Environmental heterogeneity and dispersal processes influence post-logging seedling establishment in a Chiquitano dry tropical forest

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Abstract

Selective logging is becoming more and more influential in forest use in the tropics, especially as it provides local communities and regions with timber resources. Logging greatly alters abiotic and biotic factors which are fundamental in seedling establishment and spatial heterogeneity of tree recruitment. Niche and dispersal processes may affect post-logging seedling establishment, particularly in water-constrained tropical dry forests (TDF). To understand how selective logging affects tree recruitment and how forest exploitation can become a sustainable practice; a theoretical framework has been set up based on these processes. We assessed post-logging seedling establishment in a Bolivian Chiquitano TDF by: (i) characterizing logging microsites and the variability in abiotic (canopy openness, soil compaction and soil water content) and biotic (short and long-distance dispersal) factors among them, (ii) evaluating the roles played by those factors, here considered surrogates of niche and dispersal processes, on seedling establishment, and (iii) providing guidelines to ensure tree regeneration in similar logged TDFs. One year after logging, seedling establishment of five canopy tree species was assessed in four microsite types created by selective logging and in undisturbed TDF. Dispersal processes were described by interpolated kernel estimates of abundance of adult trees, i.e. potential seed sources. After logging, the abiotic environment was considerably altered, especially in the most disturbed logging microsites, leading to significant changes in canopy openness and soil compaction, the most important factors determining seedling establishment in four out of the five studied species. Dispersal processes also influenced regeneration in three tree species. Since the spatial distribution of adult trees influences post-logging regeneration, this should be considered to improve sustainability in logging operations across the tropics.

49 **Key words:** environmental heterogeneity, tropical dry forest, soil compaction, canopy
50 openness, zero-inflated Poisson models.

51

52 **Introduction**

53 Environmental heterogeneity is one of the most important mechanisms favouring
54 species coexistence in tropical forests (Wright, 2002), which are among the most
55 diverse ecosystems on earth (Myers et al., 2000). They are subjected to profound land-
56 use changes (Wright, 2010) and face a massive loss of biodiversity (Dirzo and Raven,
57 2003). Within the tropical biomes, Tropical Dry Forests (TDF) are threatened by the
58 expanding agricultural border, since they develop on fertile soils, therefore only a very
59 small portion of them remain unaltered (Pennington et al., 2006).

60 Whereas deforestation and diversity are major consequences of abandoned
61 agriculture, pasture expansion and tree plantations, selective logging is a much less
62 disturbing practice (Gibson et al., 2011) but is increasing its extension in tropical areas
63 (Asner et al., 2005). Moreover, reduced impact logging, can be seen as a strategy to
64 reduce the use pressure on TDFs (Fredericksen and Putz, 2003), while offering viable
65 economic alternatives to local communities in developing tropical regions (Merry et al.,
66 2009). This management technique reduces canopy and ground disturbance by more
67 than half compared to conventional selective logging (Pereira Jr. et al., 2002).

68 Selective logging causes a reduction of stand basal area and damages
69 neighbouring trees, particularly those forming subcanopy layers, while affecting soil
70 conditions (Asner et al., 2005; Johns, 1988). As a result of logging abiotic conditions
71 suffer negative alterations (e.g., erosion, run-off, microclimate). Biotic interactions are
72 also changed due to modifications in the availability of resources to plants (Clark and
73 Covey, 2012). For instance, logging increases light availability and temperature,
74 decreases relative air humidity (Johns, 1985), changes rooting environments
75 (Fredericksen and Pariona, 2002), and enhances the development of understory

76 vegetation (Fredericksen and Mostacedo, 2000). Therefore, selective logging increases
77 environmental heterogeneity by creating spatiotemporal variation in the distribution of
78 abiotic resources and creates regeneration niches for tree recruitment (Denslow, 1980;
79 Grubb, 1977). These two processes are considered among the main mechanisms
80 explaining tree species coexistence in tropical forests (Wright, 2002). Natural treefall
81 gaps also play a key role in maintaining spatial heterogeneity in the composition and
82 dynamics of tropical forests (Brokaw, 1985) by generating microsite heterogeneity in
83 the distribution of abiotic resources, which determines the regeneration success of each
84 tree species (Rother et al., 2013).

