

RESEARCH ARTICLE

UN Decade on Ecosystem Restoration

Leaf functional traits predict shade tolerant tree performance in cloud forest restoration plantings

Tarin Toledo-Aceves¹  | Martha Bonilla-Moheno²  | Vinicio J. Sosa¹  |
Fabiola López-Barrera¹  | Guadalupe Williams-Linera¹ 

¹Red de Ecología Funcional, Instituto de Ecología, A.C. (INECOL), Carretera Antigua a Coatepec No. 351, Xalapa, Veracruz 91073, Mexico

²Red de Ambiente y Sustentabilidad, INECOL, Xalapa, Veracruz 91073, Mexico

Correspondence

Tarin Toledo-Aceves

Email: tarin.toledo@inecol.mx

Funding information

Consejo Nacional de Ciencia y

Tecnología, Grant/Award Number:

CB2014-01/238831; Instituto de Ecología A.C., Grant/Award Number: 20030-11218

Handling Editor: Ainhoa Magrach

Abstract

1. Restoration of tropical montane cloud forest (TMCF) landscapes is urgently required. Assisting the regeneration of endangered and shade tolerant tree species is essential for both the recovery of this vulnerable group and of ecological processes. However, there is limited species-specific information regarding tree performance under different disturbance conditions with which to implement effective interventions.
2. We assessed the performance of shade tolerant tree seedlings in restoration plantings under different disturbance settings and determined whether leaf mass area (LMA) and leaf dry mass content (LDMC)—functional traits typically associated with resource capture or stress tolerance—could serve as predictors of survival and growth among species. Since conservative leaf morphological traits can maximize survival, we expected species with higher LMA and LDMC to present higher survival. For a set of eight native cloud forest species, a total of 2,202 seedlings were planted in four pastures, five secondary forests and three forests subjected to traditional selective logging, in TMCF landscapes in Eastern Mexico.
3. Seedling survival was high after 3 years: 62% in pastures, 80% in secondary forests and 88% in logged forests. Growth rates were lowest in pastures, followed by secondary forests and highest in logged forests. LMA was a strong predictor of seedling survival in all of the environments; tree species with higher LMA presented greater survival. LDMC was related to seedling survival in the three environments, although to a lesser extent than LMA. In the pastures, higher LMA and LDMC were linked to lower growth.
4. *Synthesis and applications.* This study supports the potential of shade tolerant tree species in restoration efforts to assist the recovery of this important functional group and to accelerate succession across altered environments. Our results support the notion that conservative leaf functional traits are linked to a higher probability of survival, not only in the shaded understorey, but also under high solar radiation in transformed habitats. Leaf mass area (LMA) in particular is a reliable predictor of seedling survival for shade tolerant

species. Species selection based on LMA could thus improve restoration initiative outcomes: tree species with high LMA present higher survival probability and can be introduced into pastures, secondary forests and selectively logged forests.

KEYWORDS

enrichment planting, late successional, leaf dry mass content, leaf mass area, pasture, secondary forest, seedling survival, traditional selective logging

1 | INTRODUCTION

Shade tolerant tree species, also known as non-pioneers, are important elements of mature forest structure and composition, representing more than 80% of tree species in tropical forests (Denslow, 1987; Uhl et al., 1988). This guild recovers at a lower rate along succession because abandoned agricultural land in the tropics frequently lacks seed and seedling banks of shade tolerant species, which are typically of late successional status and display low seed dispersal reach (Martínez-Garza & Howe, 2003; Muñiz-Castro et al., 2012; Suganuma & Durigan, 2015). Since shade tolerant species are more vulnerable to habitat transformation and play a key role in ecosystem functioning, restoration focused on assisting the recovery of this guild in particular is urgently required (Aide et al., 2011; Holl et al., 2000; Martínez-Garza & Howe, 2003).

Tropical forest tree species are arranged along a continuum of shade tolerance (Wright et al., 2003), but most studies contrast the attributes and responses of pioneer versus shade tolerant species, with much still to be understood about the complexity that exists within the shade tolerant functional group (Valladares et al., 2016). Shade tolerance is associated with a conservative-use strategy, featuring biomass and energy conservation traits that maximize survival under the low light conditions of the forest understorey (Kitajima, 1994; Reich et al., 2003; Veneklaas & Poorter, 1998). While shade tolerant species display high survival in the dark conditions of the forest understorey, experimental essays have shown that shade tolerant transplants can also establish under high irradiance in early-successional environments if they arrive via ecological restoration efforts (Cole et al., 2011; Martínez-Garza et al., 2013; Pedraza & Williams-Linera, 2003). However, an important variation in survival has been found within the shade tolerant group in disturbed habitats (Benítez-Malvido et al., 2005; Camacho-Cruz et al., 2000; Hooper et al., 2002; Martínez-Garza et al., 2005; Muñiz-Castro et al., 2015). Due to the high species diversity and variation in environmental conditions across altered tropical habitats, the development of criteria to select appropriate species for restoration efforts is central to design more effective interventions.

