DO MICROHABITATS IN FOREST GAPS INFLUENCE TREE REGENERATION? A STUDY IN THE MONTANE FORESTS OF VENEZUELAN GUAYANA

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Abstract. One theory used to explain the high tree species richness in tropical forests involves niche partitioning, whereby species specialize according to the availability of environmental resources in microhabitats. We examined whether there were differences in microhabitats that could account for the composition and diversity of tree regeneration in natural small-scale montane forest canopy gaps found in the Sierra de Lema, Venezuela. Five microhabitats (fallen crown, fallen large branches, large lying trunk, undisturbed ground, and the gap border) were identified and sampled for species richness in 20-m² plots within gaps. Additionally, the cover of trees, large palm seedlings, shrubs, tree ferns, and small palms was estimated and gap age, size, and disturbance category were assessed. To test what was influencing tree species richness we developed four alternative models and used various combinations of explanatory variables: microhabitats, abiotic gap characteristics, and competition with other life forms. The importance of each variable was evaluated based on the model averages. The differences in composition were analyzed with permanova and mrpp, and an indicator species analysis was done. A total of 111 morphospecies was recorded. Species richness differed between microhabitats. Branch and crown areas had a negative impact, as did the most severe disturbance category. Gap size, however, did not have any impact on species richness at either plot or gap level. Species composition differed between crown, undisturbed, and trunk microhabitats and the most severe disturbance category also had a differentiating impact. *Sloanea* sp. and *Ocotea* sp.1 were associated with undisturbed and trunk microhabitats. The palm *Euterpe catinga* was associated with an intermediate disturbance intensity, whereas *Elaeagia maguirei*, *Ocotea* sp.1, and *Schefflera quinquestylorum* were associated with the severe disturbance category. We conclude that species richness and floristic composition of trees regenerating in the montane forest gaps of the Sierra de Lema were mainly affected by disturbance and advanced regeneration.

Resumen. Los altos niveles de riqueza arbórea que caracterizan a los bosques tropicales han sido parcialmente explicados por la hipótesis de nichos de regeneración, la cual postula que las especies se especializan a los recursos ambientales disponibles en los microhábitats. El presente estudio investiga si la riqueza y la composición florística de la regeneración arbórea es afectada por los microhábitats en claros de bosque montanos en la Sierra de Lema, Venezuela. La riqueza de la regeneración arbórea fue inventariada en parcelas de 20 m², repartidas en cinco microhábitats de claros: 1) la copa del árbol caído que formó el claro, 2) las ramas caídas, 3) el fuste del árbol caído, 4) el suelo no perturbado del claro y 5) el borde del claro. Se estimó la cobertura de la regeneración de árboles y palmas grandes, las palmas de porte pequeño, arbustos y helechos arborescentes en las parcelas, asi como la edad y tamaño de los claros y el nivel de perturbación de los mismos. Cuatro modelos fueron postulados con el fin de comprobar cuales variables (microhábitats, características abióticas del claro y la competencia de otras formas de vida) afectan la riqueza de especies. La importancia de cada variable fue evaluada en base los promedios de los modelos. La diferencia en composición florística fue analizada mediante PERMANOVA, MRPP y el análisis de especies indicadoras. Se registró un total de 111 morfo-especies. La riqueza de especies fue diferente entre los microhábitats. La misma fue afectada negativamente por las áreas de ramas y copa asi como con el nivel de perturbación más severo. Similarmente la composición florística se diferenció entre algunos microhábitats (entre la copa, suelo no perturbado y fuste) y esta también fue afectada por el nivel de pertubación más severo. Sin embargo, la riqueza y la composición florística no fueron afectadas por el tamaño del claro. Las especies *Sloanea* sp. y *Ocotea* sp.1 estuvieron asociadas a los microhabitats de suelo no perturbado y tronco, la palma *Euterpe catinga* a niveles de perturbación media y *Elaeagia maguirei*, *Ocotea* sp.1 y *Schefflera quinquestylorum* a niveles de perturbación severa. Se concluye que la riqueza y la composición florística de la regeneración arbórea, en claros del bosque montano de Sierra de Lema, son afectadas principalmente por la perturbación y la regeneración remanente.

Keywords: microhabitat, tree regeneration, forest gap, disturbance, Sierra de Lema, Guayana Shield, tropical forest.

