# Population structure and recruitment of an emergent tree, *Dipteryx micrantha*, in different habitats of a Peruvian floodplain forest

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## Abstract

To test the hypothesis that *Dipteryx micrantha* is a species that regenerates in late successional forests, we inventoried 398 ha of forest in different successional stages along the Manu River. We found no significant differences in densities of seedlings and saplings between mature and late successional forests, indicating that *D. micrantha* recruits in both forest types.  Densities of poles and juveniles also appeared similar. The results show that the decline in the number of individuals from seedlings to juveniles, and from saplings to juveniles was not different between mature and late successional forest. Higher densities of all size classes were found in the margins of lakes and swamps than in the forest interior.   The mature forest in the immediate vicinity of the Cocha Cashu biological station had significantly higher densities of adults, seedlings and saplings than the mature forests along the Manu River in general.

## Introduction

Amazonian floodplain forests typically present a dynamic mosaic of different habitats at a landscape scale (tens to thousands of meters). Laterally advancing river erosion leaves behind sequential bands of successional forests. Gradual sedimentation slowly creates relatively high ground where forests experience less severe floods, and sedimentation can also block drainage so that permanently wet swamps appear. Additionally, swamps are formed in oxbow lakes and flood channels that are gradually filled by sediments and grown over by vegetation (Huber 1906, Terborgh 1983, Encarnación 1985, Foster et al. 1986, Salo et al. 1986, Foster 1990).

Rivers and floodplains have always been important routes of traffic and areas for settlement in Amazonia and therefore floodplain forests have been utilized quite heavily. Consequently, there are few places where it has been possible to study natural sequential forest succession in Amazonian floodplains. A rare example of a relatively untouched floodplain is that of Manu River in southern Peru. Over the last century, the area has remained relatively uninhabited and has apparently only experienced some

extraction of rubber during the early 20thcentury and of mahogany and cedar during the 1960's. This area also has a relatively long history of continuous biological research due to the presence of Cocha Cashu biological station (Terborgh 1990). Accordingly, our idea of forest succession in Amazonian floodplains is very much based on observations from this particular river.

The succession that starts from the point bars of the laterally moving river channel has been described to have three or four stages of forest vegetation (Terborgh 1983, Foster et al. 1986, Salo et al. 1986, Foster 1990). The first phase is dominated by a single rather low-stature tree species, *Cecropia membranacea* Trécul (Cecropiaceae). This becomes replaced rather quickly by a more species-rich forest characterized by two big canopy trees, *Ficus insipida* Willd. (Moraceae) and *Cedrela odorata* L. (Meliaceae). After the disappearance of these two species, in the late successional forests, no tree species can be said to clearly dominate the canopy. This phase develops somewhat fuzzily into the mature phase, which is also called high ground forest as its elevated ground is reached by water only during high floods that do not necessarily occur every year. According to Terborgh (1983), one of the most prominent tree species in the mature forest is *Dipteryx micrantha* Harms (Leguminosae, Papilionoideae), which appears to be relatively abundant (0-6 individuals/ha, Cintra 1997).At Cocha Cashu the abundance is so high that the forest has been called as a *Dipteryx-Quararibea* forest (Janson and Emmons 1990). The species attains emergent heights of 50-60 meters.

*Dipteryx micrantha* is an important species because its large size creates large tree fall gaps that allow the regeneration of those species that require such large open areas. It is also important for the bird and mammal fauna. At least in southwestern Amazonia, it is one of the main tree species used as a nest site by the largest birds of prey (*Harpya harpyja* and *Morphnus guianensis*; A. Fernandini pers. com.) and macaws (*Ara* spp.; Nycander et al. 1995). Furthermore, its fruits area key resource for canopy bats during the dry season (Romo 1996) and are also an important food item for other animals like squirrels (*Sciurus* spp.) and agoutis (*Dasyprocta* spp.; Emmons 1984, Forget 1993).

Foster et al. (1986) and Foster (1990) have hypothesized that the regeneration of emergent tree species like *D. micrantha* in mature forests along the Manu River is dependent on the conditions of thin canopy in combination with a low level of root competition. According to Foster, these requirements would very rarely exist within the mature forest itself. Instead, they are met in successional forests below the thin and low canopy of *Cecropia*, in the frequent gaps caused by big fallen-down *Ficus* and *Cedrela* trees, and possibly also along lake margins where light enters laterally. However, recently, Romo and Tuomisto (2004) have found that seedlings of *D. micrantha* can survive well under low light conditions.

The hypothesis of Foster et al. (1986) and Foster (1990) of the regeneration conditions of emergent trees in Amazonian floodplain forests can be seen as a special case of the more general hypothesis that emergent trees are actually late to very late successional species which can not regenerate within climax forests (Jones 1955, Schulz 1960, Budowski 1965, Knight 1975). The special attraction of studying the relationships between forest succession and regeneration in Amazonian floodplains is that forest patches in different phases of succession are spatially segregated at a landscape resolution, not only as relatively small canopy gaps created by tree falls.

Studies relating the regeneration of emergent tropical trees to different habitats or successional stages are few, presumably mainly because young saplings recruiting to reproductive age are typically very rare. It is a significant problem to find enough recruits for making any relevant deductions of the conditions that promote their success. To our knowledge, the only such studies on the regeneration and recruitment of emergent Neotropical rain forest trees are those from Costa Rica by Clark & Clark (1987, 1992).

The first aim of the present study is to test the hypothesis that *Dipteryx micrantha* is a late successional species. For this purpose, we have made an extensive field inventory in the floodplain forests of Manu River to sample sequential forest patches representing different phases of succession, and to count individuals of *Dipteryx micrantha* in them. Higher densities of young trees in late successional forests than in mature forests would indicate a preference for regeneration in the former.

The second aim of the present study is to compare the population structure of *Dipteryx micrantha* in the immediate surroundings of Cocha Cashu to that elsewhere in Manu river floodplain forests. This question is relevant because different aspects of the reproductive biology of *D. micrantha* – including seed predation and dispersal, seedling growth and survival and regeneration (Foster et al. 1986, Foster 1990, Romo 1996, Romo et al. 2004) – have only been studied within the immediate surroundings of the biological station at Cocha Cashu. These results can reliably be assumed to be valid over a larger area only if the structure and density of the *D. micrantha* population observed at Cocha Cashu is a typical representative of the populations in the Manu River floodplain forests in general.

