## Broad-scale biodiversity pattern of the endemic tree flora of the Western Ghats (India) using canonical correlation analysis of herbarium records

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A crucial step in understanding the origin and maintenance of biological diversity is the assessment of its distribution over space and time and across environmental gradients. At the regional scale, two important attributes of species can be assessed that provide insight into speciation processes: species geographical and environmental ranges. The endemic tree flora of the Western Ghats is an interesting case for analyzing broad-scale biodiversity patterns because of the steep environmental gradients that characterize this tropical region of India. We analysed species geographical and environmental ranges by Canonical Correlation Analysis of point data from herbarium collections. We performed partial analyses to discriminate spatial and environmental correlates of species distribution, and evaluate the contribution of higher taxonomic ranks to these ranges. We identified different levels of organization in the distribution of endemism: 1) general features, such as the concentration of endemic species in the southern part of the Western Ghats, and the decrease in endemic species richness along the altitudinal and the dry season length gradients, and 2) patterns specific to genera or families, such as species niche separation along the environmental gradients. Our analyses enabled us to formulate hypotheses about the diversification of the endemic tree flora of the Western Ghats. They also confirm the value of Canonical Correlation Analysis as the suitable method for collection data analysis.

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Increasing awareness of the ongoing loss of biological diversity has heightened interest in its estimation, origin, function, and maintenance (Hawksworth 1995, Heywood and Watson 1995). The assessment of biodiversity patterns over space and time and across environmental gradients is a crucial step in the understanding of these issues. With the development of macroecology, broad-scale biodiversity patterns have been recognized (Brown 1995). These approaches have emphasized the importance of processes that act at the regional scale, combining ecological, historical and evolutionary factors (Ricklefs and Schluter 1993).

Species geographical and environmental ranges are two important attributes of species that can be assessed at such a scale and can provide insights into speciation processes. Indeed, allopatric and sympatric modes of speciation have different effects on the geographical ranges of sister taxa (Taylor and Gotelli 1994, Barraclough and Vogler 2000), whereas species niche differentiation may indicate adaptive radiation (Knox and Palmer 1995, Schluter 1996, Losos et al. 1998).

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The endemic tree flora of the Western Ghats is an interesting case for investigating broad-scale biodiversity patterns. The Western Ghats form a 1500 km-long escarpment parallel to the southwestern coast of the Indian Peninsula, recognized as one of the world biodiversity hotspots (Myers et al. 2000). The interaction of the summer monsoon winds with the relief of the Ghats results in two steep environmental gradients, a westeast decrease in rainfall and a south-north increase in dry season length, that determine strong changes in the vegetation. The western side of the Ghats supports wet evergreen forests, whereas the eastern side supports deciduous forests, with the exception of a belt of dry evergreen forests in the south (Pascal 1988). In the north, the wet evergreen forests are displaced by deciduous formations because of the lengthening of the dry season. As a consequence, the evergreen forests of the Western Ghats are isolated from their counterpart in the north-eastern part of India, a feature that may explain their high level of endemism: 63% of the evergreen tree species are endemic to this region (Ramesh and Pascal 1991). The uplift of the Western Ghats would date from the Pliocene; the concomitant decrease in rainfall and increase in dry season length would have induced the replacement of the wet evergreen forests of the Indian Peninsula by deciduous forests and the formation of dry evergreen forests in the south on the eastern side of the Ghats, while reducing the area formerly occupied by wet evergreen forests to the western side of the Ghats and the north-eastern region of Assam (Legris and Meher-Homji 1982). So the endemic tree species of the Western Ghats share a common biogeographic history since the isolation of the evergreen forests, and their geographical and ecological ranges can be compared to provide insights into speciation processes (Taylor and Gotelli 1994).

One way to assess species distributions consists of gathering available records from the collections in museums or herbaria (Mourelle and Ezcurra 1996, Skov and Borchsenius 1997, Shaffer et al. 1998, Parmesan et al. 1999, Peterson et al. 1999). However, as stressed by Ponder et al. (2001), these data suffer from several biases: they can provide reliable data about species presence, but species absence is generally dubious due to geographical gaps in the sampling effort. Moreover, each record is uniquely characterized by the identity of the collector, the place and the date of record, so it corresponds to a distinct sampling unit which does not provide any information about the presence of other species: local species diversity cannot be assessed directly from such data.

Two sets of methods have been developed to deal with collection data. The first set of methods aims at modeling individual species distribution, coupling point data with abiotic variables to define species habitat requirements (Stockwell and Peters 1999, Bonn and Schröder 2001, Ponder et al. 2001). The second set of

methods aims at modeling species communities, analyzing the spatial and environmental distribution of species diversity (Guisan et al. 1999). In the context of unimodal species response curves, Canonical Correspondence Analysis (CCA; ter Braak 1986) is very efficient to investigate niche separation along environmental gradients. CCA requires a table containing abundances or presence-absence of species at a series of sites and measurements of environmental variables for the same sites, where a site is "the basic sampling unit, separated in space or time from other sites" (ter Braak 1986, p. 1167). In principle, CCA can be extended in the case of herbarium data by dividing the study area into smaller units, such as grid cells. Number of records are then computed for each cell and variations in species diversity are analyzed from these units (Hill 1991, Bolognini and Nimis 1993, Heikkinen 1996). However, if one uses spatial units defined a posteriori, one cannot control the sampling effort, which may biase the analyses (species absences are more likely to result from a poor sampling effort). Moreover, the size of the cells can influence the results (Gaston 1994, Böhning-Gaese 1997, Donald and Fuller 1998). In particular, the relationships between species occurrences and environment will not be tightly coupled because environmental data are then averaged at the cell scale.

In this paper, we use a general method based on Canonical Correlation Analysis (CANCOR, Hotelling 1936) to assess variations in species diversity directly from a list of independent species occurrences, such as geo-referenced herbarium specimens. We show that CANCOR, which was found ineffective for ordination of real relevés (Gauch and Wentworth 1976), is especially suitable for collection data. Our aim was to analyze the distribution of tree endemism in the Western Ghats; we assessed broad-scale biodiversity patterns using different kinds of analyses in order to reveal different levels of organization.

## Material and methods

### Presentation of the data set

To depict the geographical ranges of the endemic evergreen tree species of the Western Ghats, Ramesh and Pascal (1997) gathered occurrences from three sources: 1) specimens in herbaria, 2) published data and 3) results of field surveys by the French Institute of Pondicherry and other botanists. From this database we extracted the 5142 occurrences that correspond to herbarium specimens, forming a set of reliable and independent observations, verified by the same expert (a botanist from the French Institute). Taxa represented by <5 occurrences were not considered, as their geographical range could not be assessed properly. A total of 224 endemic tree species, belonging to 104 genera and 38 families, were documented.