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INTRODUCTION

Tropical forests are known for their high tree species diversity (Ricklefs 1977, Connell 1978) although the reasons for this high diversity are not yet completely understood. Different theories have been developed to explain this diversity, especially as an outcome of regeneration processes (Clark & Clark 1984, Dalling *et al.* 1998, Hubbell *et al.* 1999, Hubbell 2005). Ricklefs (1977), for example, suggested that the high diversity in tropical forests is a consequence of differences in regeneration niches requiring species to specialize and adapt to certain environmental conditions in the early phases of their life cycles, i.e. the tree seedling and sapling phase. In the same year, Grubb (1977) suggested that the highest variety of regeneration niches can be found in forest gaps, because large gradients of environmental factors including light, temperature, humidity, etc. exist there. These gradients and their effects are expected to increase with gap size (Swaine & Whitmore 1988). Microhabitat heterogeneity within the root, bole, and crown zones in tree-fall gaps was also suggested as a partial explanation for the species richness and growth form diversity (Orians 1982). Within gaps, tree species partition resources by regenerating along environmental gradients which are influenced by gap size (Denslow 1980). Some current studies provide evidence for niche partitioning in tropical forests (Brokaw & Busing 2000, Poorter 2007, Kraft *et al.* 2008, Rüger *et al.* 2009). But so far there is no general agreement on the effects of niche partitioning. A number of studies looking at tree species regeneration in tropical forest gap microhabitats have found compositional differences (Brandani *et al.* 1988, Núñez-Farfán & Dirzo 1988) but other studies did not detect any species preferences for certain microhabitats (Uhl *et al.* 1988, Baraloto & Goldberg 2004).

In this study, we analyzed the regeneration in small gaps caused by tree falls in the Sierra de Lema montane tropical forest. This tropical forest is a part of the Guayana Shield, the world's largest remaining undisturbed tropical rainforest (Hernández *et al.* 2012). In this region, as in most other tropical regions, ecological studies have focused on lowland forest ecosystems. However, mountain forest ecosystems could have a disturbance regime different than lowland forests. We developed the hypotheses for our study based on existing knowledge about microhabitat effects on species composition in lowland forest ecosystems. Gap areas opened up by fallen tree crowns are known to have the lowest plant density within the gap types (Poorter 2002) because advance regeneration is often damaged by the falling crown and the germination and growth of seedlings under the crown could be difficult as the crown decays (Núñez-Farfán & Dirzo 1988). Another reason for the low density could be that the leaf litter from the fallen crown prevents light from reaching the forest floor. The decomposition of the crown can take several years (Poorter 2002) and release high quantities of nutrients relatively rapidly (Brandani *et al.* 1988). The fallen trunk elevated above the surrounding area could receive more light. Such conditions in combination with moist, decaying fallen wood potentially provide excellent germination conditions (Poorter 2002). Individuals germinating from seeds on still undecomposed trunks in humid forests generally have a greater chance of survival because they are positioned above the competition (van der Meer *et al.* 1998). Tree regeneration hit by the falling tree can be severely damaged whereas undamaged regeneration can benefit by being released from competition (Brandani *et al.* 1988).

In our study gaps, the largest area consisted of undisturbed forest floor (Durán-Rangel *et al.* 2011). The advanced tree regeneration in these undisturbed microhabitats had the best chances for survival and growth. However, plants that can grow beneath the advanced tree regeneration, like understory palms (Denslow *et al.* 1991) and tree ferns (Gaxiola *et al.* 2008), can also respond to the gap conditions. They compete with tree seedlings and saplings for gap resources and they can mechanically interfere with them (Royo & Carson 2006).

With this study we aimed to understand which forest canopy-gap attributes drive forest regeneration, tree species richness, and composition in montane tropical forests. Therefore we developed a set of four alternative models to estimate tree species richness as a function of multiple explanatory variables. The most parsimonious model included only the different microhabitats as an explanatory variable. The full model included the different microhabitats plus additional explanatory variables describing the gap characteristics, such as gap size and gap age as well as the cover of competing life forms. In the third model the different microhabitats were replaced by disturbance intensity. The last model included only the abiotic gap characteristics (size and age) along with disturbance intensity. We were not only interested in whether there was a quantitative impact on species richness but also in analyzing the qualitative

differentiation in tree species composition and in identifying those tree species which depended on certain niches represented by microhabitats.

METHODS

Study area. The study was carried out in the montane forests of the Sierra de Lema located in the State of Bolívar, in southeast Venezuela. These forests grow on soils derived from sedimentary rocks of the Roraima Group from the Precambrian Era and diabase intrusions of the Mesozoic Era (Huber 1995). The soils are characterized by a low nutrient content, low pH, and low cation exchange capacity (Durán-Rangel 2001, Hernández *et al.* 2012). The study area comprises 53.5 ha at approximately 1430 m a.s.l. situated on a dissected plateau (Durán-Rangel *et al.* 2011).

