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Assessing landscapes: a case study of tree and shrub diversity in the seasonally dry tropical forests of Oaxaca, Mexico and southern Honduras

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Abstract

Tropical dry forests, with their distinct and economically important diversity, are acknowledged conservation priorities because of alarming rates of forest conversion. Whilst it is realised that terrestrial conservation requires an understanding of landscape level patterns of diversity, forests are rarely assessed accordingly. Here we demonstrate that, in the case of the seasonally dry tropical forests of the Pacific watershed of Mesoamerica, landscape level assessment of woody diversity can inform decision making relevant to both between-landscape and within-landscape prioritisation. We report floristic surveys of dry forest landscapes in Oaxaca, Mexico and southern Honduras. It is noted that these forests are floristically similar to other seasonally dry tropical forests in the neotropics. By calculation of Genetic Heat Indices, a relative measure of the concentration of restricted range species in a sample, we determine that the conservation of the tree diversity of the coastal lowlands of Oaxaca should be prioritised over that of southern Honduras. The current conservation status of forested areas in Oaxaca is briefly described. We suggest that the greater degree of anthropogenic disturbance in southern Honduras may explain the relative lack of restricted range species there. We argue that some forest fallows can act as analogues of mature forest and therefore landscape elements other than mature forest need to be included in forest conservation assessments. We conclude that diversity sampling of any forest type should not be limited to mature forests, but extended to other elements of forested landscapes.
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1. Introduction

Seasonally dry tropical forests (SDTFs) rank amongst the most endangered of terrestrial ecosystems (Lerdau et al., 1991) with those of Mesoamerica (southern Mexico and Central America) being of particular concern. Janzen (1988a), writing of these forests in Central America, estimated that less than 2% of the original forest is in a state 'sufficiently intact to attract the attention of the traditional conservationist', with only 0.09% at that time having official reserve status. More recently, Trejo and Dirzo (2000) calculated that by 1990 only 27% of the original area of Mexico's SDTF remained.

The fragmentation (Casante et al., 2002; Boshier et al., in press) and conversion (Maass, 1995) of the original forest cover, which was begun in pre-Columbian times and continues today, has put at risk a distinct woody flora (Gentry, 1992) of high socio-economic importance. This importance is derived as much from the use local inhabitants make of native tree resources (Bye, 1995), as from the use to which these species have been put elsewhere in the world. Important taxa native to Mesoamerican SDTF, and now in use on other continents or whose products are traded internationally,

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include *Leucaena* (Hughes, 1998); *Guaiacum* (Grow and Schwartzman, 2001), *Gossypium* (Fryxell, 1979); *Swietenia* (Mayhew and Newton, 1988); *Cordia alliodora* (Ruiz. & Pavon.) Oken (Boshier and Lamb, 1997) and *Gliricidia sepium* (Jacq.) Steudel (Stewart et al., 1996). The conservation of Mesoamerican SDTF can therefore be considered an international priority both as a unique ecosystem and as a store of genetic variability of proven current value. However, not all SDTF in the region is the same and species composition varies (Gentry, 1995; Gillespie et al., 2000; Trejo and Dirzo, 2002) as would be expected across a region of high biophysical and socio-economic variability. This variability is also reflected in the many land-uses which make up a typical SDTF landscape following its fragmentation and conversion. In these circumstances biodiversity assessment, both within and between landscapes, is an essential tool for aiding the rational selection of sites, however, typically only forests considered well conserved or mature are subject to assessment (e.g. Lott et al., 1987; Trejo and Dirzo, 2002). Here we report a comparative study of the tree and shrub diversity of two lowland SDTF landscapes on the Pacific watershed of Mesoamerica, and discuss the significance of the results in relation to conservation priorities. The yardstick by which we compare mature forests, secondary forests and forest fallows is their relative content of species considered to be threatened by global extinction.

We use the term seasonally dry tropical forest in the broad sense of Mooney et al., (1995). Within this broad definition we distinguish two types of SDTF in the samples discussed here. Dry deciduous forest has a closed canopy reaching rarely more than 15 m in height and in which over 75% of canopy species are leafless during the dry season; this definition being equivalent to the term *bosque bajo caducifolio* in the classification of Rzedowski (1981) which is commonly used in Mexico. Dry semideciduous forest has a closed canopy reaching to 20 m height and in which between 50 and 75% of trees are leafless during the dry season, a definition which corresponds to term *bosque mediano subcaducifolio* of Rzedowski (1981). The differences between these forest types are assumed to be primarily determined by water relations, the latter has a shorter dry season and higher annual rainfall, but annual rainfall in SDTF areas is highly variable (Murphy and Lugo, 1986), and soil conditions are also likely to play a role (Mooney et al., 1995). Certainly the vegetation and structure of these forests appear to vary considerably over quite short distances, suggesting a complex set of environmental and anthropogenic factors are in play.

Two stages of sampling are described. The first is a comparison between the forests of southern Honduras and those of coastal Oaxaca, Mexico. The second is a comparison between the forests and the forest fallows of two agrarian communities in coastal Oaxaca.

2. Methods

2.1. Site selection

The lowlands of the Pacific watershed of Mesoamerica once contained probably the largest continuous area of SDTF in the region, stretching from the province of Guanacaste in northern Costa Rica to Baja California Sur in northern Mexico. The two case study areas chosen for this study, the Pacific coast of Honduras and the coast of Oaxaca in southern Mexico, form part of that area of SDTF, but their landscapes demonstrate important differences. In Oaxaca some relatively large areas of mature SDTF remain, whilst in Honduras forest is limited to small patches of secondary forest or woodlots that often measure no more than a few hectares, and never more than a few hundreds of hectares. The survey therefore contains samples from forests of highly variable size. Socio-economically, both areas are notable for their levels of poverty, ranking amongst the poorest in their respective countries. However there are important differences in social organisation. In coastal Oaxaca, which has lower human population densities than southern Honduras, communal land tenure is common whilst in Honduras land is typically privately owned.

Forests sampled in these surveys where chosen non-randomly to maximise coverage of forested areas and with a bias towards forested areas of larger size. The locations of samples are shown in Fig. 1.

Much of the forests of Oaxaca are embedded in a matrix of other land-uses particularly forest fallows which make up a considerable, but to our knowledge undetermined, proportion of the closed canopy woody vegetation of the region. The second stage of the analysis presented here considers the potential for these forest fallows to contribute to woody diversity conservation. The distinction drawn here between forest fallow and secondary forest is essentially a socio-economic one. Secondary forests are areas that have been converted from more intensive forms of land management and, given current socio-economic conditions, are likely to remain forested for the foreseeable future. Fallows remain part of the agricultural cycle and can be expected to be converted to more intensive forms of agricultural production at some point in the future, so long as current socio-economic conditions prevail.

