**Landscape context and local-scale environmental influences on the regeneration of tree species in neotropical forests treefall gaps**

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**Running title:** gaps, landscape, and microenvironment.

**ABSTRACT**

Composition of pioneer species was recorded in 23 to 76 treefalls in the forests of La Selva (LS), Barro Colorado Island (BCI), Cocha Cashu Research Station (CC) and Km41, in order to evaluate the hypothesis that distance to secondary forests which can act as seed sources influences the composition of pioneer tree species at scales of thousands of hectares, and to assess the relative importance of distance to seed sources compared to two microenvironmental factors: soil and gap size. Discriminant Function Analysis (DFA) was used to assess the relative importance of the landscape and environmental factors in controlling the presence in Gaps of *Cecropia* species that are typical of secondary forests originated in large-scale disturbances. Principal Component Analysis (PCA) was used as an ordination technique based on pioneer species composition of each gap. The PCA ordination axes were regressed against the soil, size, and forest type and distance values of each site in order to explore the relationship between composition and control factors. In the four sites, the variable best correlated to the discriminant function of gaps with and without *Cecropia* was the distance to secondary forests, although such discriminant function was statistically significant in only one site. In three of the four sites (with the exception of BCI where there are no typical young secondary forests), distance to secondary forests was correlated with at least one of the axes of the PCA at significance levels < 0.06. Other significant correlations included soil variables (CC and Km 41), gap size (Km 41) and forest type (secondary vs primary, BCI). Overall, the results provide some support for the hypothesis that at the spatial scale of this study, distance to forests originated in large scale disturbances (both natural and anthropogenic) have an influence on treefall

gap composition comparable to endogenous and exogenous microenvironmental

factors.

**RESUMEN**

Se estudió la composición de 23 a 76 claros por caída de árboles en los bosques

tropicales de La Selva (LS), Isla de Barro Colorado (BCI), Estación Biológica Cocha

Cashu (CC), y Km. 41, para evaluar la hipótesis que la distancia a bosques secundarios

que pueden actuar como fuentes de semilla influye en la composición de especies

pioneras en claros a escalas espaciales del orden de pocos miles de hectáreas, y para

evaluar la importancia relativa de la distancia a los bosques secundarios en

comparación con dos factores microambientales: suelo y área del claro. Se usó Análisis

de Funciones Discriminantes (DFA) para evaluar la importancia relativa de los distintos

factores como controladores de la presencia en claros de especies de *Cecropia* que

son características de los bosques secundarios. Se utilizó Análisis de Componentes

Principales (PCA) como una técnica de ordenamiento basada en la composición de

especies pioneras en los claros.  Para evaluar la relación entre los factores ambientales

y la composición de especies se realizaron regresiones entre los scores en los ejes

mas importantes del PCA y los valores de cada variable. En los cuatro sitios, la variable

mejor correlacionada con la función discriminante de presencia y ausencia de *Cecropia*

*spp* fué la distancia a los bosques secundarios, aunque en solo uno de los cuatro sitios

esta función fue estadísticamente significativa. En tres de los cuatro sitios (con la

excepción de BCI que no tiene bosques secundarios jóvenes típicos) al menos uno de

los ejes principales se correlaciono con la distancia al bosque secundarios a valores de probabilidad < 0.06. Otras correlaciones significativas incluyen suelos (CC y Km 41), tamaño del claro (Km 41), y tipo de bosque (secundario vs primario, BCI). En general los resultados apoyan parcialmente la hipótesis de que a la escala espacial del estudio, la distancia a bosques secundarios juega un papel en la composición de especie en los claros comparable a la de factores microambientales endógenos y exógenos.

**Keywords:** Cecropia, dispersal limitation, disturbances, forest dynamics, treefall gap.

LOCAL-SCALE SPECIES' REGENERATION is affected by the interaction of physical microenvironment and the biotic microenvironment which in turn is strongly influenced by the disturbances (Grubb 1977).  Among the physical factors, in tropical ecosystems, soil fertility is recognized as a major control of species composition (Huston 1994), whereas treefall gaps are recognized as the single most important type of endogenous disturbance in tropical forests. The intermediate disturbance hypothesis (Connell 1978, Huston 1979) indicates that treefalls should promote the coexistence of species having different resource use strategies (particularly light) and that differences in treefall regime should be reflected on differences in species diversity.  In support of this hypothesis, several studies found differential species responses to microenvironmental conditions produced by treefalls (Denslow 1987, Brokaw 1987, Veblen 1992, Brokaw and Busing 2000), being gap-size the best single descriptor of the intensity of this type of disturbance.