Plant functional traits have been proposed as a useful tool with which to predict the response of species to environmental conditions in restoration efforts (Martínez-Garza et al., 2005, 2013; Pywell et al., 2003). Based on the functional theory that establishes

that species traits reflect resource use and life-history trade-offs, plant species can also be selected according to their functional traits with the aim of restoring ecosystem functions (Ostertag et al., 2015; Reich, 2014; Zirbel et al., 2017). Leaf mass area (LMA) is a descriptor of the efficiency of light capture per unit of carbon invested, and is thus a key trait involved in carbon return and balance that influences whole plant performance (Poorter et al., 2009; Reich, 2014). Leaf dry mass content (LDMC), the ratio of leaf dry mass to fresh mass, is a trait associated with drought resistance, presumably because high fibre content increases the hydraulic integrity of leaf veins, improving tissue resistance to the cell damage caused by severe drought (Kursar et al., 2009; Markesteijn et al., 2011). Plants adapted to shaded habitats tend to exhibit a conservative leaf morphological pattern, including high LMA and LDMC, traits that minimize carbon loss through respiration and maximize tissue defence (Reich et al., 2003; Valladares & Niinemets, 2008). These leaf traits favour persistence under low-resource conditions at the expense of low growth rates (Reich et al., 2003). Plant adaptations for coping with low light conditions are generally incompatible with those required for development under high light conditions and vice versa (Wright et al., 2010; Reich, 2014). However, there is limited information about the performance of shade tolerant planted trees in different disturbance settings and the use of LMA and LDMC as criteria for species-site matching to improve restoration effectiveness in highly diverse tropical landscapes.

In this study, we examined the performance of eight shade tolerant tree species (six endangered) in restoration plantings in various disturbed environments, including pastures, secondary forests and forests subjected to traditional selective logging, in a tropical montane cloud forest (TMCF) landscape. Restoration interventions are required under a variety of conditions because TMCF landscapes are mosaics of mature, secondary and degraded forest and active and abandoned pastures (Aide et al., 2011; CONABIO, 2010; Muñiz-Castro et al., 2012; Pedraza & Williams-Linera, 2003). One of the main causes of TMCF loss has been its transformation to agricultural land (Aide et al., 2011). Such agricultural and livestock production lands are subsequently abandoned, giving rise to secondary forests worldwide (Mulligan, 2011). In remnant forest fragments, unplanned logging, frequently targeting shade tolerant species, contributes to further degradation and the depletion of locally valuable tree species (Ramírez-Marcial et al., 2001; Rüger

et al., 2008; Williams-Linera, 2002). Recruitment of many shade tolerant tree species is limited in such disturbed habitats (Muñiz-Castro et al., 2012; Ortiz-Colin et al., 2017; Toledo-Aceves et al., 2021). For instance, in Mexico, 60% of TMCF tree species face some degree of threat (González-Espinosa et al., 2011) and many of these are shade tolerant species for which no information is available regarding their performance under different altered environments. We address two questions across the three altered environments: (a) What are the survival and growth rates of seedling transplants of eight shade tolerant tree species? and (b) can LMA and LDMC be used as predictors of seedling survival and growth among shade tolerant species in restoration plantings? Given that some shade tolerant species can experience photoinhibition under high radiation (Agyeman et al., 1999) and that high air temperature and low water availability, as well as high soil compaction, are characteristic of tropical pastures (Williams-Linera et al., 1998; Loik & Holl, 1999), we expected lower seedling survival and growth in pastures than in the secondary and selectively logged forests. Under the high irradiance conditions of pastures where water deficit can be limiting (Martínez-Garza et al., 2013; Muñiz-Castro et al., 2015), we expected a strong relationship between LDMC and seedling survival. In contrast, relatively high canopy cover is maintained in cloud forests subjected to traditional selective logging (Ortiz-Colin et al., 2017; Toledo-Aceves et al., 2019), as well as in secondary cloud forests (Muñiz-Castro et al., 2012, 2015; Trujillo-Miranda et al., 2018). Given that, under low-resource conditions, conservative resource-use seedling traits can be associated with higher survival (Poorter & Bongers, 2006; Wright et al., 2010; Reich, 2014), we hypothesized that higher LMA will be related to higher seedling survival in the shaded understorey of the secondary and selectively logged forests.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study sites are located in the TMCF of central Veracruz, Mexico, a region of high priority for conservation and restoration due to the high concentration of biodiversity and considerable loss of forest cover (CONABIO, 2010). In the study region, TMCF ranges between 1,200 and 2,200 m a.s.l. The climate is mild and humid throughout the year with three seasons: a wet-warm season (June–October), a humid-cool season (November–March), and a short dry-warm season (April–May). Mean annual temperature in the study sites ranges from 14 to 19°C, and total annual precipitation between 1,523 and 1,707 mm (based on interpolations calculated by Cuervo-Robayo et al., 2014). TMCF remnant fragments in this region are immersed in a landscape matrix dominated by agricultural land and agroforestry systems (mainly shade coffee plantations; CONABIO, 2010).

The study sites comprised four pastures, five secondary forests, and three forests subjected to traditional selective logging, which together represent the most common causes of TMCF transformation (Aide et al., 2011; CONABIO, 2010). Field work permits were

secured for all sites. These agreements with the landowners were verbal, as is common in the study region. The study did not require ethical approval. Site locations and characteristics are presented in Appendix ST1. The imbalance in the number of sites was due to the limited number that shared similar management and environmental conditions and in which the landowners were interested in maintaining the restoration plantings. In all pastures, cattle had been recently excluded and the vegetation was dominated by the exotic grass *Cynodon plectostachyus* (Poaceae). The pastures presented isolated trees and shrubs, some of them remnants of the TMCF. Common tree species include *Liquidambar styraciflua* (Altingiaceae), *Quercus* spp. (Fagaceae), *Vachellia pennatula* (Fabaceae), *Trichilia havanensis* (Meliaceae) and *Turpinia insignis* (Staphyleaceae). Scattered trees in pastures are a common element in tropical landscapes, and occur in varying densities and spatial arrangements (Prevedello et al., 2018). The secondary forests, developed in areas previously used as agricultural and agroforestry lands, were between 15 and 40 years of age. Traditional selective logging in the studied sites is of low intensity, focused on the extraction of oaks to produce charcoal and other hard wood species for rural construction needs (Ortiz-Colin et al., 2017; Williams-Linera, 2002), including the species used in this study.

