# Preliminary Notes on the Phytogeography of the Osa Peninsula, Costa Rica

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## Abstract

A phytogeographic analysis of the distributions of 455 species of trees in 16 families revealed that 4.6% of the species are endemic to the Osa Peninsula and the adjacent mainland. However, nearly one-fourth of the species may be regionally endemic to Central-South Mesoamerica (Costa Rica, Nicaragua, and Panama). Our sample suggests that 54.7% of the species occur in some part of Mesoamerica and sometimes range into northwestern South America and that 45.3% of the species have wide distributions throughout tropical America. There is a strong affinity with the flora of northwestern South America with 50.2% of the species on the Osa also found there. In addition, 49.7% of the species on the Osa occur on both the Atlantic and Pacific slopes of Central America or, if they reach South America, are sometimes found on both sides of the Andes. Major contributions to the tree flora of the Osa have been made by species arriving in the Osa by 1) dispersal from South and North America to islands in proto Central America before the formation of a dry-land connection between the two continents and 2) migration from South America and North America after the closure of the Panamanian isthmus was made. This analysis demonstrates the importance of the Osa as a regional refuge for protecting species with distributions limited to the Osa and parts of Panama, Costa Rica, or Nicaragua. The Osa is also important because it harbors the last expanse of rainforest on the Pacific slope of Central America large enough to ensure the survival of the Central American populations of widely distributed plants and animals.

## Introduction

Costa Ricans and the international conservation community have recognized the Osa Peninsula (Fig. 1A) as a priority conservation area since the early 1970's and in 1975 the Corcovado National Park, a large (41,789 ha.) protected area located in the southwestern part of the Peninsula (Fig. 1B), was created (Christen, 2008). Today Corcovado is surrounded by the Golfo Dulce Forest Reserve (67,287 ha.) (García, 1997), a Guaymí Indigenous Reserve is located in the heart of the Peninsula (Fig. 1C), and much of the Osa Peninsula is part of a larger conservation area called the Área de Conservación de Osa (ACOSA, Fig. 1D), which was established between 1998 and 2000 (Kappelle et al., 2002). In addition, several non-governmental organizations contribute to preserving

the biodiversity and natural beauty of the Osa by protecting natural habitats in private reserves, conducting research, and promoting environmental education, reforestation, and ecotourism, e.g., Los Charcos de Osa (Aguilar & Bainbridge, 2008) and Friends of the Osa (Friends of the Osa, 2010 accessed).

The goal of this essay is to analyze the geographic distributions of tree species native to the Osa Peninsula. We then discuss the possible routes these species took to reach the Osa and emphasize the importance of the Osa Peninsula as a refuge for protecting regional endemics as well as populations of species with wider geographic distributions.

## Study Area

The Osa Peninsula is located in Central America in the southwestern corner of Costa Rica in the province of Puntarenas. To the north and west it is limited by the Pacific Ocean, to the east by the Golfo Dulce, and to the northeast by the Costa Rican mainland (Fig. 1). Altitude on the peninsula ranges from sea level to 745 meters at Mt. Rincón (Grayum et al., 2004). The climate of the Osa Peninsula is hot and humid, with an average temperature of 25°C, an annual average rainfall of 6,000 mm, a rainy season from August to December, and four months of reduced precipitation from January to April (Herrera, 1985; Carrillo et al., 2000). According to Holdridge (1967), the Osa Peninsula has moist, wet, and pluvial life zones in tropical to premontane altitudinal belts. Among them, the wet forest life zone is predominant and encompasses 92.48 % (=1,445.28 $km^2$) of the Osa project area.

For the purposes of this study, the northern most branch of the Río Sierpe serves as the northern limit of the project, and the southern most branch of the Río Esquinas as the eastern limit. The Río Sierpe splits into three main branches in a delta in the Sierpe-Terraba National Wetland, a vast mangrove area designated as a wetland of international significance under the Ramsar Convention (Ankersen et al., 2006). As calculated from our map (Fig. 1), the area of our study encompasses 1,573 $km^2$.