On the other hand, recent analyses of community-scale floristic patterns in tropical forests show little relationship with descriptors of treefall gap regimes. An extensive study based on a 50-hectare permanent plot in a tropical forest in Panama found no relationship between canopy disturbances frequency, and species richness at the scale of 20 by 20 meters. Species composition in treefall gaps was not predictable from descriptors of the treefall regime even for pioneer species (Hubbell et al. 1999). This study contradicts the intermediate disturbance hypothesis. Instead, it suggests the potential importance of recruitment limitation, in which a species fails to recruit in all the sites favorable to its germination, growth and survival. Thus, due to lack of timely dispersal into a site, recruitment defaults to species that may not be the best adapted for that microsite (Tilman 1994, Hurtt and Pacala 1995). This is expected to slow competitive exclusion, and potentially explains the lack of association between species composition and descriptors of the treefall gap regime (Hubbell et al. 1999, Brokaw and Busing 2000).

In addition to local environmental characteristics, species composition in a particular site is influenced by the pool of species in the surrounding area ("mass effect" or "vicinity", Shmida and Willson 1985, van der Maarel 1994). The capacity of colonizing a "safe site" (such as a canopy opening) is a function of the abundance of the safe sites and the availability of propagules (Harper 1977). Recent studies in different ecosystems have shown the importance of dispersal limitation in controlling local scale composition of successional communities (e.g. Butaye et al. 2002, Tofts and Silvertown 2002). Since treefalls are relatively small in relation to the undisturbed forest and provide differential environmental conditions during a limited period of time, availability of propagules from nearby trees is likely to be relatively important in controlling

colonization. For example, Grau (2002) found in NW Argentina subtropical forests that new treefalls are more likely to occur in the proximity of previous ones, and that the aggregations of treefalls at scales of 1000 to 2500 square meters do increase species richness, probably by reducing the dispersal limitation of pioneer trees into newly created treefall gaps. Consistently, Dalling et al (2002) found that the colonization of treefalls by pioneer species in Barro Colorado Island is limited by seed availability.

In addition to treefall gaps, many tropical forests are affected by larger scale disturbances such as extensive windblowns or meandering rivers (Clark 1991) that are typically colonized by pioneer species.  Given the growing effect of human activities, post agriculture or post grazing successional forests may also act as potential seed sources for colonizing treefall gaps in the mature forests (Janzen 1983). Consequently, tree species composition in mature forest treefalls, can potentially be affected by the distance to forest originated in larger-scale disturbances occurring in the proximity.  This paper aims to assess the effect of distance to secondary forests (both originated in human activities and large-scale natural disturbances) on the composition of pioneer species in treefalls.

One of the most common gap-dependent Neotropical tree genera is *Cecropia*. *Cecropia* trees are characterized by high growth rates, and short life spans (Denslow 1987).  Studies on *Cecropia obtusifolia*, one of the species included in this study, have shown that seed germination is trigged by light conditions occurring in treefall gaps (Vazquez-Yanez & Smith 1982).  About 50% of the seeds germinating in treefall gaps are recently dispersed seeds and the other 50% originate in short-living seed banks (Alvarez-Buylla and Martinez-Ramos 1990).  In Panama, *Cecropia insignis* had the shortest median dispersal distance over 14 species analyzed (Dalling et al. 2002.)

Two hypotheses were tested: 1) proximity to secondary forests originated both in river banks, windblowns and human disturbances increases the chances of treefall gaps being colonized by pioneer species of the genus *Cecropia* which dominate these secondary forests and 2) distance to these external sources of seeds is comparable to local microenvironmental characteristics in terms of controlling the composition of treefall gaps pioneer tree communities.

**METHODS**

DATA COLLECTION - The study was conducted in four tropical rainforest sites: La Selva Biological Station, Costa Rica (LS); Barro Colorado Island, Panama (BCI); Cocha Cashu Research Station, Manu National Park, Peru (CC); and Km 41 camp site, Biological Dynamics of Forest Fragments Project, Amazonia, Brazil (Km41). Details on location, environmental characteristics, vegetation and animal communities, and ecological characteristics are provided in Gentry (1990), Mc Dade et al. (1994), Leigh (1999), and Bierregard et al. (2002).

