How anthropogenic disturbances affect the resilience of a keystone palm tree in the threatened Andean cloud forest?

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ABSTRACT

To conserve tropical forests, it is crucial to characterise the disturbance threshold beyond which populations of tropical trees are no longer resilient. This approach is still not widely employed, especially with respect to the effects of moderate disturbances. Compensation effects, such as positive interactions among plants, are addressed even more rarely. We attempt to identify the extents to which the distribution of the keystone palm tree *Ceroxylon echinulatum* is regulated by various regimes of deforestation in a threatened tropical montane cloud forest in the North-West Andes of Ecuador. The demographic structure of this palm tree was examined in three habitats: old-growth forest, forest disturbed by selective logging, and deforested pasture. Patterns were related to stand structure, microclimate, and soil composition. Seedling desiccation owing to severe aboveground water stress led to the absence of juvenile palms in pastures, and thus was predictive of a near extinction of the species in this habitat. However, shade provided by dominant bunchgrass in pastures considerably reduced above- and belowground water stress by diminishing light intensity. Selective logging resulted in a higher density of individuals in disturbed forests than in old-growth forests, but was associated with a spoiled spatial structure. Therefore, the protection of residual old-growth forests is a prerequisite for the conservation of *C. echinulatum*, although secondary forests might act as provisional refuges that promote its resilience. The reduction of water stress by nurse grasses in pastures represents a promising approach to promote the resilience of tropical tree species and their associated communities after deforestation.

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1. Introduction

The pervasiveness of deforestation was recently evidenced on a global scale (Hansen et al., 2010). Humid Tropics present the highest portion of forests on Earth, and at the same time they lost as much as 2.4% of their total cover in the 2000–2005 period (Hansen et al., 2010). It is largely accepted that intense disturbances such as deforestation and habitat fragmentation affect the performance and abundance of plant species deeply in this biome (Debinski and Holt, 2000), and thereby influence biodiversity as well as ecosystem functions and services (Hering, 2003; Cayuela et al., 2006). However, it remains uncertain whether tropical forest species might benefit from intermediate disturbances (e.g., selective logging), although this is a central hypothesis with respect to explaining the effects of such activities on the biodiversity in species-rich ecosystems (Bongers et al., 2009).

Tropical montane cloud forests (TMCF) in the Andes are among the ecosystems with the highest biodiversity globally (Brummit and Lughada, 2003). The effects of deforestation on these ecosystems are thought to be highly negative (Goerner et al., 2007) but they remain poorly studied (however, see Svenning, 1998; Svenning et al., 2009) and are in great need of basic research as well as specific investigations from the perspectives of conservation and restoration (Wright, 2005). Especially, deforestation generates strong micro-climatic shifts at the plant scale (e.g., Holl, 1999). Resulting increasing abiotic stress may create conditions that exceed the physiological limits of juvenile trees. Accordingly, facilitative interactions with nurse plants may become a central ecological process in the survival of forest trees in deforested pastures (stress gradient hypothesis, Brooker et al., 2008). This hypothesis needs to be tested in TMCF.

Neotropical palms have been shown highly sensitive to human-induced disturbances, although each type of disturbance (e.g. habitat fragmentation, fire, hunting, non lethal harvest) may affect each palm population in a singular way (Montúfar et al., in press). We focus here on the Andean wax palm *Ceroxylon echinulatum* Galeano (hereafter *Ceroxylon*), syn. *Ceroxylon alpinum* Bonpl. ex DC. subsp. *ecuadorense* Galeano (Sanín and Galeano, in press).

The restricted, fragmented distribution of *Ceroxylon* in the TMCF of Ecuador and Northern Peru makes populations of this species particularly sensitive to anthropogenic alterations of their natural habitat (Trenel et al., 2008).

Through a demographic study of *Ceroxylon* combined with local biotic and abiotic measurements, we specifically tested (1) the extent to which populations can endure various types of disturbance related to deforestation and (2) how plant–plant interactions interfere with the dynamics and structure of populations. We hypothesised that this latter process might have a significant role in explaining the distribution of tropical trees in a highly productive system that is subject to consumer pressure (see Callaway, 2007). In light of the obtained results, we discuss possible approaches to manage the conservation of *Ceroxylon* in TMCF.

2. Materials and methods

2.1. Study area and study sites

This study was undertaken in the mountainous area of the Ecuadorian Chocó, on the western slopes of the Andes (North-West Pichincha district). Two sites that exhibit ecological conditions that are optimal for *Ceroxylon* were selected: the Inti Llacta Reserve (00°02′N, 78°43′W; mean altitude 1861 m a.s.l.) and the Rio Bravo Reserve within the Mindo–Nambillo Protected Forest (00°04′S, 78°44′S; 1548 m a.s.l.). Both sites contain TMCF and receive approximately 3200 mm of precipitation each year, as reported for an adjacent area (Svenning, 1998). Historically, the study area has been influenced by an indigenous population (Yumbo) for hundreds of years (Valarezo, 2001).