## Materials and methods

### Study site

The study was conducted at Cocha Cashu Biological Station (11°54' S, 71°18' W, 400 m.a.s.l.) and along the Manu River, in Manu National Park in southeastern Peru. The study area (Fig. 1) formed a 53 km long strip along the Manu River and covers an area of ca. 600 km$^2$. At Cocha Cashu, the mean annual temperature is 23-24 °C and the annual precipitation 2000 mm. Normally, rainfall is concentrated in the rainy season (November-May), with around 300-600 mm falling in the dry season, but considerable variation in rainfall can occur among years.

### Field inventories of *Dipteryx micrantha*

One of us (MR) made field inventories of *Dipteryx micrantha* during the dry seasons of three consecutive years (September-October of 1998, 1999, and 2000) using two different sampling schemes. In both schemes, individuals of *D. micrantha* were carefully searched for. In the first one, the search was made within one block of forest along the trail system of Cocha Cashu biological station. In the second scheme, the search was carried out along inventory lines in widely dispersed sites along the Manu River. In both methods, all individuals of *Dipteryx micrantha* were counted and classified into five different size classes: seedlings (<1 cm stem diameter), saplings

(stem diameter $\geq$ 1 cm and <4 cm), poles (diameter at breast height, dbh, $\geq$4 cm and <10 cm), juveniles (dbh $\geq$10 cm and <40 cm), and adult trees (dbh $\geq$40 cm). Trees larger than 40 cm dbh were considered as adults since that was the minimum size observed for reproductive individuals (pers. obs. from 123 individuals in Cocha Cashu). For adult trees, diameters of individual trees were also measured as follows: when a tree had buttresses higher up than 135 cm, the diameter refers to the height where the buttresses end. When they ended so high up that it was not possible to directly measure the diameter, two independent observers estimated the diameter and the average of these estimations was taken as the final measurement.

The exhaustive search at Cocha Cashu covered late successional forests (including the *Ficus-Cedrela* forests as distinguished by M. Foster) and mature forests. Seedlings and saplings were searched to a distance of 3 m on each side of the trails in the station's permanent trail system. Poles were searched to a distance of 20 m, and juveniles and adults to a distance of 30 m on each side of the trails. When a trail followed the margin of a lake or a swamp, the width of the side of the inventory line against the margin was, on average, 10 m.

In distributing inventory lines along the Manu River, the intention was to sample roughly equal amounts of forests representing the late successional and mature stages, to include as many lake margins as possible, as well as to have some samples representing young successional forests as well. In order to find these locations and to avoid swamps, unflooded terrain and bamboo forests, we used a Landsat TM 5 image (path 4, row 68, date16 September 1990) for a preliminary selection of study sites. The histogram-equalized bands 4, 5 and 7 were used for red, green and blue, respectively, in a color composite that was used as a map. In this image, each of the different vegetation types distinguished by M. Foster in Cocha Cashu (unpublished map) appeared with a relatively distinct color.

The inventory lines followed a straight compass reading when they sampled the interior of the forest, and lake curvature when they sampled lake margins. The length of the lines varied between 0.55 and 1.5 km. As in Cocha Cashu, seedlings and saplings were counted to a distance of 3 m on both sides of each line, poles to a distance of 20 m, and juveniles and adult trees to a distance of 30 m. In lines that sampled lake or swamp margins, the counting distance was only 10 m on the side of the lake. The starting point of each inventory line was georeferenced with a hand-held GPS-receiver (Garmin XL12).

In order to compare differences in *Dipteryx* population density between the Cocha Cashu area and the other forests, four virtual inventory lines were built using the data from the exhaustive search at Cocha Cashu. Each of the virtual lines represented a different combination of forest age (late successional or mature) and position within the forest (interior or margin), and was set to have the average length of those inventory lines outside Cocha Cashu that represented the same combination of forest classes. The densities of the different *Dipteryx* size classes in the virtual inventory lines were simply the averages observed for each forest class combination within Cocha Cashu.

## Classification of the forests

We classified the forests according to their successional stage and position in relation to the margin of lakes or swamps. Margins were defined to extend 40 m

perpendicularly from the border line between forests and lakes or open swamps into the forest. We consider the positions of lakes and swamps essentially permanent, whereas rivers are so mobile that their borders with forest cannot be taken as a valid criterion for defining a margin in this study. Inventory lines never began closer than ca. 30 m from the river.

The successional stage of each inventory line was determined by two different methods: by a subjective field assessment and by a mechanistic classification based on reflectance data registered in the Landsat TM image. For the subjective field classification, young successional forests were recognized by their proximity to a meander point and the abundance of *Cecropia membranacea*. Indications for late successional forest were the occurrence of intermediate-sized palms, dense patches of *Heliconia* spp., and a generally small mean diameter of palms and trees although trees of large diameters could also occur. A mature forest was characterized by a tall canopy with emergent trees, and the presence of adult palms. These successional stages refer to the age of the forest ground since it was last deposited by the river, so the determination of the successional stage was made with a rather coarse geographical resolution, not considering variation that seemed due to tree fall gaps. In general, each inventory line was planned to represent only one successional stage, but in some cases two different stages were nevertheless present. In these cases, the inventory line was split into two, and both sections that represented different successional stages were numbered and treated in the subsequent analyses as separate inventory lines. Two inventory lines were also divided into two sections because a part of them represented forest interior, and another part, lake margin.

For the forest classification based on reflectance values, we used the same Landsat TM 5 image that was used for making the map used to locate the lines. Prior to the classification, the satellite image was filtered by mean kernel of 3x3 pixels (the pixel size was defined as 28.5 x 28.5 m) and pixels representing water bodies, swamps (open, semi-open and dominated by palms) and unflooded terrain were masked out. A water mask was formed by thresholding and editing the mask manually. The mask for unflooded terrain was digitized manually according to a visual interpretation of the satellite image. We used ERDAS Imagine 8.4 to work with the image.