Between September and November 2001, treefalls of trees larger than 60 cm of diameter at the trunk base with an estimated age between a few months and approximately 10 years were surveyed along trails in the four sites. Distance to secondary forests (ranging from 0 to 2000 meters) was estimated on the basis of GPS readings and map location. At LS the secondary forests were post-pasture 20-30 years old secondary forests (Hartshorn and Hammell 1994). At BCI the secondary forest was an area of several hundreds of hectares affected by a severe windblown in the late

eighties, located south of the 50-hectares plot around Drayton trail (Joseph Wright, personal communication). At CC, the secondary forests are typical successional forests in the river banks originated by the combination of floods and fluvial geomorphology (Foster 1990). At Km41, secondary forests are the *Cecropia* dominated stands that occur along the main road which are similar in composition to non-degraded post-human disturbance secondary forests (Mesquita et al. 2001). These secondary forests varied in size, but included abundant individuals of the *Cecropia* species considered, and at least some of the other pioneer species considered in the analysis.

At each treefall, the abundance of a selected group of pioneer trees was recorded (Appendix A). Two criteria were considered to include the species: 1) they where clearly pioneer species, based on the opinion of local experts and my own observations on distribution (i.e. juveniles were not found in the absence of canopy openings), and 2) they where easy to identify based on vegetative characters. Length of the gap-maker tree from the base to a stem diameter of 30 cm was measured as a proxy for gap size. When multiple treefalls occurred in one site, I followed two criteria. If stems where in touch, I considered only the larger one. If stems where not touching each other, I considered it as separate treefall gaps.

Soil type was classified into two discrete categories in three of the four sites (alluvial and residual at LS, flooded and terrace in CC, sand and clay in Km41). Soil classification was derived from soil maps for LS, from local observations of topography and understory composition in CC, and soil texture visual analysis and topography in Km41. At BCI two variables potentially related to soils were considered: topography in three categories (ridges, slope and valley bottom) and forest age (primary vs

secondary-more than 100 years old-, based on local topographic and forest history maps).

Species' identification was based on comparisons with local herbarium for LS, BCI and CC, and Ribeiro et al (1999) for Km 41, and complemented with local experts opinions.

DATA ANALYSIS - For the species of *Cecropia* that occur in secondary forests and in gaps of mature forests, I tested if their presence in treefall gaps was significantly affected by the distance to secondary forests, by using Discriminant Function Analysis (DFA, Gardiner 1997). DFA uses a least squares approach to produce the function of the variables which best predicts group classification (presence *versus* absence of *Cecropia sp* in this analysis). Each independent variable (soil type, distance to secondary forest, and gap size in this analysis) has a discriminant function coefficient that can be interpreted as the standardized load of the variable in the discriminant function equation. Soil/topography variables in this analysis were treated as discrete variables with arbitrary values of 0,1. The significance of the analysis is tested by running a regression between the independent variables and the discriminant function equation, and by a Chi-square test that compares the group classification produced by the DFA with the classifications expected by chance. Additionally, a Kruskall-Wallis non parametric test was used to compare the values of the variables in gaps with and without *Cecropia*.

Principal Component Analysis ordination (PCA, Legendre and Legendre 1998) based on pioneer species composition was performed for each site using individual treefalls as samples. PCA was preferred as an ordination technique because it

assumes a linear relationship with the underlying environmental gradient, which is consistent with the expected pattern of composition related to distance to seed sources. For comparative purposes, Correlation analysis was performed between the scores in the ordination axes of each sample (treefall) and the variable values, in order to compare the strength of the relationships between the environmental and distance variables, and species composition. For discrete variables (soils, forest type for BCI), scores of the plots with different characteristics were compared by means of a Kruskall-Wallis non parametric test. Ordination Analysis was performed using CANOCO version 4 (all default options for PCA), and statistical analysis was performed using SPSS version 6.1.