The cloud forests studied in Sierra de Lema have been classified as "very humid submontane forest" (Ewel & Madriz 1968, Holdridge *et al.* 1971). The mean annual temperature is 18°C (Hernández & Castellanos 2006) while the mean annual precipitation is around 4800 mm (data from CVG-EDELCA climate station situated at 1412 m a.s.l., located about 20 km from the study area; data for the period 1988-2004). The monthly average precipitation is above 100 mm (Huber *et al.* 2001). The forests in this region show no signs of human influence (Duellman 1997, Huber *et al.* 2001). The main tree canopy reaches a height of 20-25 m, with emergent trees over 40 m in height. These forests are characterized by moss-covered tree trunks, abundant epiphytes and hemi-epiphytes, tree ferns (Cyatheaceae) and palms. The most diverse tree families are Lauraceae, Clusiaceae, Rubiaceae, Sapotaceae, Melastomataceae, Myrtaceae, Moraceae, Burseraceae, Chrysobalanaceae, and Euphorbiaceae (Sanoja 2009). The most frequent tree species are *Licania intrapetiolaris*, *Sextonia rubra*, *Micropholis spectabilis* and *Protium* spp. (Durán-Rangel 2001, Hernández & Castellanos 2006).

Gaps and microhabitats. The canopy gaps in the Sierra de Lema forests are created by small-scale disturbances, frequently uprooted trees. Over time, canopy gap border trees could be uprooted pushing down more trees thereby enlarging and modifying the gaps (Durán-Rangel *et al.* 2011). Canopy gaps in the Sierra de Lema had a mean size of 296 m² (gap size range c. 30-900 m²) and occupied 1.4% of the forest area (Durán-Rangel *et al.* 2011).

Because most of the gaps in the study area were found on a plateau (Durán-Rangel *et al.* 2011), in order to study tree regeneration that was representative of the regeneration dynamics occurring in the gaps, only gaps located on the plateau were considered. The age of the studied gaps was known from a monitoring of gap formation, their age ranged from a few months to older than three years. Gaps were defined employing Runkle's (1981) definition as "areas under a canopy opening that extends to the bases of the canopy trees surrounding the canopy opening" where 75% of the vegetation was less than 2 m high (Durán-Rangel *et al.* 2011). The border area, a 5-m wide zone stretching from the edge of the gap into the adjacent forest, was also included in the analysis. Although the border zone did not strictly belong to the gap, it was influenced by the changed physical (freeing up potential sites for the establishment of new individuals) and climatic conditions (irradiation, air temperature, wind, humidity) after gap creation. In a previous study (Durán-Rangel *et al.* 2011) we observed that similar numbers of pioneer species had established in the border areas and in the centers of gaps. Therefore just as Popma *et al.* (1988) considered it important to include gap borders when studying early gap regeneration, so did we.

Microhabitats were defined as areas within the gap where the abiotic conditions necessary for seedling establishment were relatively homogeneous. We distinguished the following gap microhabitat categories (Table 1): fallen crown (crown), fallen large branch with diameter < 20 cm (branches), large lying trunk with diameter ≥ 20 cm (trunk), undisturbed ground (undisturbed), and undisturbed forest floor under the closed forest bordering the gap (border).

The same plots were grouped in three disturbance intensity categories on the basis of their level of disturbance (Table 1). Plots in which the tree regeneration under the fallen crown was greatly damaged were classified as severely disturbed (severe). Branch and trunk microhabitats only partially damaged and where several individuals of the advance regeneration survived between branches or beside the trunk corresponded to the moderately disturbed (medium) category. Finally, the undisturbed patches in the gaps and in the gap borders corresponded to the negligibly disturbed (minor) category.

Vegetation data collection. We defined tree regeneration as individual trees and large palm species with heights between 0.5 and 3 m. These height classes were adopted from a previous regeneration monitoring study established in Sierra de Lema for the purposes of a broader long-term ecological study of re-

TABLE 1. Number of plots per microhabitat and disturbance intensity category.

Microhabitats	Number of plots
Crown	13
Branches	12
Trunk	14
Undisturbed	7
Border	16
Disturbance intensity categories	
Minor	13
Medium	26
Severe	25

gional forest dynamics (Hernández & Castellanos 2006). The size of the study plots was 20 m² and the shape variable to accommodate the form of the microhabitat. In 23 gaps, 62 plots were established across different microhabitats.