By laying the satellite image upon the vegetation map of Cocha Cashu, we obtained training areas for young successional, late successional and mature forests. The total numberof pixels used in training were: early successional forest 397, late successional forest 1623, and mature forest 1589 pixels. We evaluated different spectral characteristics of the forest types in the Cocha Cashu area in order to select the most appropriate feature to be used in forest classification. The evaluated spectral features were DN (digital number) values of bands 1-7, band ratios (band 4 / band 3, band 5 / band 4, band 7 / band 4), NDVI ([band 3 -band4] / [band 3 + band 4]) and band differences (band 4 - band 5, band 4- band 3). The different forest successional types of Cocha Cashu had least overlap when they were characterized by the difference of bands 4 and 5. Accordingly, we selected this criterion for classifying the rest of the study area.

After plotting the distribution of the resulted difference of bands 4 and 5 for pixels in each forest type, the DN values corresponding to the lower quartile (Q2) and the upper quartile (Q3) were selected as the values to separate the lower and upper limits of each forest type. The threshold values used to assign each pixel in the filtered image to a forest class are shown in Table 1. We filtered the classified image twice

with a 3x3 pixel majority kernel in order to exclude patches of a forest class consisting of only one or a few pixels. The classification result is shown in Fig.1. Finally, we determined the forest class of each inventory line or line section simply as the class which had most pixels within its boundaries. In some cases, an inventory line was classified differently in the field and using the satellite image (Table 2). As the distinction there between late successional and mature forest is not very clearly defined and as we ignore individual tree fall gaps, we can not expect that we would find no young trees at all in forests that we can describe as mature.

## Analyses of densities in different forest classes

We were interested in comparing the densities of *D. micrantha* plants of different size classes in different types of forests. The calculation of these densities on the basis of field observations is obvious, but the estimation of whether differences in the observed densities are statistically significant is somewhat problematic. The distribution of individuals in their natural environment is most likely to show spatial autocorrelation, i.e. to have a clumped distribution at the resolution of the particular unit of inventory. This is a logical consequence of both spatially restricted distribution of propagules, and of the usually patchy distribution of environmental characteristics, and it impedes the use of statistical tests that are based on the assumption of independence of observed individuals.

To alleviate this problem, we estimated the probabilities of type I error through the following randomization procedure. We considered the observed series of densities of individuals per size class in one inventory line as one independent measurement of the population structure of *D. micrantha* in the forests of Manu river floodplain. We estimated the probabilities of error through a randomization procedure in which we classified each inventory line randomly to the forest class relevant for any particular question while keeping constant the total number of each forest class. In detail the procedure was as follows: the rows of our table of field observations represent inventory lines or sections of lines, and columns indicate successional stage, position in relation to forest margin, and densities of individuals in different size classes (Table 2). On the basis of the information on successional stage and position in relation to forest margin, we labeled the inventory lines and line sections appropriately for each question that we investigated in our data, and added the labels as a new column to the table. Thereafter, we permuted the column of the labels and recalculated the differences using the permuted labels for lines and line sections. We used 999 permutations and subsequent recalculations of differences in order to obtain a distribution of values in which it was possible to find out the probability (the p value) of getting by chance an equal or bigger difference than the one which was actually observed. Permutations were run in Excel X for Mac.

One should note that while this method for estimating the type I error does not suffer from the probable interdependence between individuals within one inventory line, it is not devoid of problems caused by spatial autocorrelation possibly occurring in abundances between inventory lines.

## Test of the effect of the year of observation

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We inventoried *Dipteryx* individuals during three different years. The densities of large individuals can be expected to remain relatively constant from one year to the next, but seedling population densities can fluctuate strongly because some years may be better than others for germination and subsequent seedling development. Therefore, it is not necessarily justified to compare densities of seedlings at different sites if the counts were made in different years. In order to find out if the density of seedlings varied between the years of inventory, we counted the seedlings in all three inventory years along eleven trails (total length 7.7 km) in Cocha Cashu area. The results of these counts are presented in Table 3. It is evident that there was very little variation in the amount of seedlings among the three years covered by this study. Accordingly, we consider it justified to include also seedlings in the analyses.

# Results

The total inventoried area comprised 398.5 ha, of which 229.9 ha consisted of the exhaustive search area within the trail system of Cocha Cashu, and 168.6 ha of 30 inventory lines outside Cocha Cashu (Fig. 1). Five of the inventory lines outside the Cocha Cashu trail system were divided into two separate sections that were in the field classified to different phases of succession, and one line because a part of it represented forest at a lake margin and a part, forest interior. Accordingly, there were 40 separate units of line inventory (4 virtual inventory lines at Cocha Cashu and 36 inventory lines or line sections along the Manu River; Table 2). In the continuation, we refer to all these sampling units as inventory lines.

## Densities of *D. micrantha* in different forest classes

The recorded densities of seedlings and saplings were very uneven among the inventory lines. Seedlings and/or saplings were present only in 15 of the 40 lines, and their densities varied strongly: for seedlings from 1.67 up to 166.67 individuals per hectare, and for saplings from 1.42 to 12.82 individuals per hectare (Table 2). Poles were extremely rare – we found altogether only 5 individuals (0.018 individuals per hectare), all in mature forests. Compared to seedlings and saplings, the densities of juvenile and adult trees varied fairly little among the inventory lines. Juveniles were observed about 2.5 times as often as poles (in total 21 individuals, 0.053 individuals per hectare), but adult trees were found rather commonly (a total of 259 individuals, 0.650 individuals per hectare).

The density of each size class per forest class is presented in Table 4. Seedlings and saplings were found in all three different stages of succession, being most abundant in mature forests and least abundant in young successional forests. This difference was clearest in field classified forests and we performed the permutation test based on these data. The permutations produced relatively easily greater differences than those observed between the minimum and maximum densities of seedlings (p=0.115) and of saplings (p=0.232), and therefore we cannot consider the density of seedlings or saplings to be statistically significantly lower in late successional forests than in mature forest.