**RESULTS**

A total of 23 treefalls were surveyed at LS, 52 at BCI, 76 at CC , and 54 at Km 41.  For the same sites respectively, 7, 7, 14 and 15 species were considered for the analysis. Details on species composition in treefalls at the different sites are presented in Appendix A. Distance to secondary forests ranged from 0 to 2000 m, gap maker-length ranged from 12 to 55 m.

Of the four sites, Only at Km 41 the discriminant function derived from the DFA for gaps with and without *Cecropia* was highly statistically significant, whereas in CC was marginally significant (p=0.056). In the four sites, the distance to secondary forests was the variable best correlated with the discriminant function with values of correlation coefficient ranging from 0.62 to 0.84.  In the four sites distance to secondary forests of

gaps with the selected *Cecropia* species was shorter than the mean distance of gaps

without *Cecropia.* The Kruskall-Wallis comparison showed that only at CC these

differences were statistically significant. In the case of Km 41, gaps with and without

*Cecropia* differed significantly both in gap-maker length and in soil type (Table 1).

At BCI and Km41, more than 90% of the variance was explained by the first two

axes of the Principal Component Analysis, whereas at CC, and LS, the third axes still

explained about 10 % of the variance. Correlations between variables and PC axes are

presented in Figure 1. Soil type was significantly correlated to the first principal

component (PC-1) in Km 41 and CC. Gap-maker length was significantly correlated with

PC-1 in Km 41 and correlated at 0.053 probability level with PC-2 in BCI. Also in BCI,

PC-1 was significantly correlated with forest age (primary vs secondary). Distance to

secondary forests correlation with the PC-2 was significant at levels close to 0.05 in CC

and Km 41 and at LS, these variable was strongly ( r> 0.5) and significantly (p = 0.008)

correlated with the PC-3 which, however, explained only approximately 10 % of the

variance.

**DISCUSSION**

Although the statistical significance of the DFA was generally low, they showed a

consistent pattern of a higher correlation coefficient between the Discriminant Function

and the distance to secondary forests than between the Discriminant Function and the

other variables (Table 1).  This suggests that for the target species of *Cecropia*,

distance to forests originated in large scale disturbances may be an important factor

controlling their presence in treefall gaps providing some support for prediction 1. When the density of trails allowed intensive sampling in areas relatively close to secondary forests (i.e. less than 500 m along a complete gradient of distances, CC and Km41), is when this relationship was clearly documented. These results coincide with recent studies in tropical (e.g. Grau 2002, Dalling et al. 2002) and extratropical environments (e.g. Butaye et al. 2002, Tofts and Silvertown 2002) which emphasize the importance of the available species pool and the spatial dynamics of disturbances in regulating the capacity of pioneer species to colonize a treefall gap. Since pioneer species as *Cecropia spp* are characterized by fast growth rates, if present, they tend to dominate the treefall potentially affecting the microenvironmental and competitive conditions for other species in the gap. Given the strong dependence of Cecropia on seed dispersal due to the short longevity in the seed bank (Alvarez-Buylla and Martinez-Ramos 1990), and the short median dispersal distance (Dalling et al. 2002) distance to secondary forests can affect the composition and dynamics of treefalls (Janzen 1983).

The results of the PCA also suggest that the distance to secondary forests plays a role in controlling pioneer communities composition in treefall gaps. Although I did not evaluate the presence of these species in the secondary forests, by being strongly light demanding species, they area likely to occur in larger densities there. Beyond the levels of significance the statistical tests and the limitation of such analysis due to multiple comparisons, the correlations between the ordination axes and distance to secondary forests was comparable to the correlations with the microenvironmental variables, which have been typically recognized as relevant factors controlling regeneration in treefalls (Denslow 1987, Veblen 1992), thus providing support for prediction 2. Correlations between distance to secondary forests and PC-1 was in

general lower than the correlations with soil variables, but the correlations between distance and second and third PC axes of ordination was consistently high in three of the four sites. Only in BCI there were no correlations with distance to secondary forests approaching statistical significance. This can be partially explained by the fact that the secondary forest considered in BCI is a post windblown patch with a very heterogeneous composition, and because other similar types of disturbances occurred across the island potentially producing similar effects in terms of providing seed sources for pioneer species.  La Selva is the site that showed the lower levels of significance in the correlation with the ordination axes, probably because of the low sample size.