## Methods

A checklist of the flowering plant species of the Osa Peninsula was prepared based mostly on the collections of Reinaldo Aguilar (see Fig. 1D for tree collection localities). This checklist includes 2,200 native species and is available at the *Vascular Plants of the Osa Peninsula, Costa Rica* web site (Aguilar et al., 2008 onward). Each of the species in our database was classified as being a tree or not being a tree by consulting published descriptions and habit information provided on herbarium collections from the Osa. Although most species were easily classified as either trees or not trees, some species are described as trees and/or shrubs in the literature or on herbarium specimens. In those cases, the species were considered trees and included in the analysis. Cultivated trees, e.g., *Anacardium occidentale* L. and *Bixa orellana* L., were not included. Using these criteria, 821 species were classified as native trees (Table I).

Seven distribution categories were established (Tables II, III). Category one includes only species found on the Osa Peninsula and adjacent mainland. Each successive category includes a larger distribution range until category seven which encompasses

species distributed within the borders of the entire Neotropics (defined as the area between the Tropics of Capricorn and Cancer). For the purposes of this study, Mesoamerica is defined as covering the area from the Isthmus of Tehuantepec in southern Mexico throughout all of Central America to the border of Panama with Colombia. This definition is more-or-less the same area covered by the Flora Mesoamericana project (Missouri Botanical Garden, 2010 accessed).

Publications, especially monographs and floras, and online data from Atta (INBio, 2010 accessed) and Tropicos (Missouri Botanical Garden, 2009 accessed) from specimens identified by specialists were consulted to get an approximation of the geographic distributions of the species found on the Osa in the following families: Anacardiaceae, Annonaceae, Arecaceae, Burseraceae, Capparaceae, Chrysobalanaceae, Fabaceae (appearing as Mimosaceae, Caesalpiniaceae, and Fabaceae in our online checklist), Humiriaceae, Lauraceae, Lecythidaceae, Meliaceae, Moraceae, Myristicaceae, Olacaceae, Proteaceae, and Sapotaceae. Most of the species in these families are characteristic of Neotropical lowland rain forests. Of the 821 species classified as trees from all families in our database, distribution ranges were obtained for 455 (55.4 %) species from these 16 families.

## Results

Table III provides a list of the 455 species of trees included in this analysis with a description of their geographic distribution, the source of the information, and the category in which each species was assigned. Our sample revealed 4.6% of the species as Osa endemics (Category 1, Fig. 2A), 6.2% in Osa/Costa Rica (Category 2, Fig. 2B), 14% in Osa/Costa Rica/adjacent countries (Category 3, Fig. 2C), 13.2% in Osa/Mesoamerica (Category 4, Fig. 2D), 14.9% in Osa/Mesoamerica/ NW South America (Category 5, Fig. 3A), 1.8% in Osa/Mesoamerica/ NW South America /West Indies (Category 6, Fig. 3B), and 45.3% in Osa/widespread in tropical America (Category 7, Fig. 3C).

## Discussion

The Osa Peninsula is considered to be one of the most diverse areas of Costa Rica (Herrera-Mcbride et al., 1997; Zamora et al., 2004). Estimates of species diversity on the Osa are based on many collections deposited in different herbaria and recorded in several databases. For example, 2,334 species of vascular plants based on 11,319 collections from the Osa are found in the ATTA database of INBio (Zamora et al., 2004) and 2,709 species of vascular plants have been reported for the Osa by Weissenhofer et al. (2001). Our Osa database includes 8,671 records of collections representing 2,240 species, 950 genera, and 167 families of vascular plants. Because of the difficulty in making sure that the names used for duplicates of the same collections in the different databases are the same and the problem of confirming that collections come from the same area as our study area (Fig. 1), we opted to use only our database for this analysis; thus, we consider this study preliminary.

### Osa endemics

Only 4.6% of the species in this sample are endemic to the Osa Peninsula and areas adjacent to it (Fig. 2A). Within the Osa, we found no common distribution patterns for endemic species, and this can be explained by two main factors. In the first place, the predominance of the wet forest life zone does not provide the opportunity for species to diversify in response to strikingly different habitat selection. In the second place, there are no effective orographic or aquatic barriers within the Osa that limit species to particular areas or prohibit them from migrating to and from the mainland.