The observed greater abundance of seedlings and saplings in mature forests, as well as the practically equal densities of juveniles in mature and late successional forests (although not testable statically due to small sample size), can be taken as evidence against the hypothesis that *D. micrantha* is a late successional species. However, the hypothesis would still remain viable if the recruits at a later phase of development encounter much heavier mortality within mature forests than in late successional forest. If this were the case, we would observe a more rapid decline of population densities from one size class to the following one(s) in mature forests than in late successional forests. Obviously, a comparison of this decline would be relevant only up to the juvenile size class. Adult densities are practically bound to be lower in late successional forests, because *Dipteryx micrantha* is a long-lived species, and adult trees can be much older than the maximum age of late successional stage for a given patch of forest.

The decline from seedling densities to sapling densities was practically equal in late successional and mature forests, no matter whether field classification or image classification of the forests was used (Table 4). In contrast, the observed decline in density from seedlings to juveniles, from saplings to juveniles, and from poles to juveniles was greater in mature forests than in late successional forests. However, this difference cannot be considered statistically significant, as an equal or larger difference was relatively easily obtained through permutations (p=0.094 in the case of seedlings to juveniles, and p=0.123 in the case of saplings to juveniles, both calculated for the field classification of forests). Poles were too few in our data to allow meaningful testing of the difference in decline from poles to juveniles.

The densities were higher in forest margins than in forest interior for all size classes and in both successional and mature forests (Table 4). This pattern was observed almost similarly in both the field and image classified forests. In field classified forests, randomizations only rarely produced (p<0.006) an equal or bigger sum of relative differences in densities of separate size classes than the sum that we observed. Considering the different size classes individually, the permutation tests indicated significant differences between forest margin and interior in adults (p=0.008) and juveniles (p=0.014), marginally significant differences in seedlings (p=0.065) and saplings (p=0.061) and non-significant difference in poles (p=0.240). We did not test these differences with the image classified forests, as there the difference between the densities with forest interior and forest margin was even greater than in field classified forests.

## Comparison between Cocha Cashu and other forests along Manu river

We observed that in all four forest classes, densities of seedlings were higher in Cocha Cashu than in the surrounding areas (whether field or image classified) (Table 5). Sapling densities were also mostly higher in Cocha Cashu, but pole and juvenile densities were lower in almost all forest classes. Adult densities were higher in Cocha Cashu in mature forests but not in late successional forests. The high density of adults in Cocha Cashu is illustrated in Fig. 2, which also shows the clumped distribution of *D. micrantha* trees.

These observations can be interpreted so that the mature forests in Cocha Cashu have more adults than the mature forests outside Cocha Cashu, and, consequently, seed production is also higher, which is reflected in higher seedling densities not only in the

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mature forests of Cocha Cashu but also in the nearby late successional forests. This interpretation can be tested by asking if it would be easy to randomly get an equal or bigger difference in densities of the different size classes between Cocha Cashu and the surrounding areas. In practice we did the testing by first dividing the inventoried paths within mature interior forest of Cocha Cashu into 24 path sections (mean length 867.5 m, maximum 1000 m, and minimum 560 m). Then we placed these path sections into the same table with the 13 inventory lines of field classified mature interior forests outside Cocha Cashu. Finally, we randomly assigned 24 rows of the table as "Cocha Cashu lines" and 13 rows as "outside Cocha Cashu lines", and calculated after each of the 999 randomizations the average densities for both of these categories. This testing indicated that mature interior forests of Cocha Cashu are significantly denser in *D. micrantha* adults (p=0.011), seedlings (p=0.002) and saplings (p=0.019) than the surrounding field classified mature interior forests. Juvenile density in Cocha Cashu can hardly be considered different from its surroundings (p=0.574), and for poles we did not even perform the test as poles were so rare. We did not perform the testing for image classified forests either, as in adults and saplings the difference was even more extreme and for seedlings and juveniles the image classified forests gave very closely similar densities as field classified forests.

## Discussion

Our general conclusion is that we did not find support for the hypothesis of Foster et al. (1986) and Foster (1990) that *Dipteryx micrantha* is a late successional species. Instead, it appears that *D. micrantha* can readily regenerate within mature forests. We observed sub-adult individuals of all size classes at relatively similar densities in late successional and in mature forests, and if there were differences in densities, they were in favor of mature forests. The densities of the smallest size classes were observed to decline more abruptly to lower densities of juveniles in mature forests than in late successional forests, and this in principle could indicate that recruits survive better in late successional than in mature forests. However, this difference was not statistically significant. Probably mortality events need to be measured at very long time scales to find such differences in decline between late successional and mature forest. Thus, even if the mortality of the smaller size classes (seedlings to juveniles) were higher in mature forests, the end result seems to be that the same amount of individuals are entering to the fertile stage of *D. micrantha* life cycle in both mature and late successional forests.

It is interesting to note that our conclusion on *D. micrantha* not being a late successional species, was unaffected by the method of classifying the successional stage of the studied forest areas, although image classification allocated some inventory lines that had been classified as mature forest in the field to late successional.

The hypothesis that *D. micrantha* is a late successional species can still be accepted if we have actually failed to sample the really mature forests, and instead have only sampled transitional stages between mature and late successional forest. The present understanding of forest succession and forest types in the area does not allow an evaluation of this possibility, and therefore this remains an open question for further investigation.

We did not find that *D. micrantha* had preference for certain successional stage, but this does not mean that the species would be indifferent to variation in habitat quality. Lake and swamp margins seemed to constitute a preferred habitat, where densities of adults and possibly juveniles are higher than in the forest interior. This result is in accordance with the prediction of Foster (1990), but we are not convinced that the mechanism for this pattern is only the one suggested of higher light level due to thin canopy.   We believe that the preference of *D. micrantha* for lake and swamp margins can equally well be understood as a result of the ability of the smaller size classes (seedlings-poles) to withstand relatively long periods of low light supply that might also occur at margin habitats due to the presence of lianas covering the lower strata. This, together and alternating with higher light levels that also occur there might favor the survival of several size classes, but specially survivorship after passing to poles or juveniles. Forest edges, such as lake and swamp margins, are typically characterized by higher tree mortality, higher density of vines and lianas (Lawrence et al 1998) and higher penetration of lateral light (Kapos et al. 1997) than the forest interior. It is conceivable that lianas form a dense stratum which actually prevents light from entering to the forest floor, where seedlings of light-demanding tree species have low probabilities of surviving but where more tolerant species can survive. On the other hand, once a young tree can get through the layer of lianas – possibly aided by occasional and short-lived openings caused by dying trees – the growing tree can suddenly get to an "upper-level gap" (Clark and Clark 1992) where it will survive well if it manages to escape the continuously growing lianas.  So, perhaps *D. micrantha* is not so much a late successional species demanding light, but a species that tolerates shade as seedlings, saplings, but who requires better light at subsequent size classes (as was found for *D. panamensis*, Clark and Clark 1992).