The 5142 species occurrences occupy 8 degrees of latitude, from 8° to 16°, the area covered with evergreen forests delimited towards the east by the isohvet 2000 mm (Fig. 1). In this region, the escarpment of the Ghats consists almost exclusively of archean rocks with varying degrees of metamorphism, and the soils (saturated acidic soils) appear homogeneous (Bourgeon 1989). Studies carried out by the French Institute of Pondicherry (e.g. Pascal 1992, Ramesh et al. 1997) have shown that, at the regional scale, species turnover is driven by three climatic factors: variation in total annual rainfall, rainfall seasonality (dry season length) and temperature, associated with altitude. So, we assessed species environmental ranges by compiling these data for each occurrence (Fig. 2). Altitude was recorded for each specimen in the database, while mean total annual rainfall and mean annual dry season length were deduced from bioclimatic maps of the Western Ghats (Pascal 1982). The dry season is defined by the number of months during which the amount of rainfall measured in mm is lower than twice the temperature expressed in °C (Bagnouls and Gaussen 1953).

# Canonical Correlation Analysis of species occurrences

Species information concerning the 5142 occurrences gathered from natural history institutions is contained in a species by occurrences table X with  $x_{ij} = 1$  if the ith occurrence belongs to the jth species, otherwise  $x_{ii} = 0$ .



Fig. 1. Study area and location of the 5142 herbarium specimens.

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A table Y describes the environmental features at each locality where  $y_{ik}$  represents the measurements of the kth environmental variable recorded for the ith occurrence (Fig. 3). As noted above, species occurrences such as herbarium specimens are independent observations, so they represent the actual statistical units. As a consequence, tables X and Y represent two sets of variables measured on the same statistical units, the 5142 occurrences. In this case, the number of observations is much higher than the number of variables. Such characteristics correspond exactly to the requirements of CAN-COR, a method that finds the linear combinations of one set of variables that are maximally correlated with linear combinations of another set of variables (Gittins 1985).

As X is formed by variables indicating species membership, the CANCOR of X and Y finds linear combinations of environmental variables that best discriminate the species. This is equivalent to Discriminant Analysis (DA) of Y by the specific groups of occurrences in X (Lebart et al. 1984), also known as Canonical Variates Analysis (James and McCulloch 1990). DA has been used in ecology by Green (1971), and Lebreton et al. (1988) demonstrate that Green's DA is mathematically equivalent to the CCA of ter Braak (1986). ter Braak and Verdonschot (1995) admit this link and specify that "the main difference between CCA and discriminant analysis is that the unit of the statistical analysis in discriminant analysis is the individual, whereas it is the site in CCA". Hence, just like CCA, our CANCOR approach provides linear combinations of environmental variables that maximize species niche separation. CANCOR of occurrence data can be viewed as a CCA without any sampling site. Contrary to multivariate analyses based on a partition of the study area into grid cells, CANCOR computes species environmental means directly from the list of occurrences, i.e. only from species presences. Sampling bias associated with the use of cells is thus removed. The analysis allows a direct comparison of species environmental ranges, i.e. abiotic realized niches. We defined species niches by ellipses containing 50 percent of species occurrences on the canonical planes, following the procedure described by Thioulouse and Chessel (1992) and Pélissier et al. (2002).

We analyzed species geographical ranges in a similar way, with the table Y containing now polynomial functions of the geographic coordinates of species occurrences, i.e. the variables x, y,  $x^2$ , xy,  $y^2$ , etc., where x and y are, respectively, occurrence longitude and latitude. The CANCOR of X and Y becomes a Canonical Correlation Trend Surface Analysis (CCTSA) (cf. Gittins 1968, Wartenberg 1985). This analysis identifies multispecies spatial patterns, i.e. gradients of species composition or areas of high endemism, according to the degree of overlap among species ranges. In order to



visualize these patterns, we computed contour curves from the canonical scores mapped on the study area, following Thioulouse et al. (1995).

### Partial analyses

CANCOR permits partial analyses to study the relationships between X and Y. In this case, Y contains variables from which the effect of another set of explanatory variables has been removed. Principles of the method are the same as those used for partial CCA (ter Braak 1988). The mathematical details are explained in Pélissier et al. (2002), following Méot et al. (1998). We used these partial analyses in two ways: 1) to remove the effect of environmental factors on the multispecies spatial patterns and identify other correlates of species distribution, such as geographical barriers to dispersal, and 2) to analyze the contribution of higher taxonomic levels to species geographical and environmental ranges. In the latter case, the partial analyses are similar to within-group analysis, depicting species-environment relationships or multispecies spatial patterns within genera or within families.

#### Permutation test

The statistical significance of the results of CANCOR can be evaluated by a random permutation test (Manly 1991). First, the number of eigenvalues of interest (l) is determined from the graph of the decrease in CAN-

Fig. 3. Occurrences-by-species (X) and occurrences-byenvironment (Y) tables obtained from a list of n occurrences distributed among s species and characterized by p environmental variables. Species appear as dummy variables indicating species identity, while the environmental factors are considered as quantitative variables.



COR eigenvalues, and the sum of the l first eigenvalues is computed; CANCOR eigenvalues are equal to the square of the canonical correlation coefficients, so the sum of eigenvalues measures the strength of the correlation between X and Y. Then the rows of Y are permuted randomly and CANCOR analysis is performed between X and the permuted table Y. We performed 1000 permutations and computed the sum of the l first eigenvalues for each one. We compared the results obtained from the original data set with those obtained after permutations of the rows of Y to obtain a p-value.

All calculations and related graphs were generated with ADE-4 software (Thioulouse et al. 1997), available on the internet at < http://pbil.univ-lyon1.fr/ADE-4/>. The maps were generated with Arcview 3.2.

### Results

#### **Multispecies spatial patterns**

To obtain a general picture of the distribution of endemism in the Western Ghats, we first analyzed the changes in endemic species composition in the study area by means of CCTSA, using polynomial functions of the geographic coordinates of order less than four, i.e. the 9 variables x, y,  $x^2$ , xy,  $y^2$ ,  $x^3$ ,  $x^2y$ ,  $xy^2$  and  $y^3$  (x and y are, respectively, occurrence longitude and latitude).

