly to SDTF (Lavin & Sousa 1995) and the rain forest genus *Inga* (Pennington 1997; **Figure 4**). Robinieae are represented by many herbarium collections of highly localized species because local abundance ensures that such species

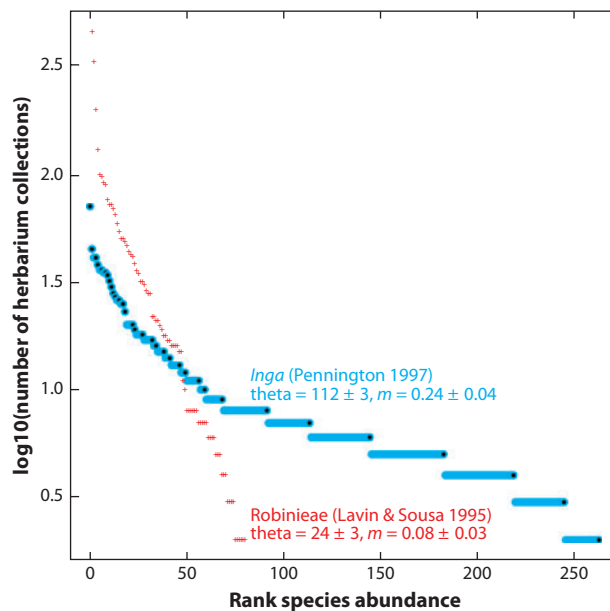


Figure 4

Relative species abundances (RSA) derived from herbarium collections with associated estimates of diversity, theta, and immigration rate, m . The RSA profiles are illustrated for two legume clades, Robinieae mainly confined to seasonally dry tropical forest (SDTF) (*red data points*) and *Inga* mainly from rain forest (*blue data points*), and are sampled from herbarium collections cited in respective monographs. Pennington (1997) did not list all collections for the most commonly collected species, so the upward inflection to the most abundant categories in *Inga* is underestimated, and the theta and m estimates are thus biased low. Regardless, these results are consistent with other findings comparing SDTFs and other neotropical forests reported in Hubbell (1979, 2001) and meet the prediction that high levels of dispersal limitation in SDTF cause a low incidence of widespread abundant species and a high incidence of locally abundant species. Relative to the cerrado (savanna woodland) or rain forest biomes, this is manifest as a less pronounced upward inflection to the most abundant species, a relatively greater representation of middle abundant species and a smaller representation of rare abundance categories. Parameter estimates were made with Tetame 2.0 (Chave & Jabot 2008).

are often collected (**Figure 4**), whereas *Inga* species are more often represented by few specimens. These relative species abundance profiles taken from numbers of herbarium collections are similar to the rank abundance distributions generated by Hubbell (1979, 2001; see figures 1.1 and 5.1 from the latter) from inventory plot data sampled in rain forest (Manaus, Brazil, where *Inga* species are common) and SDTF (Guanacaste, Costa Rica, where Robinieae species are common). This pattern of global rarity and local abundance is seen in many species from Mesoamerican SDTF (Williams et al. 2009), and we expect it to be found in South American SDTF.

The hypothesis positing high immigration rates in rain forest and savanna could be tested by examining whether geography structures population genetic variation within species or phylogenetic variation among species, which inhabit these biomes. Dick et al. (2003) used nuclear ribosomal ITS sequences to investigate the phylogeography of *Symphonia globulifera*, a rain forest tree species with an enormous distribution, including both the neotropics and Africa. Much geographic structure was evident in Mesoamerica and the Caribbean, where rain forests are more patchily distributed. Across 2500 km of lowland forest east of the Andes, little ITS diversity was detected (Dick et al. 2003). The same pattern of higher structure in Mesoamerican rain forests than in Amazonia has

also been described in microsatellite studies of the mahogany tree *Swietenia macrophylla* (Lemes et al. 2003). In the cerrado, despite its continuity, there are hints of a fundamental biogeographic division splitting the biome into an eastern and western partition. The division is suggested by species distribution patterns (reviewed by Pennington 2003) and also by the single well-sampled population genetic study of a cerrado tree species, *Hymenaea stigonocarpa* (Simoes-Ramos et al. 2007). Populations of *H. stigonocarpa* on either side of this north-south division, however, show little sign of geographic structure, with many containing multiple, geographically widespread chloroplast haplotypes.