Our hypothesis that *D. micrantha* is shade tolerant as seedling and sapling, but requires light at later phases of development would obviously need to be tested through other data. This aspect in the biology of the species is by no means easy to study but, the effort should be made as it appears that shade tolerance of saplings may be one of the key characteristics that determine the landscape-scale abundance of a tropical tree species (Svenning et al. 2004). Preferably, one would gather measurements of growth and survival of individuals of various sizes growing in a variety of conditions of light and other environmental characteristics. However, it is very hard to find enough individuals that represent the mid and late phases of recruitment (poles). Despite having surveyed about 285 ha of forest, we found only five poles. Yet, one would preferably investigate at least some tens of them in order to get a reliable idea of factors affecting their growth and survival, and therefore one should be prepared to comb through an area on the order of 1500 ha or even more.

Furthermore, one should be aware of possible problems in extrapolating the results from a restricted area to areas nearby. Our study has shown that the density of *D. micrantha* can vary considerably at two different geographical scales. Locally, within tens to hundreds of meters, the distribution of the species appears to be quite strongly clumped, as illustrated in Fig. 2. There also seem to be significant density differences at scales from one to some tens of kilometers. This patchiness in the distribution obviously should be taken into account when planning any sampling effort, like for the estimation of the population size in a larger forest area. Besides describing the aggregation pattern, we would like to understand the reasons behind it. Although

we have too few observations to give well substantiated explanations, we want to mention some possibilities.

We observed only one area of very high density of adult *Dipteryx micrantha* trees – the patch in Cocha Cashu. We think that this area represents the oldest forests included in our inventories. This is suggested by the fact that there are no recent marks of river channel movement (oxbow lakes, open swamps) between the Cocha Cashu forest and the unflooded terrain to the north of it. If *D. micrantha* is a shade-tolerant and long-lived species, it should attain its highest density in those forests that have experienced the longest history without major large-scale disturbance. In general, species with hard wood have comparatively low mortality rates (Putz et al 1983), which suggests that *Dipteryx*, which has very hard wood, might persist in the forest until a major disturbance occurs. It can be seen in the satellite image (Fig. 1) that outside Cocha Cashu, only one of the inventory lines (number 22) represents what seems to be very old mature forest. All other mature forests that we sampled are situated between the present river channel and relatively fresh marks of fluvial dynamics, which suggests that they are younger.

The high density of seedlings and saplings in Cocha Cashu (in both late successional and mature forests) may be only a reflection of the high abundance of adult trees, if higher seed production also implies higher seedling recruitment (see De Steven and Wright 2002). Naturally, it is also possible that the network of trails in Cocha Cashu in itself plays a role. The main dispersers of *Dipteryx* seeds are canopy bats, which are known to use open corridors in the forest, like man-made paths, as their preferred flying routes (Palmeirim and Etheridge 1985).

The exceptionally high population density at Cocha Cashu serves as a sign of caution when one wants to generalize from the results on the biology of *D. micrantha* obtained there. For example, estimations of seed predation and mortality of recruits may be affected by the special circumstances in Cocha Cashu, as these processes may reflect the overall density of seeds and seedlings/saplings (Romo et al 2004). However, the exceptionally high density of individuals of *D. micrantha* in Cocha Cashu is probably not a problem when generalizing the results of seedling growth. The physiological responses of the individuals are likely to be the same whatever the density of the population. In any case, geographical variation in the density of *D. micrantha* serves as a reminder that results obtained from just one locality should not be generalized uncritically for other areas.

In addition to the purely academic interest in resolving the question of biological characteristics of *D. micrantha*, there is also an applied aspect here. The species produces valuable timber, and obviously its utilization should be planned to follow the principle of sustainability. Sustainable use is only possible if one has knowledge of the species' autecology, including its habitat preferences and life cycle. At the moment we can rather confidently say that the eventual planting and/or enrichment takes place most easily along the margins of lakes and open swamps, but to clarify other aspects that are relevant for sustainable use, more studies are needed.

## Acknowledgements

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**Table 1.** Threshold digital numbers (DN) of the difference between band 4 and band 5 for distinguishing three successional stages along Manu river flood plain forests, southeastern Peru.

| Successional stage | Lower limit (DN) | Upper limit (DN) |
|---|---|---|
| Early successional forest | 37.1 | 47 |
| Late successional forest | 28.6 | 37 |
| Mature forest | 23 | 28.5 |

**Table 2.** Density and number of individuals (in parenthesis) of *Dipteryx micrantha* in inventory lines at forests of different successional stages, along the margins of water bodies (max. 40 m from water) and in forest interior, in floodplain forests of Manu river and around the biological research station of Cocha Cashu.