The analysis produced two highly significant factors representing 52% of total variance (p < 0.001). The canonical correlation coefficients of these first factors were respectively 0.747 and 0.655. The first factor reveals a strong change in endemic species composition from the coast towards the top of the Ghats, and the progressive disappearance of this  $\beta$ -diversity gradient in the northern part of the study area (Fig. 4a). The second factor highlights the floristic distinctness of the southeastern part of the study area, revealing that

several endemic species are restricted to this region (Fig. 4b). However, the variation in endemic species composition from the southeast is not uniform, with steep gradients of  $\beta$ -diversity observed towards the coast and the tops of the Ghats, whereas the change in endemic species composition towards the north appears much less marked.

# Multispecies spatial patterns independent of environmental factors

We performed a partial CCTSA to remove the effect of environmental variables and analyze the residual component of species distribution (the same polynomial functions of geographical coordinates were used).

The first two factors were highly significant, representing 52% of total variance (p < 0.001). The canonical correlation coefficients were smaller than in the previous analysis, 0.483 and 0.466. They reveal more complicated spatial patterns, confirming the strong correlation between environmental factors and species distribution (Fig. 5). Species canonical scores (obtained as the centroid of their occurrence scores) allows the identification of species groups sharing the same spatial features; the occurrences of species representing each group can then be mapped by their physical coordinates.

The first axis highlights species with narrow latitudinal ranges (Fig. 5a). At the negative end, there are species whose distributions are limited to the central part of the study area between 10 and 12°N, such as *Pithecolobium gracile* at low elevation or *Euonymus angulatus* at medium elevation, whereas at the positive end, there are two kinds of species: 1) species whose geographical ranges are limited to the southern mountains, and more specifically occurring on their eastern side, such as *Garcinia travancorica* and *Diospyros foliolosa*, and 2) species restricted to the northwestern part of the study area, such as *Mammea suriga*. Three



Fig. 4. Multispecies spatial patterns obtained by CCTSA. Mapping of occurrence canonical scores by contour curves computed over the 500 nearest neighbours. a) first factor, b) second factor. The colours reflect variation in occurrence scores (cf. insert).

floristic regions are thus delineated, each of which harbours a specific endemic tree flora (Fig. 5a).

The second axis highlights species with narrow longitudinal ranges, i.e. with different altitudinal ranges, pointing to the floristic homogeneity of the western slopes of the Ghats (Fig. 5b). At the positive end, are species whose distributions correspond to these middle elevation slopes, such as *Litsea mysorensis* and *Humboldtia brunonis*, whereas at the negative end, are two kinds of species: 1) species whose distributions are restricted to the coastal area, such as *Buchanania lanceolata* in the south and *Garcinia indica* in the north, and 2) species located on the top and/or the eastern slopes of Palni and Nilgiri mountains, such as *Microtropis microcarpa* and *Rhododendron nilagiricum*. An overlap of species geographical ranges is observed on the western slopes of the Ghats, as shown by the mapping of species occurrences (Fig. 5b).

### Environmental ranges of endemic species

We then analyzed the role of environmental factors by assessing species niche differentiation along the three main environmental gradients. This was done by performing a CANCOR between the occurrences-by-species and occurrences-by-environment tables (cf. Fig. 3).



Fig. 5. Multispecies spatial patterns obtained by partial CCTSA removing the effect of environmental variables. Mapping of occurrence canonical scores by contour curves computed over the 500 nearest neighbours, and projection of the occurrences of species characteristic of the spatial patterns identified. The colours reflect variation in occurrence scores (cf. insert). See Appendix for species names.

The first two factors were highly significant, representing 87% of total variance (p < 0.001). The canonical correlation coefficients were equal to 0.803 and 0.573. The first factor represents the altitudinal gradient, whereas the second factor corresponds to the gradient of dry season length and, to a less extent, the rainfall gradient (Fig. 6a). On the first canonical plane, the projection of species at the centroid of their occurrences forms a triangle, showing the correlation between altitude and dry season length (Fig. 6b). The tips of this triangle are occupied by three kinds of species with a narrow ecological range: 1) species restricted to the lowlands with a short dry season, such as *Myristica fatua* var. *magnifica* and *Gymnacranthera canarica*, two species typically associated with swamps, 2) species restricted to the high elevations, such as the unique species of Magnoliaceae *Michelia nilagirica* and of Caprifoliaceae *Viburnum hebanthum*, and 3) species re-



Fig. 6. Results of CANCOR of occurrences-by-endemic tree species and occurrences-by-environment tables. a) correlation of the environmental variables with the first two canonical factors, b) projection of species at the centroid of their occurrences. Species with the highest scores are represented by their names, with the other species represented by dots. See Appendix for species names.

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Fig. 7. Species environmental ranges within the most species-rich genera. a) *Litsea*; b) *Diospyros*; c) *Syzygium*. Species represented by ellipses containing 50% of their occurrences. See Appendix for species names.

stricted to the lowlands with a long dry season, such as *Diospyros angustifolia* and *Garcinia indica*. Between these species, are species with a broader environmental range, with the generalists located near the origin of the canonical plane.

#### Species niche separation among congeneric species

In order to assess the importance of species niche separation among congeneric species, we plotted the results separately for the three most species-rich genera, *Litsea* (Lauraceae), *Diospyros* (Ebenaceae) and *Syzy-gium* (Myrtaceae); the low number of species per genus allowed the visualization of species niches by ellipses containing 50% of their occurrences (Fig. 7).

Litsea species occupy most of the environmental space, displaying rather wide ecological amplitudes, except three species with a narrow altitudinal range, L. travancorica, restricted to the lowlands, L. keralana, occurring at middle elevation, and L. wightiana var. tomentosa, inhabiting the tops of the mountains (Fig. 7a); the highest niche overlap is observed at middle elevation (800–1400 m) under medium dry season length (3–4 months).

Contrary to *Litsea*, *Diospyros* is primarily located in the lowlands (Fig. 7b). Only one species is observed at

medium elevation, *D. nilagirica*, and none occurs at high elevation. The length of the dry season in addition to the amount of rainfall appears as the main factor of species niche differentiation. For example, the second canonical factor separates species tolerating a long dry season, such as *D. angustifolia*, from species inhabiting the lowlands under a short dry season, such as *D. bourdillonii*. Within this last group, it distinguishes *D. foliolosa*, a species located on the eastern side of the Ghats, where the annual rainfall is lower than on the western side. The highest niche overlap is observed at low elevation under a short dry season.

With 20 endemic species, *Syzygium* represents the most species-rich genus of the endemic tree flora of the Western Ghats, but the majority of its species are rare. Compared with the two previous genera, species niche differentiation among the 8 most abundant *Syzygium* species is especially high (Fig. 7c).