Based on hemispherical photographs and convex densitometer measurements taken at the study sites (see methodology below), the mean percentage of canopy cover in pastures was 35.5 ± 2.41 ($\pm SE$; mean values of canopy cover per site are shown in Appendix ST1). In the secondary forests, this value was 90.8 ± 0.3 and in the logged forests it was 95.2 ± 0.2 . Important variation in canopy cover occurred within each environment, but particularly in the pastures (minimum–maximum: 0%–77%) due to the presence of scattered trees, and in the secondary forests (61%–99%). Lower variation characterized the logged forests (86%–99%). To characterize the soil, six samples were collected across each site and mixed into one compound sample for the following laboratory analysis: pH, soil bulk density, total carbon (C), nitrogen (N) and phosphorus (P) (see Appendix ST1).

2.2 | Species

Eight native cloud forest tree species were used to establish the plantings, all of which were reported as being shade tolerant *sensu* Swaine and Whitmore (1988) (Table 1). Seedlings were grown in polythene bags (30 × 16 cm) with a mixture of forest soil and fine gravel (3:1) at the Instituto de Ecología A.C. (INECOL), Xalapa, Veracruz, until transplantation in the field. All seedlings were produced from the same set of seeds collected in the study region but, due to interspecific differences in species phenology and growth rates, the seedling age and size varied among species. One to two-year-old seedlings were planted in 2015 with manual weeding conducted before planting. Seedlings were planted at a minimum distance of 1.5 m apart and in distance from trees already present in the sites. The species arrangement was random in each site. A total of 2,202 seedlings were planted: 496 seedlings in pastures, 986 in secondary

Species	Family	Status
<i>Fraxinus uhdei</i> (Wenz.) Lingelsh.	Oleaceae	Least concern ^a
<i>Juglans pyriformis</i> Liebm.	Juglandaceae	Endangered ^a
<i>Magnolia vovidesii</i> A. Vázquez, Domínguez-Yescas & L. Carvajal.	Magnoliaceae	Endangered ^b
<i>Oreomunnea mexicana</i> J.F. Leroy	Juglandaceae	Endangered ^a
<i>Quercus germana</i> Schlttdl. & Cham.	Fagaceae	Critically endangered ^a
<i>Quercus sartorii</i> Liebm.	Fagaceae	Endangered ^a
<i>Sideroxylon contrerasii</i> (Lundell) T.D.Penn.	Sapotaceae	Vulnerable ^a
<i>Ulmus mexicana</i> (Liebm.) Planch.	Ulmaceae	Endangered ^a

^aGonzález-Espinosa et al. (2011).

^bRivers et al. (2016).

TABLE 1 Family and conservation status of tropical montane cloud forest tree species

forests and 720 in logged forests. The number of planted seedlings per species varied due to differences in seed availability and germination. As a result of the different months of the establishment of plantings, initial seedling height varied among environments (pastures = 69.3 cm \pm 2.5; secondary forests 46.4 cm \pm 1.47; logged forest = 34.8 cm \pm 0.87). The number of seedlings planted and their mean initial size per species in each environment is detailed in Appendix ST2.

Seedling survival and height were recorded in all the plants a month after planting and again 3 years after. Relative growth rate (RGR) in height was calculated as follows: $RGR = (\ln H_2 - \ln H_1) / (t_2 - t_1)$, where H is plant height; t is time, and the initial and final measurements are denoted by subscripts 1 and 2, respectively (Hunt, 1982).

At each site, 10 seedlings per species were selected at random and one mature undamaged leaf (developed after planting) was collected from each seedling (including the petiole) to quantify LMA and LDMC (following Pérez-Harguindeguy et al., 2013). Leaves were collected 1 year after planting, which provided information regarding the plant response to the environment. In a previous study, we measured leaf traits under two levels of shade in controlled conditions for the same set of species, with the exception of *J. pyriformis* (reported in Toledo-Aceves et al., 2017; LMA values per species are shown in Appendix SF3). Due to the reduced number of leaves in some plants, and to minimize the effect of leaf removal on seedling performance, only one leaf per individual was collected. Leaf traits were not measured for *J. pyriformis* in the pasture due to the high mortality of the species in this environment and because the few live individuals presented leaves in poor condition. Each leaf was deposited in a sealed plastic bag in a cooler and transported to the laboratory at INECOL, where they were placed on a tray with the petiole submerged in water for ~12 hr for rehydration. After this period, excess water was removed with a cloth and the remnant petiole was cut. The fresh weight was recorded with an analytical balance and the leaf scanned with an Epson Expression 11000XL and leaf area measured using the program WinFolia version Pro (Regent Instruments Inc.). The leaves were then dried in an oven at 80°C for 48 hr and weighed. The following formulas were used

to determine the functional traits: LMA = leaf dry mass/leaf area, and LDMC = leaf dry mass content/leaf fresh mass content (Pérez-Harguindeguy et al., 2013).

Light affects tree seedling performance and leaf traits (Rüger et al., 2009; Poorter et al., 2009); therefore, for each of the 10 seedlings selected, canopy cover was measured using hemispherical photographs at the time of leaf collection. For this purpose, a camera (Canon Eos rebel XSi) equipped with a fisheye lens was set up at height 1.3 m above the ground on a tripod, levelled and orientated northwards. The photographs were analysed using Gap Light Analyzer (Version 2.0.).

2.3 | Data analysis

A generalized linear model (GLM; binomial family and logit link function) was used to assess the survival of each species as a function of environment. Environment was included as a factor with three categories (pasture, secondary forest, logged forest). The GLMs were performed using the proportion of surviving seedlings per site. A linear mixed effects model (LMM) with a Normal error distribution was used to assess the relative growth rate (RGR) of each species as a function of environment (factor with three categories); site was included as a random factor.