The two communities in Oaxaca whose forest fallows were surveyed were chosen from four communities that formed part of a wider socio-economic survey of tree use in the area. The first of the two, La Jabalina, represents a group of farm dwellings among several dispersed communities or *rancherías* that contain areas of forest and forest fallow, much of it under communal tenure, around the watershed of the Tangolunda River. This area is compared below to forests immediately to their

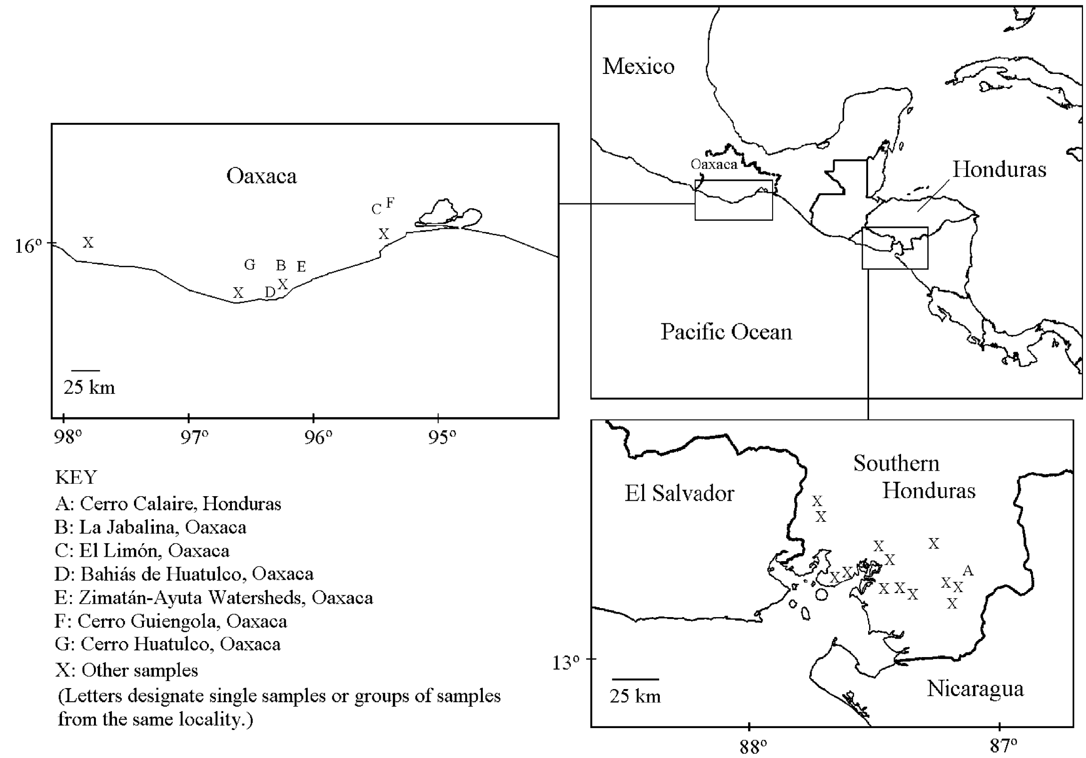

Fig. 1. Location of plant diversity samples: Oaxaca and Honduras.

west in the several watersheds between the Zimatán River and the Ayuta River. Many of the human inhabitants of La Jabalina are relatively new arrivals having been relocated from land expropriated for the nearby Bahı́as de Huatulco tourist development. The sandy soils and flat to undulating topography of La Jabalina contrast with the more accidented and rocky topography of the Zimatán-Ayuta watersheds. The second community, El Limón, is approximately 100 km northeast of La Jabalina. The land controlled by this long established community is under communal tenure. The sandy soils and undulating terrain within El Limón contrast with the steep slopes and rocky outcrops of Cerro Guiengola, 15 km to its east and with which it is compared.

The two communities were selected not because they were considered representative of coastal Oaxaca but because they contained significant areas of forest fallow in the proximity of forest areas that were determined to be of conservation importance (see below). Samples sites in these two communities were also selected non-randomly depending upon the degree of accessibility granted by members of those communities.

2.2. Sampling

Sampling followed the plotless, rapid botanical survey methodology described by Hawthorne and Abu-Juam (1995) with minor modifications described below. This methodology was chosen because of its speed and efficiency, compared to plot based methodologies, for broad scale assessments across structurally diverse landscapes. It sacrifices detailed information on vegetation structure for landscape level information on species composition eliminating the 'bias' inherent in ignoring species seen in the forest but not present in a plot (Vanclay, 1998). In the case of small forest patches each sample site was delimited by the pre-existing boundaries of the forest. In larger forest patches where distinct forest types could be identified by visual inspection, for example where hillside forest and riverine forest were contiguous, each forest type was surveyed separately. Each sample consisted of a species inventory derived from 4.5 person-hours of searching. In each survey a species was scored as present if it could be identified as a woody individual with a stem diameter at ground level of at least 2 cm, resulting in a very broad definition of woody vegetation and allowing the inclusion of live stumps. Woody climbers were not included in the analysis except those species that were found to have both climbing and shrub habits.

Many of species could be identified in the field, for those that could not specimens were taken, often of sterile material, for later herbarium identification. Oaxacan specimens were identified in the National Herbarium, Mexico City (MEXU) whilst Honduran specimens were identified in the Paul C. Standley Herbarium, El Zamorano (EAP). Voucher specimens were left in these respective herbaria.

2.3. Determination of species conservation status

The conservation status of each species identified was determined by estimation of its natural distribution; therefore range size is taken to be a surrogate of extinction risk with those species occupying smaller ranges deemed more at risk of extinction than those of greater range size. This may appear to be an over simplification; abundance per unit area, rate of habitat loss and other factors are often considered when evaluating the threat status of a tree species (Oldfield et al., 1998), however for most of the 375 species dealt with such information is simply not available. We thus employed the terminology of Hawthorne (1996) assigning each species to one of four star categories based solely on this parameter (Table 1). The most narrowly distributed species were put into the *black star* category, then follow the *gold star* and *blue star* categories for species with increasing distributions but whose status is still of concern. Finally the *green star* category was used for those of no conservation concern. The distributions were determined principally from herbarium specimen data but also from monographs, reliable checklists (e.g. Janzen and Liesner, 1980; Lott, 1993; Martin et al., 1998) and from on-line databases such as w^{3}Tropicos (accessed 2002). Given the variable quality of information on herbarium specimen labels, the number of Mexican states/Central American countries in which a species had been collected was the imprecise, but practical, unit of measurement used for estimating distributions.