## Contribution of higher taxonomic ranks to species distribution

Species geographical and environmental ranges are expected to differ among genera and families, as these higher taxonomic ranks may be characterized by a

Table 1. Contribution of higher taxonomic levels to species ecological ranges. Canonical correlation coefficient (r) and percentage of total variance (% V) of the first two factors compared for three analyses: CANCOR between the occurrences-by-species and occurrences-by-environment tables (SE), and same analysis after partialling out the effect of genus (SE-G) or family (SE-F) (see text for further details).

| Axis | Analysis | SE    | SE-G  | SE-F  |
|------|----------|-------|-------|-------|
| 1    | r        | 0.803 | 0.651 | 0.756 |
|      | % V      | 57.85 | 59.48 | 58.52 |
| 2    | r        | 0.573 | 0.453 | 0.539 |
|      | % V      | 29.51 | 28.87 | 29.02 |

Table 2. Contribution of higher taxonomic levels to species geographical ranges. Canonical correlation coefficient (r) and percentage of total variance (% V) of the first two factors compared for three analyses: partial CCTSA removing the effect of environmental variables (Sxy), and same analysis after partialling out the effect of genus (Sxy-G) or family (Sxy-F) (see text for further details).

| Axis | Analysis | Sxy            | Sxy-G          | Sxy-F          |  |
|------|----------|----------------|----------------|----------------|--|
| 1    | r<br>% V | 0.483<br>26.92 | 0.392<br>29.28 | 0.459<br>27.02 |  |
| 2    | r<br>% V | 0.466<br>25.06 | 0.356<br>24.24 | 0.444<br>25.29 |  |

series of traits influencing species dispersal capacities or environmental tolerance. We analyzed the contribution of genus and family to species ranges by means of partial CANCOR. If genera (or families) are not randomly distributed, the results of these partial analyses should differ from the previous ones.

After partialling out the effect of genus or family on species ranges, the canonical correlation coefficients decrease, indicating that these higher taxonomic levels partly determine species environmental and geographical ranges (Tables 1 and 2). In both cases, the influence of family is lower than the influence of genus. In terms of patterns however, no difference is observed regarding species-environment relationships: niche separation along the environmental gradients occurs primarily within genera, i.e. at the species level. Regarding the multispecies spatial patterns independent of environment, slight differences are observed after removing the effect of genus (Figs 5 and 8). On the first factor, of the three floristic regions identified previously, the southeastern region remains unchanged whereas the others are less clear, being divided into different subregions (Fig. 8a). On the second factor, the pattern is almost unchanged, with the floristic homogeneity of the middle elevation slopes being even more strongly underlined than in the previous analysis (Fig. 8b).

In order to compare the multispecies spatial patterns within genera, we joined the canonical scores of congeneric species by a polygon (Fig. 9). The size of the polygon decreases with the overlapping of geographical ranges among congeneric species, whereas its shape reflects the diversity of species ranges (congeneric species may have narrow latitudinal extents and/or narrow longitudinal extents). Four types of patterns were identified: 1) genera represented by a large polygon, such as *Diospyros, Garcinia* and *Syzygium,* 2) genera with a large variance of species scores on the first factor, such as *Actinodaphne, Goniothalamus* and *Symplocos,* 3) genera with a large variance of species scores on the second factor, such as *Litsea* and *Microtropis,* and 4) genera represented by a small polygon, such as *Psychotria.* 

These multispecies spatial patterns were visualized by mapping the occurrences of congeneric species with contrasted factorial scores. For instance, if one considers the genus *Actinodaphne*, at the positive end of the first factor one finds *A. angustifolia*, a species occupying the northern part of the Ghats, and *A. campanulata* var. *campanulata*, a species restricted to the southeast,



Fig. 8. Multispecies spatial patterns obtained by partial CCTSA removing the effect of environment and genus. Mapping of canonical scores by contour curves computed over the 500 nearest neighbours, and location of species within genera that have high and contrasted factorial scores. a) first factor, b) second factor. The colours reflect variation in occurrence scores (cf. insert). See Appendix for species names.



Fig. 9. Species factorial map obtained by a partial CCTSA removing the effect of environment and genus. The species represented at the centroid of their occurrences (black squares) are joined within each genus. The size of the polygon reflects the importance of spatial segregation among species belonging to the same genus. ACTI, Actinodaphne; AGLA, Aglaia; DIOS, Diospyros; EUON, Euonymus; GARC, Garcinia; GONI, Goniothalamus; LITS, Litsea; MALL, Mallotus; MICR, Microtropis; PSYC Psychotria; SAPR, Saprosma; SYMP, Symplocos; SYZY, Syzygium.

while at the negative end one finds *A. lawsonii*, a species restricted to the central part of the Ghats, essentially the Nilgiri Mountains, and *A. tadulingami*, a species present both in the northern and in the central regions but absent from the southeastern area (Fig. 8a). If one considers the genus *Litsea*, at the positive end of the second factor one finds *L. bourdillonii*, *L. floribunda*, *L. keralana*, *L. ligustrina* and *L. mysorensis*, five species occupying the middle elevation slopes of the Ghats, while at the negative end one fiftinds *L. glabrata*, *L. wightiana* var. *tomentosa* and *L. wightiana* var. *wightiana*, three taxa occurring on the tops of the Ghats, and *L. travancorica*, a species occupying the low elevation slopes of the southern part of the Ghats (Fig. 8b).

#### Environmental profiles of the endemic tree families

Another way to assess the contribution of family to the observed species ranges is to analyze family environmental profiles. This was done by CANCOR of occurrences-by-families and occurrences-by-environment tables.

The analysis produced two highly significant factors representing 93% of total variance (p < 0.001). As expected, the correlation between taxa and environment was lower for families than for species: the canonical correlation coefficients were 0.548 and 0.269. The

patterns obtained for both analyses were similar (Figs 6 and 10).

Within the triangle formed by the projection of occurrences on the first canonical plane, the overlap of family ecological profiles is not uniform and indicates that most of the families are present at low to medium elevation under a short to medium dry season (Fig. 10b). The narrow profiles observed at the tips of the triangle often correspond to "monospecific" families (i.e. families with only one tree species endemic to the Western Ghats), such as Caprifoliaceae, Ericaceae and Magnoliaceae at high elevation, and Apocynaceae, Combretaceae and Rhizophoraceae at low elevation under a short dry season. Conversely, the families having the largest environmental profiles correspond to the most species-rich families, notably Euphorbiaceae, Lauraceae and Rubiaceae, suggesting a link between clade diversification and species niche differentiation.