As a measure of the occupancy of the microhabitat by different vegetation forms, namely tree regeneration, shrubs, tree ferns, and small or understory palms, the respective cover was estimated using the Braun-Blanquet cover abundance scale (Matteucci & Colma 1982); for each cover abundance class the class mean was used: 5 = 87.5%, 4 = 62.5%, 3 = 37.5%, 2b = 20%, 2a = 10%, 1 = 2.5%, + = 0.1%, and r = 0.02.

Regenerating trees were identified by their indigenous local names (by Leandro Salazar, a native guide from the research area) after which they were identified to the species, genus, or family level. Where this was not possible, trees were classified to morphospe-

cies. The nomenclature used follows the Flora of the Venezuelan Guayana (Berry *et al.* 1995) and for species not listed there we consulted the Tropicos botanical information system of the Missouri Botanical Garden (http://www.tropicos.org/), Missouri Botanical Garden 2010).

Statistical analysis. Differences in cover of the different life forms between microhabitats and disturbance categories were tested with the Kruskal-Wallis test and Wilcoxon test for pairwise comparisons. These tests were carried out using the R package "stats" (Venables & Ripley 2002).

The tree regeneration species richness was estimated using individual-based rarefaction (Gotelli & Colwell 2001) to control for differences in abundances between microhabitats, using the "vegan" package of R (Oksanen *et al.* 2010). The rarefied species richness was used for all further analysis.

To test if the microhabitats and other gap characteristics influenced species richness we developed four alternative models to estimate species richness as a function of multiple explanatory variables, described in the Introduction and in Table 2. A generalized linear model with Poisson distribution and log link function was applied. To evaluate the models we used the information theoretic framework (Burnham & Anderson 2002, Anderson 2008). The evaluation of the models was performed using the package "AICcmodavg" version 1.24 (Mazerolle 2012). The second order of Akaike´s Information criterion (AICc) for small samples was applied to evaluate the different models (Burnham & Anderson 2002). Additionally, we calculated two more measures to compare the models: the first one is delta AICc, which measures the difference of each model relative to the best model. A second measure for the strength

TABLE 2. Candidate models for estimating species richness, including the value of the maximized log-likelihood function (Max log), the number of estimated parameters (K), Model selection criterion (AICc), the differences compared to the best model (Delta i), and the Akaike weights (weight i).

Model#	Model	Max log (LL)	K	AICc	Delta i	Weight i
1	Mhab+Gap+Comp	-146.6813	11	321.1018	0.0000	0.9871
2	Gap+Dist+Comp	-154.0394	9	329.8288	8.7270	0.0126
3	Gap+Dist	-161.8851	6	337.4173	16.3155	0.0003
4	Mhab	-167.0866	5	345.2446	24.1427	0.0000

K: Parameter count includes intercept and variance; Mhab: the factor microhabitat; Gap: includes the factors gap size and the factor gap age; Dist: the factor disturbance intensity; Comp: includes the three competing life forms (tree ferns, small palms, and shrubs)

of evidence of each model is the Akaike weight, which indicated the probability that the model is the best among the whole set of candidate models (Burnham & Anderson 2002). Akaike weights were calculated as the ratio of the delta AICc of a given model relative to the whole set of models.

The magnitude of the effect of each explanatory variable on the response variable was assessed with an estimated average across all models. To conduct the model averaging, the estimate (i.e. the regression coefficient) of each of the variables for each model was weighted by the Akaike weights (Mazerolle 2012). The precision of the estimation (SE) of the models averaged estimate was calculated in the same way.

A simple linear model was fitted in order to explain the richness of tree regeneration in gaps with gap sizes. The species richness for this model was rarefied according to an individual-based approach (Gotelli & Colwell 2001).

In order to test for differences in species composition within microhabitats and disturbance categories, the permutational multivariate analysis of variance or PERMANOVA (Anderson 2001) was used. This is a non-parametric test of differences in species composition (tree regeneration) between samples from different groups (microhabitats and disturbance intensity categories). As the species composition in plots may be spatially autocorrelated, given that several plots were positioned within each gap, the plot location (termed Gap ID) was included in the PERMANOVA test. Other explanatory variables were the gap age, which is the time passed since gap formation (recent < 1 year, middle-aged between 1 and 3 years, and old > 3 years), and the gap size (small < 150 m², medium 150–300 m², and large > 300 m²). The effects of these explanatory variables were tested stepwise in the PERMANOVA analysis. Pairwise comparisons were performed using the non-parametric multi-response permutation procedure (MRPP, McCune & Grace 2002). The T statistic shows the floristic "separation" between the groups. The A value describes the within-group homogeneity compared with the random expectation, whose maximum value is 1, which would indicate that all individuals in the groups belong to one species. In community ecology, a value higher than 0.3 is deemed to be fairly high (McCune & Grace 2002). Both tests were performed with "vegan" version 1.17-3 (Oksanen *et al.* 2010).