In the other three sites ordination axes showed associations with variables affecting edaphic conditions. In BCI there were significant differences between gaps in the primary and secondary forests. These may be associated to edaphic differences (secondary forests recovered from anthropogenic pastures of the XIX century) or due to differences in the treefall regime (primary forest seems to have a more open canopy in general, probably due to higher frequency of large treefalls).

At CC, treefalls in the lower flooded areas differed in composition from the gaps occurring at locations in the micro topography less affected by floods. One potential explanations for this pattern is the differential tolerance to flooding or high water table of the pioneer species.  Another potential factor is the competition with understory plants: in the flooded areas the understory is dominated by monocotiledoneae plants (mostly Heliconiaceae, Marantaceae, and Zingiberaceae) that produce a dense cover with low light availability and low seedlings recruitment. In these microenvironments the effects of treefalls is not so much one of opening the tree canopy but one of disrupting the understory providing a smaller scale increase in light availability and less competition

with advanced regeneration, two factors that can influence differential performances in pioneer species.

Soil differences in Km41 were often associated to differences in topography, since clay soils tend to occur in plateaus and sandy soils occur in concave reliefs (*baixios*). Therefore, their influence on species composition may be attributed to differences in both nutrient and water availability. Differences in pioneer composition depending on gap size have been extensively documented (see reviews in Denslow 1987, Veblen 1992, Brokaw and Busing 2000), and were also found in this study.

Overall, despite limitations due to sample sizes, differences in logistics to conduct the study (e.g. differences in the trail system of the different sites), and differences in landscape spatial configuration, the study provided some support to the general hypothesis that at the scale of the study (1000-2000 has in the different sites) distance to secondary forests that can act as potential seed sources has an effect on species composition of treefall gaps that is relatively comparable to both the effect of exogenous microenvironmental factors such as soil/topography and endogenous microenvironmental factors such as gap size.  This result implies that studies looking at local-scale effects of treefall regimes (e.g. Welden et al 1991, Lieberman et al. 1995, Hubbell et al 1999) are missing a major factor controlling species composition: the effect of spatial configuration controlling seed input.

Treefall gaps have received a strong attention as potential contributors to the maintenance of tropical species richness (Rickelfs 1977, Connell 1978, Huston 1979), Brokaw 1987).  Dispersal limitation is supposed to reduce the effect of local environmental conditions on species composition if the species best adapted to a particular microenvironment are not available (Tilman 1994, Hurt and Pacala 1995).

Since colonization of treefall gaps (and consequently its role in maintaining diversity) is partially dependent on the distance to forest originated on larger scale disturbances, future research should focus on the spatial interactions between treefall gaps and other disturbances such as windblown, river banks, and anthropogenic deforestation (which has important implications for the ecological dynamics of fragmented and protected areas, Janzen 1983), as well as the spatial relationships among treefalls of different ages (Grau 2002).

## ACKNOWLEDGMENTS

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**TABLES**

Table 1. Discriminant Function Analysis of gaps with and without *Cecropia* based on distance to secondary forests, gap-maker length, and soil type at the four sites. r = Pearson's correlation coefficient between the variables and the discriminant function. DF coefficient = Standardized discriminant function coefficient of each discriminating variable. Mean = mean value of each independent variable in the with and without *Cecropia* classes. Values in parentheses indicate significant level of Kruskall-Wallis test of the differences in the variable values between gaps with and without *Cecropia*.

La Selva. $X^2 = 1.4$, p = 0.69

| Variable | r | DF coefficient | Mean with | M. without (p) |
|---|---|---|---|---|
| Distance | 0.84 | 0.75 | 291 | 489 (0.29) |
| Gap length | -0.64 | -0.52 | 36 | 19 (0.40) |
| Soil type | 0.59 | 0.04 | .52 | .46 (0.39) |

BCI. $X^2 = 2.3$, p=0.50

| Variable | r | DF coefficient | Mean with | M. without (p) |
|---|---|---|---|---|
| Distance | 0.62 | 0.56 | 1080 | 1280 (0.33) |
| Gap length | -0.55 | -0.73 | 28 | 26 (0.39) |
| Topography | 0.41 | 0.61 | 1.5 | 1.6 (0.55) |