85 Abiotic factors related to the dry season play a far-reaching role not only in tree
86 regeneration but in overall dynamics (Ceccon et al., 2006; Comita and Engelbrecht,
87 2009; Powers et al., 2009). Seasonality in the availability of water is an important driver
88 of growth, reproduction and survival patterns in TDFs (McLaren and McDonald, 2005;
89 Mendivelso et al., 2013; Murphy and Lugo, 1986). Whereas in wet tropical forest the
90 tree regeneration dynamics are directly related to light availability in the understory, in
91 TDFs the relationship is considered to be less relevant (Chazdon et al., 1996; Rozendaal
92 et al., 2006). Drought creates a more open canopy structure, given the deciduous habit
93 and the compound leaf structure of the most abundant trees (Killeen et al., 1998;
94 Murphy and Lugo, 1986). It is to a large extent the ability of each species in TDFs to
95 tolerate distinct levels of light irradiance and water availability that channels the
96 response of seedling establishment to changing abiotic resources (Rozendaal et al.,
97 2006; Poorter and Markesteijn, 2008a).

98 In TDFs the dominance of wind dispersed trees over animal and gravity-
99 dispersed trees also determines seed dispersal processes and seedling establishment
100 (Bullock et al., 1995; Lebrija-Trejos et al., 2008). Another important mechanism

favoring species coexistence is recruitment limitation. This process, depending on species dispersal syndromes and requirements for seedling establishment, occurs if seeds of a species do not reach available microsites for regeneration (Wright, 2002).

There is a need to increase our knowledge about regeneration niches of many TDF tree species since these are among the most threatened types of tropical forests (Ceccon et al., 2006; Fredericksen and Mostacedo, 2000). The existence of unknown biotic factors involved in tree regeneration processes, besides environmental factors, may led to an important portion of variance in the results unexplained (Fredericksen and Pariona, 2002; Park et al., 2005). Therefore, we used a spatially explicit model to gain insights into the niche and dispersal processes influencing seedling regeneration after selective logging of a TDF. We selected a forestry concession for selective logging located in the Chiquitano forest, in the Bolivian lowlands, a type of TDF that has long been threatened and stated as a global conservation priority (Parker III et al., 1995). We analyzed the distribution of seedlings and resprouts of the most abundant timber tree species one year after selective logging in order to: (i) describe logging microsites and the variability in biotic and abiotic microsite variables; (ii) evaluate the role of abiotic factors (canopy opening, soil disturbance), and dispersal processes on seedling establishment; and (iii) provide guidelines to improve management in order to ensure seedling establishment in logged TDFs.

Materials and methods

Study site

This study was conducted in a Chiquitano TDF located in the eastern lowlands of Bolivia. It has a distinct dry season of five months, from May to September, where precipitation is below 100 mm. Meteorological data obtained from the Concepción

station (16° 15' S, 62° 06' W; data available for the period 1949–2009; station located 35 km away from the study site) show that mean annual temperature is 24.3 °C and mean annual rainfall is 1177 mm. The terrain in the site is typical of the Brazilian Shield, with rolling hills of Precambrian origin located between 300 and 550 m a.s.l. and superficial, reddish-brown inceptisols and oxisols.

The Chiquitano forest is located in the transition between the dry Chaco in the south and the humid Amazon Basin in the north. It is probably the largest remaining patch and one of the most floristically diverse TDF in the Neotropics (Killeen et al., 1998; Parker III et al., 1995). Floristically it is considered a distinct floristic region from the Chaco and the Amazonian forest (Killeen et al., 2006), but with few endemic species. The forest structure is characterized by an open 25-35 m tall canopy allowing the development of a high density of sub-canopy trees, shrubs and lianas (Killeen et al., 1998). There are locally abundant ground bromeliad species that can occupy most of the forest floor. Most canopy trees species are deciduous or semi-deciduous, while most sub-canopy tree species are evergreen (Justiniano and Fredericksen, 2000).

The study site is located in a 30,000 ha forest concession for sustainable management (INPA Parket company; 16° 07' S, 61° 43' W, 380 m a.s.l.) located near Concepción, Santa Cruz Department. Roughly 10 % of the total area is a reserve, and permanent sample plots are monitored regularly by the Instituto Boliviano de Investigación Forestal (IBIF), a non-governmental forest conservation and research agency. Before logging operations begin a forest census is carried out, where commercial timber tree species above 40 cm at breast height (DBH, diameter measured at 1.3 m) are mapped and tagged. Approximately, 20 % of the mapped individuals are left for seed production. The minimum cutting cycle in INPA is 25 years according to the Bolivian forestry law.

Sampling design

We selected areas with distinct post-logging light and rooting environments and defined five microsite types, four of them created by selective logging. In order to compare these microsites with forest areas not affected by logging, undisturbed forest microsites were selected (Fig. 1). Logging microsites included logging roads, log landings, skid trails, logging gaps and undisturbed forests, each with differing soil and canopy disturbance intensities. Undisturbed microsites had high canopy cover and no soil disturbance. To avoid site effects caused by environmental heterogeneity (soil, topography, etc.) we used a block sampling design with the five aforementioned microsite types in each block taking the log landing as the epicentre of each block. We established 24 blocks in two different study areas. These areas covered 600 and 1000 ha, respectively. The first block number was given to the log landings, the least abundant microsite types, after searching thoroughly within the two study areas. Then, we located the rest of logging microsite types with a minimum distance of 50 m between them.