In modern times, Mindo–Nambillo has been affected very little by human-related disturbances owing to its remoteness; therefore, it constitutes an old-growth forest with the presence of the long-lived trees *Licaria limbosa, Ocotea cernua* and the palms *Aiphanes erinacea* and *Geonoma undata*, representative of undisturbed TMCF (Svenning, 1998). In contrast, Inti-Llacta has recently experienced deforestation and selective logging, as indicated by a loss of 41% of forested areas from 1966 to 1990 in an adjacent zone (Guevara et al., 2001). Pastures were established during the same period, and were soon dominated by the bunchgrass *Setaria sphacelata*. This species can reach more than 2 m in height and is almost mono-dominant in the current pastures. Forests are dominated by a patchwork of early- and late-successional trees, which include *Cecropia pentandra, Cinchona pubescens*, and several arboreal ferns (*Cyathea* spp.). The presence of the palm *Chamadorea linearis* is indicative of a moderately disturbed environment (Svenning, 1998). In the pastures, residual trees are dominated by *Ceroxylon* and *Alnus acuminata*.

2.2. Target species

Ceroxylon echinulatum is an endemic, long-lived palm tree that reaches an average stem height of 20 m (Paredes-Ruiz, 1995) and displays keystone properties owing to a local high density and intense interactions with seed dispersers (Mejía Londoño, 1999). From a socio-economic point of view, the important harvest of its leaves and, to a lesser extent, its stems (Borchsenius and Moraes, 2006) might be detrimental to its long-term conservation. Although the current distribution of *Ceroxylon* in Ecuador might be underestimated, some populations in the western Andes of Ecuador are thought to be threatened by extinction through deforestation (Svenning and Balslev, 1998). However, during its long establishment phase – or rosette phase – *Ceroxylon* develops a short subterranean stem and a rosette of leaves very difficult to

eradicate when the area is cleared out, which may increase its resilience in the face of deforestation (R. Bernal, pers. com.).

2.3. Sampling design

The population structure of *Ceroxylon* was observed through a snapshot study along a gradient of increasing intensity of human activities in old-growth forests (Mindo), disturbed forests where selective logging of large tree species is taking place (Inti-Llacta), and deforested pastures dominated by *S. sphacelata* with a few residual trees (Inti-Llacta), following a protocol developed within the international project PALMS (see Anthelme et al. (2010) for details on the method). Although old-growth forest was not at the same site as the other habitats and its altitude was slightly lower, all habitats displayed comparable volcanic bedrock and climate. A total of 91 square plots of 400 m² in size were set randomly, separated by at least 40 m, at 1412 to 1985 m a.s.l. A total of 20 plots were established in old-growth forests, 46 in disturbed forests, and 25 in pastures, in accordance with the structural heterogeneity of each habitat.

Plot randomisation consisted of identifying the nearest stemmed individual of *Ceroxylon* from a random point within a habitat, and using it as one of the four corners of the plot.

2.4. Biotic observations

Demographic observations were carried out in June and July 2008 by counting the number of individuals within each plot, classifying them into one of five life stages (Table 1) and separating males and females among adults.

Seedling stage was observed using a specially designed method because of the particularly high density of individuals in some areas. Three types of zone were identified within each plot: high density (>300 individuals/m²), medium density (between 30 and 300 individuals/m²), and low density (less than 30 individuals/m²). Within the high-density zone, individuals were counted in 1 m² subplots to estimate the total number of individuals. In the two other zones, seedlings were counted directly.

The stand structure of each plot was estimated by measuring the basal area of all trees ⩾10 cm in diameter at breast height.

2.5. Abiotic measurements

The locations of the plots were determined using a Garmin GPS 60 (UTM coordinates, WGS 84). Slope inclination was calculated with a clinometer (Sunnto Tandem) from three 20-m-long measurements along the direction of the slope.

During a relatively dry period (March 2009), we measured various micro-climatic parameters in disturbed forests and pastures. Pastures were divided into two sub-habitats on the basis of the presence or absence of neighbouring *S. sphacelata* to provide an indication of potential plant–plant interactions between palms and grasses. We concentrated the acquisition of data at the Inti-Llacta site (disturbed forests and pastures only) to ensure more comparable data between forests and pastures instead of observing differences between old-growth forests and disturbed forests.

Vapour pressure deficit (VPD, kPa) was monitored with HOBO-Pro RH/Temp data loggers as an indicator of atmospheric water stress for plants, with 4 (5) spatial repetitions at each habitat assigned randomly in the initial plot design. Relative humidity in the soil at a depth of 5 cm was determined using U23-01 data loggers (three spatial repetitions at each habitat). Light intensity was measured using UA-002 data loggers (eight spatial repetitions at each habitat). All data loggers (Onset Computer Corporation, Pocasset, MA) generated data every 15 min during a 12-day period, from which daily maximal and/or minimal values were extracted

Table 1
Mean density of *Ceroxylon* individuals among life stages and habitats (±S.E.). Differences among treatments are compared using the Kruskal–Wallis test. Common letters indicate no difference among pairs of treatments within each life stage ($p < 0.05$, Mann–Whitney test, hypothesis: not equal, adjusted for ties). Sign.: significance; ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$.

Life stages	Description	Old-growth forest	Disturbed forest	Pasture	Sign.
Seedlings	Leaves not divided	14.04 ± 3.11[a]	2159.72 ± 637[b]	1326.46 ± 871[a]	***
– High density		0[a]	1979.28 ± 623[b]	1292.11 ± 859[b]	***
– Medium density		0[a]	101.97 ± 18.2[b]	30.05 ± 14.8[c]	***
– Low density		14.04 ± 3.11[a]	84.11 ± 9.83[b]	5.80 ± 3.61[c]	***
J1	Leaves divided, <2 m	3.08 ± 0.83[a]	48.09 ± 7.94[b]	2.35 ± 1.97[c]	***
J2	>2 m, absence of stem	0.96 ± 0.34[a]	7.89 ± 2.45[b]	0[c]	***
Sub-adults	Stem easily identifiable	0.32 ± 0.13[a]	0.50 ± 0.09[a]	0[b]	**
Adults	Reproductive material	1.00 ± 0.10[a]	1.61 ± 0.22[ab]	1.65 ± 0.25[b]	–

to detect physical stresses for plants in the habitats. Data loggers in pastures with *Setaria* were placed directly at the base of *Setaria* stems.