To evaluate the power of the functional traits LMA and LDMC as predictors of seedling survival (binomial response variable), a GLM was used including the three environments, irrespective of tree species. In the first full models, environment was included as a factor with three categories (pasture, secondary forest, logged forest), while LMA or LDMC, canopy cover and seedling initial height were included as covariables. The interactions of functional traits with canopy cover or environment and environment with canopy cover were included. Seedling initial height was included because it can affect the establishment of plantings (Benítez-Malvido et al., 2005) and this parameter varied within and among species (Appendix ST2). Models were constructed for each functional trait separately because LMA and LDMC are highly correlated ($R = 0.88$,

$p < 0.0001$). Since the interactions environment \times LMA and environment \times LDMC were significant ($p < 0.05$; Appendix ST4), and in order to understand and gain further insight into the relationship between functional traits and species performance, a separate model was fitted for each environment. For these models, the leaf traits (LMA or LDMC), canopy cover, height and the statistical interactions LMA \times Canopy or LDMC \times Canopy were included (see Appendix ST4). In all cases, the step-wise procedure based on the Akaike information criterion ($\Delta AIC > 2$) was used for selection of the best fitting model except in the case of tied values, in which case the most parsimonious model was selected (Crawley, 2013).

To evaluate relative growth rate (RGR) as function of the leaf traits (LMA or LDMC), LMM including the three environments were used, irrespective of tree species, in a similar manner to the procedure described above. In these models, site was included as a random factor. Since the interactions environment \times LMA and environment \times LDMC were significant ($p < 0.05$; Appendix ST4), a separate model was fitted for each environment in order to better understand the relationships between leaf functional traits and species growth. Models included the leaf traits (LMA or LDMC), canopy cover and their interaction (LMA \times Canopy or LDMC \times Canopy) in each environment, with site included as a random factor. The best fitting model was selected based on the criteria described above. All analyses were carried out in R with the MASS and nlme libraries (R Core Team, 2019).

3 | RESULTS

3.1 | Survival and growth in restoration plantings

Overall, proportion of survival was highest in logged forests (0.875 ± 0.028), followed by secondary forests (0.798 ± 0.034) and finally pastures (0.624 ± 0.055) after 3 years. Six species presented high survival (>0.70) across all the environments (Figure 1). Survival was significantly lower in the pastures than in the secondary or logged forests in seven species (Figure 1; Appendix ST5). Only *Fraxinus uhdei*, *Juglans pyriformis* and *Magnolia vovidesii* displayed significantly lower survival in secondary forests than in logged forests (Figure 1). *Juglans pyriformis* had the poorest performance, with the lowest survival of all species.

Including all species, RGR was highest in the logged forests ($0.290 \pm 0.01 \text{ cm cm}^{-1} \text{ year}^{-1}$), intermediate in secondary forests ($0.261 \pm 0.01 \text{ cm cm}^{-1} \text{ year}^{-1}$) and lowest in pastures ($0.159 \pm 0.03 \text{ cm cm}^{-1} \text{ year}^{-1}$). Significantly lower RGR was displayed in *Oreomunnea mexicana* in the pastures compared to the secondary and logged forests (Figure 1; Appendix ST5). A tendency for lower RGR in the pastures could be observed for other species but, probably due to high variation within the environments, the differences were not significant. The RGR of *J. pyriformis* in pastures was not included in the analysis because growth data was available for only three individuals. The average height values reached per species after 3 years are presented in Appendix ST2.

3.2 | Leaf functional traits as predictors of survival and growth

LMA was a strong predictor of seedling survival in the three environments (Table 2). LDMC was also significantly related to survival (Table 2). In the three environments, the species with higher LMA displayed higher probability of survival and, those species with higher LDMC also had a higher probability of survival (Figure 2; Appendix SF6). In addition to the functional trait LMA, canopy cover contributed to a better model fit in the pastures and secondary forests (Table 2). However, canopy cover had no significant effect on the logged forest models. For the models that included LMA as a predictor of seedling survival, initial tree height was not significant in the pastures, but contributed to a better model fit in the secondary and logged forests. In the models that included LDMC, tree height also contributed to predicted survival in the two environments. The magnitude of this contribution is much lower compared to that of the functional traits (see regression coefficients in Table 2). Models with LMA as a predictor of survival explained more variation (Deviance: 27%–68%) than models with LDMC (21%–50%). Selection of models based on ΔAIC can be found in Appendix ST4.

LMA was also a predictor of RGR in the pastures and secondary forests, but not in the logged forests (Table 3). In the pastures, lower RGR was related to higher LMA. In contrast, the opposite relationship was found in the secondary forests (Figure 3). Lower RGR was related to higher LDMC in the pastures but no significant relationship was found in the secondary and logged forests (Table 3). Canopy cover contributed to a better fit for models that included LMA as a predictor of RGR in pastures and logged forests, but had no significant effect on secondary forests (Table 3; Appendix ST4). For models that included LDMC as a predictor of RGR, canopy cover also contributed to a better model fit in the three environments (Table 3; Appendix ST4).

4 | DISCUSSION

Our results regarding the relationship between leaf traits and seedling performance within the shade tolerant functional group support a higher probability of survival in species with higher LMA under different disturbed environments. LDMC is also linked to seedling survival among the shade tolerant species, but to a lower extent than LMA. Overall, the high seedling survival found supports the potential of the studied species for use in restoration plantings, in particular under the canopy of secondary and selectively logged forests. While conservative leaf attributes were linked to higher survival, this occurred at the expense of low growth under the conditions of the pastures, thus potentially reducing the establishment success of species of high LMA and LDMC in these altered environments.