Measured variables

In July 2012, one year after selective logging, 120 square plots (2 x 2 m) were set out at the five microsite types, i.e. 24 plots per microsite. An undisturbed forest plot was also located in the nearest undisturbed forest fragment, located at least 50 m away from the disturbed microsites to reduce effects due to positive spatial autocorrelation. All plots had their location noted with an approximate resolution of 10 m based on GPS measures, which we assume would impact similarly the interpolated kernel density values across the study plots. In logging roads and skid trails we measured the width of

the road, while in logging landings and logging gaps we measured the length of the two major perpendicular axes and calculated their areas assuming they were ellipses. At the four corners of each plot we measured soil compaction (in N m^{-2}) with a hand penetrometer (Eijkelkamp, Giesbeek, the Netherlands) and volumetric soil water content (%) in the upper soil layer (10 cm) using a TDR probe (Theta Probe Soil Moisture Sensor, Delta-T, Cambridge, UK). Canopy openness (%), i.e. the area not covered by the canopy, was measured at the center of each plot with a spherical densitometer (Stumpf, 2008). Percent cover of trees, shrubs, woody vines, herbaceous vines and herbs or forbs was estimated in each plot. We proceeded to the identification of species together with a census of all newly emerged seedlings and resprouts of the most abundant canopy tree species within the plots. We differentiated seedling from resprouts by looking for cotyledon scars only present in seedlings.

Determining seed sources and distances from adult trees

Prior to selective logging in 2011, forest censuses of the timber tree species were carried out by the INPA company and the IBIF. In those censuses, every tree with a DBH > 40 cm was identified to species and mapped. We used mapped tree populations from the commercial censuses to calculate kernel density maps of the three most abundant timber tree species. In this way, we obtained a quantitative estimate of seed sources in the study area, with reference to potential ‘mother’ trees capable of reaching a reproductive size or age. Those maps represented interpolated intensity values, i.e. the mean number of points per unit area (tree density).

We used two different criteria for bandwidth selection to build two kernel density maps of the most abundant species: one with a lower bandwidth and the other with a higher bandwidth. This allowed us to consider each species density map as a

surrogate of density of seed sources under two scenarios: short- (SDD) and long-distance dispersal (LDD), respectively. Using tree species as a mark, we started off by creating a marked point pattern with the two censuses. A kernel density map of each species was then calculated in order to select the two dispersal scenarios. This step involved the use of a function where the effects of intensity variation can be separated from the effect of clustering in heterogeneous point processes (Baddeley and Turner, 2005; Diggle, 1985). This produced a value of sigma (the smoothing bandwidth parameter) for all tree species between 40.69 and 66.25 m in the 600 and 1000-ha large areas, respectively. For the higher bandwidth, we did the kernel density map for each species separately, applying a common bandwidth with information from each species (Baddeley and Turner, 2005; Kelsall and Diggle, 1995), which returned a value of sigma of 149.49 and 188.55 m in the 600 and 1000-ha large areas, respectively. Then for each species we obtained the density of potential seed sources at each plot by sampling the kernel maps at the coordinates of the 120 plots. It is important to note that the density of seed sources in each sampled plot is based not only on the adult trees nearby but also on the whole adult tree population.

Statistical analyses: zero-inflated Poisson mixed models

Using the package *agricolae* in the R statistical package (R Core Team, 2013), we conducted Kruskal-Wallis tests to test for differences in the biotic and abiotic variables between logging microsites and also to test if seedling establishment differed between microsites.

The next step was to evaluate the role played in seedling establishment by factors such as the abiotic variables, the competition with resprouts of selected tree species and the dispersal processes. Since establishment data followed a zero-inflated

Poisson distribution we applied zero-inflated generalized linear mixed models with a Poisson distribution (referred throughout the text as zero-inflated Poisson mixed models; Zuur et al. 2012). Using seedling density (individuals m^{-2}) as a response variable, we conducted a set of models, with soil compaction, canopy openness, soil water content, vegetation cover, resprout abundance and density of seed sources (both SDD and LDD data) as explanatory variables. Since our response variables are counts and contain more zeros than expected by the Poisson distribution, they follow a zero-inflated Poisson distribution (Zuur, 2009). Therefore, we used a zero-inflated Poisson model (Zuur et al. 2012) where the zeros are classified differently. The structural or true zeros refer to the absence of a species in the plot due to the unsuitability of the conditions in the plot. On the other hand, the false or sampling zeros are caused by errors in design, sampling or observation. Hence, some zeros were included in a binomial model to model the probability that a zero value is observed (zero vs. non-zero values), and some zeros were modeled with a Poisson model including all counts (zeros and positive values).