Soil was collected in disturbed forests, pastures (February 2009), and old-growth forests (June 2009) from a sub-sample of 10 plots that were selected randomly within each habitat after a relatively dry climatic period. Soil samples (at a depth of 0–20 cm) were collected at the four corners and the centre of each plot. The concentrations of available macro- and micronutrients, organic matter (%), and pH were measured following standardized methods described by OSU (2009).

2.6. Data analysis

Data were analysed using Kruskal–Wallis and Mann–Whitney non-parametric tests, except when indicated otherwise in the text. On a landscape scale, the density of *Ceroxylon* individuals with stems was calculated using the basic distance to the closest individual estimator (BDCI; Cottam and Curtis, 1956):

$$\text{BDCI (individuals/ha)} = 1/(4[\Sigma Ri/N]^2) * 10,000,$$

where *R* is the distance between a random point and the closest stemmed *Ceroxylon*, and *N* is the number of random points. Density at plot level was later divided by density extracted from BDCI, which provided an aggregation index for stemmed individuals.

The combined effects of biotic and abiotic parameters on the demography of *Ceroxylon* at each plot were tested through stepwise regressions (alpha to enter = 0.10; alpha to exit = 0.15). Spatial repetitions of micro-climatic data (from three to eight) were assembled to yield 12 mean values (corresponding to 12 days), which we correlated with demographic data. We considered that the potential temporal autocorrelation from day to day was insignificant considering the robustness of the data obtained (mean values from several spatial locations) and the high day-to-day climatic variability in this region. Statistical analyses were conducted with MINITAB and the ADE-4 package available in *R*.

3. Results

3.1. Habitat structure

Slope inclination varied among habitats ($p < 0.001$). Slopes were steeper in old-growth forests (25.01° ± 1.95), and to a lesser extent in disturbed forests (19.25° ± 1.16), than in pastures, which contained gentle slopes (14.24° ± 1.68).

Overall, basal area (BA) varied among habitats ($p < 0.001$, Fig. 1), but was not significantly different between old-growth forests and disturbed forests (618.5 m²/ha and 641.6 m²/ha, respectively). BA was 10 times lower in pastures (64.5 m²). BA assignable to *Ceroxylon* ($p < 0.001$) reached 12.4% of total BA in disturbed forests
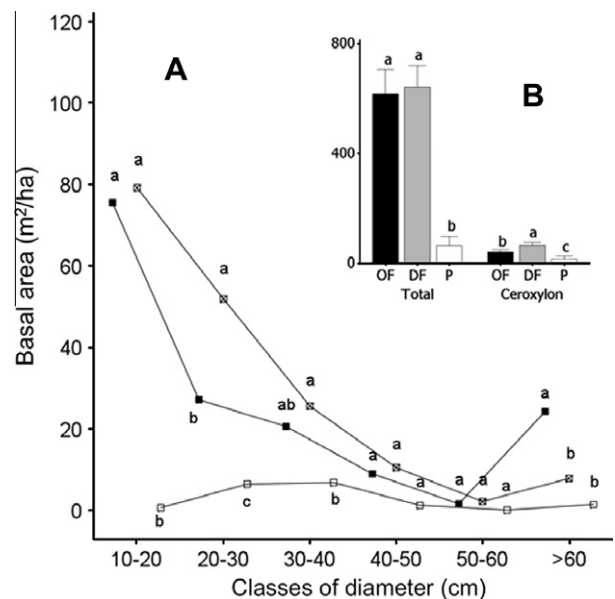

Fig. 1. Mean basal area (BA) among classes of tree diameter at each habitat (A), and total BA with relative BA assignable to *Ceroxylon* (B). Common letters indicate no difference among pairwise treatments for each diameter and each habitat (Mann–Whitney test, $p < 0.05$). Error bars represent 95% confidence intervals. OF: old-growth forest; DF: disturbed forest; P: pasture.

and 7.1% of that in old-growth forests. It clearly dominated tree cover in (40.0%).

The BA distribution of diameter classes in disturbed forests was typical of regenerating tropical forests ("inverted J shape"; La Torre-Cuadros et al., 2007). Old-growth forests displayed less slender trees (20–30 cm in diameter) than disturbed forests and a larger number of old trees, as expected in mature forests.

3.2. Demography of Ceroxylon among habitats

A total of 129,069 individuals were included in the analysis, 98% of which were seedlings. The rarity of juveniles 1 (J1) and the absence of juveniles 2 (J2) and sub-adults (J3) in pastures denoted a highly abnormal demographic structure. In contrast, seedlings were particularly frequent, and adults seemed to be present at the same density as in disturbed forests at the plot level (Table 1). Seedlings in old-growth forests were very scarce, especially when compared with the number in disturbed forests – 14.04 and 2159.72, respectively – but the estimated rate of survival from seedlings to J1 was far higher in old-growth forests (21.9%) than in the other two habitats (up to 2%). All life stages were represented in forested habitats. Almost all seedlings found in pas-

tures were concentrated in small high-density areas, very close to female trees (Table 1). In disturbed forests, seedlings were also concentrated in high-density areas but a few seedlings were observed in low- and medium-density areas as well. The few seedlings detected in old-growth forests were found systematically at a low density.