### Discussion

## Distribution of endemism in the Western Ghats

The comparison of the pattern identified by the first factor of CCTSA (Fig. 4a) with variation in altitude

Fig. 10. Results of CANCOR of occurrences-by-families and occurrences-by-environment. a) correlation of the environmental variables with the first two canonical factors, b) representation of the 38 families by ellipses containing 50% of their occurrences. Anac, Anacardiaceae; Anno, Annonaceae; Apoc, Apocynaceae; Aqui, Aquifoliaceae; Aral, Araliaceae; Arec, Arecaceae; Aste, Asteraceae; Capr, Caprifoliacae; Cela, Celastraceae; Clus, Clusiaceae; Comb. Combretaceae; Corn, Cornaceae; Dipt, Dipterocarpaceae; Eben, Ebenaceae; Elae, Elaeocarpaceae; Eric, Ericaceae; Euph, Euphorbiaceae; Faba, Fabaceae: Flac, Flacourtiaceae; Laur, Lauraceae; Magn, Magnoliaceae; Mela, Melastomataceae; Meli, Meliaceae; Mora, Moraceae; Myri, Myristicaceae; Myrs, Myrsinaceae; Myrt, Myrtaceae; Olea, Oleaceae; Pitt, Pittosporaceae; Rhiz, Rhizophoraceae; Rubi, Rubiaceae; Ruta, Rutaceae; Sapi, Sapindaceae; Sapo, Sapotaceae; Stap, Staphylaceae; Ster, Sterculiaceae; Symp, Symplocaceae; Thea, Theaceae.



(Fig. 2a) indicates that the change in endemic species composition is mainly driven by the altitudinal gradient and the related decrease in temperature, while the homogenization of floristic composition observed in the northwestern part of the study area can be explained by the effect of an increase in dry season length being counterbalanced by the effect of an increase in the amount of occult precipitation with elevation (Fig. 2b). The second factor emphasizes the concentration of endemic species in the southeastern part of the Ghats and the concomitant decrease of endemic species richness along the altitudinal and the dry season length gradients. Indeed, the steep gradient of  $\beta$ -diversity towards the coast in the southern part, can be explained by a severe decrease of endemic species richness due to the high anthropogenic pressure that characterizes the coastal area (Fig. 4b).

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### Biogeographic history of the Western Ghats

The analysis of family environmental profiles by CAN-COR can be interpreted in the light of the biogeographic history of the Western Ghats. Indeed, the fact that most of the families are present at low to medium elevation under a short dry season (Fig. 10) indicates that this habitat is associated with a larger pool of endemic evergreen species than high elevation areas or lowlands with a long dry season, and this could be related to its older age, as compared to the other habitats (cf. Taylor et al. 1990). After the uplift of the Western Ghats, wet evergreen taxa would have been faced with a physiological barrier to occupy the new habitats, i.e. high elevation areas and lowlands with a long dry season. As a consequence, the current latitudinal and altitudinal gradients of endemic species richness (Fig. 4) could result from these historical and evolutionary factors. A similar hypothesis has been formulated by Latham and Ricklefs (1993) regarding the northern temperate tree flora.

The environmental profiles of the "monospecific" families can be related to the Quaternary history of the Western Ghats. On the one hand, families restricted to high elevation areas (> 1800 m) have a Laurasian affinity (cf. Raven and Axelrod 1974), so these species most probably migrated from Himalaya during glacial periods and took refuge at the highest elevations of the Ghats, as postulated by Vishnu-Mittre (1974) for the Ericaceae Rhododendron nilagiricum (Fig. 10). Indeed, the Western Ghats experienced a cooler and drier climate during the glacial cooling in the Quaternary (cf. Rostek et al. 1997). On the other hand, families restricted to low and middle elevations with a short dry season have a Gondwanan affinity, so these species may be relictual or recently evolved taxa, with the southern part of the Ghats representing a former refuge for species of the wet evergreen forest, or alternatively an active centre of speciation (cf. De Franceschi 1993). Indeed, summer rainfall would have persisted in this region in the Quaternary (Van Campo 1986), and the topographic complexity of the middle elevation reliefs of the southern part of the Ghats could have favoured species survival as well as species formation (cf. Fjeldså and Lovett 1997).

## Speciation processes in the endemic tree flora of the Western Ghats

The analysis of multispecies spatial patterns by partial CCTSA allowed the identification of three groups of species with a narrow latitudinal range that define three floristic areas, with the strongest floristic differentiation observed between the southeastern and the central part of the study area (Fig. 5a). Variation in the three environmental factors measured here shows that the northern region is characterized by a long dry season (Fig. 2b), while the central region is located around Palghat Pass, an interruption in the relief of the Ghats isolating Nilgiri from Palni Mountains (Fig. 2a), and the southern region mainly corresponds to the eastern side of the Ghats, also characterized by a low total annual amount of rainfall (Fig. 2c). So the existence of distinct endemic floras can be explained by physical and/or climatic barriers that would have limited species migration or adaptation, also enhancing range contraction and species extinction processes.

The second pattern identified by this analysis concerns the floristic homogeneity of the western slopes of the Ghats, in contrast to the coastal area and the top of Palni and Nilgiri Mountains (Fig. 5b). As shown by the overlap in *Litsea* species ranges at middle elevation (Fig. 8b), this pattern seems to result from the intermediate position of the slopes of the Ghats along the altitudinal gradient. This allows the co-existence of species from the lowlands or from the tops of the Ghats with species typical of middle elevation forests, a phenomenon emphasized by the decrease in endemic species richness towards the coast and the tops of the Ghats (Fig. 4b). So the middle elevation slopes of the Ghats appear as an area of species accumulation rather than a centre of speciation.

### Allopatric speciation

The analysis of multispecies spatial patterns within genera provides an insight into the origin of the three floristic regions. Indeed, the limits of the southeastern region remain unchanged while the other regions become less clearly delimited (Fig. 8a). This result suggests a general phenomenon of geographical vicariance for evergreen species between the eastern and the western sides of the Ghats, whereas independent adaptations to the long dry season would have occurred on the western side, as shown by the relative distributions of Actinodaphne species (Fig. 8a). The phylogenetic analyses of Indian Sapotaceae and Ebenaceae by De Franceschi (1993) are consistent with the hypothesis of allopatric speciation: Diospyros foliolosa and D. paniculata would derived from a widely distributed ancestor that underwent differential selection on each side of the Western Ghats.

### Adaptive radiation

The analysis of species environmental ranges reveals the importance of species niche separation along the altitudinal and the dry season length gradients (Fig. 6). This general feature holds among congeneric species, suggesting a link between speciation and niche evolution. While altitude appears as the main factor of species niche separation within *Syzygium* (Fig. 7c), the length of the dry season plays this role within *Diospyros*, primarily located at low elevation (Fig. 7b), and both factors contribute to species niche separation within *Litsea* (Fig. 7a). The steepness of the environmental gradients in the Western Ghats could have favoured the diversification of the evergreen tree flora by parapatric or sympatric speciation (cf. Endler 1982, Hodges and Arnold 1994, Schneider et al. 1999).