When categories that include other parts of Mesoamerica in close proximity to the Osa are combined, the importance of the Osa as a refuge for plants with relatively limited distributions becomes more significant. For example, 24.8% of the tree species in the sample belong to the first three categories; thus, nearly one-fourth of all of the species found on the Osa may be regionally endemic to Central-South Mesoamerica (Costa Rica, Nicaragua, and Panama). With further botanical exploration, additional endemics, such as the recently described *Miconia osaensis* (Kriebel et al., 2008), will be discovered. On the other hand, species once thought to be endemic to the Osa (e.g., *Miconia dissitiflora*) will be found outside of the Osa and adjacent mainland and will have to be removed from the list of endemics. As Hammel et al. (2004) have made clear, continued study and exploration can lead to decreased levels of endemism. They point out that Standley's (1938) estimate of 37% endemism for Costa Rica is far above the 11 to12% endemism they calculated for the country in 2004. Also, the high level of endemism estimated by Standley was to some extent due to the oversplitting of some taxonomists, e.g., Trelease recognized 537 species of Piperaceae in the Flora of Costa Rica, of which only 200 are accepted (Hammel et al., 2004).

Mesoamerican species

In our sample, 54.7% of the species only occur in some part of Mesoamerica and NW South America (Figs. 2-3), of these 14.9% reach northwestern South America and usually extend into the Chocó of Colombia and sometimes reach northwestern Ecuador (Fig. 3A). These species apparently do not occur east of the Andes. However, if the Osa/Mesoamerica/NW South America/West Indies (Fig. 3B) and widespread species (Fig. 3C) are added to the total, 50.2 % of the tree species on the Osa are also found in northwesternmost South America. This supports the conclusion of Kappelle et al. (2002) that the flora of the Osa has a strong affinity with the flora of northwestern South America.

Osa West Indies

Species that occur on the Osa and in the West Indies (Fig. 3B) make up only 1.8% of our sample. None of the species in this category are disjunct between the Osa and the West Indies and all of them have relatively wide Mesoamerican distributions; for example, *Grias cauliflora* is distributed from Belize into northwestern South America (Fig. 3B).

Widespread

In our sample, 45.3% of the species have a widespread distribution in tropical America (Fig. 3C). Many of these species occur from Mesoamerica to Brazil and Bolivia (e.g., *Prestoea acuminata*), and a few species even range from north of the Isthmus of Tehuantepec in Mexico to Paraguay and northern Argentina in the south (e.g., *Crateva tapia*). Among these species, 37.4% occur in the Amazon but none are found only there and on the Osa. Some species that appear to be more narrowly distributed belong to species complexes that when considered together are found in essentially all lowland forest areas of Tropical America. For example, *Gustavia brachycarpa* Pittier, endemic to southwestern Costa Rica (including the Osa) and northwestern Panama, is part of a species complex that ranges from Costa Rica into northwestern South America and is also found throughout the Amazon (Prance & Mori, 1979). Our analysis demonstrates that there is a high percentage of tree species on the Osa that have distributions throughout much of the moist to wet lowlands of tropical America.

Transmontane distribution

This analysis shows that 49.7% of the tree species on the Osa occur on both the Atlantic and Pacific slopes of Mesoamerica and, if they reach South America, some of these species are found on both sides of the Andes (Table IV). For example among the Osa species found in the Chocó, 30.7 % of them (e.g., *Couratari guianensis*) are found on both sides of the Andes. This distribution pattern is found in Mesoamerican species (e.g., *Rustia occidentalis*), widespread species (e.g., *Ruptiliocarpon caracolito*), as well as in Costa Rican endemics (e.g., *Eschweilera biflava* [Fig. 2B)] and *Osa pulchra*). These species were either once continuous populations separated by the uplifting of mountain ranges or dispersed from one side of the mountains to the other after the mountains were uplifted.