3.3. Density and aggregation of stemmed individuals

Taking BDCI into account, the density of adults reached 15.6 individuals/ha in disturbed forests but only 5.2 in pastures. In old-growth forests, the R distance exceeded 30 m almost systematically; therefore, the density of *Ceroxylon* could not be calculated, but it was certainly less than that in pastures.

The aggregation index, which was extracted from the ratio of local density/BDCI of stemmed individuals, was 2.95 in pastures and 1.85 in disturbed forests. Both habitats were significantly aggregated (one-sample T-test that tested the hypothesis that local density was greater than BDCI, $p < 0.05$).

3.4. Interdependence between life stages and basal area

Stepwise regression models provided evidence of key effects of the number of female palms and BA on the distribution of *Ceroxylon* (Table 2). Seedlings in low-density areas were less dependent on female density than seedlings in higher density areas and showed a higher degree of correlation with the presence of older life stages than the total number of seedlings. BA affected the abundance of several life stages positively in all habitats. In disturbed forests, this was due to the high density of young, regenerating trees (effects of BA 20–30 cm diameter on J1 and J2; Fig. 2), whereas the effects of old, large trees (>60 cm diameter) were neutral or slightly negative. Positive effects of BA in old-growth forests (J1) and pastures (seedlings at low density) were not correlated with the density of young or old trees (Fig. 2). In pastures, seedling distribution was accurately predicted by tree canopy plus the presence of females (Table 2). Finally, the distribution of low-density seedlings in disturbed forests was not predictable, which was probably indicative of an efficient dispersal of these few individuals.

3.5. Micro-climatic variations

Maximal light intensity (MLI) decreased drastically from pastures (113,295 lux) to forests (13,097 lux, $p < 0.001$, Fig. 3). Interestingly, the shading effect provided by *Setaria* reduced MLI by more than one-half in pastures (49,787 lux).

Aboveground water stress (maximal VPD) was significantly variable among habitats ($p < 0.001$). It peaked at 1.01 kPa in pastures, with the absolute highest value exceeding 2 kPa on day 9. With respect to MLI, *Setaria* in pastures reduced VPD by one-half, whereas canopy virtually eliminated VPD in forest. MLI affected maximal VPD strongly in pastures without *Setaria* (Appendix A: $R^2 = 0.82$, $p < 0.001$) and in pastures with *Setaria* ($R^2 = 0.87$, $p < 0.001$), but not in disturbed forests ($R^2 = 0.08$, $p = 0.35$).

Minimal values of relative humidity in the soil atmosphere were especially low in pastures (35.3%) whereas protection by *Setaria* helped to maintain a similar level of minimal humidity to that in disturbed forests (76.6% and 73.6%, respectively, Fig. 3). This variable was also affected by MLI in pastures (Appendix A: $R^2 = 0.38$, $p < 0.05$), but not in the two other habitats.

3.6. Soil composition

The most notable variations in the availability of soil nutrients among habitats concerned NH_4, Fe, and phosphorus (Table 3). The concentrations of NH_4 and Fe increased significantly along the gradient of disturbance, and, for Fe, reached a level 10 times higher than the initial content in pastures. Levels of phosphorus were lower in old-growth forests than in the other habitats, as was the case for Cu. Zn was present at a higher concentration in pastures than in the two types of forests. Finally, the soil was more acidic in old-growth forests than in the two other habitats.

4. Discussion

In general, the high level of diversity of tropical forests results in a low density of most plant species (Lieberman and Lieberman, 2007). In the present study, *Ceroxylon* was found to form up to 12% of the stand BA in TMCF, which has itself been shown to correlate strongly with leaf cover and net throughfall input (Ponette-
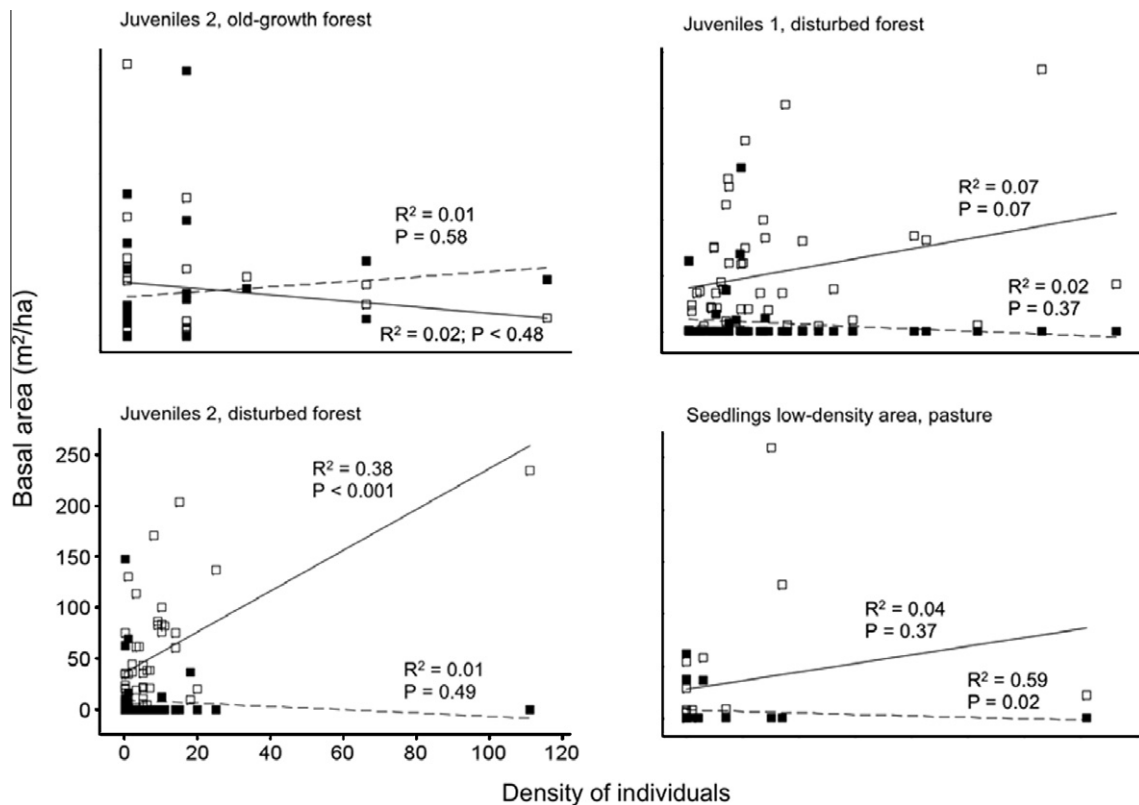
Table 2