To identify tree species which would be promoted by certain microhabitats, we performed an Indicator Species Analysis (ISA, Dufrene & Legendre 1997). This analysis is based on the frequency of species occurring in plots corresponding to a group, for example to a microhabitat. The ISA value is 1 when a species is found in all the plots belonging to a group (Legendre & Legendre 1998).

For PERMANOVA, MRPP, and ISA analysis, species occurring in less than 5% of the plots were excluded. We used the Bray-Curtis dissimilarity index and ran 10 000 permutations. All statistical analyses were conducted using R version 2.15.1 for Linux (R Development Core Team 2012).

RESULTS

Tree species richness. A total of 111 morphospecies was recorded in the regeneration plots, two of them large palm species (*Euterpe catinga* and *Dictyocaryum ptarianum*). The most abundant species were all shade-tolerant, including *Duguetia rigida*, *Elaeagia maguirei*, *Myrcia bracteata*, *Licania intrapetiolaris*, the palm *Euterpe catinga*, and the pioneer *Ocotea* sp. 1 (Durán-Rangel 2011).

The percentage cover of the various life forms were, in most cases, significantly different between the microhabitats (Fig. 1a, Kruskal-Wallis chi-squared for border = 42.62, undisturbed = 22.05, trunk = 29.73, branches = 23.39, and crown = 24.60; all with df = 3 and P < 0.05) and within disturbance categories (Fig. 1b, Kruskal-Wallis chi-squared for minor = 63.09, middle = 52.15, and severe = 24.60; all with df = 3 and P < 0.05).

The results in Table 2 indicate that model 1, the full model including microhabitats, gap age, gap size, and the competition from other life forms (cover of tree ferns, shrubs, and small palms) with an Akaike weight of 321.10, is the best of the four candidate models. Only the first two models have a reasonable level of support (Delta i < 10). As a rule of thumb, a delta < 2 suggests substantial evidence for the model (Anderson 2008) (Table 2). The full model including the microhabitats (Mhab+Gap+Comp) is 78.53 times more likely to be the best model than the model with disturbance intensity (Gap+Dist+Comp) based on the evidence ratio (0.9871/0.0126).