4.1 | Survival and growth in restoration plantings

The overall survival found after 3 years (76%) surpassed the average survival of 62% reported in a metaanalysis of restoration

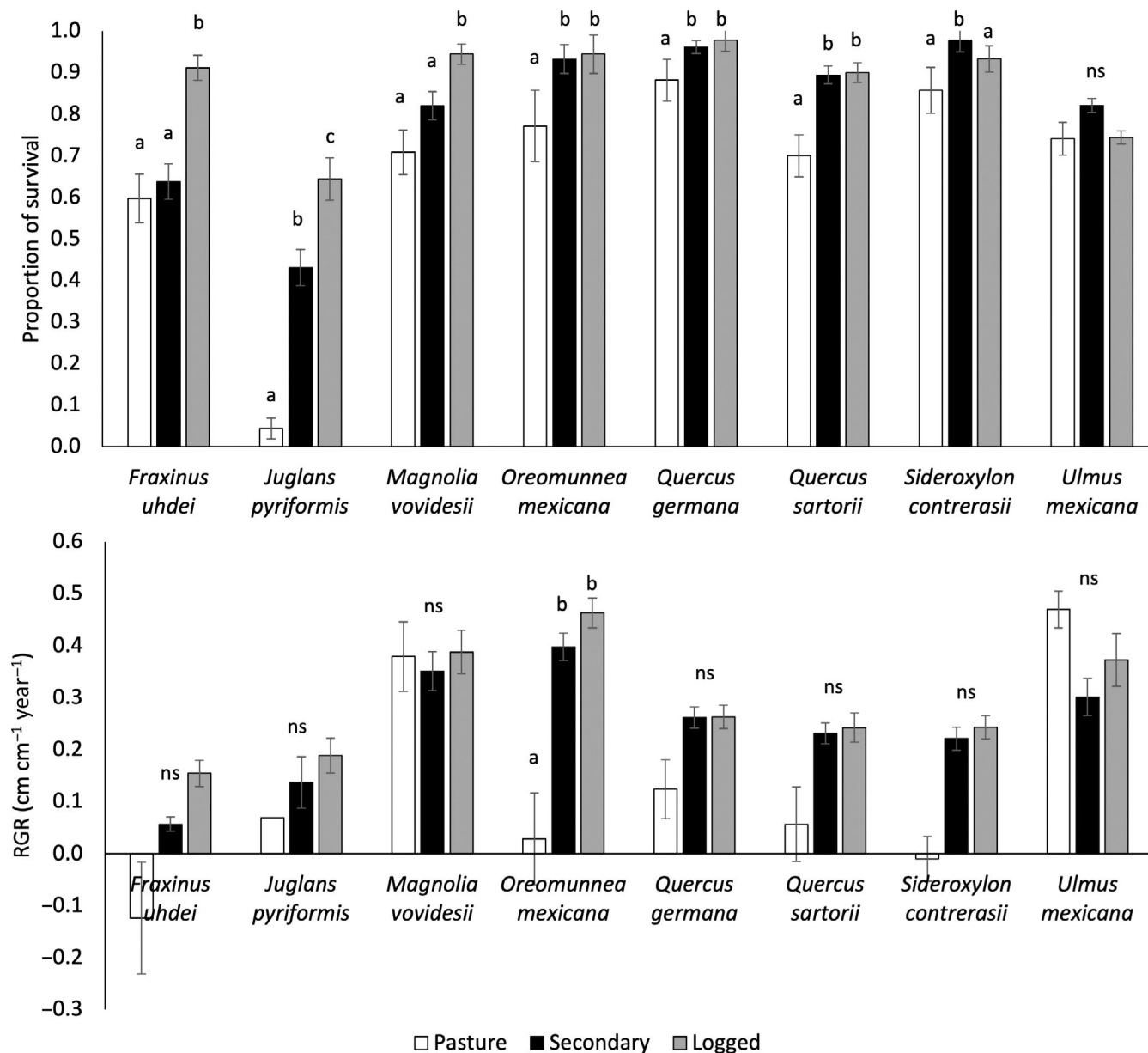


FIGURE 1 Survival proportions (top) and relative growth rate (RGR; bottom) of cloud forest tree seedlings in restoration plantings established in pastures (white), secondary forests (black) and forests subjected to selective logging (grey). Values are mean \pm standard error. Different letters denote significant differences within species among environments ($p < 0.05$). ns, not significant

seedling plantings in varied ecosystems (Palma & Laurance, 2015). Important interspecific variation in transplant performance occurred among environments. However, due to differences among environments in terms of the size of transplants, time of planting and site characteristics (such as orientation, topography, soil conditions and prior land use) comparisons of performance among environments should be treated with some caution. The high variation in survival and growth in the pastures not only denotes the differential responses of the species to the environment, but also highlights the important heterogeneity present within and among the pastures, probably as result of variation in the soil conditions and in grass and canopy cover. Overall lower survival and growth in the pastures, in comparison to the secondary and logged forests,

denotes that while most of the shade tolerant species were capable of resistance, they were probably stressed due to the extreme environmental conditions, such as high radiation and temperature accompanied by lower soil water availability, soil compaction, as well as the dominance of exotic grasses as reported for tropical pastures (Benítez-Malvido et al., 2005; Loik & Holl, 1999; Williams-Linera et al., 1998). Plants in high irradiance conditions have lower leaf area and greater investment in roots and stem support in order to meet the greater demand for nutrients and water imposed by greater transpiration (Poorter et al., 2019), although compacted soil can limit root expansion (Alameda & Villar, 2008). Shade tolerant tree seedlings exposed to high solar radiation can also experience photoinhibition, which involves a reduction