| | | | successional stage | | | Density per ha (no. of individuals.) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Line no. | Line length (km) | Inventoried area for juv. and adults (ha) | field id. | Image id. | Margin (mrg)/ Interior (in) | seedlings <1cm | saplings ≥1cm and <4cm | poles ≥4 cm and <10 cm | juveniles ≥10 cm and <40 cm | adults ≥40cm |
| 1a | 0.15 | 0.75 | ls | m | mrg | 12.82(1) | 12.82(1) | 0 | 0 | 1.33(1) |
| 1b | 0.85 | 5.1 | m | m | in | 0 | 0 | 0 | 0 | 0.20(1) |
| 2a | 0.5 | 3 | ls | ls | in | 0 | 0 | 0 | 0 | 0 |
| 2b | 0.5 | 3 | m | ls | in | 0 | 3.33(1) | 0 | 0 | 0.33(1) |
| 3 | 0.7 | 4.2 | ls | ls | in | 0 | 0 | 0 | 0 | 0.48 (2) |
| 4 | 0.65 | 3.9 | ys | ys | in | 0 | 0 | 0 | 0 | 0 |
| 7 | 1 | 6 | m | ls | in | 0 | 0 | 0 | 0 | 0.83(5) |
| 8 | 1 | 6 | m | m | in | 0 | 0 | 0 | 0.33(2) | 0.17(1) |
| 14 | 0.97 | 5.82 | ys | ls | in | 0 | 0 | 0 | 0 | 0 |
| 15 | 1 | 6 | ys | ls | in | 0 | 0 | 0 | 0 | 0 |
| 16a | 1.05 | 6.3 | ys | ys | in | 3.17(2) | 1.59(1) | 0 | 0 | 0 |
| 16b | 0.1 | 0.6 | m | m | in | 16.67(1) | 0 | 0 | 0 | 0 |
| 17a | 1.175 | 7.05 | m | m | in | 18.44(13) | 1.42(1) | 0.21(1) | 0 | 0.43(3) |
| 17b | 0.325 | 1.95 | ls | ls | in | 20.51(4) | 0 | 0 | 0.51(1) | 0 |
| 18 | 1 | 6 | m | m | in | 0 | 0 | 0 | 0 | 0.33(2) |
| 19 | 1 | 6 | m | m | in | 0 | 0 | 0 | 0 | 1.17(7) |
| 20a | 0.138 | 0.828 | ys | ys | in | 0 | 0 | 0 | 0 | 0 |
| 20b | 0.862 | 5.172 | ls | ls | in | 0 | 0 | 0 | 0 | 0.19(1) |
| 21 | 1 | 6 | m | m | in | 0 | 0 | 0 | 0 | 0.17(1) |
| 22 | 1 | 4 | m | m | mrg | 0 | 0 | 0 | 0.25(1) | 1.25(5) |
| 23 | 1 | 6 | m | m | in | 0 | 0 | 0 | 0.17(1) | 0.67(4) |
| 24 | 1 | 6 | ls | ls | in | 0 | 0 | 0 | 0 | 0.33(2) |
| 25 | 1 | 6 | m | ls | in | 0 | 0 | 0 | 0 | 0.33(2) |
| 26 | 1 | 6 | ls | ls | in | 5.00(3) | 3.33(2) | 0 | 0 | 0 |
| 27a | 1.11 | 6.66 | m | m | in | 10.51(7) | 0 | 0.23(1) | 0 | 0.30(2) |
| 27b | 0.04 | 0.24 | m | m | ma | 166.67(4) | 0 | 0 | 0 | 4.17(1) |
| 28 | 1.1 | 6.6 | ls | ls | in | 0 | 0 | 0 | 0 | 0.30(2) |
| 29 | 1 | 4 | ls | ls | mrg | 0 | 0 | 0 | 0.25(1) | 0.75(3) |
| 30 | 1 | 6 | ls | ls | in | 0 | 0 | 0 | 0.17 (1) | 0 |
| 31 | 0.65 | 3.9 | m | m | in | 0 | 0 | 0 | 0 | 0.51(2) |
| 32 | 1 | 4 | m | ls | mrg | 28.33(17) | 5.00(3) | 0.25(1) | 0 | 1.00(4) |
| 33 | 1 | 6 | ls | m | in | 0 | 0 | 0 | 0 | 0 |
| 34 | 1 | 6 | ls | ls | in | 0 | 0 | 0 | 0.17(1) | 0.17(1) |
| 35 | 1 | 6 | ls | ls | in | 1.67(1) | 0 | 0 | 0 | 0 |
| 36 | 0.88 | 3.52 | ls | ls | mrg | 0 | 0 | 0 | 0 | 0.57(2) |
| 37 | 1 | 4 | ls | ls | mrg | 0 | 0 | 0 | 0.50(2) | |
| Cocha Cashu | | | | | | | | | | |
| ls-mrg | 0.758 | 3.032 (22.64) | ls | ls | mrg | 8.09(27) | 0.90(3) | 0 | 0.09(2) | 0.22(5) |
| ls-int | 0.862 | 5.172 (62.57) | ls | ls | in | 9.04(59) | 1.99(13) | 0 | 0.03(2) | 0.06(4) |
| m-mrg | 0.68 | 2.72 (17.8) | m | m | mrg | 32.04(79) | 11.35(28) | 0 | 0.22(4) | 1.69(30) |
| m-in | 0.876 | 5.256 (126.9) | m | m | in | 23.81(303) | 7.15(91) | 0.02(2) | 0.02(3) | 1.30(165) |

**Table 3.** CC trail system checked for seedlings(1-9.9mm)  and saplings (10-39.9mm ) 1998 and 1999

| Forest type/ trail id. | distance (m) | 1998 seedlings | saplings | 1999 seedlings | saplings | 2000 seedlings | saplings |
|---|---|---|---|---|---|---|---|
| **Mature** | | | | | | | |
| margin trails | | | | | | | |
| 6.0-800 | 800 | 48 | 1 | 50 | 2 | 50 | 2 |
| 7.0-350 | 350 | 9 | 2 | 5 | 4 | 5 | 4 |
| total | | 57 | 3 | 55 | 6 | 55 | 6 |
| interior trails | | | | | | | |
| 3.0-575 | 575 | 26 | 3 | 23 | 4 | 21 | 4 |
| 4.0-350 | 350 | 11 | 1 | 13 | 4 | 26 | 3 |
| 5.430-1100 | 670 | 40 | 5 | 35 | 7 | 32 | 7 |
| 10.0-800 | 800 | 11 | 1 | 17 | 2 | 22 | 0 |
| 33.0-900 | 900 | 26 | 0 | 24 | 1 | 19 | 0 |
| 34.0-500 | 500 | 13 | 0 | 14 | 2 | 10 | 2 |
| total | | 127 | 10 | 126 | 20 | 130 | 16 |
| **Late successional** | | | | | | | |
| margin trail | | | | | | | |
| 14.0-2000 | 2000 | 3 | 0 | 22 | 3 | 11 | 0 |
| interior trails | | | | | | | |
| 18.0-600 | 600 | 7 | 0 | 8 | 0 | 5 | 1 |
| 40.0-150 | 150 | 4 | 0 | 5 | 0 | 5 | 0 |
| total | | 11 | 0 | 13 | 0 | 10 | 1 |