Cocha Cashu. $X^2 = 7.6$; p = 0.056

| Variable | r | DF coefficient | Mean with | M. without (p) |
|---|---|---|---|---|
| Distance (m) | 0.7 | 1.21 | 899 | 1240 (0.046) |
| Gap length | 0.03 | -0.15 | 30.4 | 30.1 (0.96) |
| Soil type | 0.17 | 0.8 | .25 | .19 (0.23) |

Km 41 $X^2 = 26.8$ ; p<0.001

| Variable | r | DF coefficient | Mean with | M. without (p) |
|---|---|---|---|---|
| Distance (m) | 0.80 | -0.35 | 538 | 711 (0.22) |
| Gap length | 0.51 | 0.80 | 43.3 | 25.8 (0.01) |
| Soil type | -0.20 | 0.56 | .52 | .34 (0.03) |

**FIGURE CAPTIONS**

Figure 1. Correlation coefficients between different environmental and distance factors, and the ordination axes of a Principal Component Analysis based on pioneer species composition in treefall gaps. Numbers on the top of the bars indicate statistical significance levels of the correlations. Factors in the x axis: 1= Distance to secondary forests, 2= gap size, 3=soil type, 4=forest successional type.

## APPENDICES

| Sp | Family | Site | Rel.frec. | Abundance |
|---|---|---|---|---|
| Urera caracasana | Urticaceae | CC | 47 | 62 |
| Urera laciniata | Urticaceae | CC | 3 | 2 |
| Jacaratia caracasana | Caricaceae | CC | 42 | 45 |
| Cecropia polystachia | Cecropiaceae | CC | 18 | 36 |
| Cecropia sciadophylla | Cecropiaceae | CC | 1 | 1 |
| Luahea grandiflora | Tiliaceae | CC | 7 | 5 |
| Ochroma pyramidalis | Bombacaceae | CC | 18 | 26 |
| Triplaris americana | Polygonaceae | CC | 2 | 16 |
| Sapium marmeri | Euphorbiaceae | CC | 74 | 123 |
| Miconia elata | Melastomataceae | CC | 8 | 7 |
| Pouruma cecropifolia | Cecropiaceae | CC | 13 | 11 |
| Guazuma crinita | Ulmaceae | CC | 15 | 14 |
| Trema micrantha | Ulmaceae | CC | 2 | 2 |
| Matisia cordata | Bombacaceae | CC | 3 | 2 |
| Cecropia insignis | Cecropiaceae | BCI | 55 | 118 |
| Pouruma aspera? | Cecropiaceae | BCI | 1 | 5 |
| Zantoxylon sp | Rutaceae | BCI | 2 | 1 |
| Laetia procera | Flacourtiaceae | BCI | 16 | 7 |
| Trema micrantha | Ulmaceae | BCI | 18 | 9 |
| Ochroma lagopus | Bombacaceae | BCI | 4 | 4 |
| Jacaranda copaia | Bignoniaceae | BCI | 10 | 8 |
| Cecropia obtusifolia | Cecropiaceae | LS | 39 | 12 |
| Pouruma aspera | Cecropiaceae | LS | 39 | 19 |
| Laetia procera | Flacourtiaceae | LS | 30 | 5 |
| Caesaria arborea | Flacourtiaceae | LS | 30 | 9 |
| Trema micrantha | Ulmaceae | LS | 22 | 5 |
| Ochroma lagopus | Bombacaceae | LS | 10 | 2 |
| Castilla elastica | Moraceae | LS | 13 | 3 |
| Miconia dispar | Melastomataceae | km41 | 18 | 12 |
| Miconia pyrifolia | Melastomataceae | km41 | 2 | 1 |
| Miconia biglandulosa | Melastomataceae | km41 | 11 | 13 |
| Yrianthera sp | Miristicaceae | km41 | 5 | 3 |
| Vismia sp | Clusiacee | km41 | 5 | 3 |
| Palicourea guianensis | Rubiaceae | km41 | 11 | 6 |
| Cecropia distachia | Cecropiaceae | km41 | 7 | 2 |
| Cecropia purpurescens | Cecropiaceae | km41 | 7 | 5 |
| Cecropia sciadophylla | Cecropiaceae | km41 | 7 | 25 |
| Aparisthimum cordatum | Euphorbiaceae | km41 | 5 | 3 |
| Pouruma ferruginea | Cecropiaceae | km41 | 2 | 2 |
| Pouruma tomentosa | Cecropiaceae | km41 | 2 | 1 |
| Pouruma cecropifolia | Cecropiaceae | km41 | 5 | 3 |
| Streptodendron pulcherrimum | Mimosaceae | km41 | 2 | 1 |
| Goupia glabra | Celasteraceae | km41 | 7 | 7 |