Relationships between densities of each life stage, habitat, and basal area (stepwise multiple regression: alpha to enter: 0.10; alpha to remove: 0.15). The effects of slope and sub-adults were not significant and are not shown in the table. The response of adults to other life stages was not taken into account nor was the effect of BA on adults in pastures nor the effects of older life stages on target stages. LD: low-density area. R^2 was adjusted when two or more variables were included in the analysis. + indicates a positive effect, − indicates a negative effect. Significance: n.s.: not significant; (*): $p < 0.10$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Habitat/life stage	Basal area	Seedlings	Seedlings LD	J1	J2	Males	Females	R^2
Old-growth forest								
Seedlings							***	0.43
Seedlings LD							***	0.43
J1		**						0.27
J2	*							0.20
Sub-adults					***			0.46
Adults								0.13
Disturbed forest								
Seedlings							***	0.45
Seedlings LD							(*)	0.06
J1	*		(*)				**	0.28
J2	***			**				0.41
Sub-adults			(−)					0.10
Adults								n.s
Pasture								
Seedlings	(*)					**	**	0.61
Seedlings LD	***						(*)	0.74
J1			***					0.87
J2								n.s
Sub-adults								n.s
Adults								n.s

Fig. 2. Relationships between the densities of young trees (20–30 cm diameter, white boxes, solid line) and old trees (>60 cm diameter, black boxes, dashed line) and the density of *Ceroxylon* individuals for the life stages that are influenced significantly by total basal area (see Table 2).

Gonzalez et al., 2010). Therefore, *Ceroxylon* was shown to be a locally dominant component of the TMCF, although it is fragmented on a larger scale (Trenel et al., 2008). Combined with its dominant treelike structure and its high level of production of fleshy fruits (Anthelme, pers. obs.), the palm acts as an ecosystem engineer or keystone species, as reported for many palms in South America (Scariot, 1999; Galetti et al., 2006), and especially in the Andes (Svenning, 1998; Borchsenius and Moraes, 2006). However, it is likely that the arrangement of *Ceroxylon* populations in clusters on a landscape scale is due to a failure to achieve long-distance dispersal (see Trenel et al., 2008). The result is a high level of fragmentation of relatively dense populations. For these reasons, and taking into account its socio-economic value (Pintaud and Anthelme, 2008), *Ceroxylon* is an appropriate target genus for ecosystem conservation in TMCF.

4.1. Ceroxylon virtually extinct in deforested pastures?

A strong hypothesis when considering the altered demographic structure in pastures is that the residual adults in this habitat only reflected the earlier existence of forests from which *Ceroxylon* was spared. Therefore, the dense stands that have been observed in open areas (Paredes-Ruiz, 1995) would represent the remnants of virtually extinct populations. However, the higher density found in pastures than in old-growth forests indicates very likely the occurrence of a preliminary intermediate disturbed phase favourable to the development of the palm. This applies to *C. echinulatum*, but also to gregarious species such as *Ceroxylon quindiuense* and *C. alpinum*, which display a similar pattern of distribution (Sanín and Galeano, in press; Vergara-Chaparro, 2002). The relatively high number of seedlings in pastures indicates a positive response of germination to light intensity, but is probably negated by higher mortality through desiccation in this habitat, as suggested for the palm *A. erinacea*, which is found in adjacent old-growth forests (Svenning, 1998).

The presence of very few J1 individuals might indicate that it is extremely difficult for *Ceroxylon* to establish itself in pastures. The spatial association between JI individuals and seedlings, which are themselves influenced by the presence of residual trees and palms, indicates that their persistence is due to the presence of protecting trees that provide local shade (see Table 2).