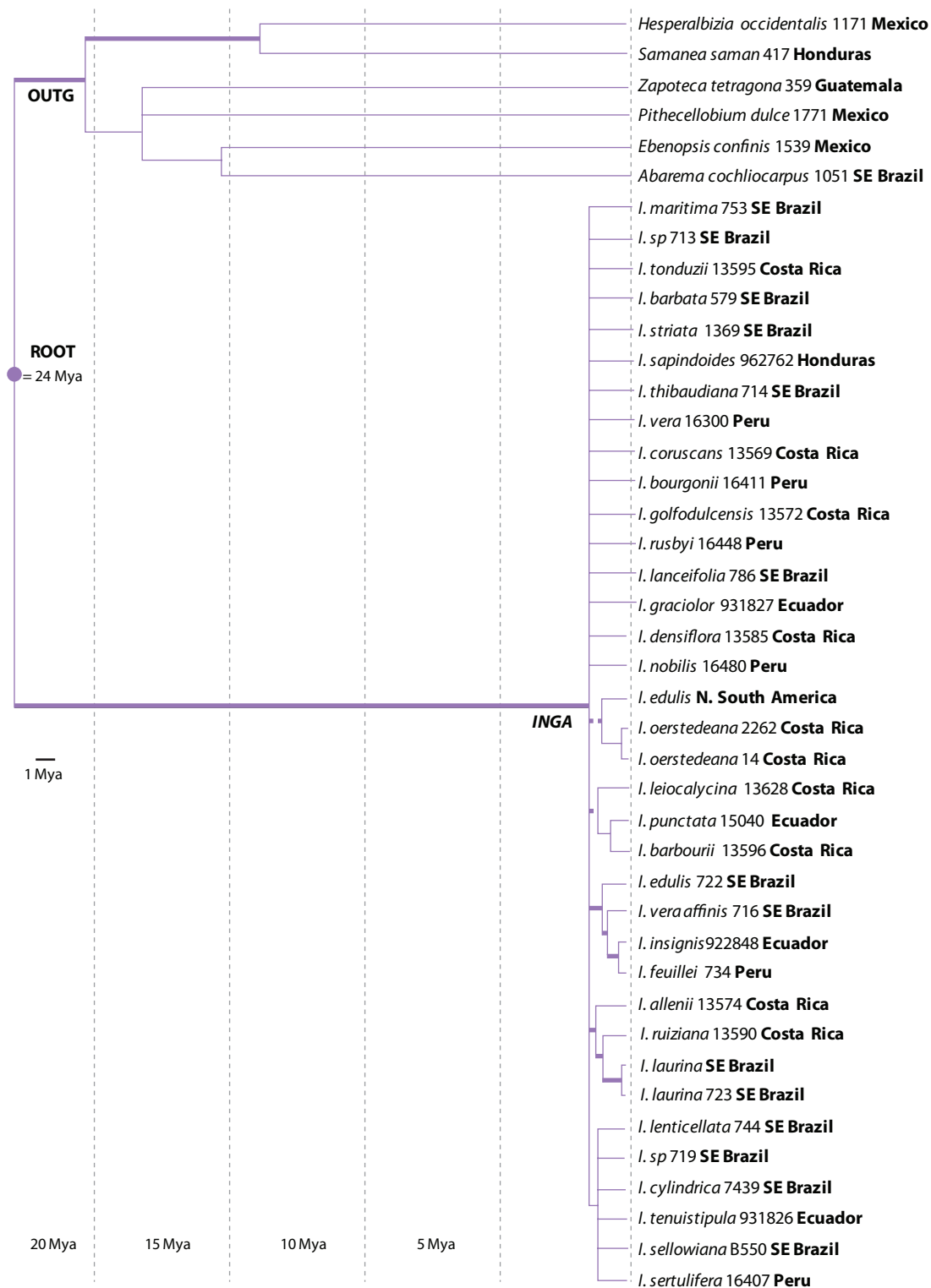
We are aware of no published phylogenies with thorough species sampling in cerrado clades. However, phylogenies of clades of species confined to rain forests display remarkably low phylogenetic geographic structure in comparison to those of clades confined to SDTF. For example, there is little evidence of phylogenetic geographic structure in *Inga* (Richardson et al. 2001, Lavin 2006; **Figure 5**, see especially the Costa Rican and SE Brazilian samples), a result confirmed by subsequent sequencing of more species for c. 5000 bp of cpDNA (Kursar et al. 2009; R.T. Pennington, unpublished data). Such low geographic phylogenetic structure implies that historical dispersal over long distances has been important in *Inga*. The pattern of low geographic phylogenetic structure in *Inga* is mirrored in the neotropical rain forest genera *Clusia* (Gustafsson & Bittrich 2003), *Guatteria* (Erkens et al. 2007), *Renealmia* (Sarkinen et al. 2007), *Ruellia* (Tripp 2008), and *Swartzia* (Torke & Schaal 2008). In these genera, phylogenetic geographic structure is especially low in Amazonia and the Guianas. There is evidence of higher geographic structure in smaller areas of rain forest that are isolated from Amazonia, for example, clades confined to the Atlantic coastal rain forest of Brazil (e.g., in *Andira*; Pennington 2003) or the Pacific Chocó region of Colombia (Pirie et al. 2006, Trénel et al. 2007). This underlines our argument that the scattered distribution of SDTF is one cause of dispersal limitation.