TABLE 2 Parameters of the best generalized logistic linear models to evaluate seedling survival as a function of leaf mass area (LMA) and leaf dry mass content (LDMC), canopy cover, initial tree height and the interaction LMA \times Canopy or LDMC \times Canopy, in restoration plantings established in pastures, secondary forests and forests subjected to traditional selective logging. B_i = coefficient \pm standard error; P = probability of type I error; D^2 = deviance (%) explained by the model

	Pastures				Secondary forest				Logged forest			
	B_i	z	p	D^2	B_i	z	p	D^2	B_i	z	p	D^2
Intercept	-2.24 \pm 1.36	-1.652	0.098	68.5	-13.00 \pm 2.19	-5.94	<0.0001	51.3	1.1 \pm 0.36	3.01	0.002	27.4
LMA	66791 \pm 20741	3.22	0.001		886.11 \pm 90.89	9.74	<0.0001		485.31 \pm 90.98	5.33	<0.0001	
Canopy	0.02 \pm 0.03	0.64	0.521		0.13 \pm 0.02	5.58	<0.0001					
Height					-0.01 \pm 0.00	-2.85	0.004		-0.02 \pm 0.01	-3.44	0.0005	
LMA \times Canopy	-8.56 \pm 5.44	-1.57	0.11									
Intercept	-0.71 \pm 0.98	-0.725	0.468	50.3	-11.45 \pm 2.20	-5.20	<0.0001	34.1	-27.22 \pm 13.58	-2.00	0.045	20.7
LDMC	7.64 \pm 2.3	3.27	0.001		11.42 \pm 1.35	8.47	<0.0001		7.24 \pm 1.59	4.56	<0.0001	
Canopy	0.02 \pm 0.02	0.82	0.41		0.11 \pm 0.02	4.83	<0.0001		0.29 \pm 0.14	2.07	0.038	
Height					-0.01 \pm 0.00	-3.25	0.001		-0.02 \pm 0.01	-3.61	0.0002	
LDMC \times Canopy	-0.13 \pm 0.05	-2.35	0.018									

of light use efficiency in photosynthesis (Agyeman et al., 1999; Lovelock et al., 1994). Previous studies also report lower survival of shade tolerant transplants in pastures than in young secondary and mature tropical forests (Alvarez-Aquino et al., 2004; Benítez-Malvido et al., 2005; Muñiz-Castro et al., 2015). Nevertheless, the overall 62% survival recorded in the pastures after 3 years in our study is an indicator of an acceptable restoration success (Palma & Laurance, 2015) in this harsh environment, thus supporting the use of transplants of shade tolerant species in early successional environments to assist the recovery of this vulnerable group and its associated functions.

In the pastures, *J. pyriformis* in particular displayed very high mortality indicating that this species is unsuitable for these environments. These results confirm the findings of previous experiments in which *J. pyriformis* attained poor survival in open sites in comparison to seedlings under the canopy of *Pinus patula* plantations (Avendaño-Yanez et al., 2016). However, they contrast with the c. 60% survival of *J. pyriformis* reported after 20 months in a recently abandoned pasture (Pedraza & Williams-Linera, 2003). *Oreomunnea mexicana* and *S. contrerasii* also presented very low RGR in the pastures. This indicates that, although they were able to persist, the conditions were unfavourable for their development. In contrast, the similar performance across environments in *M. vovidesii*, *Q. germana*, *Q. sartori* and *U. mexicana* support their potential for establishment in varied disturbed habitats.

The range of conditions presented by the secondary forests is more favourable than those in pastures, where the developing canopy cover reduces intense radiation and buffers temperature and humidity (Alvarez-Aquino et al., 2004; Muñiz-Castro et al., 2015), resulting in higher survival and RGR. However, in comparison to mature forests, secondary forests are highly heterogeneous and have a higher tree density and dominance of the herbaceous strata (Kappelle et al., 1996; Muñiz-Castro et al., 2012; Trujillo-Miranda et al., 2018), factors that could be less favourable for tree early establishment. In the traditional selectively logged forests, the highest survival and RGR values were reached for most species. While lower growth rates could be expected in the low light environment of the forest understorey (Poorter & Bongers, 2006), the overall higher survival and growth rates found in the logged forests denote the high potential for successful establishment for all species under the prevalent conditions, which tend to be comparable to those of mature forests. Oscillations in humidity and temperature are also buffered in the understorey, which can have an important influence on plant carbon balance (Valladares et al., 2016). Interestingly, some species that presented high survival in the shaded logged forests also presented high RGR in the sun exposed pastures (e.g. *M. vovidesii* and *U. mexicana*), while others with high survival in the logged forests had very low or even negative RGR in the pastures, suggesting that they had experienced stress (e.g. *F. uhdei*, *O. mexicana* and *S. contrerasii*). Such idiosyncratic responses within the so-called shade tolerant group emphasize the importance to study their responses for adequate selection of species for restoration efforts in varied altered habitats.