Hawthorne (1996) introduces other variables into the categorisation of species by stars which are not used here. His economic index, which reflects a concern for timber production not inherent in the current context, was based on detailed forest inventory data not available to us. He also increased the importance (i.e. moved up a star category) of species congeneric with species of high current socio-economic importance on the basis that they have greater potential for future use. We omitted this from the current analysis as the same argument could be applied to many other species, (e.g. many woody species have the *potential* to become marketable species) and detracts from the fundamental objective of the current study, that is, the identification of endangered species, and the sites in which they are found *regardless* of their socio-economic importance, either potential or actual. See Appendix for the complete list of priority species found in the samples discussed here.

2.4. Calculation of relative area of occupancy of species of each star category

After surveying and species categorisation, the next step in the methodology was to assign a numeric weight to each star category inversely proportional to the average area occupied by species in that category (Table 2). This weighting then allowed a mean score to be calculated for each sample. These average areas were estimated from the subset of species in each star category (about 10%) for which there were detailed distribution maps published in recent monographs. The unit of measurement of area was the degree-square with the distribution of each species being the total number

Table 1
Categorisation by *stars* of seasonally dry tropical forest (SDTF) tree and shrub diversity from southern Honduras and coastal Oaxaca, Mexico

Criterion	Rank
Endemic to the Pacific SDTF zone of Honduras or Oaxaca	Black star
Endemic to the Mesoamerican Pacific SDTF zone and present in two to four Central American countries/Mexican states	Gold star
Endemic to the Mesoamerican Pacific SDTF zone and present in five to eight Central American countries/Mexican states OR Not endemic to the Mesoamerican Pacific SDTF zone but present in one to four Central American countries/Mexican states	Blue star
Endemic to the Mesoamerican Pacific SDTF zone but present in more than eight Central American countries/Mexican states OR Not endemic to the Mesoamerican Pacific SDTF zone and present in five or more Central American countries/Mexican states	Green star

Table 2
Calculation of weightings for star categories

	Black star	Gold star	Blue star	Green star
Area of occupancy (Mean no degree squares: x)	1.67	4.5	10.33	53.68
$x/53.68$ $(=y)$	0.031	0.084	0.192	1
$1/y$	32.14	11.93	5.19	1
Weighting	32	12	5	0

Table 3
Summary statistics of seasonally dry tropical forest tree diversity survey

	Total samples	Individuals identified (%)	Mean sample size	Families	Genera	Species	Possible new species
Honduras	22	97	40.3	56	139	194	0
Oaxaca	21	91	38.4	63	160	252	4
Total	43	94	39.3	70	210	375	4

of degree-squares from which botanical samples had been collected (x in Table 2). These areas were then divided by the mean green star area (y in Table 2) so that each category was weighted relative to a value of one for the *green stars*. The weights were then inverted, thus giving higher values to 'rarer' species, and rounded to the nearest integer ($1/y$ in Table 2). Finally the green star weighting was arbitrarily reduced from one to zero to reflect the lack of conservation concern we wished to give to these species.

2.5. Calculation of genetic heat indices

Using the weights calculated in Table 2, the mean score for each sample was calculated as a *Genetic Heat Index* (GHI, Hawthorne, 1996) for each sample using the formula:

$$\mathrm{GHI} = \frac{[(\text{No black star spp.} \times 32) + (\text{No of gold spp.} \times 12) + (\text{No of blue star spp.} \times 5)] \times 100}{N}$$

GHIs reflect the proportion of restricted range species in a sample. Because the denominator, N, is all species in the sample, an average is produced that allows comparison of samples with different numbers of species. Ideally N should be reasonably large (>30) to ensure GHIs are not overly sensitive to the inclusion or loss of single black or gold star species.

3. Results

3.1. Floristic description of Honduran and Oaxacan forest samples

Table 3 shows the Oaxacan samples to be more diverse than the Honduran samples at the level of family, genus and species.

Amongst the Honduran samples the most speciose families were Mimosaceae with 16 species in nine genera, Papilionaceae with 11 species in eight genera, Euphorbiaceae with 11 species in eight genera, Caesalpiniaceae with 10 species in five genera and Rubiaceae with 10 species in nine genera. The most speciose genera encountered were *Ficus* (Moraceae) and *Cordia* (Boraginaceae) with five species each and *Annona* (Annonaceae), *Senna* (Caesalpiniaceae), *Solanum* (Solanaceae) and *Trichilia* (Meliaceae) each with four species.

The most speciose familes encountered in Oaxaca were Mimosaceae with 25 species in 13 genera, Papilionaceae with 24 species in 15 genera, Euphorbiaceae with 19 species in nine genera, Caesalpiniaceae with 15 species in five genera and Rubiaceae with 10 species in nine genera. The most speciose genera encountered were *Bursera* (Burseraceae) and *Caesalpinia* (Caesalpiniaceae) with eight species each, *Acacia* (Mimosaceae), *Croton* (Euphorbiaceae) and *Lonchocarpus* (Papilionaceae) with seven species each, *Ficus* with six species, *Cordia* with five species and *Capparis* (Capparidaceae) and *Jatropha* (Euphorbiaceae) with four species each.

These results are broadly similar to the patterns of tree diversity described by Gentry (1995) for other areas of neotropical dry forest. In comparison with paleotropical dry forests, the dominance of the Leguminosae appears to be pantropical, however, in Central African Republic and Gabon there is evidence that the Apocynaceae make a greater contribution to diversity than in the neotropics, (Phillips and Miller, 2002) and Sussman and Rakotozafy (1994) report dominance of Tiliaceae in Madagascar.

Fig. 2 shows the relationship between Honduran and Oaxacan samples. The lower between-sample diversity of the Honduran samples is reflected in the greater clustering of those samples.

Two Way Indicator Species Analysis (TWINSPAN) of the samples reveals species characteristic of both the Honduran and Oaxacan samples to be (in descending order of occurrence) *Bursera simarouba* (L.) Sarg. Burseraceae, *Cochlospermum vitifolium* (Willd.) Spreng. (Cochlospermaceae), *Jacquinia macrocarpa* Cav. (Theophrastaceae), *Plumeria rubra* L. (Apocynaceae), *Spondias purpurea* L. (Anacardiaceae), *Thevetia ovata* (Cav.) A.DC. (Apocynaceae) and *Tabebuia rosea* (Bertol.) DC. (Bignoniaceae).