In the exploratory analysis prior to this, after checking for collinearity between the explanatory variables by calculating the variance inflation factor (VIF), we removed those variables with $\text{VIF} > 3$ (Zuur et al., 2010). Highly correlated variables such as tree and shrub percent cover were also removed, whereas canopy openness and soil compaction were retained, since these are two correlated variables which relate to different physical processes.

Before fitting the models we standardized all explanatory variables, so they all had mean of zero and standard deviation of one. We used the *glmmADMB* package (Fournier et al., 2012; Skaug et al., 2012) to fit zero-inflated Poisson mixed models in the R statistical package (RCore Team, 2013). Each model included a Monte Carlo

procedure, run with 50000 iterations, to obtain samples from a posterior distribution of the model parameters in order to find confidence intervals (Zuur et al., 2012).

To check for the presence of spatial autocorrelation in the response variable (seedling density) we calculated spline correlograms of the raw establishment data and used the bootstrap method (1500 replications) to calculate 95% confidence envelopes (Bjørnstad and Falck, 2001). Furthermore we also calculated spline correlograms of the Pearson residuals of the zero-inflated Poisson mixed models to inspect whether some spatial autocorrelation remained after accounting for the spatial autocorrelation of the explanatory variables (Zuur, 2009).

Finally, we generated a series of alternative zero-inflated Poisson mixed models for every species with different combinations of the explanatory variables. All models were ranked according to the Akaike Information Criterion (AIC). We calculated the Akaike weights (W_i) -the relative probability of each model being the best- and established the 95% confidence set of models (Zuur, 2009). To calculate the relative importance of each variable, we used the sum of the Akaike weights of all models where that specific variable was found.

Results

Selective logging

Selective logging removed 8550 trees of 16 timber tree species, and 77% of those trees had DBH > 40 cm. On average 5.29 individuals ha⁻¹ and 7.56 m³ ha⁻¹ in volume were removed. Consequently, numerous logging microsites were created, differing in area, soil and canopy disturbance and vegetation cover (Fig. 1, Table 1).

Log landings occupied significantly larger areas than logging gaps ($W = 437$, $P < 0.0001$; see Table 1). Log landings showed the highest soil and canopy disturbance,

followed by logging roads, skid trails and log gaps, the latter microsites showing partial soil disturbance and moderate canopy disturbance. Logging landings presented the highest soil compaction and high canopy openness, whereas logging roads had similarly high soil compaction and lower canopy openness (Table 1, Fig. 2). Skid trails had lower soil compaction and canopy openness while logging gaps had low soil compaction and intermediate canopy openness. The undisturbed sites had the lowest canopy openness and the second lowest soil compaction. Soil water content significantly differed between microsites (ANOVA, $F = 3.58$, $P = 0.009$) with logging landings showing the maximum value (Table 1).

Seedling establishment

We found 360 recently-emerged seedlings in the sampled plots, corresponding to 20 tree species. Among the five most abundant tree species (Table 2), *Acosmium cardenasii* was the most abundant, followed by *Machaerium acutifolium*. The rest of species had similarly lower seedling densities. As in the case of *Centrolobium microchaete* and *Tabebuia impetiginosa*, some species appeared mainly as resprouts rather than seedlings. *A. cardenasii*, the most abundant species, also had an important number of resprouts, as had three of the studied species (Table 2).

Seedling establishment in all five main tree species differed between logging microsites (Fig. 3). In *A. cardenasii* establishment was very low in highly disturbed microsites (e.g., log landings and roads), but high in undisturbed forest. In the case of *Caesalpinia pluviosa* there was no establishment in the most disturbed microsites, establishment was low in intermediately disturbed microsites (e.g., logging gap, skid trail) and much higher in undisturbed forest. Similarly, in *M. acutifolium* establishment was very low in disturbed microsites and high in undisturbed forest. On the other hand

Anadenanthera macrocarpa did not establish in undisturbed forest, while its establishment was high in logging gaps. Lastly, *Astronium urundeuva* established successfully in logging roads and skid trails.

Density of adult trees

The Kernel density maps of the three selected tree species revealed how density of seed sources varied across both study areas for each species (Figs. 4 and 5). The different bandwidth selection methods showed how density changed as a surrogate of short- and long distance-dispersal from the adult “mother” trees. The estimated densities of seed-source trees for the 600- and 1000-ha large study areas were, respectively, 2.10 and 1.48 ind ha⁻¹ for *A. macrocarpa*, 0.11 and 0.04 ind ha⁻¹ for *C. pluviosa* and 0.49 and 0.08 ind ha⁻¹ for *A. urundeuva*.