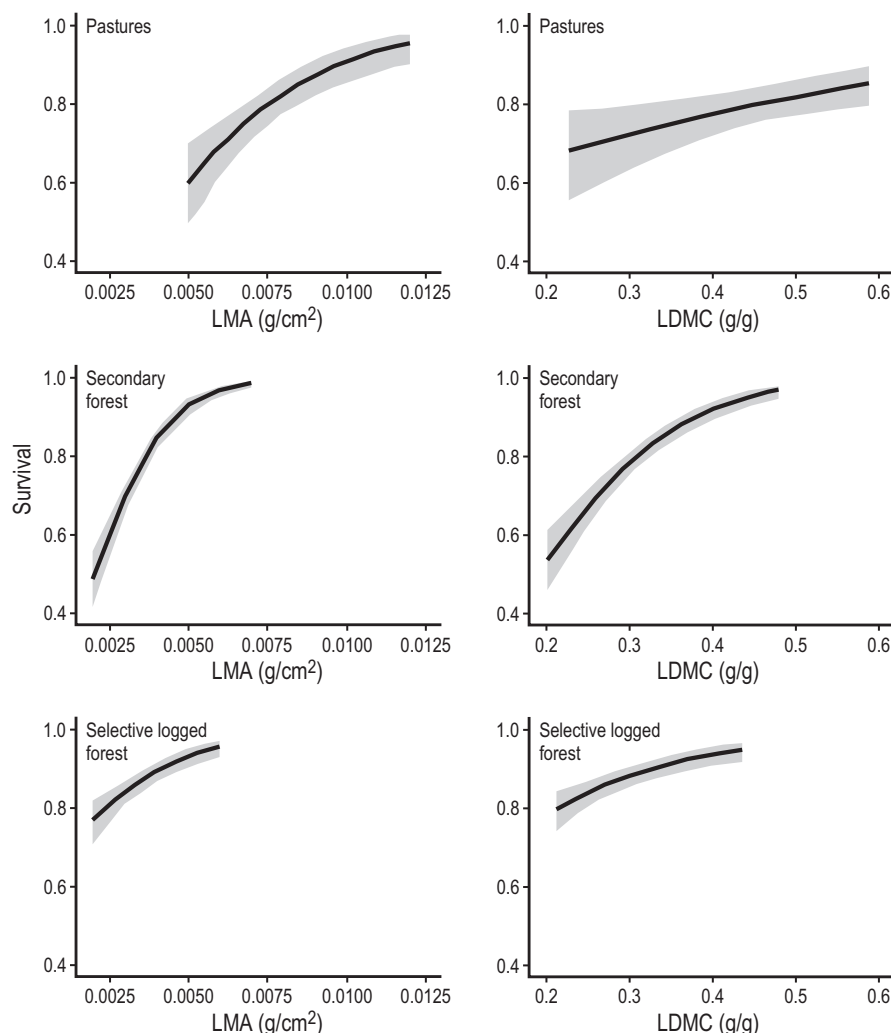


FIGURE 2 Relationship between proportion of survival and leaf mass area (LMA; left) and leaf dry mass content (LDMC; right) in cloud forest tree species in restoration plantings established in pastures, secondary forests and forests subjected to traditional selective logging. The solid line is the fitted logistic linear model. Grey area represents 95% confidence intervals

4.2 | Leaf functional traits as predictors of survival and growth

Our results support that LMA is a strong predictor of seedling performance within the shade tolerant guild in disturbed habitats, ranging from recently abandoned pastures to secondary and selectively logged forests. Despite the smaller range of trait values expressed in the understorey of the selectively logged forests, a strong pattern emerged in which the species of higher LMA displayed higher survival. In a previous study, LMA was also found to be a strong predictor of seedling survival among 13 shade tolerant tree species along an elevation gradient in the TMCF understorey (Toledo-Aceves et al., 2019). Under the low light conditions in the forest understorey, conservative resource-use seedling traits can be associated with higher survival (Poorter & Bongers, 2006; Reich, 2014). Additionally, our results denote that this conservative leaf trait provides resistance to the seedlings established in the transformed habitats. Indeed, higher LMA was also linked to higher survival in the pastures. Higher LMA is also associated with increased longevity and better protected leaves with lower nutrient concentrations, which lead to higher plant persistence (Poorter et al., 2009), but this leaf investment strategy occurs at the expense of lower growth in the pastures. Leaves with high

LMA constrict potential growth under high irradiance due to lower light interception and less efficient carbon gain (Jantse-ten Klooster et al., 2007; Kitajima, 1994). Thus, a negative relationship between LMA and seedling growth rates has been widely documented (Poorter & Bongers, 2006; Poorter et al., 2009; Wright et al., 2010). Overall, our results are in line with previous studies showing the significant role of LMA in plant performance under controlled and natural forest conditions (Kitajima, 1994; Poorter & Bongers, 2006; Wright et al., 2010). However, most studies have contrasted pioneer versus shade tolerant species, leaving an important gap in the information regarding differential performance within the shade tolerant functional group and, in particular, our results add to previous findings by providing support for the inclusion of shade tolerant species with high LMA in early successional habitats for restoration purposes.

Plastic adjustments in LMA could contribute to acclimatization to contrasting environments. Intraspecific LMA values were higher in the pastures and lower in the secondary forests, with the lowest values occurring in the selectively logged forests. Seedlings in the pastures were continuously exposed to high radiation and it is known that plant individuals exposed to high radiation display increased LMA (Poorter et al., 2009). Under high irradiance, a greater photosynthetic biomass per unit of leaf area enhances photosynthetic

TABLE 3 Parameters of the best linear mixed models to evaluate seedling relative growth rate (RGR) as function of leaf mass area (LMA), and leaf dry mass content (LDMC), canopy cover and the interaction LMA × Canopy or LDMC × Canopy, in restoration plantings established in pastures, secondary forests and forests subjected to traditional selective logging. B_i = coefficient ± standard error; p = probability of Type I error