If we consider the influence of the individual explanatory variables, it was crown microhabitat or disturbance intensity which had the highest impact on species richness (Table 3, Fig. 1). Compared to the reference microhabitat (the undisturbed situa-
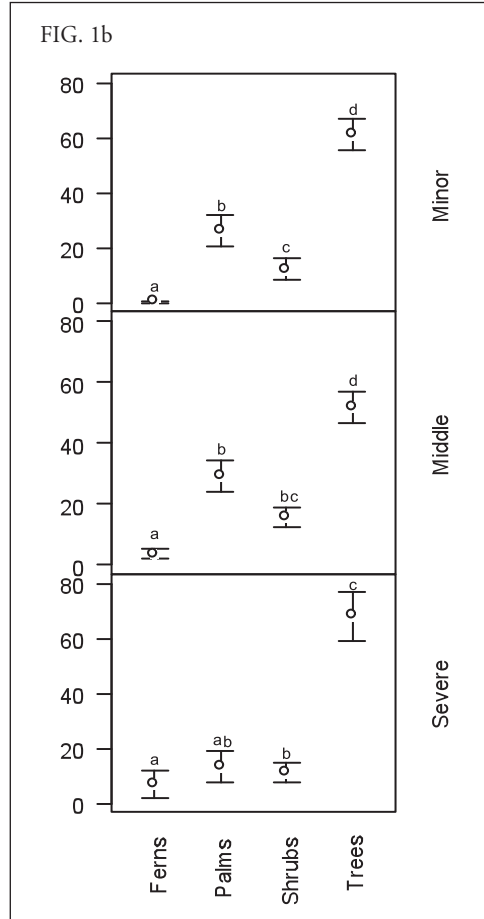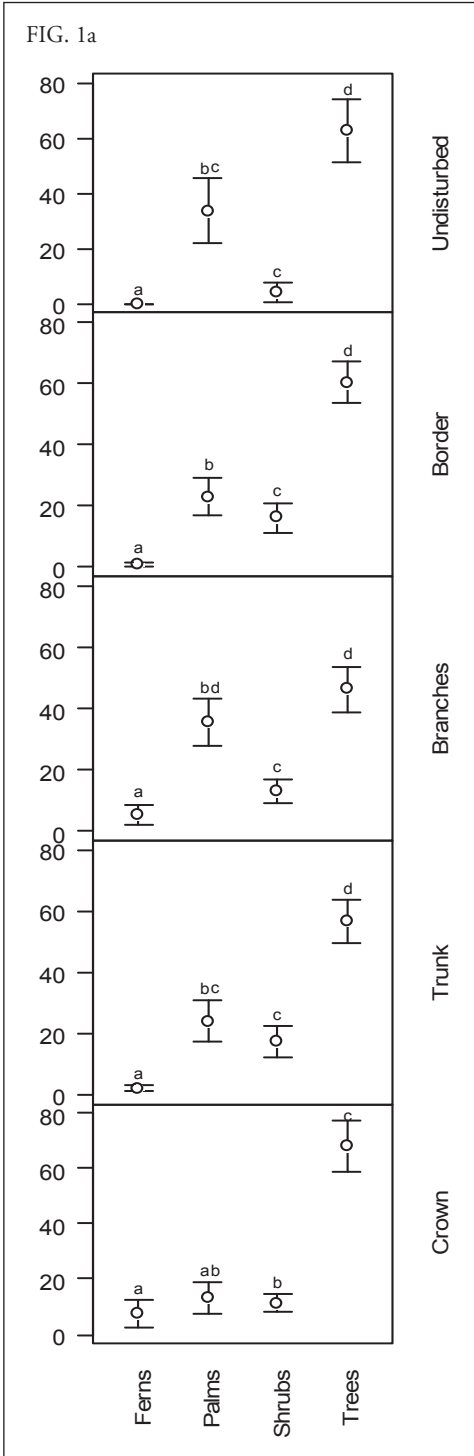
FIG. 1. Differences in the cover (%) of the vegetation forms present in the gaps: tree ferns, small palms, shrubs, and trees regenerating in a) the gap microhabitats (border, undisturbed, branches, trunk and crown) and in the b) disturbance intensity categories (minor, medium, and severe). The y-axis indicates percentage cover. The vertical lines correspond to the ± standard error of the mean (white circle) cover of a particular life form. Different letters above the lines indicate significant differences.

tions; not in the model because microhabitat was a factor and Microhabitat 1 [undisturbed] was treated as a baseline) in the gap, it was crown, followed by branch that supported lower species richness. When considering the disturbance intensity categories instead, it was severe disturbance (Disturbance [severe]) which reduced species richness compared with the

low disturbance baseline. A reduction in species richness was also detected for middle-aged gaps (age-f2 [Mid]) compared with the baseline immediately after disturbance. Gap size as well as competition from tree ferns, small palms, and shrubs did not have an impact on species richness.

The gap size also had no influence on tree regeneration richness when using rarefied richness based on each gap (R^2: 0.05, Adjusted R^2: 0.00, P > 0.05). *Tree species composition.* Overall there was a significant difference in species composition between all gap microhabitats (PERMANOVA F = 1.79, df = 4, P < 0.05). Species composition was observed to differ between crown and undisturbed and trunk microhabitats (Table 4). But the differences (*T*-values) between the gap microhabitats in general were very small and the within-group heterogeneity (*A* value in MRPP analysis, Table 4) was high. Species composition between the disturbance intensity categories differed significantly (PERMANOVA F = 2.19, df = 2, P < 0.05). The species composition in severely disturbed areas differed significantly from that of the medium and minor disturbance categories, albeit with relatively small differences (see *A* and *T* values of MRPP analysis in Table 4). Plots within the same gap were autocorrelated in terms of species composition (PERMANOVA F = 1.54, df = 22, P < 0.05). Neither gap age (PERMANOVA F = 0.71, df = 1, P > 0.05) nor gap size (PERMANOVA F = 1.24, df = 3, P > 0.05) had an influence on floristic composition.