Niche and dispersal effects on seedling establishment

In four out of five tree species, models including niche variables were the best predictors of seedling establishment (Tables 3 and 4). Both *A. cardenasii* and *M. acutifolium* were influenced by niche variables, whereas *A. macrocarpa* and *C. pluviosa* were significantly influenced by niche variables and by dispersal processes together, and *A. urundeuva* was only influenced by dispersal processes (Table 4).

Regarding the two species whose establishment was only related to niche variables, *A. cardenasii* establishment decreased significantly with soil compaction and canopy openness, while *M. acutifolium* preferably established in microsites with closed canopies (Tables 3 and 4; see also Fig. 6). In the case of species whose establishment was linked to niche and dispersal variables, *A. macrocarpa* establishment increased significantly with increasing canopy openness, while it augmented with increasing

short-distance seed dispersal (Table 4; Fig. 6). In the case of *A. urundeuva* establishment increased with increasing dispersal over long distances (Fig. 6), while the rest of variables played a minor role. Finally, *C. pluviosa* establishment decreased as canopy openness and soil compaction increased, while it increased in response to dispersal over short distances (Fig. 6).

Discussion

Effects of logging on environmental heterogeneity

Logging intensity in the study area was lower than in other exploited TDFs (Baraloto et al., 2012; Villela et al., 2006) and nearby humid tropical forests (Fredericksen and Pariona, 2002; Peña-Claros et al., 2008), and much lower than the average selective logging intensity of 23 m³ ha⁻¹ applied in some sites of the Amazon Basin (Asner et al., 2005; Pereira Jr. et al., 2002). This relatively low logging intensity is consistent with the lower basal area, canopy height and growth rates of TDFs as compared to wet tropical forests. As we expected, this led to a clear gradient of canopy and soil disturbances.

Logging landing, characterized by very open canopies and highly disturbed soils (soil scarification and compaction) emerged as the most disturbed microsite. Logging roads, with similar soil conditions but lower canopy disturbance, was the second most disturbed microsite. Skid trails had intermediate soil disturbance and little canopy disturbance, while logging gaps presented low soil disturbance and higher canopy disturbance. In undisturbed sites, soil compaction may be increased as a result of the dense network of roots often found in such sites. This could be an explanation for the higher values of soil compaction in undisturbed sites in comparison to that of logging sites. These results are in accordance with the findings of Fredericksen and Mostacedo (2000) six months after logging in another Chiquitano dry forest site. They found

significant differences in tree cover in the most disturbed logging landings and roads, in comparison to the least disturbed logging gaps and undisturbed microsites. They also found soil disturbance was much higher in logging landings and gaps than in the rest of logging microsites. Fredericksen and Pariona (2002) also reported that scarified areas varied across logging gaps in a nearby humid tropical forest in Guarayos, Santa Cruz.

Effects of environmental heterogeneity on seedling establishment

After logging, the abiotic environment was considerably altered, especially in the most disturbed logging microsites, leading to changes in light, soil moisture and rooting conditions, which are important factors determining seedling establishment (Oliver and Larson, 1996).

High canopy openness significantly reduced the establishment of three tree species (*A. cardenasii*, *C. pluviosa* and *M. acutifolium*), and affected recruitment of all species. Overall average seedling establishment was low, with *A. cardenasii*, *A. macrocarpa* and *M. acutifolium* showing the highest values. This is consistent with the relative abundances of these species found by the Long Term Silvicultural Research Program (LTSRP) plots monitored every 2-3 years in INPA by IBIF since 2002, with these species ranked, respectively, as first, second and fifth (unpublished data). These abundances were also similar to the ones found in another Chiquitano forest in the Lomerio site (Fredericksen and Mostacedo, 2000).

Functional groups of species with distinct ability to regenerate under different light conditions (Poorter et al., 2006), have been reported to respond differently to selective logging (Arets et al., 2003; Berry et al., 2008; DongKai et al., 2010). The observed differences in seedling establishment were in agreement with the characteristic shade tolerance of the species guilds (Table 2). The shade-tolerant *A. cardenasii* and the

partially shade-tolerant *C. pluviosa* and *M. acutifolium* showed similar patterns of decreasing seedling establishment with logging disturbance, mainly due to the differences in light availability and also in soil compaction. Accordingly, the long-lived-pioneers *A. macrocarpa* and *A. urundeuva* had the highest establishment in intermediately disturbed microsites. These results indicate that logging causes an increase in the abundance of pioneer and mid-tolerant species. As for the shade-tolerant species, they remain dominant in undisturbed forest (DongKai et al., 2010; Peña-Claros et al., 2008).