Data on the African oil palm showed that stomatal conductance and photosynthetic activity are affected negatively by VPD values greater than 1.8 kPa, even with a sufficient level of water in the soil (Dufresne and Saugier, 1993). In comparison with *Ceroxylon*, the African oil palm shows a better adaptation to water stress because it grows in areas adjacent to *Ceroxylon* where the environment is slightly more stressful (Anthelme, pers. obs.). Accordingly, when the VPD reaches more than 2 kPa, as observed in pastures, seedling desiccation and mortality owing to aboveground water stress might occur. Together with edaphic water stress and predation by herbivores, it is likely that this physiological limitation is responsible for the failure of *Ceroxylon* to survive beyond the seedling stage in open areas, as has been shown for other mid-and late-successional species in the same region (Gunter et al., 2009). The high level of soil nutrients, especially nitrogen, in pastures indicates that soil composition, which is a major constraint for reforestation in TMCF (Gunter et al., 2009), is not responsible for the absence of *Ceroxylon* regeneration in this habitat. Similarly, a high level of iron, which might inhibit photosynthesis in wet anoxic soils but not in the well-drained soils that were observed, was not responsible (Lucassen et al., 2006). The altered seed dispersal in pastures (Holl, 1999) may reduce even more the probability of palm recruitment but appears not to be a central factor when compared with physiological limitations in our study.

An alternative hypothesis to explain the current distribution pattern of *Ceroxylon* in pastures, suggested by Rodrigo Bernal (pers. comm.), is that the presence of adults would result from J1 and J2
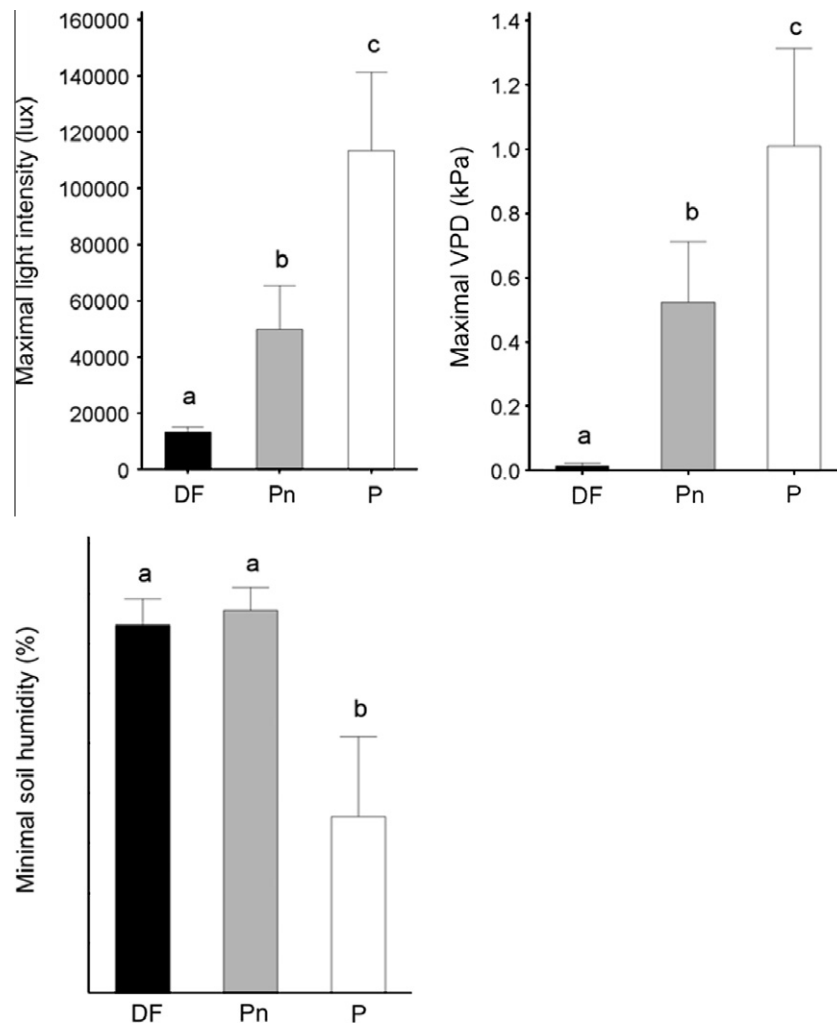
Fig. 3. Variations in the abiotic environment in disturbed forests (DF), pastures with *Setaria sphacelata* (Pn), and pastures without *S. sphacelata* (P). Common letters indicate no difference among pairwise treatments (Mann–Whitney test, *p* < 0.05). Error bars represent 95% confidence intervals.

Table 3
Variation in the soil nutrient content, pH, and organic matter (MO) among habitats. Significance was determined using the Kruskal–Wallis test for each variable. Common letters indicate no difference among pairwise habitats (Mann–Whitney test). Sign.: significance, ***: *p* < 0.001; **: *p* < 0.01; *: *p* < 0.05.