However, the comparison of congeneric species spatial patterns shows that the hypothesized phenomena of geographical and environmental vicariances have not affected all genera equally. Indeed, the six species of *Psychotria* have largely overlapping ranges, compared with the five species of *Garcinia* (Fig. 9). This means that diversification of congeners is not necessarily correlated with species separation in physical or environmental spaces. Several factors could explain these discrepancies. For instance, sympatric speciation could have occurred by polyploidy. An alternative hypothesis would be a high dispersal ability or low competition among congeners, as noted for *Psychotria* (Valladares et al. 2000).

Phylogenetic analyses would be necessary to test the hypotheses formulated above to explain the diversification of the endemic tree flora of the Western Ghats, notably by plotting species ecological profiles and species geographical ranges on the phylogenetic trees. The link between speciation and niche evolution could then be tested (cf. Barraclough et al. 1998). The data available for Diospyros suggest that the Indian species do not form a monophyletic group (De Franceschi 1993). If this were true for the other genera as well, Indian endemic congeneric species should be split into several groups of closely related taxa, but this would not alter the patterns identified in the present study. More information is also needed regarding the genetics and the life-history traits of Indian taxa to investigate speciation processes. For instance, De Franceschi (1993) suggests that the adaptive flexibility of Diospyros could result from its high number of chromosomes allowing frequent rearrangements. Lastly, the mean phylogenetic relatedness of taxa could be assessed along the environmental gradients of the Western Ghats, following Webb (2000) who noted that species of tropical tree communities in a stressful environment are less closely related of communities in a favorable than species environment.

### Methodological issues: perspectives

Since its first use in ecology (Austin 1968), CANCOR has been a neglected ordination method, notably because of collinearity problems and related difficulties in presentation and interpretation (ter Braak 1990). Our analyses confirm the value of CANCOR as the suitable method for collection data analysis. Conversely, herbarium records offer the most accurate information about species distribution, provided that they are numerous and evenly distributed in the area under study. Moreover, such data could be used to analyze the correlation between biological attributes of taxa and environmental factors, allowing the identification of functional diversity patterns (cf. Lavorel et al. 1999). More generally, the unifying framework of CANCOR would be especially suitable for assessing the relative roles of biological and environmental factors in the variation of species-richness between clades (cf. Barraclough et al. 1998).

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Appendix. List of species names identified by Canonical Correlation Analysis (Figs 5-8).

| Species code | Species name   | Family           |
|--------------|--|------------------|
| actiangu     | Actinodaphne angustifolia (Bl.) Nees   | Lauraceae        |
| acticaca     | Actinodaphne campanulata var. campanulata J. Hk.                             | Lauraceae        |
| actilaws     | Actinodaphne lawsonii Gamble   | Lauraceae        |
| actitadu     | Actinodaphne tadulingamii Gamble   | Lauraceae        |
| aglaelbo     | Aglaia elaeagnoidea (Juss.) Benth. var. bourdillonii (Gamble)<br>K.K.N. Nair | Meliaceae        |
| aglalawi     | Aglaia lawii (Wt.) Saldanha  | Meliaceae        |
| aporbour     | Aporosa bourdillonii Stapf.  | Euphorbiaceae    |
| ardirhom     | Ardisia rhomboidea Wt.   | Myrsinaceae      |
| bacccour     | Baccaurea courtallensis M. Arg.  | Euphorbiaceae    |
| bentcoda     | Bentinckia codapanna Berry   | Arecaceae        |
| blaccaly     | Blachia calycina Benth.  | Euphorbiaceae    |
| blacdenu     | Blachia denudata Benth.  |                  |
| buchlana     | Buehanania lanecolata Wt   | Angeardiageag    |
| byrstetr     | Bursonhullum tetrandrum (Bedd.) I. Hk. ex. Bedd                              | Rubiaceae        |
| cantnene     | Canthium neilaberrense Wt var neilaberrense                                  | Rubiaceae        |
| casewyna     | Casearia wynadensis Bedd   | Flacourtiaceae   |
| cinnripa     | Cinnamomum riparium Gamble   | Lauraceae        |
| cinnwigh     | Cinnamomum wightii Meissn.   | Lauraceae        |
| cleimala     | Cleistanthus malabaricus M. Arg.   | Euphorbiaceae    |
| diosangu     | Diospyros angustifolia (Miq.) Kosterm.                                       | Ebenaceae        |
| diosassi     | Diospyros assimilis Bedd.  | Ebenaceae        |
| diosbarb     | Diospyros barberi Ramas.   | Ebenaceae        |
| diosbour     | Diospyros bourdillonii Brand.  | Ebenaceae        |
| dioscand     | Diospyros candolleana Wt.  | Ebenaceae        |
| diosfoli     | Diospyros foliolosa Wall. ex DC.   | Ebenaceae        |
| diosghat     | Diospyros ghatensis Ramesh & De Franceschi                                   | Ebenaceae        |
| dioshumi     | Diospyros humilis Bourd.   | Ebenaceae        |
| diosnila     | Diospyros nilagirica Bedd.   | Ebenaceae        |
| diospani     | Diospyros paniculata Dalz.   | Ebenaceae        |
| diospiul     | Diospyros pruriens Dalz.   | Ebenaceae        |
| dipthour     | Diospyros saluannae Kosterin.<br>Dinterocarnus hourdilloni Brandis           | Dipterocarpaceae |
| drypconf     | Drynetes confertiflorus (I Hk) Pax & Hoffm                                   | Fuphorbiaceae    |
| elaerecu     | Elaeocarnus recurvatus Corner  | Elaeocarpaceae   |
| eugemacr     | Eugenia macrosepala Duthie   | Mvrtaceae        |
| euonangu     | Euonymus angulatus Wt.   | Celastraceae     |
| euoncren     | Euonymus crenulatus Wall. ex Wt. & Arn.                                      | Celastraceae     |
| flacmont     | Flacourtia montana Grah.   | Flacourtiaceae   |
| garcindi     | Garcinia indica (Thouras) Choisy   | Clusiaceae       |
| garctrav     | Garcinia travancorica Bedd.  | Clusiaceae       |
| garcwigh     | Garcinia wightii T. Andr.  | Clusiaceae       |
| glocbour     | Glochidion bourdillonii Gamble   | Euphorbiaceae    |
| glocjohn     | Glochidion Johnstonei J. Hk.   | Euphorbiaceae    |
| glocnell     | Glochidion nelignerrense WL.   | Apagardiagana    |
| giutitav     | Guia Indunconca Beau.  | Anacardiaceae    |
| gordobtu     | Gordonia obtusa Wall ex Wt & Arn   | Theaceae         |
| gymncana     | Gymnacranthera canarica (King) Warb  | Myristicaceae    |
| holibedd     | Holigarna beddomei J. Hk.  | Anacardiaceae    |
| homatrav     | Homalium travancoricum Bedd.   | Flacourtiaceae   |
| hopepong     | Hopea ponga (Dennst.) Mabb.  | Dipterocarpaceae |
| hoperaco     | Hopea racophloea Dyer  | Dipterocarpaceae |
| hopeutil     | Hopea utilis (Bedd.) Bole  | Dipterocarpaceae |
| humbbrun     | Humboldtia brunonis Wall.  | Fabaceae         |
| humbdecu     | Humboldtia decurrens Bedd. ex Oliv.  | Fabaceae         |
| humbvahl     | Humboldtia vahliana Wt.  | Fabaceae         |
| nyanmama     | <i>Hyanocarpus macrocarpa</i> Bedd. Warb. ssp. <i>macrocarpa</i>             | Flacourtlaceae   |
| isonperr     | Isonanara perrollellana DC.<br>Isona notoniana Wall, av. G. Don              | Pubiaceae        |
| ivorpoly     | Ixora novantha Wt  | Rubiaceae        |
| lasirost     | Lasianthus rostratus Wt  | Rubiaceae        |
| litovenu     | Litosanthes venulosus (Wt & Arn ) Deh & Gang                                 | Rubiaceae        |
| litsbour     | Litsea hourdillonii Gamble   | Lauraceae        |
| litscori     | Litsea coriacea J. Hk.   | Lauraceae        |
| litsflor     | Litsea floribunda Gamble   | Lauraceae        |
| litsglab     | Litsea glabrata J. Hk.   | Lauraceae        |
| litskera     | Litsea keralana Kosterm.   | Lauraceae        |