Abundance of pioneer species also decreases with increasing time since logging in sites logged long time ago (Verburg and van Eijk-Bos, 2003). Similarly we can refer to another Chiquitano TDF study near our study site. The establishment of *A. macrocarpa* and *A. urundeuva* was higher in the most disturbed sites one year after selective logging, while *C. pluviosa* had similarly high establishment in the least disturbed sites (Fredericksen and Mostacedo, 2000). Similar responses have been found in a dipterocarp forest in Borneo, where pioneer species were dominant in logged forests, suggesting successful establishment shortly after logging (Berry et al., 2008). In a Bolivian wet tropical forest soil scarification due to skidder disturbance had some positive effects in seedling density (Fredericksen and Pariona, 2002), although other unknown factors influenced seedling establishment. In the same site pioneer species dominated establishment in recent gaps, although some timber tree species also ended up dominating logging gaps (Park et al., 2005). Moreover, functional guilds also show different growth rates in response to disturbance. In the INPA site it has been found that the increase in growth rates due to silvicultural treatments is higher in pioneer than in shade-tolerant tree species (Villegas et al., 2009).

400 Taking into account the differences found in soil water content among logging
401 microsites, we found the effect of soil water content on seedling establishment to be
402 insignificant. The importance of soil water content in explaining tree recruitment was
403 low as compared to other abiotic factors as canopy openness or soil compaction. This
404 could be due to the shallow soil layer considered or to the period when soil water
405 content was measured. Although soil water content was measured during the dry
406 season, the availability of local soil water could have been altered notably after a few
407 rainy days. Moreover, soil water availability could also be affected by differences in soil
408 texture, depth and organic matter content in the logging microsites.

409 There is a contrast between these results and other studies. Drought intensity and
410 water availability have been seen to play a major role in the distribution of plant species
411 in moist tropical forests (Engelbrecht et al., 2007; Condit et al., 2013). The reason for
412 such contrasting results could be the difference in the scales used in each study and the
413 types of forests compared. Their calculations were based on tree drought sensitivity,
414 which is the relative difference in seedling survival over the dry season, comparing dry
415 plots to experimentally irrigated ones. This information was then related to the regional
416 and local abundance of each species. In contrast to this method, in our study we
417 estimated shallow soil water content as an on the spot reference to water availability and
418 related it to local seedling abundance. There are, of course, differences in the annual
419 precipitation, which is much lower at INPA than in Barro Colorado Island (2612 mm),
420 where these studies were performed (Windsor, 1990). One final point to bear in mind is
421 the influence of seedling traits in drought survival (Poorter and Markesteijn, 2008b).
422 These traits could buffer soil conditions and be of long-lasting importance in
423 determining a species regeneration niche (Poorter, 2007).

424

Dispersal effects on seedling establishment

Seed dispersal is considered to be fundamental in determining recruitment and expansion rates in tree species particularly at large spatial scales (Nathan and Muller-Landau, 2000). To study the effect of dispersal from parent trees on seedling establishment we estimated seed rain. We did so using kernel density maps of adult trees, as we considered adult trees as density of seed sources a surrogate of seed rain. The heterogeneous patterns of the kernel density maps suggested that the distribution of some of the study tree species could related to dispersal limitation when the availability of seeds is limiting recruitment at the landscape level (Münzbergová and Herben, 2005).

Density of seed sources and location of adult reproductive trees played an important role in seedling establishment in three out of the five study species. The relative importance of dispersal and niche factors in seedling establishment (Table 3) could be directly related to the availability of seeds (seed limitation) and the availability of suitable microsites (establishment limitation), respectively. For instance, in *A. macrocarpa*, the availability of seeds, when compared with the availability of suitable microsites, revealed similar contributions on seedling establishment. However, our inferential analyses should be complemented with additional data on fruit production and seed censuses to strengthen our conclusions. Furthermore, the location of adult reproductive trees could be a legacy of past events including logging or fires.

In *A. urundeuva*, seed limitation contributed much more whilst in *C. pluviosa* establishment limitation had a greater effect on seedling establishment. Our results suggest that effective regeneration can be fulfilled through different pathways modulated by biotic and abiotic factors and their interactions (Pulido et al., 2010).

Implications for the management of logged tropical dry forests

The low logging intensity in the study site in terms of individuals harvested per area could be considered high if the overall damage caused per logged tree is taken into account (Panfil and Gullison, 1998). Nevertheless, we consider that harvest intensity in the study site is already optimized to cause little residual damage, i.e. damage to non-logged trees. This research provides further understanding of the specific environmental and biotic constraints of tree recruitment as the dominant roles played by canopy openness and soil compaction in the study TDF. This knowledge would lead to a deeper understanding of the reasons for regeneration success or failure in some commercial tree species after logging. Silviculture management techniques based on species guilds (Park et al., 2005) are essential in this context. Examples of the negative effects of overharvesting can be seen in the INPA forest and in other Neotropical TDFs, where some of the most valuable timber tree species have been depleted (Gullison et al., 1996; Grogan and Galvão, 2006). Careful management is needed to restore these forest stands to be sustainable. Therefore our management recommendations are to carefully plan logging operations species by species according to local abundances and the knowledge of their recruitment strategies after logging disturbance.