Species commonly encountered in the Honduran samples but rarely or never in the Oaxacan samples, i.e. indicative species of the Honduran samples, include *Gyrocarpus americanus* Jacq. (Hernandiaceae), *Trichilia americana*, (Sessé & Moc.) T.D.Penn. and *Swietenia humilis* Zucc. (Meliaceae), *Lonchocarpus minimiflorus*

Donn.Sm., *Bunchosia odorata* (Jacq.) Kunth (Malpighiaceae), *Alvaradoa amorphoides* Liebm. (Simaroubaceae), *Guazuma ulmifolia* Lam. (Sterculiaceae), *Coutarea hexandra* (Jacq.) K.Schum. (Rubiaceae) and *Albizia niopoides* (Benth.) Burkart var. *niopoides* (Mimosaceae).

Species indicative of the Oaxacan samples include *Amphipterygium adstringens* (Schltdl.) Standl. (Anacardiaceae), *Guaiacum coulteri* A.Gray (Zygophyllaceae), *Forchhammeria pallida* Liebm. and *Crataeva tapia* L. (both Capparidaceae), *Bursera excelsa* (Kunth) Engl. (Burseraceae), *Jacaratia mexicana* A.DC. (Caricaceae), *Apoplanesia paniculata* C.Presl (Papilionaceae) and *Comocladia engleriana* Loes. (Anacardiaceae).

3.2. Conservation importance of Honduran and Oaxacan forest samples

Only those records identified to species, plus those unidentified records which were considered to be possible undescribed species (and therefore of considerable potential conservation importance and thus categorised as black stars), are included in the calculation of GHIs.

Table 4 shows the genetic heat indices of the forest samples. There is clear disparity in the highest scores found in the two regions, with the Oaxacan forests, on this measure, containing areas of far greater potential for the conservation of threatened woody diversity than the Honduran samples. This is a direct result of the disparity in the numbers of black, gold, and blue stars species that were found in the two sets of samples. Tree and shrub species of limited distribution are very uncommon in the samples from southern Honduras (see Appendix).

3.3. Between-sample diversity of forests and forest fallows in Oaxaca

The second stage of the analysis presented here considers the potential for landscape elements other than mature forest, e.g. forest fallows, to contribute to woody diversity conservation. Given the clear difference in GHI scores obtained for Honduran and Oaxacan forest samples, Oaxacan fallows were the subject of this additional sampling carried out in the two communities described.

In La Jabalina, a community which contains significant fragments of mature forest, 10 of these fragments (three semideciduous, and seven deciduous forests) were sampled for comparison with samples from six forest fallows, all considered to be of deciduous forest origin. On the other hand, El Limón is a community with extensive areas of forest fallow and little or no forest. From this community seven forest fallows, also assumed to be of deciduous forest origin, were sampled for comparison with the three samples taken from the neighbouring Cerro Guiengola included in the forest samples described above. The total number of samples analysed here is therefore 26, in which 92% of individuals where identified to species. Sample size was relaxed here to accommodate the fewer species present in forest fallows of small size. Thus a per sample average of 37.8 identified species were entered into the analysis. These additional samples contributed a further 72 species to the 252 species identified in the forest samples (Table 3). The floristic relationships between these samples are shown in Fig. 3.

As in Fig. 2, Fig. 3 reveals the samples from semideciduous forest (in this case only from La Jabalina) to

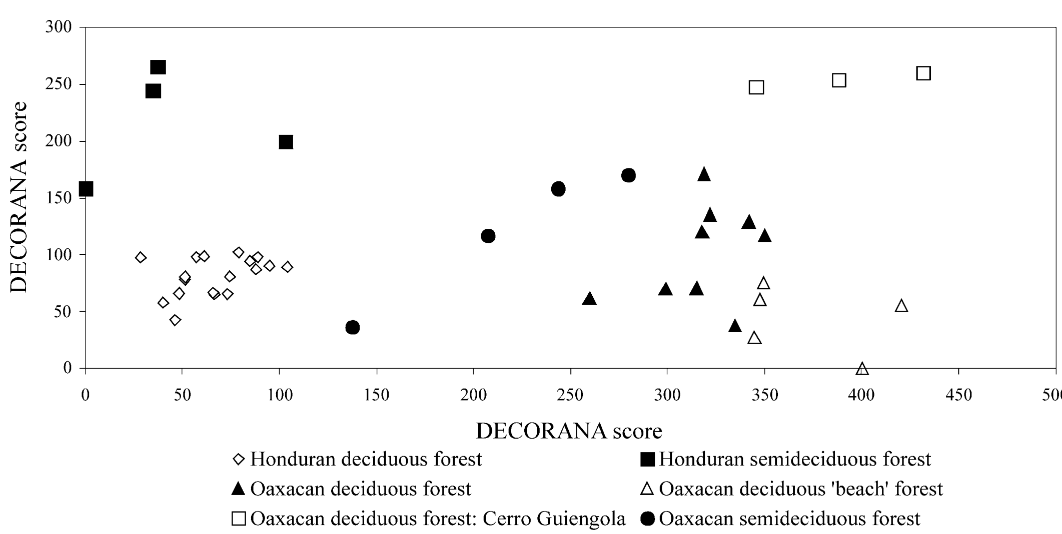

Fig. 2. Detrended correspondence analysis (unweighted) of Honduran and Oaxacan seasonal forest tree and shrub diversity.

Table 4
Forest quality as measured by genetic heat indices (descending order) of seasonally dry tropical forests sampled in southern Honduras and coastal Oaxaca, Mexico

Location	Type	GHI
Mexican forests		
Cerro Guiengola, Tehuantepec	Mature deciduous forest	358
Puente Coralito	Mature deciduous forest	333
Playa Entrega, Huatulco	Deciduous forest bordering beach	277
Cerro Guiengola, Tehuantepec	Mature deciduous forest	263
Cerro Huatulco, Huatulco	Mature semideciduous forest	246
Playa Entrega, Huatulco	Deciduous forest bordering beach	232
San Isidro Chacalapa[a]	Secondary deciduous forest	226
Tehueca, Pochutla	Hurricane damaged deciduous forest	202
Zimatán[a]	Mature deciduous forest	168
Cerro Huatulco, Huatulco	Mature semideciduous forest	150
Zimatán[a]	Mature deciduous forest	138
Playa San Agustín, Huatulco	Deciduous forest bordering beach	134
Cerro Guiengola, Tehuantepec	Secondary deciduous forest	132
Rio Ayuta[a]	Mature deciduous forest	131
Zimatán[a]	Mature deciduous forest	93
La Cañada, Tututepec	Secondary semideciduous forest	93
Zimatán[a]	Mature deciduous forest	73
Playa El Organo, Huatulco	Deciduous forest bordering beach	61
Playa Chachacual, Huatulco	Deciduous forest bordering beach	45
San Pedro, Tututepec	Secondary semideciduous forest	36
Puente Aguacate, Pochutla	Hurricane damaged semideciduous forest	14
Honduran Forests		
Cerro Calaire, Choluteca	Secondary deciduous forest	77
Los Hermanos, Choluteca	Secondary deciduous forest	54
Cerro Las Tablas, Choluteca	Secondary deciduous forest	50
Cerro Zurquillas, Choluteca	Secondary semideciduous forest	41
Cerro Mapachin, Valle	Secondary deciduous forest	40
Cerro El Tambor, Choluteca	Secondary deciduous forest	38
Cerro Las Tablas, Choluteca	Secondary deciduous forest	33
Cerro Las Tablas, Choluteca	Secondary deciduous forest	30
Cerro Las Tablas, Choluteca	Secondary deciduous forest	30
Cerro Guanacaure, Choluteca	Secondary deciduous forest	27
Cerro El Avion, Valle	Secondary deciduous forest	26
Cerro Las Tablas, Choluteca	Secondary deciduous forest	25
El Chaparal, Valle	Secondary deciduous forest	13
Pavana, Choluteca	Secondary deciduous forest	13
Pavana, Choluteca	Secondary deciduous forest	13
El Corpus, Choulteca	Secondary semideciduous forest	12
El Ricon Orocuina, Choluteca	Secondary deciduous forest	11
Cerro El Avioncito, Valle	Secondary deciduous forest	0
El Chaparal, Valle	Secondary deciduous forest	0
Cerro Palin, Valle	Secondary deciduous forest	0
Pavana, Choluteca	Secondary deciduous forest	0
Cerro Guanacaure, Choluteca	Secondary semideciduous forest	0