It is also notable that several of these phylogenies of rain forest plants (e.g., *Inga*, *Guatteria*, *Renealmia*) show evidence of remarkably recent diversification of species in Amazonia. For example, the crown group of *Inga* (c. 300 species) dates only to a maximum of 6 Mya (Richardson et al. 2001; Pennington et al., unpublished data), and many of its species must have arisen in the Pleistocene (**Figure 5**). This recent diversification of an entire clade lacking geographical structure stands in stark contrast to the older geographically structured species lineages characteristic of SDTF such as those resolved in robinoid legumes (**Figure 2**).

TESTING THE HYPOTHESIS THAT BIOME TYPE INFLUENCES EVOLUTION AND BIOGEOGRAPHY

A key point of this review is that SDTFs represent a distinctive theater of evolution for neotropical woody plants that is separated from other biomes by niche conservatism. This implies that species with an ancestry not adapted to the SDTF metacommunity will be unlikely to evolve the necessary adaptations to thrive in this biome. The SDTF biome can be evolutionarily defined to include a group of communities that reciprocally and preferentially serve as sources of immigrants over evolutionary time. Such an evolutionary definition of biomes is consistent with the metacommunity definition of Hubbell (2001).

This metacommunity definition applies best to biomes with high levels of biodiversity within particular taxa or trophic groups and that cover broad geographical scales. Only in such biodiverse systems are stochastic immigration and fluctuations in relative species abundances likely to have a strong effect on community composition. Spatial autocorrelation (dispersal limitation) of community composition should thus be an expectation within such a metacommunity and deviations from this are expected between hypothesized metacommunities. Designing a study that samples



species diversity in inventory plots both within and between two hypothesized biodiverse meta-communities can address how the type of biome (that is, its broad ecological setting), its size, and its geographic distribution structure woody plant biodiversity.

The Phylogenetic Community Perspective

Studies of community phylogenetic structure have asked whether the distribution of species in a community is nonrandom with respect to a phylogeny of the local species pool (e.g., Webb 2000, Webb et al. 2002). Community phylogenetics has been used to explain community diversity maintained by ecological filtering, competitive exclusion (e.g., Emerson & Gillespie 2008, Webb et al. 2002, Vámosi et al. 2009), or over ecological gradients (e.g., Graham & Fine 2008, Hardy 2008, Hardy & Senterre 2007). We suggest that community phylogenetics has a further use in modeling phylogenetic niche conservatism. Phylogenetic community metrics (e.g., the net relatedness index, Webb et al. 2002; phylogenetic differentiation statistics such as the Pst, Hardy & Senterre 2007, Hardy & Jost 2008) can be used to compare sample sites that share few or no species in common and to reveal their relatedness. These phylogenetic community metrics can be used as a response variable and tested against environmental variables that determine the hypothesized metacommunities to see if phylogenetic community relatedness is determined by ecology.

A community rather than taxon phylogenetic approach may raise concern among phylogeneticists who focus on monophyletic groups as part of a well-executed phylogenetic study. We argue that community phylogenetic biogeography carried out within and among biodiverse metacommunities has many advantages over phylogenetic biogeographical studies that infer geographic history from selected taxon phylogenies (e.g., Becerra & Venable 2008, Crisp et al. 2009). First, the community phylogenetic approach sidesteps taxon sampling issues that can comprise the taxon phylogenetic approach. For example, which constituent clades best reflect the geographical history of a biodiverse metacommunity? How exhaustively should such exemplar clades be sampled? Are such clades representative of all life forms in the metacommunity (e.g., herbaceous versus woody groups, see Tuomisto et al. 2003)? Second, testing for niche conservatism requires exemplar clades to be about equally diverse in both hypothesized metacommunities, which may rarely be the case unless clades of large size are well sampled. Third, ecological explanatory variables such as geographic position, elevation, precipitation, temperature, substrate, etc., can be much more readily captured for a limited number of sample sites than for a potentially unlimited set of terminal taxa.