Migration

Species of plants may have directly or indirectly colonized the Osa 1) by long distance dispersal, including island hopping, from South and North America to islands in proto Mesoamerica before the formation of a dry-land connection between the two continents or 2) from South and North America after a land bridge connection was made with the closure of the Panamanian isthmus in the late Pliocene 3.5–2.5 million years ago (Hammel et al., 2004). The Osa is one of the more recent additions to the Central American isthmus having emerged from the Pacific Ocean about two million years ago (Burgess, 2009) and, therefore, many species probably reached the Osa from parts of the isthmus that had already been established. In our sample, 75.4% of the species are found beyond Panama/Costa Rica/Nicaragua which demonstrates the ability of many of the tree species of the Osa to migrate over long distances if given sufficient periods of time to do so.

In an analysis of the role of migrants in the South America tree flora, Pennington and Dick (2004) use molecular phylogenies to demonstrate that migration played a significant role in determining the current distributions of Neotropical trees. They challenge the long-held assumption that the fauna and flora of South America evolved in isolation and suggest that long distance dispersal had an important if not predominant

role in determining the composition of the Neotropical flora. The high percentage of species with very wide distributions in the tree flora of the Osa supports this hypothesis.

Hammel et al. (2004) suggest that species of some genera may have been dispersed to islands in proto-Central America before the land bridge connection formed. Fifteen of the 18 genera cited by these authors as having early migration from South America are represented on the Osa (*Alchornea*, *Allophylus*, *Apeiba*, *Astronium*, *Bauhinia*, *Casearia*, *Dendropanax*, *Erythrina*, *Eugenia*, *Luehea*, *Mabea*, *Ochroma*, *Pouteria*, *Tapirira*, and *Trichilia*). Another example is provided by the Proteaceae, a family best represented in Australia and South Africa (Johnson & Briggs, 1975). In the Neotropics, Proteaceae are represented by eight native genera with 90 extant species (Prance et al., 2007), and are most species rich in South America where macrofossils have been collected in the southern part of the continent (González et al., 2007). In Central America, the family is represented by *Panopsis* and *Roupala*, two predominantly South American genera consisting of only nine native species, of which four occur on the Osa. In a study of Malpighiaceae using phylogenetic analyses based on molecular data combined with fossil evidence and molecular divergence time, Davis et al. (2002) propose that this family originated in northern South America, repeatedly migrated into North America, and from there subsequently dispersed into the Old World via the North Atlantic land connection. They argue that vicariance caused by the separation of West Gondwana can not explain the presence of Malpighiaceae in South America and Africa because these two continents had separated long before the origin of the family.

Hammel et al. (2004) point out that a large group of Gondwanan plants of African origin appear to have reached Central America from the north before the land bridge connection formed. Fifteen of the 18 genera cited by these authors as having this type of migration are represented by native species on the Osa (*Acacia*, *Beilschmiedia*, *Bursera*, *Caesalpinia*, *Cedrela*, *Chrysophyllum*, *Dalbergia*, *Diospyros*, *Ficus*, *Lonchocarpus*, *Nectandra*, *Ocotea*, *Sapium*, *Sterculia*, and *Terminalia*). Another example is *Ruptiliocarpon caracolito* which was described in 1993 as the first and as yet only recognized New World species of Lepidobotryaceae. This tree, ranging from Nicaragua to western Colombia and possibly even to Amazonian Peru, is sometimes locally common on the Osa. All other species of Lepidobotryaceae are found in Africa (Hammel & Zamora, 1993) which, along with South America, formerly formed part of Gondwanaland. Similarly, *Meliosma* (Sabiaceae) is another genus of Boreotropical origin represented by numerous fossil leaves and endocarps, mostly from the lower Eocene into the later Pliocene in the northern hemisphere of western Europe, eastern Asia, and North America. At least 13 extinct fossil species of *Meliosma* from the lower Eocene (50-40 Ma), long before the closure of the Isthmus of Panama, have been found in eastern North America (van Beusekom, 1971; Bestland & Retallack, 1994; Retallack, 2004). Recent studies based on molecular phylogenies support the hypotheses that the Annonaceae (Erkens et al., 2006; Richardson et al., 2004) and Rubiaceae (Antonelli et al., 2009) were also part of a boreotropical flora from which species migrated into tropical America.