Considering the large number of species found, only very few species were associated with a particular microhabitat and disturbance category. *Sloanea* sp. and *Ocotea* sp. 1 were associated with the undisturbed (ISA = 0.21, P < 0.05) and trunk microhabitat (ISA = 0.39, P < 0.05) respectively. The palm *Euterpe catinga* was associated with a middle disturbance intensity (ISA = 0.35, P < 0.05), whereas *Elaeagia maguirei*, *Ocotea* sp. 1, and *Schefflera quinquestylorum* were associated with the severe disturbance category (ISA = 0.50, 0.40, 0.21 respectively; all with P < 0.05).

DISCUSSION

Tree species richness in gaps was best explained by the model combining microhabitats, gap age, size, and competition with other life forms. When disturbance intensity was used instead of microhabitats, the species richness was explained much less. But both models included most of the different gap characteristics, indicating that species richness is determined by a complex set of conditions rather than by one driving factor.

If we consider the individual explanatory variables, it was microhabitats and disturbance intensity which had the highest influence. Comparing the microhabitats, the crown and branch areas had the lowest species richness. In the models without the microhabitats, the most severe disturbance category had the lowest number of species. This could mean that species richness was less likely to have been influenced by niche partitioning due to the ecological characteristics of the different microhabitats but rather, by the severity of the disturbance in the microhabitats.

The results for species richness were confirmed by the effects of microhabitats and disturbance intensity on species composition. The differences between microhabitats were very small (see *T* statistic in MRPP results), and only two of the seven species detected as indicators for overall microhabitats and disturbance categories showed a relatively high association to a group, namely to severely disturbed areas within the gaps. These species (*Ocotea* sp. 1 and *Schefflera quinquestylorum*) were two of the few pioneer tree species found in the gaps studied in the Sierra de Lema (Durán-Rangel 2011) and might therefore be adapted to disturbances.

Overall, several of the tree species regenerating in the gaps studied, such as *Catostemma lemense*, *Dictyocaryum ptarianum*, *Duguetia rigida*, *Elaeagia maguirei*, *Myrcia bracteata* and one morphospecies of the Lauraceae, were abundant. A large group of species was present in two or more microhabitats and therefore not very specific (for example *Dacryodes roraimensis*, *Dimorphandra macrostachya*, *Licania intrapetiolaris*, *Myrcia bolivarensis*, *Pleurothyrium amapaense* and *Pseudolmedia laevigata*). Finally, some species were found to be very scarce, such as *Alchornea glandulosa*, *Chrysophyllum sanguinolentum* and an unidentified species of the genus *Solanum*. The majority of the species that we found occurred in all microhabitats studied.

Neither gap size nor gap age influenced tree regeneration composition. Hence we surmise that also the advanced regeneration (juvenile trees) was not influenced by microhabitat differentiation. Poorter (2002) reported a smaller number of trees, less cover, and lower height of tree regeneration for crown compared with trunk and undisturbed microhabitat in four other neotropical forests in La Selva (Costa

TABLE 3. Parameter estimate (regression coefficients) and standard error by model and the multimodel averages based on AICc.

Model	Model ranking	Mhab_f2 (Border)	Mhab_f3 (Branches)	Mhab_f4 (Crown)	Mhab_f5 (Trunk)	age_f2 (Mid)	age_f3 (Old)	Disturbance (Middle)	Disturbance (Severe)	Gap size (m²)	Tree ferns (%cover)	Small palms (%cover)	Shrubs (%cover)
Mhab+Gap+Comp	1	-0.08 (0.15)	-0.37 (0.16)	-0.76 (0.18)	0.16 (0.15)	-0.23 (0.13)	0.07 (0.1)			0 (0)	0.01 (0)	0 (0)	-0.01 (0)
Gap+Dist+Comp	2					-0.29 (0.13)	0.07 (0.1)	0.0 (0.1)	-0.7 (0.15)	0 (0)	0.01 (0)	0 (0)	-0.01 (0)
Gap+Dist	3					-0.28 (0.13)	0.04 (0.1)	0.04 (0.09)	-0.65 (0.15)	0 (0)			
Mhab	4	-0.06 (0.14)	-0.27 (0.16)	-0.77 (0.17)	0.20 (0.14)								
Model average (unconditional SE)		-0.08 (0.15)	-0.37 (0.16)	-0.76 (0.18)	0.16 (0.15)	-0.23 (0.13)	0.07 (0.1)	0.0 (0.1)	-0.70 (0.15)	0 (0)	0.01 (0)	0 (0)	-0.01 (0)

Unconditional SE: not restricted to a single best model but based on the whole set of models

TABLE 4. Pairwise comparison (multi-response permutation procedure, MRPP) of the species composition of the tree regeneration between pairs of gap microhabitats and disturbance intensity categories. T = T statistic, A = chance corrected within-group agreement. P-value: < 0.05 = *, > 0.05 = ns (not significant). T and A values are in the lower and upper part of the table for the microhabitat and disturbance intensity categories respectively.