The “Isolation by Distance” Community Phylogenetic Analog

Leibold (2008) stated that niche and neutrality vie for prominence in ecology. In population genetics and molecular evolution, however, neutrality has a biological expectation from which

Figure 5

A chronogram of the genus *Inga* (adapted from Lavin 2006 with permission) represented by samples originally reported in Richardson et al. (2001). Extrapolating from this sample suggests that the approximately 300 extant species of this primarily rain forest inhabiting clade probably arose in a single rapid diversification event within the past few million years. Little evidence of geographical phylogenetic structure combined with the long stem branch leading to the *Inga* clade suggests constant extinction, recolonization, and rediversification of *Inga* species within neotropical rain forests. The thicker solid horizontal lines represent branches supported by Bayesian posterior probabilities (p.p.) of 0.90–1.00, the thinner solid horizontal lines represent branches supported by p.p. 0.60–0.89, and the dashed horizontal lines represent branches with posterior probabilities of below p.p. 0.60. The labels refer to the area from which the sample was taken.

deviations serve as evidence of selection. Models designed to test for deviations from neutral expectations in population genetics and molecular evolution include the Hardy-Weinberg equilibrium (e.g., Latch et al. 2008), linkage disequilibrium (e.g., Ramirez-Soriano et al. 2008), coalescent theory (e.g., Nee 2006), dN/dS ratios (e.g., Rocha et al. 2006), the MacDonald-Kreitman test (e.g., Nielsen 2005), and isolation by distance models (e.g., Grefen et al. 2004). None of these approaches are null models *sensu* Anderson et al. (2000), because they involve parameter estimates for both the neutral and non-neutral biological processes that shape biodiversity. Although ecologists have considered the population genetic and molecular evolutionary approach to detecting deviations from neutral expectations (e.g., Harte 2003, Hubbell 2001), this approach has not yet been used for modeling phylogenetic niche conservatism.

A promising approach to test for the effects of niche conservatism in structuring biodiversity is the isolation by distance model (e.g., Grefen et al. 2004). According to this model, demes belonging to a hypothesized breeding population would be expected to have spatially autocorrelated or geographically structured genetic variation. Demes belonging to different breeding populations would have genetic variation potentially structured by factors other than geographical proximity.

By analogy, if the ecology of the savanna woodland and adjacent SDTF are structuring biodiversity over evolutionary timescales, then sample sites distributed between these two hypothesized metacommunities should share not only few species in common, but also few closely related species, especially sister species. In contrast, sample sites distributed within either one of the hypothesized metacommunities would share closely related species, and community composition would be predicted to be geographically structured or perhaps homogeneous.

An Example

Oliveira-Filho et al. (2006 and unpublished data) have been sampling woody plant diversity from the various forest types from eastern Brazil. Especially well sampled are the cerrado, a savanna, and the caatinga, which is an SDTF formation that adjoins the cerrado (**Figure 1**). Legume phylogenetics suggests that different clades occupy these two forest types and that speciation between these biomes may have been infrequent. For example, the legume genus *Coursetia* includes at least three endemic caatinga species and is otherwise found throughout neotropical SDTF but is unknown from the cerrado. The genus *Andira* does not grow in caatinga forest but inhabits the cerrado. This suggests that the woody flora in general might show a phylogenetic distinction between these two forest types.

Do the ecologies that determine the caatinga and the cerrado structure woody plant biodiversity over evolutionary time? This question can be addressed in a straightforward manner by using a phylogenetic distance as the response variable and geographic distance interacting with forest type as the explanatory variables. In this sense, forest type is a proxy for all of the ecological variables that determine the caatinga and cerrado.

The results of a study using the above approach strongly suggest that the ecologies determining the caatinga and the cerrado also structure woody plant diversity over evolutionary time (**Figure 6**). The isolation by distance model using Bray-Curtis floristic dissimilarity as the response variable strongly suggests that lineage diversity (proxied by the incidence of angiosperm genera) is structured by distance within a forest type but by niche conservatism between the two forest types (**Figure 6a**). Community phylogenetic distances arrayed in two dimensions also reveal strong geographical structure interacting with the ecology that determines the caatinga and cerrado (**Figure 6b**). Thus, there is evidence that the cerrado and caatinga have different phylogenetic composition and that, despite being adjacent, transitions between these biomes by speciation have not been frequent (A. Oliveira-Filho, M. Lavin, R.T. Pennington, and J. Rotella, in preparation).