	pH	NH$_4$	P	S	K	Ca	Mg	Zn	Cu	Fe	Mn	B	MO
PF	5.17[a]	58.9[a]	5.7[a]	10.26[a]	0.242[ab]	8.24[a]	2.23[a]	2.64[a]	3.16[a]	91[a]	8.86[a]	0.52[a]	14.03[a]
DF	5.61[b]	85.3[b]	16.0[b]	8.66[a]	0.186[a]	8.27[a]	1.43[ab]	2.97[a]	5.68[b]	344[b]	8.25[a]	0.42[a]	11.12[a]
P	5.74[b]	98.4[c]	15.3[b]	8.82[a]	0.349[b]	8.97[a]	1.27[b]	6.47[b]	5.78[b]	1105[c]	8.55[a]	0.48[a]	9.35[a]
Sign.	**	***	***	–	*	–	–	***	**	***	–	–	–

individuals that survived complete deforestation (including adult palms). According to Bernal, during their rosette phase (J1, J2), that may reach as much as 57 years (Vergara-Chaparro, 2002), *Ceroxylon* individuals are particularly resilient, as their meristem is subterranean or almost so. Other sympatric palms, such as *Wettinia kalbreyeri* or *Euterpe precatoria*, which do not go through this rosette phase, are usually absent in deforested pastures, as their survival depends on adults being intentionally spared (R. Bernal pers. com.). Future empirical research may resolve this crucial point, especially by dating remnants adult palms in pastures (see Vergara-Chaparro (2002) for detailed methods).

Finally, it appears unlikely that *Ceroxylon* will survive in pastures after deforestation without intervention, as suggested for many mid- or late-successional tree species in TMCF (Hubbell et al., 2008; Gunter et al., 2009), including palms (Arroyo-Rodriguez et al., 2007).

4.2. Antagonistic responses to an intermediate disturbance

When compared with the effects of complete deforestation, the effects of intermediate disturbances on biodiversity in the TMCF remain poorly studied and the results obtained are controversial (Bongers et al., 2009; Montúfar et al., in press; however, see Svenning, 1998), although TMCF will probably be subjected to greater disturbances in the future (Wright, 2005). In the case of *Ceroxylon*, the high density of individuals and the persistence of nutrient-rich soils in forests undergoing selective logging (disturbed forests) suggest what appears to be a positive effect of the intermediate disturbance, as documented previously for the understory palms *Chamadorea linearis* and *Chamadorea pinnatifrons* (Svenning, 1998).

At the same time, we interpret the high concentration of *Ceroxylon* seedlings at the foot of females and the high rate of mortality during development from seedlings to juveniles as an indication of

an altered structure of *Ceroxylon* populations (see e.g. Blundell and Peart, 2004; Silva Matos et al., 1999). Moreover, local aggregation of stemmed individuals and seedlings – often a specific feature of rare species within inhospitable habitats (Hubbell, 1979) – indicates deterioration in the fitness of populations of *Ceroxylon* in disturbed forests. This is about to be confirmed by preliminary results on the population genetics of *Ceroxylon* within the same sampling design, which tend to indicate that intra-specific diversity is higher in old-growth forests than in disturbed forests (Montúfar, unpublished data).

Accordingly, the effects of the intermediate disturbance appear to be antagonistic. We raise the hypothesis that our disturbed forests were affected by both selective logging and adjacent fragmentation within a growing matrix of pastures. Although we did not analyse these two factors separately, our results suggest that the high density of individuals would be due to the positive effects of partial clearing by the logging of old live trees. By taking advantage of these clearings *Ceroxylon* displays an interesting tolerance to moderate disturbance.

Reversely, *Ceroxylon* may be negatively affected by concomitant forest fragmentation through dispersal limitation and dissemination limitation, patterns that are reported commonly for neotropical palms (Fleury and Galetti, 2006; Galetti et al., 2006; Aguirre and Dirzo, 2008). Weak dispersal is suggested to be a potentially critical factor in explaining the distribution of palms in TMCF (Svenning et al., 2009), especially through the alteration of populations of seed dispersers (Wright and Duber, 2001; Jorge and Howe, 2009). The populations of birds and mammals that disperse *Ceroxylon* (Mejía Londoño, 1999; Krabbe, 2000) have thus very likely been altered by fragmentation as these types of animals have been shown especially sensitive to fragmentation (Lefevre and Rodd, 2009; Chapman et al., 2010). This would explain the genetic bottleneck found, as commonly documented in neotropical forests (see Lowe et al. (2005) for a review).

4.3. Distribution of Ceroxylon and plant–plant interactions

Our data indicated that canopy cover is obligatory for the regeneration of *Ceroxylon* without intervention. The shade provided by trees drastically reduced the effects of light intensity on evapotranspiration and the relative humidity of soil, two well-documented mechanisms by which the tree canopy promotes plant fitness (Callaway, 2007). The resulting absence of water stress explains the balanced demographic structure of *Ceroxylon* in forests. However, the higher density of individuals of all life stages in disturbed forests as compared with old-growth forests indicated that the wax palm takes advantage of selective logging of large trees in disturbed forests. This mid-successional status makes it very sensitive to deforestation, because its development can be facilitated by selective logging but inhibited by complete deforestation. Future studies should determine more accurately the threshold between these two states, which might also be relevant for other mid- and late-successional species in the TMCF.

In pastures, the reduction in water stress above and below ground that is generated by *S. sphacelata* and the absence of a negative effect on nutrient availability indicate that grass – or other nurse plants – might exert a net positive effect on seedlings of *Ceroxylon* under stressful conditions, despite the highly competitive nature of this grass. This hypothesis, which needs to be explored in detail, is supported by the assertion that the probability that facilitation will occur increases with distance from the fundamental niche optimum of a target species (see Gomez-Aparicio (2009) for a review). This hypothesis is rarely considered with respect to TMCF, in contrast to its frequent consideration for marginal alpine or desert ecosystems (Brooker et al., 2008; Maestre et al., 2009) or even for dry tropical ecosystems (Gomez-Aparicio,

2009). The meta-analysis of Gomez-Aparicio demonstrated that tropical plant communities are prone to be driven by facilitation processes, but the author did not observe a difference between wet and tropical environments. Nonetheless, these environments might display very different responses to stress and disturbance (e.g., Bongers et al., 2009). We recommend that studies should be undertaken to test the stress gradient hypothesis on gradients caused by deforestation in wet tropical forests, and to identify more precisely the impact of this ecological process on the conservation of these exceptionally rich ecosystems (see Maestre et al. (2009) for adapted sampling designs).