| InslaveLinea laceigara GambleLauraceaelisingiLinea Ingustrini J. HK.LauraceaelisingiLinea mysorensis GambleLauraceaelisingiLinea mysorensis GambleLauraceaelisingiLinea manacorica GambleLauraceaelisingiLinea virghiana (Nees) J. HK. var. tomentosa Meissn.LauraceaelisingiLineav virghiana (Nees) J. HK. var. wightianaLauraceaemammsuriMammea surige (Buch. Ham. ex Roxb.)CelastraceaemammsuriMammea surige (Buch. Ham. ex Roxb.)CelastraceaememcheynMence/olon heyneanum Benth, ex Wt. & Arn.MelastomataceaemicrinicaMichelia Aliagirica Zenk.MagnoliaceaemyrifamaMyristica fatua Houtt, var. magnifica (Bedd.) SinclairMyristica caeeechrmissOchrinaucicea fasoloris (Wall). Rand.RubiaceaecottorayOrtinaucicea missionis (Wall, ex G. Don.) Ridsd.RubiaceaeortorayOrnosia travancorica Bedd.FabaceaeplabburPalaeantharicus Bedd.FabaceaeplabburPalaeantharicus Bedd.FabaceaepithgracPittosporane deglerenses Wt. & Arn.PittosporaceaepittasyPittosporane deglerenses Wt. & Arn.PittosporaceaepsycoldPopovia beddomean J. Hk. & Thoms.AnnonaceaepsycoldPopovia beddomean J. Hk. & Thoms.AnnonaceaepsycoldPopovia beddomean J. Hk. & Arn.SubiaceaepsycoldPopovia beddomean J. Hk. & Arn.SubiaceaepsycoldPopovia beddomean J. Hk. & A  | Species code | Species name  | Family          |
|--|--------------|---|-----------------|
| <ul> <li>Itsingu Litseu ligarina J. Hk.</li> <li>Lauraceae</li> <li>Itsinyso Litseu anysorenis Gamble</li> <li>Lauraceae</li> <li>Itsitsov Litseu stockvil J. Hk.</li> <li>Lauraceae</li> <li>Itsitsov Litseu viehtiana (Nees J. Hk. yar. tomentosa Meissn.</li> <li>Lauraceae</li> <li>Itsiwito Litseu viehtiana (Nees J. Hk. yar. tomentosa Meissn.</li> <li>Lauraceae</li> <li>Itsiwito Litseu viehtiana (Nees J. Hk. yar. tomentosa Meissn.</li> <li>Lauraceae</li> <li>Itsiwito Mallotta attrotirens J. Hk.</li> <li>Euaraceae</li> <li>mammsuri Mammea suring (BuchHam. ex Roxb.)</li> <li>Clusiaceae</li> <li>maytroth Maytenus rohhana (Walp.) Ramam.</li> <li>memcheyn Menecylon hymenoamm Benth. ex Nt. &amp; Arn.</li> <li>Melastomataceae</li> <li>micrinic Microtropis microcarpa Wt.</li> <li>Celastraceae</li> <li>micrinic Microtropis microcarpa Wt.</li> <li>Celastraceae</li> <li>eofmis Ochinaucle Missionis (Wall. ex G. Don.) Ridsd.</li> <li>Rubiaceae</li> <li>cottrav Octoropis trauncorica Bedd.</li> <li>Fabaceae</li> <li>pahaemala Phacenthum ngathericus Bedd.</li> <li>Fabaceae</li> <li>pittasy Phitosopran datyzeulon Mig.</li> <li>Pittosoporaceae</li> <li>pittasy Phitosopran datyzeulon Mig.</li> <li>Pittosoporaceae</li> <li>pittasy Phitosopran datyzeulon Mig.</li> <li>Pittosoporaceae</li> <li>pittasy Pittosopran adyzeulon Mig.</li> <li>Pittosoporaceae</li> <li>pisycolat Psychotria tudicifiar UM. &amp; Arn.</li> <li>Rubiaceae</li> <li>pisycolat Psychotria tudicifiar UM.</li> <li>Araliaceae</li> <li>pisycolat Psychotria tudicifiar UM.</li> <li>Araliaceae</li></ul>   | litslaev     | Litsea laevigata Gamble   | Lauraceae       |
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| litsto Litsea stocksi J. Hk. Lauraceae<br>Litswito Litsea travancorica Gamble Lauraceae<br>litswito Litsea wightima (Nees) J. Hk. var. vightima Lauraceae<br>mallatro Mallotus atrovirens J. Hk. var. vightima Lauraceae<br>mamsuri Mannea suriga (Buch-Ham. ex Roxb.) Clusiaceae<br>mamsuri Mannea suriga (Buch-Ham. ex Roxb.) Clusiaceae<br>memeleyn Menecylon heyneanum Benth. ex Wt. & Arn. Melastomataceae<br>memelab Menecylon tabbotianum Brandis Melastomataceae<br>michnila Michelia nilagirica Zenk. Magnoliaceae<br>michnila Michelia nilagirica Zenk. Magnoliaceae<br>michnila Michelia nilagirica Zenk. Magnoliaceae<br>coltrave Octoropis microcarpa Wt. Clastraceae<br>motelise Neolitise fischeri Gamble Lauraceae<br>coltrave Octoropis travancorica Bedd. Rubiaceae<br>cotortav Octotropis travancorica Bedd. Rubiaceae<br>plababur Palaquium bourdillon Brand. Sapotaceae<br>plababur Palaquium bourdillon Brand. Sapotaceae<br>plababur Palaquium bourdillon Brand. Sapotaceae<br>pittdasy Pittosporun acgigeneae Wt. & Arn. Pittosporaceae<br>pittdasy Pittosporun acgigeneae Wt. & Arn. Pittosporaceae<br>pittdasy Pittosporun acgigeneae Wt. & Arn. Pittosporaceae<br>psycolo Psychotria adcelli J. Hk. Rubiaceae<br>psycola Psychotria midflora Wt. & Arn. Sterculiaceae<br>psycola Psychotria midflora Wt. & Arn. Sterculiaceae<br>psycola Psychotria midglora Dun. Annonaceae<br>spycola Psychotria midglora Dun. Annonaceae<br>sagegara Sageraea grandflora Dun. Annonaceae<br>sagerari Sageraea grandflora Dun. Maccaea<br>sagerari Sageraea grandflora Dun. Annonaceae<br>sagerari Sageraea grandflora Dun. Annonaceae<br>sagerari Sageraea grandflora Dun. Annonaceae<br>symptona Symplocos macrophyll Wall. ex A. DC. Sp. rosea (Bedd.) Not.<br>Symplocaceaea<br>Symptoro Symploc | litsmyso     | Litsea mysorensis Gamble  | Lauraceae       |