More recent migration from South America into the Osa seems to have made a significant contribution to the peninsula's tree diversity. Eleven of the 15 genera cited by Hammel et al. (2004) as examples of migration from South America into Central America and Mexico after the establishment of a dry land connection are found on the

Osa (*Clytostoma*, *Coussapoa*, *Crematosperma*, *Dicella*, *Herrania*, *Mansoa*, *Maripa*, *Peritassa*, *Selysia*, *Siparuna*, and *Socratea*).

A migration type that does not appear to have contributed significantly to the diversity of the Osa tree flora is that of North American species dispersing along higher elevations into Central America after the formation of the land bridge. Of the 19 genera cited by Hammel et al. (2004) with this type of pattern, only *Prunus subcorymbosa* (collected from sea level to 600 m), *Quercus rapurahuensis* (500 m), *Salvia occidentalis* (0–30 m), *Scuttelaria costaricana* (300–500 m), and *Viburnum costaricanum* (900 m) are represented on the Osa. With the exception of *Salvia occidentalis*, these species tend to be found at higher elevations on the Osa. A large number of Laurasian species probably do not reach the Osa because they grow at higher elevations in habitats absent or not well represented there. In addition, there are no direct connections between higher elevation habitats on the Osa and similar habitats on the mainland.

## Conservation

Hammel et al. (2004) commented that "What we witness today is the steady deforestation of the Osa Peninsula forest reserves and, basically, all of the other forest reserve areas that buffer the national parks." In spite of conservation efforts on the Osa Peninsula, forest cover there declined from 97% in 1979 to 89% by 1997 (Sánchez-Azofeifa et al., 2002). Sánchez-Azofeifa et al. (2002) also noted that only 44% of the forest remaining on the Osa is old growth and that deforestation occurring less than one kilometer away negatively impacts the borders of mature forest in the Corcovado National Park. These authors emphasize that only 977 $km^2$ (both in the park as well as in unprotected areas outside the park) remain in forest and that 1,500 $km^2$ are essential for ensuring a viable population of at least 50 reproductive jaguars—a species that is key to protecting overall biodiversity on the Osa. Loss of forest cover also reduces ecosystem services (Foley et al., 2007) such as water supply and purity, sequestration of carbon, maintaining a stable climate, providing the beauty and biodiversity needed by tourism, and protecting genetic diversity, including that of plants with medicinal or other direct economic potential.

If the slow but steady reduction of forest cover on the Osa continues, the biodiversity that Osa forests harbor and the ecosystem services they provide will continue to be compromised. Because the Osa includes the last large tract of lowland rain forest on the Pacific coast of Central America, it is especially critical to protect the remaining forest cover on the peninsula. This would ensure that nearly one-quarter of the species of Osa trees endemic to Central-South Mesoamerica would have a least some proportion of their populations protected. In addition, maintaining forest cover on the Osa will provide much-needed protection of some Central American populations of wide spread species even if lowland rain forests outside of the Osa become so fragmented that they are no longer large enough to harbor viable populations of old growth plants and animals.