[a] Samples within the Zimatán–Ayuta watersheds.

be the most heterogeneous group in the sample. TWINSPAN does not distinguish these samples as a group, it does however select *Astronium graveolens* Jacq. (Anacardiaceae), *Chrysophyllum mexicanum* Brandegee ex Standl. (Sapotaceae), *Trichilia hirta* L. (Meliaceae) and *Andira inermis* (Wright) Kunth (Papilionaceae) as indicators of the two samples with the lowest y axis score, whilst the latter two of these species are also present in the third semideciduous forest sample.

The intimate mixing of the fallow and deciduous forest samples shown in Fig. 3, implies that these land-uses share a large proportion of their species and therefore that forest fallows may have a role in forest tree diversity conservation. The following species identified as conservation priorities (Appendix) were found both in forest fallows and deciduous forest fragments in La Jabalina: *Achatocarpus oaxacanus* H.Walter (Achatocarpaceae), *Brongniartia bracteolata* Micheli and

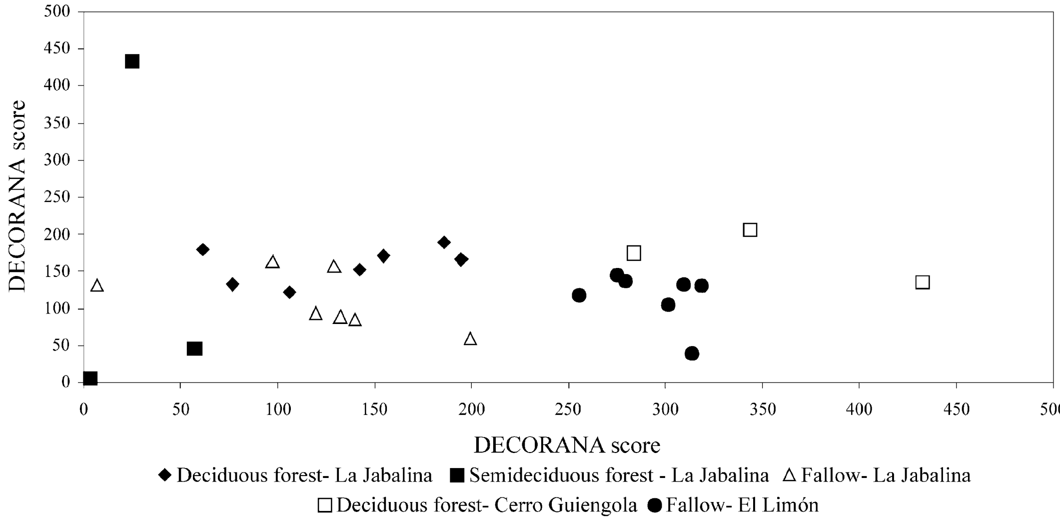

Fig. 3. Detrended correspondence analysis (unweighted) of seasonal forest tree and shrub diversity in two agrarian communities in Oaxaca, Mexico.

Caesalpinia hughesii, G.P.Lewis (both Caesalpiniaceae), *Croton septemnervius* McVaugh (Euphorbiaceae), *Bucida macrostachya* Standl. (Combretaceae) and *Recchia mexicana* Moc. & Sessé ex DC. (Simaroubaceae).

The principal division made by TWINSPAN is between the samples from La Jabalina and those of Cerro Guiengola and El Limón combined (see also Fig. 2). Species which show a preference for the La Jabalina samples include *Ceiba aesculifolia* (Kunth) Britton & Baker f. (Bombacaceae), *Achatocarpus mexicanus*, *Cordia elaeagnoides* A.DC. and *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae), *Crataeva tapia* L. (Capparidaceae), *Spondias purpurea* (Anacardiaceae) and *Calycophyllum candidissimun* (Vahl) DC. (Rubiaceae).

Species which are indicative of Cerro Guiengola and the El Limón fallows include *Gyrocarpus mocinnoi* Espejo (Hernandiaceae), *Bursera excelsa* (Kunth) Engl. and *Bursera schlechtendalii* Engl. (Burseraceae), *Randia thurberi* S.Watson (Rubiaceae) and *Thouinia serrata* Radlk. (Sapindaceae).

The relationship between the forest fallows of El Limón and the forests of Cerro Guiengola is less intimate but there is some overlap of species, including the conservation priorities, *G. moccinoi*, *Jatropha sympetala* Standl. & Blake and *Jatropha alamani* Muell. Arg. (Euphorbiaceae), *Havardia campylacanthus* (L.Rico & M.Sousa) Barneby & J.W.Grimes (Mimosaceae) and *Bucida macrostachya*. It should, however, be noted that the sample from Cerro Guiengola which has the lowest *x* axis score and that is therefore most like that of the fallows of El Limón is the secondary forest sample listed in Table 3. Forest disturbance may therefore being having a homogenising effect on vegetation in this area (McKinney and Lockwood, 1999).