Moreover, the results in our study make it clear that the way to guarantee adequate regeneration of some timber tree species is by focusing on the spatial distribution of the adult trees which represent future harvestable trees. This information can be used to detect areas where local abundance of a species is high enough for adequate regeneration. Rather than harvesting a species only if the harvestable individuals attain a minimum density threshold on average on a large enough area (e.g., 600 ha), we also suggest using size thresholds on smaller areas (5-10 ha) that take into account the local variations in density of seed sources. This is especially important for species with heterogeneous spatial distributions either caused by spatial

heterogeneity in the distribution of abiotic resources (slope, soil features) (Punchi-
Manage et al., 2013) or by clustering processes caused by dispersal syndromes or by
species interactions (Seidler and Plotkin, 2006; Wiegand et al., 2007).

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688
689 **Tables**

690
691 **Table 1.** Logging microsites described by mean values of variables measured to
692 characterize them. The χ^2 statistics correspond to Kruskal-Wallis tests based on multiple
693 comparisons between microsites performed for each variable. For Area, a Wilcoxon-
694 rank test was used. Different uppercase letters indicate that mean variables significantly
695 differed between microsites. Significance levels: *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Microsites						
Variables (units)	log landings	logging roads	skid trails	logging gaps	undisturbed	χ^2
Length (m)	34.16 ^a	4.83 ^b	3.71 ^c	13.54 ^d	---	69.51 ^{***}
Area (m ²)	1165.68 ^a	---	---	129.12 ^b	---	---
Trees (%)	3.17 ^a	36.09 ^a	70.21 ^b	21.30 ^b	81.25 ^c	69.29 ^{***}
Shrubs (%)	37.13 ^a	26.48 ^a	20.33 ^{ab}	39.78 ^{bc}	42.92 ^c	17.34 ^{**}
Woody vines (%)	9.04 ^a	4.70 ^{ab}	7.33 ^{abc}	10.91 ^{bc}	20.54 ^c	10.45 [*]
Herbaceous vines (%)	7.25 ^a	6.48 ^a	15.96 ^{ab}	18.13 ^{bc}	10.13 ^c	17.15 ^{**}
Herbs (%)	1.58 ^a	1.04 ^a	4.75 ^{ab}	6.04 ^{bc}	4.29 ^c	16.85 ^{**}
Canopy openness (%)	62.06 ^a	37.29 ^a	14.01 ^c	28.13 ^d	4.38 ^c	88.54 ^{***}
Soil water content (%)	19.22 ^a	16.76 ^{ab}	17.22 ^{ab}	16.19 ^{ab}	15.02 ^b	3.58 ^{**1}
Soil compaction (N m ⁻²)	362.81 ^a	342.41 ^a	174.06 ^b	144.07 ^{bc}	151.44 ^c	76.33 ^{***}

696 ¹This statistic corresponds to the F value of an ANOVA and a Tukey post-hoc test.

697
698 **Table 2.** The five most abundant species with guilds and the observed seedling and
699 resprout density. Values are means $\pm$ SE.

Species	Guild	Seedling density (ind. m ⁻²)	Resprout density (ind. m ⁻²)
<i>Acosmium cardenasii</i>	shade-tolerant	0.341 $\pm$ 0.052	0.194 $\pm$ 0.052
<i>Anadenanthera macrocarpa</i>	long-lived pioneer	0.097 $\pm$ 0.024	—
<i>Astronium urundeuva</i>	long-lived pioneer	0.025 $\pm$ 0.019	—
<i>Caesalpinia pluviosa</i>	partially shade- tolerant	0.049 $\pm$ 0.016	0.027 $\pm$ 0.009
<i>Machaerium acutifolium</i>	partially shade- tolerant	0.25 $\pm$ 0.1340	0.021 $\pm$ 0.007

Table 3. Main results of the zero-inflated Poisson mixed models showing their ranking and the relative importance of variables explaining the abundance of seedlings of the most abundant tree species. The symbol “✓” indicates that the corresponding variable entered that model. Variables abbreviations are: COPEN, canopy openness; SCOMP, soil compaction; SWC, soil water content; RESPA, resprout abundance; SDD, density of short-distance dispersal “mother” trees; LDD, density of long-distance dispersal “mother” trees. The ranking of the models according to their parsimony was based on the Akaike Information Criterion (AIC) and Akaike weights (W_i). The relative importance of a variable is the sum of the W_i of all models including that variable.