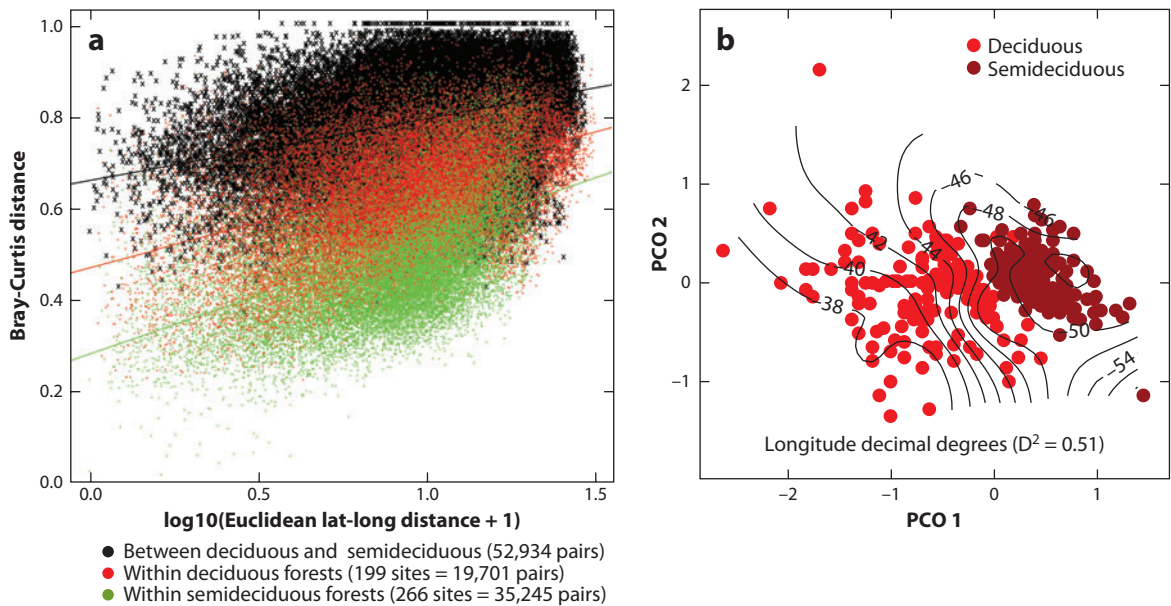


Figure 6

A model showing the relationship between geographical (Euclidean) and community composition or phylogenetic distance. (a) Community composition (Bray-Curtis) distances derived from the incidences of 450 woody angiosperm genera distributed among 465 sample sites from deciduous (199 sites mainly from the caatinga) and semideciduous (266 sites mainly from the cerrado) vegetation. A model selection approach suggests that among the deciduous sites (*red data points*) or among the semideciduous sites (*green data points*), diversity at the genus level is moderately structured geographically. This is not the case with pairwise comparisons that involve sample sites from both the deciduous and semideciduous vegetation (*black data points*). Indeed, nearly all of the pairwise comparisons involving no shared genera came from comparisons between the deciduous and semideciduous vegetation. These pairwise comparisons with large community composition distances and little geographical structure represent a deviation from neutral expectation that implicates phylogenetic niche conservatism (genus-level incidence data are serving as a proxy for phylogenetic distance). (b) A model showing the relationship between geographical (Euclidean) and community phylogenetic distance (Rao's intersample distances; Webb et al. 2008) with respect to the 356 legume species distributed among 465 sample sites from deciduous (*red dots*) and semideciduous (*dark red dots*) vegetation.

A similar result of little speciation between temperate and subtropical biomes was described by Crisp et al. (2009), though their approach analyzed multiple taxon phylogenies rather than the community phylogeny perspective suggested here.