Appendix A. Species considered in the analysis, botanical families, sites where they

were recorded, Relative frequency (gaps in which they were present / total number of
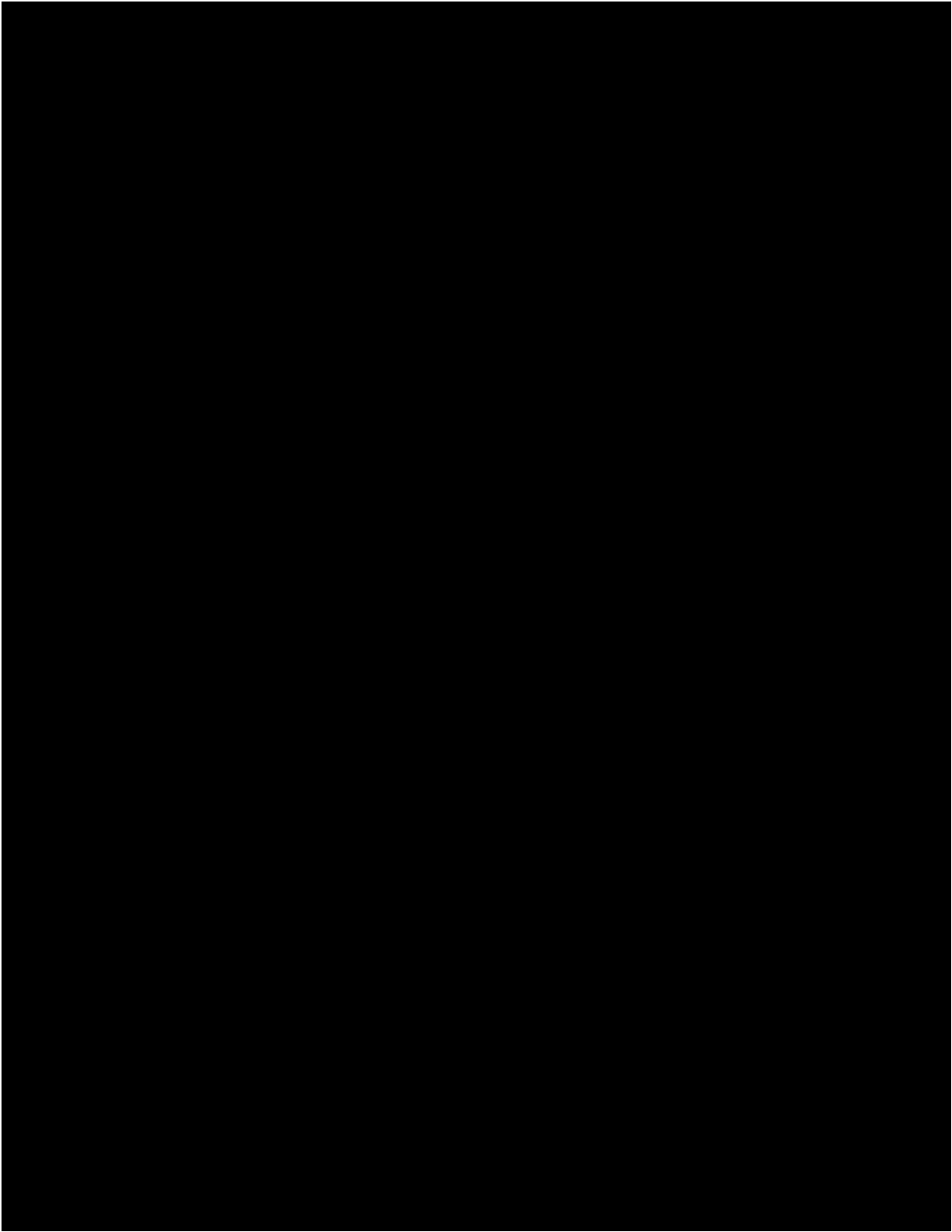
gaps), and total abundance recorded at the site.

Figure 1