Gap microhabitat	Border	Undisturbed	Branches	Trunk	Crown
Border	-	-0.00 ns	0.01 ns	0.01*	0.00 ns
Undisturbed	0.08	-	0.02 ns	-0.02 ns	0.02*
Branches	-1.10	-1.21	-	0.01 ns	0.01 ns
Trunk	-1.92	1.56	-1.58	-	0.03*
Crown	-0.68	-2.61	-1.04	-5.68	-

Disturbance intensity categories	Minor	Medium	Severe
Minor	-	0.00 ns	0.01 *
Medium	-0.88	-	0.02*
Severe	-2	-3.94	-

Rica), Barro Colorado Island (BCI, Panama), Cocha Cashu (Peru), and Manaus (Brazil). This was in agreement with the density pattern of the tree regeneration in the gap microhabitats of our study. One reason could be that advanced regeneration was severely damaged by the falling crown. Another reason could be that the dense crown litter cover restricts seedling recruitment (Dalling & Hubbell 2002).

As mentioned above, we detected only a small difference in the species composition of regenerating trees, while other studies report clear differences. In Costa Rica, Lawton & Putz (1988) found a higher number of saplings, often hemiepiphytes, growing on trunks and in disturbed soil rather than in other microhabitats in gaps in montane forests. However on BCI, pioneers in gaps established more successfully on mineral soil than on elevated microhabitats such as tree trunks (Dalling *et al.* 1998). The species composition of the tree regeneration differed remarkably between gap microhabitats in the lowland forests of Los Tuxtlas in México (Núñez-Farfán & Dirzo 1988) and in La Selva (Brandani *et al.* 1988). In their study, Brandani *et al.* (1988) found that gap age and the spatial proximity of the gap microhabitats did not influence regeneration patterns, concluding that the tree regeneration was determined by the gap microhabitats.

Observations similar to ours were made in lowland tropical forests in Paracou, French Guiana (Baraloto & Goldberg 2004), where tree regeneration bore no relation to environmental variables such as light, litter depth, soil compaction, soil moisture, total soil nitrogen, total soil carbon, soil phosphorus, and soil pH. In the Venezuelan Amazon, near San Carlos de Río Negro, gap size and microhabitat had negligible effects on the establishment and density of tree regeneration (Uhl *et al.* 1988). These findings were explained by the predominance of advanced regeneration.

In the forests of the Sierra de Lema, nutrient-demanding pioneer species, such as *Cecropia* and *Alchornea*, were rare in the gaps (Durán-Rangel 2011), and also in the neighboring Gran Sabana forests (Hernández 1999). We therefore argue that the regeneration dynamics, in gaps, on the infertile soils of the Sierra de Lema might differ from those found in tropical forests growing on more fertile soils. It could be assumed that regeneration in these forests, on infertile soils, is dominated by the non-pioneer tree species present before gap formation. If the advanced growth survives the creation of the gap, sur-

vivors are most likely to form the next generation of canopy trees.

As an example, the few mature *Cecropia* trees, typically a pioneer species, were found established on old fallen trunks. These decaying trunks are the primary source of nutrients (Brandani *et al.* 1988). In the case of gaps in San Carlos de Río Negro in the Venezuelan Amazon, which is also part of the Guayana Shield, it has been suggested that the nutrients released from the fallen trees are quickly taken up by the advanced regeneration (Uhl *et al.* 1988). Consequently, advanced regeneration has an advantage over newly establishing pioneer tree species. In the tropical lowland forests of Nouragues, French Guiana, individuals of *Cecropia* also established on dead wood (van der Meer *et al.* 1998). A study, in Ecuadorian tropical mountain forests, typically found pioneers in gaps located in valleys but absent in gaps on mountain ridges. The authors go on to suggest that this could be related to higher soil nutrients in valleys compared with on ridges (Homeier & Breckle 2008). In the more fertile lowland forests of La Selva and the montane forests of Monteverde in Costa Rica, Lawton & Putz (1998) found numerous *Cecropia* seedlings and saplings on trunks, in contrast to our findings.

We conclude that species richness and the composition of trees regenerating within gaps in the montane forests of the Sierra de Lema are mainly influenced by disturbance intensity and the occurrence of advanced regeneration.

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