The Global Seasonally Dry Tropical Forest Metacommunity

We hypothesize that neotropical SDTFs are part of a global metacommunity of tropical vegetation on fertile soils that experiences erratic water availability. For example, it is possible that the Sonoran and Chihuahuan deserts and the Tamaulipan matorral represent geographical extensions of a SDTF metacommunity into northern Mexico and southern United States. The global SDTF metacommunity could also include the bush thickets and other types of seasonally dry vegetation from the Old World, such as can be found in the Somalia-Masai region of the Horn of Africa, the southwest African Karoo-Namib, the southern Arabian peninsula, western Madagascar, and the Island of Socotra, as posited by Schrire et al. (2005a,b). These Old World regions of dry scrub or low forest vegetation resemble the drier forms of SDTF in the neotropics, but Cactaceae are replaced by other succulent families, especially Euphorbiaceae *sensu lato*, as well as Aizoaceae and

other Caryophyllales families. The biogeography of the plant family Leguminosae has prompted the hypothesis of a global “succulent biome” (Schrire et al. 2005a,b), because of the phylogenetic connection among the abovenamed regions.

Tropical Asian forests growing in monsoon climates in Thailand, Burma, Indo-China, the Indian subcontinent, and Sri Lanka (see overview of Whitmore 1975), or the tropical dry forests of Australia and the Pacific Islands, could be part of the same global SDTF metacommunity, as suggested by the climate where they grow, which matches that of areas where neotropical SDTF occurs. These Asian dry forests, however, lack the succulent flora element so characteristic of neotropical, Afro-Madagascan, and Arabian SDTFs, and many are less rich in Leguminosae (e.g., in Thailand; Rundel & Boonpragob 1995) than African, Arabian, or neotropical forests. Thus, a working hypothesis is that SDTF and related succulent-rich vegetation does not occur in central and eastern tropical Asia and is confined to the neotropics, Africa, Madagascar, and adjacent Asia.

Determining the extent of the global SDTF metacommunity could be accomplished with a modeling approach as illustrated above. When two different types of seasonally dry vegetation are analyzed using the isolation by distance approach, finding a best-fit model that explains phylogenetic diversity by geographical distance significantly interacting with vegetation type would be good evidence that the two types of seasonally dry vegetation belong to two different metacommunities. In contrast, a best-fit model explaining phylogenetic diversity by geographic distance alone would suggest that the two seasonally dry types of vegetation belong to the same metacommunity. We predict, for example, that floristic samples taken from sites in Pacific coastal Mexico northward into the Sonoran Desert will show only a geographical distance effect, thus implicating the Sonoran Desert as part of the same metacommunity as the Mexican SDTF.

CONCLUSIONS, PREDICTIONS, AND THE FUTURE OF SEASONALLY DRY TROPICAL FOREST

We predict that many clades will show evidence of phylogenetic niche conservatism to SDTF, thus bolstering its status as a metacommunity. SDTF is a highly dispersal-limited system as evidenced by the geographically structured phylogenies of SDTF constituent clades. This phylogenetic finding suggests that additional community diversity studies like that of Trejo & Dirzo (2002) will show high levels of β diversity among the SDTF nuclei. We predict that because of high levels of dispersal limitation in the SDTF metacommunity, endemic species confined to a single SDTF area will often be monophyletic and relatively old. Furthermore, such highly localized endemic species are predicted to be locally common—a pattern often seen in species that are globally rare but locally common. This is because ecological drift plays out in the absence of high effective immigration rates and causes at least some of the local endemics to drift to high frequency. Finally, we predict that RSA distributions taken from sites in the hypothesized SDTF metacommunity will lack the upward inflection to the most abundant categories because of the paucity of widespread and abundant species. This RSA distribution indicative of the SDTF metacommunity will also show elevated middle abundance categories because of the pattern of global rarity and local abundance, as well as a short rare tail because isolated nuclei will tend to lose the rarest endemics via ecological drift.

SDTF has been impacted by human activities over millennia (Piperno & Dillehay 2008) because of its fertile soils, and it is widely recognized as the most threatened tropical forest biome (e.g., Miles et al. 2006, Pennington et al. 2006a). For example, only 2% of Mesomamerican dry forests were intact in 1988 (Janzen 1988), and only 3.2% of the caatinga in Brazil is unaltered (Queiroz 2006). We hope that the improved understanding and definition of SDTF as a biome with a distinct and long evolutionary history and biogeography will provide impetus to its urgent conservation in the face of such destruction.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Antje Ahrends, Catherine Kidner, Tiina Sarkinen, John Williams, and our editor for constructive comments that greatly improved this paper. We thank Reynaldo Linares-Palomino and John Williams for access to their unpublished work and data. Toby Pennington acknowledges the Leverhulme Trust Study Abroad Fellowship RF/2/2006/0142 for support for a six-month study visit to Matt Lavin's laboratory, where many of the ideas in this manuscript were developed.

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Errata

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