| listrav Lisca tracencorica Gamble Lauraceae<br>liswito Litsca wightiona (Nees) J. Hk. var. tomentosa Meissn. Lauraceae<br>mallatro Mallous attoricens J. Hk. var. tomentosa Meissn. Lauraceae<br>mallatro Mallous attoricens J. Hk. var. tomentosa Meissn. Culsiaceae<br>mammsuri Mammea suriga (Buch-Ham. ex Roxb.) Clusiaceae<br>memeheyn Menecylon heyneanum Benth. ex Wt. & Arn. Melastomataceae<br>memeheyn Menecylon heyneanum Benth. ex Wt. & Arn. Melastomataceae<br>memeheyn Menecylon heyneanum Benth. ex Wt. & Arn. Melastomataceae<br>micrimicr Microtropis microaerpa Wt. Celastraceae<br>micrimicr Microtropis microaerpa Wt. Celastraceae<br>myrifama Myristica fatua Houtt. var. magnifica (Bedd.) Sinclair Magnoliaceae<br>coltins Neolitea fischer Gamble Lauraceae<br>ochrmiss Ochrinauclea missionis (Wall. ex G. Don.) Ridsd. Rubiaceae<br>octotrav Octorapis transmoorica Bedd. Fabaceae<br>platenual Platenthis malabaricus Bedd. Fabaceae<br>phatenala Platenthis malabaricus Bedd. Fabaceae<br>phyrittegol Plitosportum neelfgherrense Wt. & Arn. Pittosporaceae<br>psyciola Psychotria malfifora Mit. & Arn. Rubiaceae<br>psyciola Psychotria malfifora Mit. & Arn. Sterculiaceae<br>psyciola Psychotria malfifora Mit. & Arn. Sterculiaceae<br>sagegara Sageraea gandfifora Dun. Annonaceae<br>sagegara Sageraea gandfifora Dun. Annonaceae<br>sagegara Sageraea gandfifora Dun. Annonaceae<br>sagegara Sageraea gandfifora Dun. Annonaceae<br>sagegara Sageraea gandfifora Dun. Annonaceae<br>sapport Symploces macrophylla Wall. ex A. DC. sp. neare   | litsstoc     | Litsea stocksii J. Hk.  | Lauraceae       |
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| mallato       Mallotis atrovieries J, Hk.       Euphorbiaceae         mammsuri       Mamnea suriqa (Buch, Ham, ex Roxb.)       Clusiceae         maytroth       Maytenus rothiana (Walp.) Raman.       Celastraceae         memethyn       Mencylon heyneanun Benth, ex Wt. & Arn.       Melastomataceae         micmichia       Micnoropis microcarpa Wt.       Celastraceae         micrmicr       Microtropis microcarpa Wt.       Celastraceae         myrifama       Myristica fatua Houtt. var. magnifica (Bedd.) Sinclair       Myristicaceae         ochrmiss       Ochrinauclea missionis (Wall. ex G. Don.) Ridsd.       Rubiaceae         octoray       Ormosia traancorica Bedd.       Fabaceae         ormotrav       Ormosia traancorica Bedd.       Fabaceae         pithary       Pitosoporum dasycaulon Miq.       Pittosoporaceae         pithary       Pitosoporum dasycaulon Miq.       Pittosoporaceae         popobedd       Popovia beddomeana J. Hk. & Thoms.       Annonaceae         psycylob       Psychorir adlifora Wt. & Arn.       Rubiaceae         psycylob       Psychorir adlifora Wt. & Arn.       Rubiaceae         psycylob       Psychorir adlifora Wt. & Arn.       Rubiaceae         psycylob       Psychorir adlifora Wt. & Arn.       Sterculliaceae         psycylob <td>litswiwi</td> <td>Litsea wightiana (Nees) J. Hk. var. wightiana</td> <td>Lauraceae</td>   | litswiwi     | Litsea wightiana (Nees) J. Hk. var. wightiana                           | Lauraceae       |
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| verntrav Vernonia travancorica J. Hk. Asteraceae<br>vibuheba Viburnum hebanthum Wt. & Arn. Caprifoliaceae  | termtrav     | Terminalia travancorensis Wt. & Arn.                                    | Combretaceae    |
| vibuheba Viburnum hebanthum Wt. & Arn. Caprifoliaceae  | verntrav     | Vernonia travancorica J. Hk.  | Asteraceae      |
|  | vibuheba     | Viburnum hebanthum Wt. & Arn.   | Caprifoliaceae  |