3.4. Conservation importance of forest fallows

Table 5 shows that the forest fragments of La Jabalina have comparable conservation importance to the forests of the neighbouring Zimatán–Ayuta watersheds. It also clearly indicates that the best forest samples as measured by GHIs are better than the best forest fallows. None the less, four of the fallows samples score 100 or more which compares well with many of the forests listed in Table 4, and five score higher than *any* of the Honduran forests sampled. Furthermore, as noted above, there are several priority species common to both the fallow areas and to the forest with which they are compared. It is interesting to note that there appears to be little relationship between the estimated age of the sample, which was determined by asking the community member who controlled the fallow, and the GHI. It appears that in this community with access to ample land and correspondingly large areas of fallow, the restricted range species which contribute to high GHIs can establish quickly after a field is allowed to go to fallow, either from stumps, the seed bank or from the arrival of propagules.

4. Discussion

4.1. Floristics

The greater tree and shrub diversity of the Oaxacan SDTF compared to that of southern Honduras accords with Gentry's (1988, 1995) conclusions that tropical dry forests, in contrast to wet forests, may be more diverse at higher latitudes than lower latitudes. The state of Oaxaca is considered to be of outstanding biological diversity even by the standards of megadiverse Mexico (Mittermeier and Mittermeier, 1992), so a naturally

Table 5
Forest quality as measured by genetic heat indices (GHIs) of vegetation samples in two agrarian communities in coastal Oaxaca, Mexico

Land-use type	Vegetation type	GHI
Forests 'La Jabalina'	Mature lightly intervened deciduous forest	240
	Mature deciduous forest intervened by humans and hurricane	197
	Mature lightly intervened deciduous forest	193
	Mature lightly intervened deciduous forest	161
	Mature semideciduous forest with minimal human intervention	136
	Mature deciduous forest with minimal human intervention	94
	Mature semideciduous forest with minimal human intervention	33
	Mature lightly intervened deciduous forest	28
	Mature semideciduous forest with hurricane damage	25
	Secondary deciduous forest	13
Forest fallows, 'La Jabalina'	Deciduous forest regeneration, 7 years old	183
	Deciduous forest regeneration, 15 years old	74
	Deciduous forest regeneration, 2 years old	73
	Deciduous forest regeneration, 33 years old	33
	Deciduous forest regeneration, 6 years old	29
	Deciduous forest regeneration, 7 years old	17
Deciduous forest Cerro Guiengola	Mature deciduous forest	358
	Mature deciduous forest	307
	Secondary deciduous forest	132
Forest fallows, El Limón	Deciduous forest regeneration, >20 years old	228
	Deciduous forest regeneration, 4 years old	178
	Deciduous forest regeneration, 15 years old	100
	Deciduous forest regeneration, >15 years old	97
	Deciduous forest regeneration, >15 years old	71
	Deciduous forest regeneration, 2 years old	61
	Deciduous forest regeneration, >15 years old	45

greater diversity in Oaxaca might be expected. In relation to the forests in this survey this may be due in part to a greater variation in habitats in Oaxaca. No forests of equivalent topology or geology to those of Cerro Guiengola were found in southern Honduras, neither were significant areas of dry forest found on dunes and rocky out-crops around sandy beaches. Both these forest types clearly increase between-sample diversity in Oaxaca (Fig. 1).

However a second factor, successional status, may be of equal if not greater importance in explaining the differences between Honduran and Oaxacan samples. Visual inspection of the forests sampled in Honduras, and consideration of aerial photographs, lead the field teams involved in this work to conclude that all the dry forest patches of southern Honduras were of relatively recent secondary origin, probably of the order of a few decades at most. This does not discount the possibility that some individual trees may be remnants of more mature vegetation. In coastal Oaxaca much more mature forest (we avoid the term primary as none of the forests could confidently have been described as completely undisturbed) are still to be found and the emphasis on the sampling discussed here was on the larger, and therefore possibly more mature forests of the region. The overall greater species count obtained for coastal Oaxaca (Table 3) may well therefore at least in part be due to the presence of later successional species in Oaxaca. Certainly successional status may explain the surprising result that species such as *Guazuma ulmifolia* and *Swietenia humilis* are indicative of the Honduran samples alone. Even though they are well known and common in coastal Oaxaca, they are pioneer type species not often encountered in mature forest. The preference of several other species for the Honduran samples also disguises the fact that they are commonly encountered species in Oaxaca outside of mature forest, and include *Luehea candida* (Moc. & Sessé ex DC.) M. Mart. (Tiliaceae), *Acacia hindsii*, Benth. and *Acacia collinsii* Saff. (Mimosaceae), *Gliricidia sepium* and *Trema micrantha*. (L.) Blume (Ulmaceae). However, in the case of *Swietenia humilis*, its rarity in mature forest in Oaxaca may also be, at least partially, a result of selective logging. There are however various species amongst those commonly encountered in the Oaxacan samples that may also be early successional species. These include the ubiquitous *Cochlospermum vitifolium* and *Tabebuia rosea*, the former of which appears particularly resistant to hurricane damage (Gordon, pers. obs.), and amongst those exclusive to the Oaxacan samples *Jacaratia mexicana*, *Apoplanesia paniculata* and *Comocladia engleriana*. Thus the distinction between the 'mature' Oaxacan samples and the secondary Honduran ones is not absolute, but a matter of degree.

The importance of anthropogenic disturbance and successional status in explaining regional patterns of diversity in neotropical SDTF may also go some way to explaining the latitudinal gradient in diversity discussed by Gentry (1988, 1995). Two of the data sets he used are from Chamela in the state of Jalisco, Mexico and Guanacaste, Costa Rica. Rather than be an effect relating to latitude per se, the higher diversity levels in the former may reflect the more mature status of this forest (Gordon, pers. obs.) compared to the latter which is dominated by secondary successions established on old, fire maintained cattle pasture (Janzen, 1986). Gillespie et al. (2000) in discussing Nicaraguan and Costa Rican dry forests note that the least diverse of the forests they surveyed was also the most fire affected. However Trejo and Dirzo (2002) also offer compelling evidence for a relationship between potential evapotranspiration and floristic diversity in Mexican SDTF, and we do not discount that this may also be a factor.

4.2. Conservation importance

Given the clear contrast between the GHI scores of the Honduran forest samples and those of Oaxaca, we focus our discussion on the potential role of these Oaxacan forests in Mesoamerican SDTF conservation. However, we do so acknowledging the limitations outlined by Possingham et al. (2002) of the use of rare species lists in conservation planning, and we emphasise three important caveats. First we stress that our analysis, like so many biodiversity assessments, is partial, limited as it is to tree and shrub diversity. The degree to which these conclusions hold for other groups of plants and for animals remains untested, although Gillespie and Walter (2001) provide evidence for species richness correlations between birds and woody vegetation elsewhere in Central American SDTF. The second is that we offer no analysis of other areas of SDTF in Honduras, which include several dry interior valleys where rarity and endemism might be greater. The third is to emphasise that this analysis takes a global approach to determining the importance of diversity, based as it is on the proportion of species in a sample that are considered to be in some danger of global extinction. A more locally orientated approach is likely to take a different but equally valid view of a species' importance, the uses of each species probably being a more important consideration than the sizes of their distributions (Gordon et al., in press). Some aspects of the conservation of tree and shrub diversity in southern Honduras relating to the surveys discussed here are further discussed in Barrance et al. (in press), Boshier et al. (in press) and Gordon et al. (2003).