**Table 4.** Densities of *D. micrantha* of different size classes in margins and interior in young successional, late successional and mature forest (transects along the Manu River and Cocha Cashu virtual transects together).

| Type of forest/Forest habitat | Density/ha | | | | |
|---|---|---|---|---|---|
| | seedlings <1cm | saplings ≥1cm and <4cm | poles ≥4 cm and <10 cm | juveniles ≥10 cm and <40 cm | adults ≥40cm |
| **Field classification** | | | | | |
| *Young successional* | 0.88 | 0.44 | 0 | 0 | 0 |
| *Late successional* | | | | | |
|   margin | 2.07 | 0.62 | 0 | 0.21 | 0.44 |
|   interior | 2.04 | 0.49 | 0 | 0.05 | 0.13 |
|   margins and interior | 2.05 | 0.52 | 0 | 0.08 | 0.19 |
| *Mature forests* | | | | | |
|   margin | 20.88 | 4.68 | 0.09 | 0.15 | 1.33 |
|   interior | 4.56 | 0.78 | 0.04 | 0.04 | 0.51 |
|   margins and interior | 7.67 | 1.56 | 0.05 | 0.06 | 0.62 |
| *Late successional and mature* | | | | | |
|   margin | 9.95 | 2.32 | 0.04 | 0.19 | 0.81 |
|   interior | 3.40 | 0.65 | 0.02 | 0.05 | 0.34 |
| **Image classification** | | | | | |
| *Young successional* | 1.81 | 0.91 | 0 | 0 | 0 |
| *Late successional* | | | | | |
|   margin | 7.43 | 1.23 | 0.05 | 0.18 | 0.52 |
|   interior | 1.53 | 0.49 | 0 | 0.04 | 0.20 |
|   margins and interior | 3.01 | 0.67 | 0.01 | 0.06 | 0.26 |
| *Mature forests* | | | | | |
|   margin | 16.28 | 5.07 | 0 | 0.21 | 1.50 |
|   interior | 5.19 | 0.74 | 0.05 | 0.05 | 0.46 |
|   margins and interior | 6.82 | 1.37 | 0.04 | 0.07 | 0.57 |
| *Late successional and mature* | | | | | |
|   margin | 9.95 | 2.32 | 0.04 | 0.19 | 0.81 |
|   interior | 3.13 | 0.60 | 0.02 | 0.04 | 0.31 |

**Table 5.** Average densities of *Dipteryx micrantha* of different size classes in the immediate surroundings of Cocha Cashu biological station and elsewhere along the Manu River.

| Forest type | Average density (individuals/ha) | | | | |
|---|---|---|---|---|---|
| | seedlings, <1cm | saplings, ≥1cm and <4cm | poles, ≥4cm and <10cm | juveniles, ≥10cm and < 40cm | adults, ≥40cm |
| **Cocha Cashu** | | | | | |
| late successional, forest interior | 9.04 | 1.99 | 0 | 0.03 | 0.06 |
| late successional, forest margin | 8.09 | 0.90 | 0 | 0.09 | 0.22 |
| mature, forest interior | 23.80 | 7.15 | 0.02 | 0.02 | 1.30 |
| mature, forest margin | 32.04 | 11.35 | 0 | 0.22 | 1.69 |
| **Along Manu River** | | | | | |
| **Field classification** | | | | | |
| late successional, forest interior | 1.41 | 0.35 | 0 | 0.05 | 0.14 |
| late successional, forest margin | 0.55 | 0.55 | 0 | 0.24 | 0.49 |
| mature, forest interior | 3.07 | 0.29 | 0.04 | 0.04 | 0.45 |
| mature, forest margin | 17.16 | 2.45 | 0.12 | 0.12 | 1.21 |
| **Image classification** | | | | | |
| late successional, forest interior | 1.03 | 0.39 | 0 | 0.04 | 0.21 |
| late successional, forest margin | 7.30 | 1.29 | 0.06 | 0.19 | 0.58 |
| mature, forest interior | 3.54 | 0.17 | 0.05 | 0.05 | 0.39 |
| mature, forest margin | 7.12 | 1.42 | 0 | 0.20 | 1.40 |

## List of Figures

**Figure 1.** Study area showing the transect lines (dark gray rectangles) over the Landsat TM image (left images) and the image classification of the area (right image). The dotted area in the far left image represent the Cocha Cashu area where the trees were inventoried.