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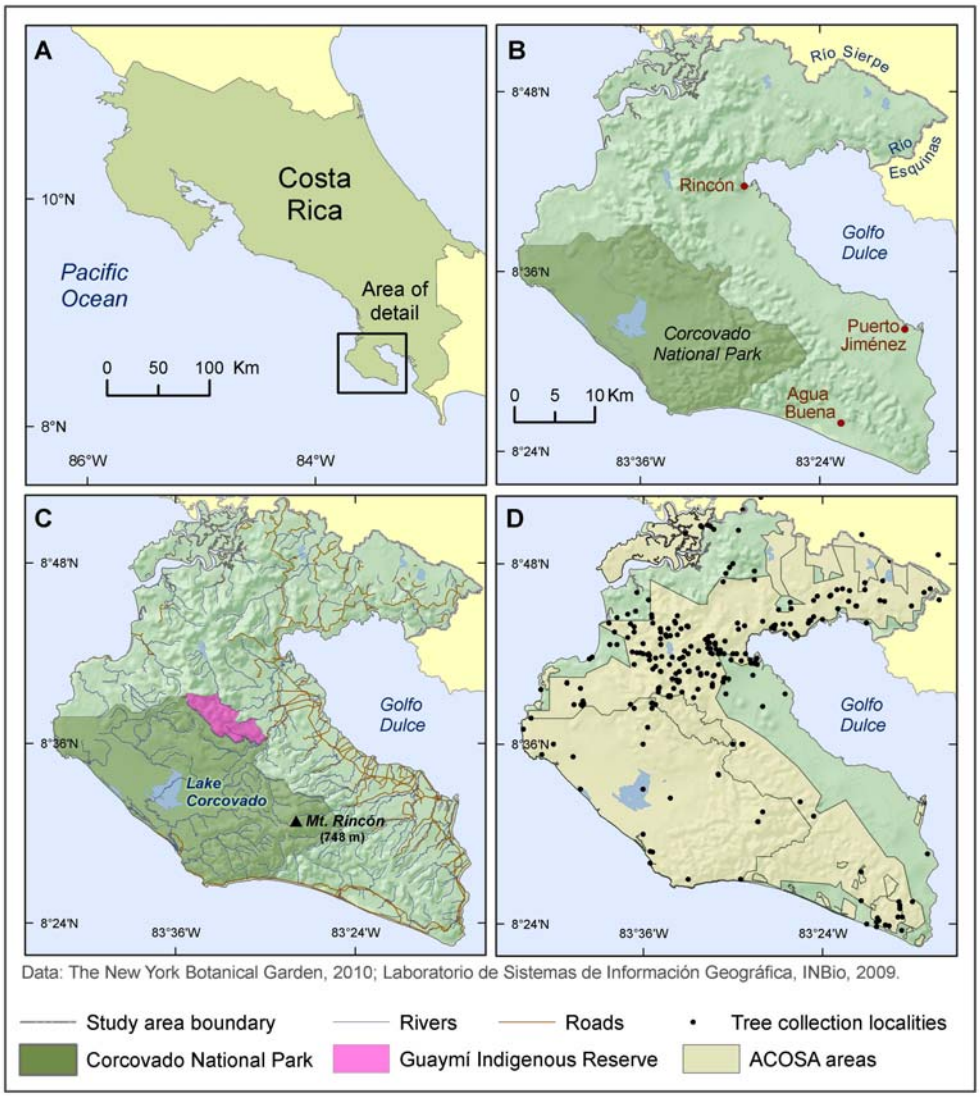


Fig. 1. The Osa Peninsula, Costa Rica. A. Location in Costa Rica. B. Major towns and the Corcovado Nacional Park. C. Roads and the Guaymí Indigenous Reserve. D. Tree collection localities indicated by black symbols. The light green area represents the part of ACOSA that occurs within the area of this study.