4.4. Resilience and conservation

The most appropriate option for the conservation of *Ceroxylon* would be to protect existing old-growth forests, because these are: (1) the primary habitat of *Ceroxylon*; (2) the habitat where interactions with other taxa, especially birds and mammals, are the most intense (e.g. Becker et al., 2008); and (3) the habitat where dispersal is most efficient, which is likely to generate a higher intra-specific diversity. The latter is a key factor when considering the long-term conservation of populations.

At the same time, disturbed forests might provide a complementary approach to the protection of old-growth forests to enhance the conservation of populations. This is supported by the observation of a higher density of individuals in disturbed forests than in old-growth forests, which agrees with the assertion that tropical secondary forests can serve as habitat refuges for mature tropical forest tree species (Norden et al., 2009). One concrete application might be to use disturbed forests as a source of seedlings for transplantation to locations where adults are absent; however, the rare seedlings that are found in low-density areas should be preserved as beneficiaries of efficient dispersal.

Any attempt to regenerate *Ceroxylon* in pastures might appear idealistic at first glance. Although it has been shown experimentally that it is difficult to recover TMCF after decades of pasture activity in areas dominated by *S. sphacelata* (Myster, 2007), the reduction of abiotic stress by the grass provides a suitable habitat for seedlings. The grass might also protect the seedlings from large herbivores by providing cover (predator avoidance; Milchunas and Noy-Meir, 2002). These findings support the hypothesis of Gunter et al. (2009) that if *S. sphacelata* is not subjected to manual weeding, it might facilitate reforestation. However, this species is known to inhibit succession through the limitation of dispersal owing to its spatial structure (Myster, 2004), as detected in our dataset. Therefore, to benefit from the protective effects of the grass, it would be necessary helping seeds or seedlings recruitment by transplanting them inside the nurse plant, a location that they cannot reach by themselves. This was not attempted in Myster's experiment.

Alternatively, abandonment of pastures can be considered a passive pathway to promote the survival of *Ceroxylon*. This type of intervention is appropriate when it is considered that, worldwide, 15% of areas that were subjected to deforestation in the 1990s have been rehabilitated through natural secondary succession (Wright, 2005). Seed dispersers in tropical pastures tend to avoid open areas (Laborde et al., 2005); therefore, the presence of female trees in the pastures is a prerequisite for palm resilience, corroborating the necessity of presence of remnant trees in pastures for promoting forest regeneration (Schlawin and Zahawi, 2008). This approach might be improved by the transplantation of shrubs in order to mimic classical grass-shrub-tree succession, which has been shown to be far more efficient for forest restoration than grass-tree succession (two-phase restoration strategy; Gomez-Aparicio, 2009).

Facilitation is still considered infrequently during the development of approaches to restore species within a habitat (Padilla and Pugnaire, 2006), despite it being recognised increasingly as a major ecological process in the structuring of plant communities (Brooker et al., 2008). A recent example of grass-to-tree facilitation (Anthelme and Michalet, 2009) can be used as an ecological precedent to expand the use of this type of positive interaction to the rehabilitation of endangered forest trees and their associated communities in the face of massive deforestation in TMCF.

Acknowledgements

Appendix A

Influence of maximal light intensity on minimal soil humidity and maximal VPD among habitats (DF: disturbed forest; Pn: pasture with *Setaria sphacelata*; P: pasture without *S. sphacelata*). Lines represent linear regressions for each habitat.
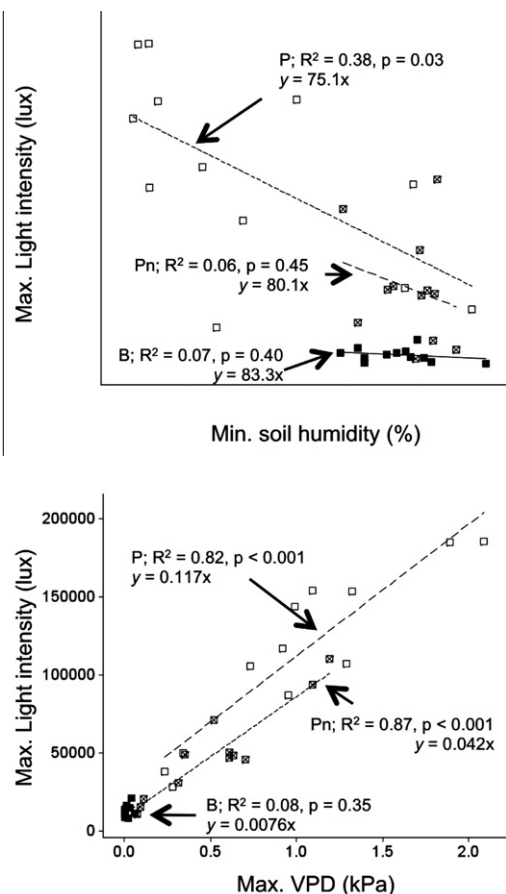
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