From the Oaxacan forest samples we identify four areas which should be given particular consideration for conservation (Fig. 1 and Tables 4 and 5). The deciduous forest of Cerro Guiengola; the deciduous forests and fallows of La Jabalina and the Zimatán-Ayuta watersheds which form several of the 'Oaxacan Deciduous Forest' samples of Fig. 2; the semideciduous forest of Cerro Huatulco which are the two 'Oaxacan Semideciduous Forest' samples nearest the centre of Fig. 2; and the deciduous 'beach' forests on the dunes and rocky outcrops of the Oaxacan coastline around the Bahías de Huatulco.

Both Cerro Guiengola and Cerro Huatulco are protected by their steep topography (*cerro* = hill). Cerro Guiengola is further protected as an archaeological site, as it contains a precolombian ruin. It is currently little visited by tourists and it cannot be considered in immediate danger, however, should often suggested plans for its more complete development as a tourist site become reality, conservation agencies will need to ensure this does not compromise its outstanding importance for biodiversity conservation. It is an isolated hill top forest and the degree to which other land-uses, especially forest fallows in neighbouring communities such as those of El Limón, can contribute to increasing the effective area of forest cover under some form of conservation management may prove important in the long-term maintenance of its diversity. The analysis presented here suggests that, at least in terms of their species content, such forest fallows could indeed have such a role.

The importance of maintaining forest cover on Cerro Huatulco is not locally in doubt as it protects the water supply of the town of Santa María de Huatulco. It has the status of a Communally Managed Protected Area and has attracted the interest of local conservation organisations. Its immediate future as a site of important woody diversity therefore appears relatively secure.

Beach-based tourism development along this coast is already considerable and is increasing. The forests around several sandy bays along this coast are at least nominally protected by their inclusion in the approximately 6 000 ha of forest that forms part of the Parque Nacional Huatulco (Escamirosa Tinoco and Hernández, 2000). This protected area was created as a by-product of the expropriation of land required for the development of the relatively new Bahías de Huatulco tourist resort. However the rocky slopes around Playa Entrega (*playa* = beach) from which samples with the highest GHI scores come is not within this protected area, and even those within it already receive considerable numbers of visitors and are likely to receive more as tourism grows. At the very least, therefore, monitoring of this vegetation type will be important, as will be the identification and protection of other forested bays along the coast that are more isolated from sites of mass tourism.

The largest expanse of SDTF in the coastal region is formed by the forests and fallows of La Jabalina and in the Zimatán-Ayuta watersheds. This area includes the 'Copalita' area sampled by Trejo and Dirzo (2002) which they identify as one of Mexico's outstandingly diverse SDTF areas. Furthermore, in contrast to the 'moderate to steep slopes and rocky outcrops' on which most of the forests they sampled were found, this area also includes significant amounts of forest cover on low lying sandy soils, especially around La Jabalina. Communal forms of land ownership are the norm here, and it seems likely that the restrictions on the number of people who can use communal land has allowed considerable areas to be maintained under mature forest and long-cycle forest fallows. Furthermore, social capital in the form of communal management structures results in a high degree of awareness of the collective importance of natural resources and facilitates their protection, as is evidenced by the creation of a Communally Managed Protected Area in part of this forest around La Jabalina.

As we have argued, forest fallow can also make a contribution to the conservation value of the area and so it would seem that current land-use practices have much to offer conservation initiatives. Indeed we advocate an approach to forest conservation in the region which integrates the cycle of forest fallow regeneration into conservation planning. This positive view of communal management contrasts with the more negative conclusions drawn by Stedman-Edwards (2000) on the effects of communal land tenure in the SDTF of the Calakmul Biospehere reserve in Campeche, Mexico.

Recent national law changes, however, threaten the stability of the *ejido* system, one of the forms of communal tenure common in the area. It is now legally possible for a community to privatise land ownership, potentially allowing increased pressure on available land in coastal Oaxaca through division and sale of land to immigrants. As yet there is no evidence that this option has been taken up with any enthusiasm by the communities of coastal Oaxaca.

5. Conclusions

For the conservation of restricted range tree and shrub diversity, coastal Oaxaca would represent a far better investment for those organisations promoting SDTF conservation than would southern Honduras. Fortunately, several international agencies in collaboration with many local non-government organisations are already active in conservation in this part of Mexico. We encourage further funding of these local organisations. We conclude that forest fallows and forest fragments (Janzen, 1988b) can act as an analogue of mature, larger forest areas, both in terms of species content and to a lesser, but significant, extent in their content of restricted range species. Thus continued conservation efforts in the region should work with, rather than against, traditional systems of social organisation and landscape management. This insight would not have been gained if we had not considered within-landscape patterns of diversity. Conservation planning should therefore go beyond consideration of only the most extensive and 'pristine' (Denevan, 1992) elements of the landscape and adopt an agroecosystem focus (Vandemeer and Perfecto, 1997). Indeed some Oaxacan organisations have taken this approach for some time.

We conclude that further efforts to identify suitable sites for SDTF tree diversity conservation should begin with areas of relatively extensive and under-explored mature forest, i.e. those similar to coastal Oaxaca, still found along Mexico's Pacific coast. In this recommendation we concur with Ceballos et al. (1998) who consider priorities amongst Mexico's mammalian fauna. However, such surveying, whether it be of Mesoamerican SDTF or any other forest type, should not discount a priori other tree containing elements in the landscape.

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APPENDIX ON NEXT PAGE

Appendix. Species conservation priorities identified in the seasonally dry tropical forests of southern Honduras and coastal Oaxaca, Mexico

Honduran species in bold, *Rondeletia deemii* being the only priority species to appear in both sets of samples. Family level nomenclature follows that of Mabberley (1997), except that for brevity Caesalpinioideae, Mimosoideae and Papilionoideae are treated as separate families. Those species marked * are not primarily limited to SDTF forests.