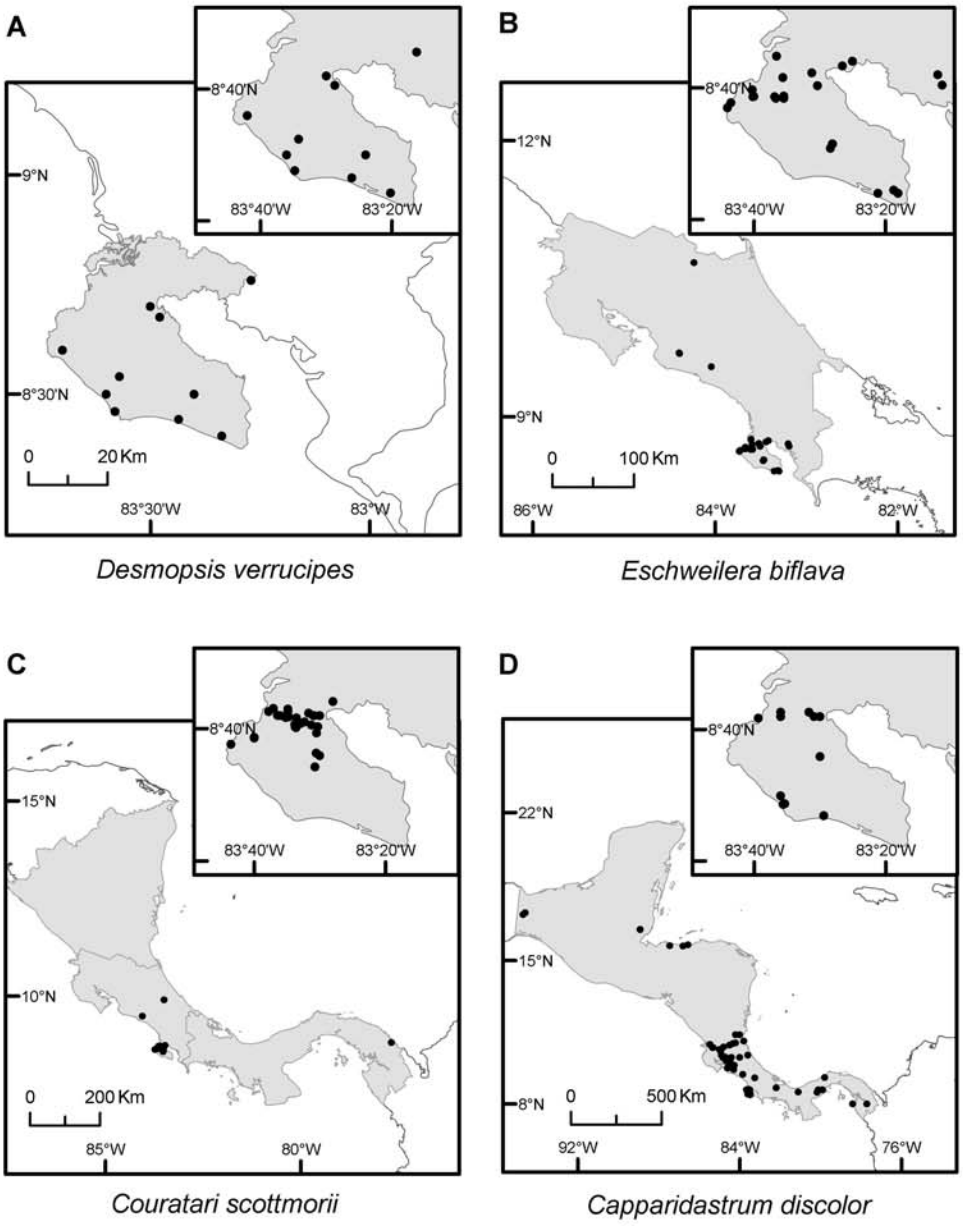


Fig. 2. Categories one through four: A. Osa endemics. B. Osa/Costa Rica. C. Osa/Costa Rica/adjacent countries. D. Osa/Mesoamerica.