Species	Rank	COPEN	SCOMP	SWC	SDD	LDD	AIC	W_i
<i>Acosmium cardenasii</i>	1	✓	✓				338.070	0.583
	2	✓	✓	✓			339.994	0.223
	3		✓				340.924	0.140
	4		✓	✓			342.850	0.053
Relative importance		0.806	0.999	0.276				
<i>Anadenanthera macrocarpa</i>	1	✓			✓		169.663	0.261
	2	✓	✓			✓	170.130	0.206
	3	✓	✓		✓		170.462	0.175
	4	✓		✓	✓		171.387	0.110
	5	✓	✓	✓		✓	171.575	0.100
	6	✓	✓	✓	✓		171.672	0.095
Relative importance		0.948	0.577	0.306	0.641	0.307		
<i>Astronium urundeuva</i>	1					✓	39.009	0.328
	2	✓				✓	40.454	0.160
	3			✓		✓	40.685	0.141
	4		✓			✓	40.997	0.121
	5	✓					41.314	0.103
	6	✓		✓		✓	41.846	0.080
	7	✓	✓				42.189	0.067
Relative importance		0.409	0.067	0.221	0	0.829		
<i>Caesalpinia pluviosa</i>	1	✓	✓		✓		102.577	0.336
	2	✓	✓			✓	103.758	0.186
	3	✓	✓	✓	✓		104.503	0.128
	4	✓	✓	✓		✓	105.625	0.073
	5	✓				✓	106.087	0.058
	6	✓	✓				106.179	0.055
	7		✓				107.027	0.036
	8	✓		✓		✓	107.997	0.022
	9		✓			✓	108.034	0.022
	10	✓	✓	✓			108.159	0.021
	11		✓		✓		108.630	0.016
Relative importance		0.880	0.874	0.244	0.480	0.362		
<i>Machaerium acutifolium</i>	1	✓					225.428	0.531

	2	✓	✓		227.404	0.198
	3	✓		✓	227.410	0.197
	4	✓	✓	✓	229.390	0.073
Relative importance		0.999	0.271	0.270		

Table 4. Parameters of the most parsimonious fitted Zero-Inflated Poisson Mixed Models for seedling establishment of the five most abundant tree species. Soil water content was not significant in the best-fitted models. Significance levels are indicated as in Table 1 and variables abbreviations are as in Table 3.

Species	intercept	COPEN	SCOMP	SDD	LDD
<i>A. cardenasii</i>	-0.13	-0.42*	-1.07***	—	—
<i>A. macrocarpa</i>	0.22	0.94***	—	0.41**	
<i>A. urundeuva</i>	-1.87	—	—	—	1.26***
<i>C. pluviosa</i>	-4.39***	-1.97*	-1.82*	0.70*	—
<i>M. acutifolium</i>	-1.79***	-1.31***	—	—	—

727
728 **Figure 1.** Overview of the sampling design and illustrations of log landing, skid trails
729 and logging road.
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Figure 2. Boxplots showing the variability of variables measured in logging microsites: a, soil compaction; b, canopy openness; c. soil water content; d, tree cover. Logging microsites are indicated by numbers as in Figure 1 (1, log landing; 2, logging road; 3, skid trail; 4, logging gap; 5, undisturbed forest).

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744 **Figure 3.** Mean seedling abundances of the studied tree species in each logging
745 microsite. Error bars are standard errors. Different letters over bars indicate significant
746 differences ($P < 0.05$) according to Kruskal-Wallis tests used for doing multiple
747 comparisons among microsites. Logging microsites are indicated by numbers as in
748 Figure 1 (1, log landing; 2, logging road; 3, skid trail; 4, logging gap; 5, undisturbed
749 forest).

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753 **Figure 4.** Kernel maps showing interpolated tree density data (ind ha⁻¹, color scales)
 754 with locations of adult individuals of three canopy trees (a, *Anadenanthera macrocarpa*;
 755 b, *Caesalpinia pluviosa*; c, *Astronium urundeuva*) in the first study area. The two
 756 columns show different bandwidth selection methods used to estimate tree density as a
 757 surrogate of short- (SDD, left column) and long-distance seed dispersal (LDD, right
 758 column), respectively. The *x* and *y* axes correspond to UTMX and UTMY coordinates,
 759 respectively.

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764 **Figure 5.** Kernel maps showing interpolated tree density data (ind ha⁻¹, color scales)
 765 with locations of adult individuals of three canopy trees (a, *Anadenanthera macrocarpa*;
 766 b, *Caesalpinia pluviosa*; c, *Astronium urundeuva*) in the second study area (1000 ha).
 767 The rest of explanations are as in Figure 4.

771 **Figure 6.** Scatter plots showing seedling density of selected tree species as related to the main
772 explanatory variables revealed by the Zero-Inflated Poisson Mixed Models (see Tables 3 and 4).
773 SDD and LDD refer to short- and long-distance seed dispersal, respectively.