Family	Species	Summarised distribution
Black star species		
Achatocarpaceae	*Achatocarpus oaxacanus* Standl.	Oaxacan dry forest endemic
Caesalpiniaceae	*Caesalpinia coccinea* G.P.Lewis & J.L.Contr.	Oaxacan dry forest endemic
Compositae	*Trixis silvatica* B.L.Rob. & Greenm.	Oaxacan dry forest endemic
Euphorbiaceae	*Jatropha alamani* Muell. Arg.	Oaxacan dry forest endemic
Euphorbiaceae	*Jatropha sympetala* Standl. & Blake	Oaxacan dry forest endemic
Euphorbiaceae	*Manihot oaxacana* D.J.Rogers & Appan	Oaxacan dry forest endemic
Malpighiaceae	*Bunchosia discolor* Turcz. ex Char.	Oaxacan dry forest endemic
Mimosaceae	*Mimosa albida* Humb. & Bonpl. ex Willd. var. *pochutlensis* R.Grether	Oaxacan dry forest endemic
Mimosaceae	*Zapoteca tehuana* H.M.Hern.	Oaxacan dry forest endemic
Simaroubaceae	*Castela retusa* Liebm.	Oaxacan dry forest endemic
Sterculiaceae	*Waltheria conzatii* Standl.	Oaxacan dry forest endemic
Gold star species		
Annonaceae	*Sapranthus foetidus* (Rose) Saff.	Jalisco, Guerrero, Oaxaca
Boraginaceae	*Bourreria purpusii* Brandgee	Jalisco, Oaxaca
Caesalpiniaceae	*Brongnartia bracteolata* Micheli	Oaxaca, Chiapas
Caesalpiniaceae	*Caesalpinia hughesii* G.P.Lewis	Oaxaca, Guerrero, Colima
Capparidaceae	*Capparis angustifolia* Kunth	Michoacan Guerrero, Oaxaca
Capparidaceae	*Forchhammeria lanceolata* Standl.	Oaxaca, Guerrero
Combretaceae	*Bucida wigginsiana* Miranda	Guerrero, Oaxaca
Compositae	*Trixis pterocaulis* B.L.Rob. & Greenm.	Sinaloa, Jalisco, Colima, Oaxaca
Malvaceae	*Hibiscus kochii* Fryxell	Guerrero, Oaxaca
Mimosaceae	***Leucaena salvadorensis* Standl.**	**El Salvador, Nicaragua, Honduras**
Myrtaceae	***Eugenia hondurensis* Ant. Molina**	**Oaxaca? Honduras, Nicaragua**
Myrtaceae	*Eugenia salamensis* Donn.Sm. var. *rensoniana* (Standl.) McVaugh	Oaxaca, Guatemala, Costa Rica
Nyctaginaceae	***Grajalesia fasciculata* (Standl.) Miranda**	**Oaxaca? Guatemala, El Salvador, Honduras, Nicaragua**
Papilionaceae	*Lonchocarpus emarginatus* Pittier	Oaxaca, Chiapas
Papilionaceae	*Lonchocarpus longipedicellatus* Pittier	Jalisco, Guerrero, Oaxaca
Rubiaceae	***Guettarda deamii* Standl.**	**Guatemala, El Salvador, Honduras, Nicaragua**
Rubiaceae	*Guettarda galeottii* Standl.	Sinaloa, Nayarit, Oaxaca
Rubiaceae	*Randia cinerea* (Fernald) Standl.	Oaxaca, Guerrero
Simaroubaceae	*Recchia mexicana* Moc. & Sessé	Oaxaca, Jalisco
Sterculiaceae	*Physodium oaxacanum* Dorr & Barnett	Oaxaca, Chiapas
Blue star species		
Achatocarpaceae	*Achatocarpus mexicanus* H.Walter	Oaxaca, Chiapas*
Amaranthaceae	*Lagrezia monosperma* (Rose) Standl.	Jalisco, Michoacan, Colima, Guerrero, Oaxaca

(continued on next page)

Appendix (*continued*)

Family	Species	Summarised distribution
Blue star species		
Anacardiaceae	***Actinocheitia filicina* (DC.) F.A. Barkley**	**Guerrero, Oaxaca, Chiapas, Honduras***
Burseaceae	*Bursera instabilis* McVaugh & Rzed.	Nayarit, Jalisco, Michoacan, Colima, Guerrero, Oaxaca
Caesalpiniaceae	*Caesalpinia mollis* (Kunth) Spreng.	Oaxaca, Chapas, Yucatán*
Combretaceae	*Bucida macrostachya* Standl.	Oaxaca, Chiapas, Guatemala, Honduras, Nicaragua
Compositae	*Verbesina oaxacana* DC.	Oaxaca*
Euphorbiaceae	*Croton axillaris* Muell. Arg.	Oaxaca, Chiapas, Tamaulipas, Guatemala, Nicaragua
Euphorbiaceae	*Croton ramillatus* Croizat	Guerrero, Oaxaca, Veracruz*
Euphorbiaceae	*Croton septemnervius* McVaugh	Jalisco, Guerrero, Oaxaca*
Flacourtiaceae	***Casearia williamsiana* Sleumer**	**Honduras***
Flacourtiaceae	*Samyda mexicana* Rose	Jalisco, Guerrero, Oaxaca, Veracruz*
Hernandiaceae	*Gyrocarpus mocinnoi* Espejo	Guerrero, Chiapas, Oaxaca, Puebla, Guatemala
Labiatae	*Hyptis tomentosa* Poit.	Oaxaca Chiapas Veracruz*
Lauraceae	***Persea caerulea* (Ruiz & Pav.) Mez**	**EL Salvador, Honduras, Nicaragua, Costa Rica, Panama**
Malvaceae	*Abutilon grandidentatum* Fryxel.	Oaxaca, Chiapas*
Mimosaceae	*Havardia campylacanthus* (L.Rico & M.Sousa) Barneby & J.W.Grimes	Michoacan, Guerrero, Oaxaca, Nicaragua, Honduras*
Mimosaceae	*Mimosa eurycarpa* B.L.Rob.	Michoacan, Colima, Oaxaca*
Nyctaginaceae	*Torrubia macrocarpa* Miranda	Jalisco, Michoacan, Oaxaca, Puebla, Morelos
Papilionaceae	*Lonchocarpus constrictus* Pittier	Jalisco, Michoacan, Colima, Guerrero, Oaxaca
Papilionaceae	*Indigofera platycarpa* Rose	Guerrero, Oaxaca, Puebla, Morelos*
Rubiaceae	*Randia nelsonii* Greenm.	Sinaloa, Michoacan, Oaxaca, Veracruz*
Rubiaceae	***Randia pleiomeris* Standl.**	**Guatemala, EL Salvador, Honduras***
Rubiaceae	***Rondeletia deamii* (Donn.Sm.) Standl.**	**Oaxaca, Guatemala, Honduras, Nicaragua***
Tiliaceae	*Heliocarpus occidentalis* Rose	Guerrero, Oaxaca*
Trigoniaceae	***Trigonia rugosa* Benth.**	**Guatemala, EL Salvador, Honduras, Nicaragua***

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