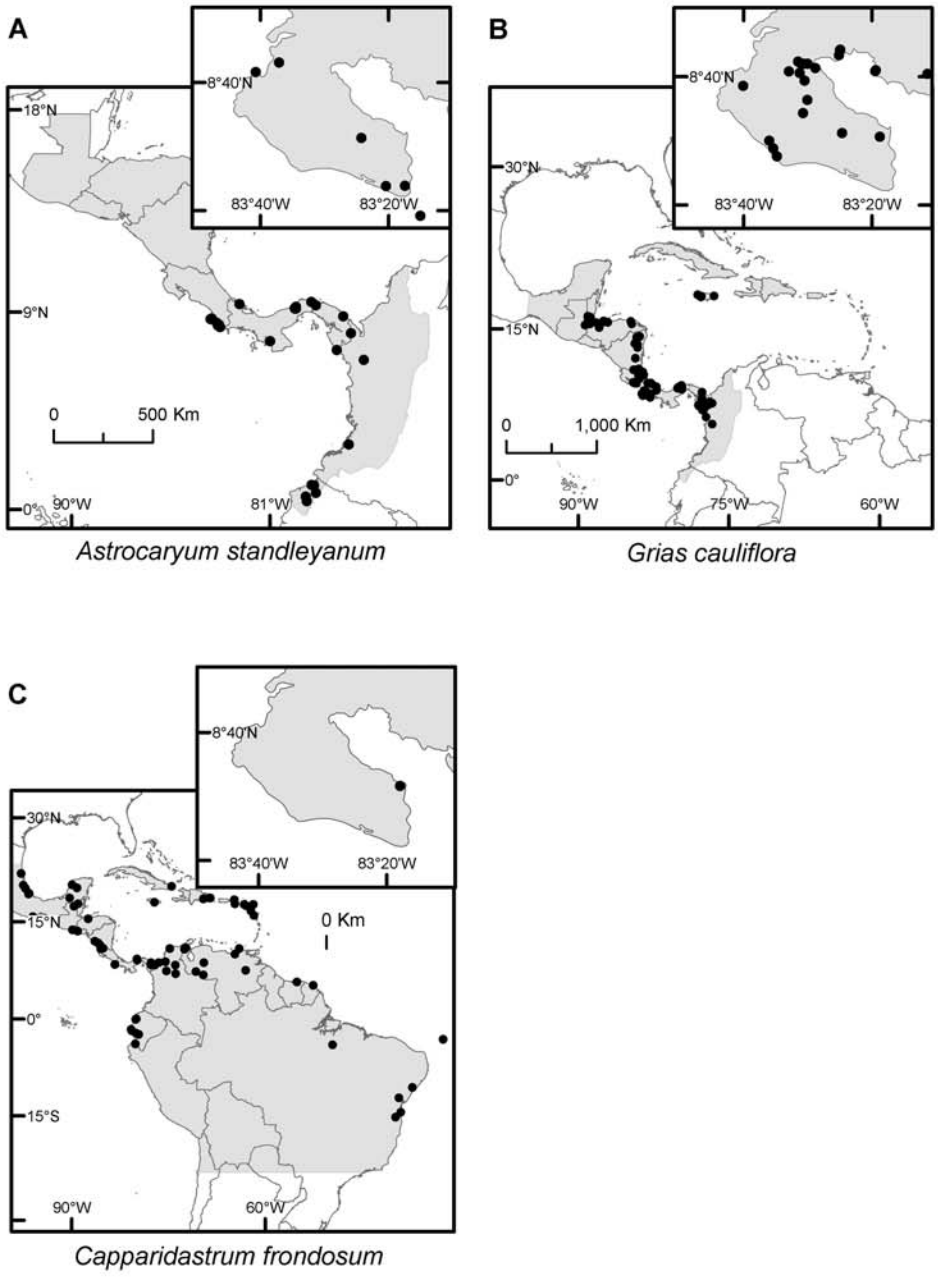


Fig. 3.Categories five through seven: A. Osa/Mesoamerica/NW South America. B. Osa/Mesoamerica/NW South America/West Indies. C. Osa/widespread in tropical America.

| Category number | Category definition | % |
|---|---|---|
| 1 | **Osa endemics:** Includes species only known to occur on the Osa Peninsula and sometimes on the adjacent mainland. | 4.6 |
| 2 | **Osa/Costa Rica:** Includes Osa endemics and found elsewhere within Costa Rica. | 6.2 |
| 3 | **Osa/Costa Rica/adjacent countries:** Includes Osa endemics, found sometimes elsewhere in Costa Rica, and in one or both of the adjacent countries (Nicaragua and Panama). | 14 |
| 4 | **Osa/Mesoamerica:** Includes Osa endemics, found sometimes elsewhere in Costa Rica, and in Mesoamerica generally including but beyond Panama and/or Nicaragua to the vicinity of the Isthmus of Tehuantepec in Mexico. | 13.2 |
| 5 | **Osa/Mesoamerica/NW South America:** Includes Osa endemics, found in some other part of Mesoamerica from Panama to the vicinity of the Isthmus of Tehuantepec in Mexico, and into either or both the Magdalena Valley and the Chocó of Colombia as far south as NW Ecuador. | 14.9 |
| 6 | **Osa/Mesoamerica/ NW South America/West Indies:** Includes Osa endemics, found in some other part of Mesoamerica from Panama to the vicinity of the Isthmus of Tehuantepec in Mexico, into either or both the Magdalena Valley and the Chocó of Colombia as far south as NW Ecuador, and the West Indies. | 1.8 |
| 7 | **Osa/widespread in Tropical America:** Includes Osa endemics, also found in Mesoamerica, elsewhere within the borders of the entire Neotropics, and sometimes even as far south as northern Argentina. | 45.3 |
| Total | | 100 |

Table II. Category number, definition, and percentage of tree species in each category.

List of figures and tables