**Figure 2.** Cocha Cashu area showing the inventoried trees. Limits of forest types were based on the forest classification by M. Foster (unpublished). Dark and light gray represent the lake and swampy areas respectively. Insert shows densities of poles, juveniles and adult trees at d mature forest of inventory lines (first bar) and Cocha Cashu (second bar) and densities at margin habitats (black fill) and interior forest are shown (gray fill).
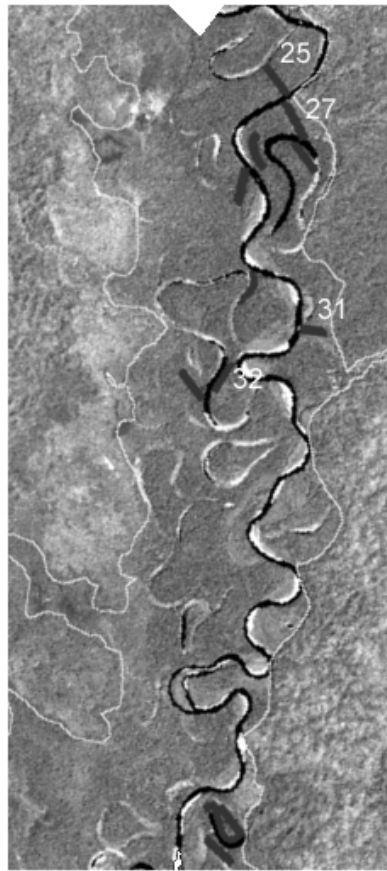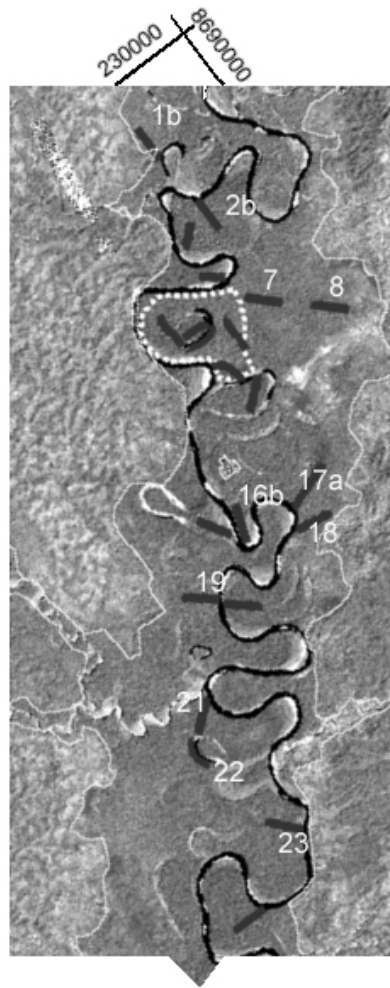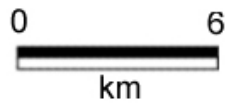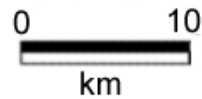
**Landsat TM 5 (band 5)**
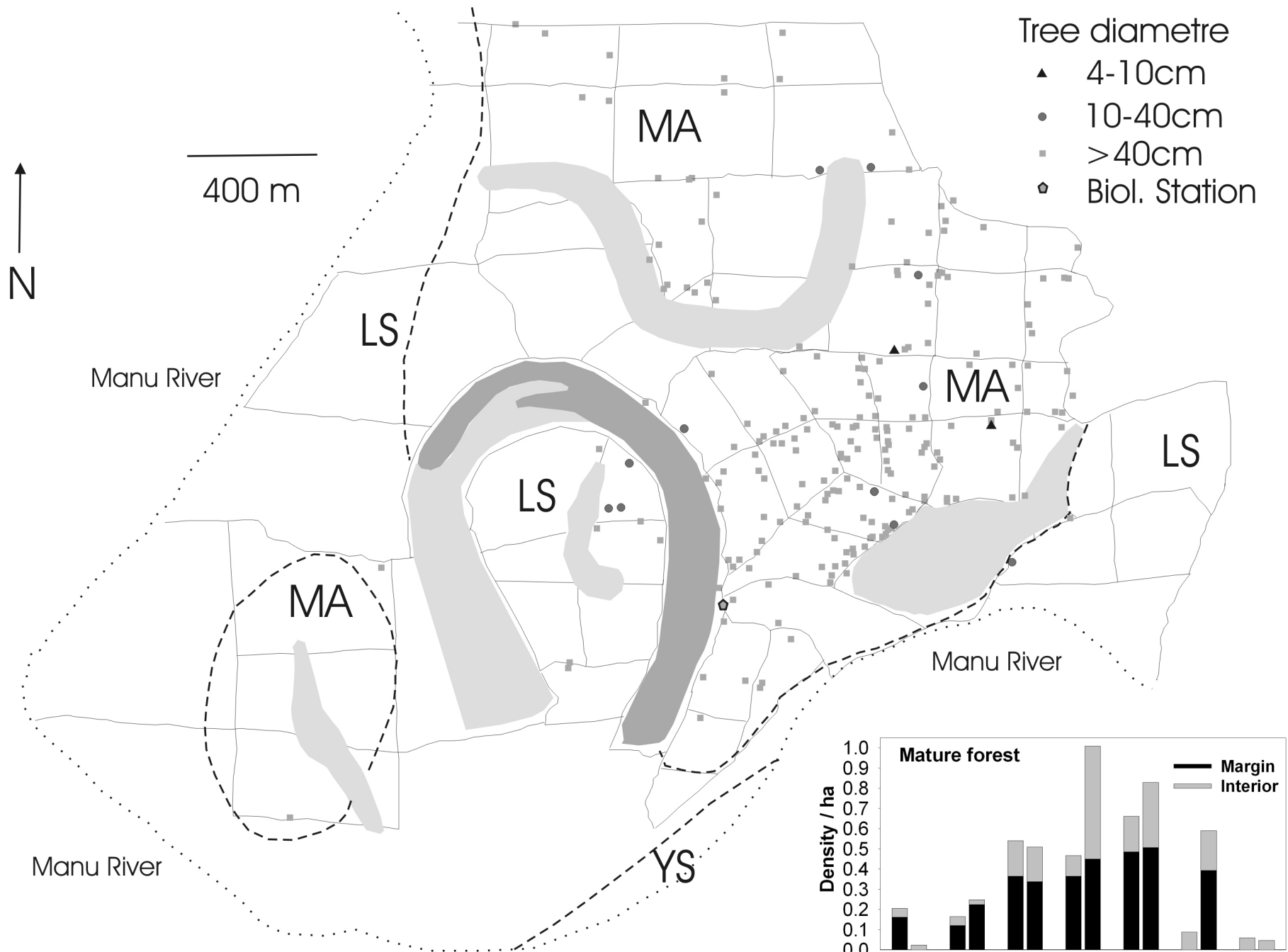
- - - - - Cocha cashu
▬▬▬ Transect line
▭ Edge of Tierra firme

**Forest type classification**

**Succession forest**

Mature

Old successional

Young successional

**Other**

Tierra firme

River

0 ——— 6
km

N

0 ——— 10
km

Tree diametre
▲ 4-10cm
● 10-40cm
■ >40cm
⬠ Biol. Station

N

400 m

Manu River

MA

LS

LS

MA

LS

MA

Manu River

YS

Manu River

Mature forest

Density / ha

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0

■ Margin
▨ Interior

4-10    10-40    40-60    60-80    80-100    100-120    >120

Diameter class (cm)

This article is chapter IV of the Doctoral Dissertation:

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