	Pastures			Secondary forest			Logged forest		
	B_i	t	p	B_i	t	p	B_i	t	p
Fixed effects									
Intercept	0.211 ± 0.181	1.165	0.260	0.658 ± 0.256	2.567	0.010	3.851 ± 1.24	3.09	0.002
LMA	-50.34 ± 20.48	-2.458	0.024	15.956 ± 7.076	2.254	0.024	-454.39 ± 281.94	-1.61	0.108
Canopy	0.009 ± 0.001	4.925	0.0001	-0.004 ± 0.002	-1.806	0.072	-0.037 ± 0.013	-2.89	0.004
LMA × Canopy							4.869 ± 2.960	1.64	0.101
Random effects									
Site residual standard deviation (RSD) = 0.207				RSD = 0.176			RSD = 0.170		
Fixed effects									
Intercept	0.335 ± 0.111	3.008	0.003	2.138 ± 0.657	2.79	0.005	2.019 ± 0.44	4.49	<0.0001
LDMC	-0.670 ± 0.152	-4.400	<0.001	-3.382 ± 1.849	-1.82	0.068			
Canopy	0.004 ± 0.001	3.548	0.0006	-0.021 ± 0.008	-2.49	0.013	-0.018 ± 0.004	-3.87	0.0001
LDMC × Canopy				0.038 ± 0.020	1.89	0.059			
Random effects									
Site residual standard deviation (RSD) = 0.190				RSD = 0.176			RSD = 0.171		

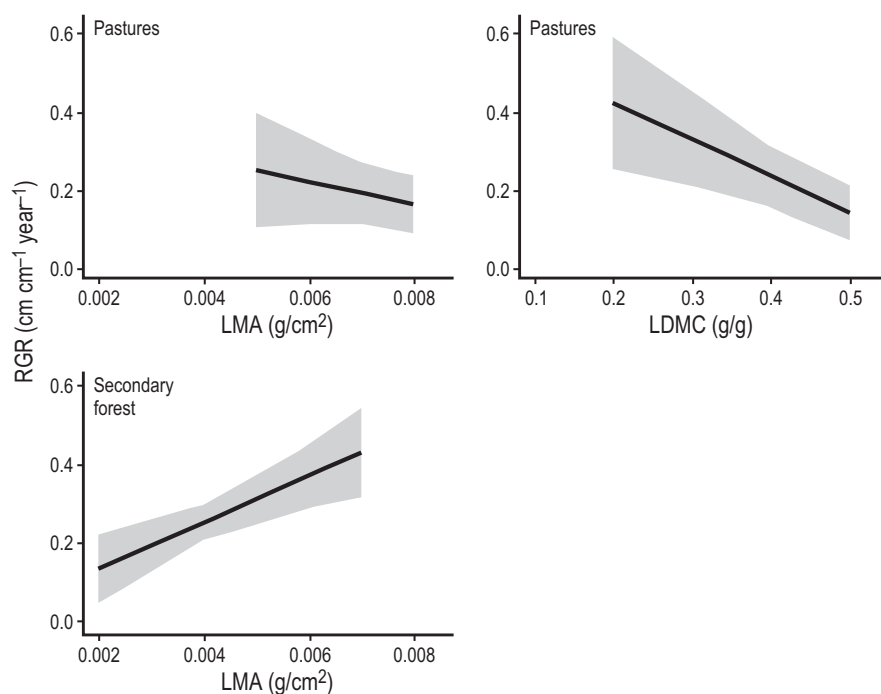


FIGURE 3 Relationship between seedling relative growth rate (RGR) and leaf mass area (LMA; left) and leaf dry mass content (LDMC; right) in cloud forest tree species in restoration plantings established in pastures and secondary forests. Solid line is the fitted linear model. Grey area represents 95% confidence intervals

capacity, while under low irradiance (under the canopy cover), light interception is augmented by increasing the area per unit of leaf biomass (Gratani et al., 2006; Poorter et al., 2009). While shade tolerant species display low plasticity in shaded environments (Toledo-Aceves et al., 2019; Valladares & Niinemets, 2008), the plastic leaf response to the varying levels of solar radiation present across the disturbed habitats may play a role in their establishment success.

Supporting our prediction, we found a relationship between LDMC and seedling survival under the high irradiance conditions of pastures where water deficit can be limiting, as was reported in non-pioneers planted in a pasture in prior tropical lowland rain forest (Martínez-Garza et al., 2013). LDMC also had a significant relationship with survival in the secondary and logged forests. Higher LDMC is associated with thicker, tougher leaves, which can be better protected from the damage caused by drought and herbivory and is also associated with longer leaf lifespans (Méndez-Alonzo et al., 2012; Pérez-Harguindeguy et al., 2013). Well-defended and long-lived leaves allow plants to maintain a positive carbon balance, enhancing plant survival (Coley & Barone, 1996; Poorter & Bongers, 2006; Reich et al., 2003). Overall, the models that included LMA accounted for a greater variation in seedling survival, compared to those that included LDMC. LMA can therefore be considered a better predictor of seedling performance for shade tolerant species in cloud forest restoration plantings.

The canopy cover had a stronger influence on seedling survival and growth within the pastures than in the secondary forests, but no effect in the logged forests. Canopy cover plays an important role in the establishment of tree seedlings in early successional habitats. The development of canopy cover as forest succession progresses acts to reduce light availability in the understory, directly affecting tree recruitment (Bazzaz & Pickett, 1980). The absence of or low canopy cover in pastures leads to high levels of irradiance, higher variation in temperature, lower humidity and competition with grasses, which can limit

establishment of shade tolerant species. However, our results indicate that most of the species introduced as 1- to 2-year-old seedlings could establish. The presence of scattered trees and shrubs contributes to a high heterogeneity in tropical pastures and can provide favourable conditions as they may act as nurse species and regeneration nuclei (Douterlungne et al., 2015; García-Orth & Martínez-Ramos, 2011). The higher establishment success of the introduced seedlings under the canopy of the secondary forests indicates the occurrence of facilitation by the secondary vegetation of forest development into advanced successional stages (Brown & Lugo, 1990). The small variation in canopy cover in the selectively logged forests may have led to the lack of a significant effect of this structural variable on seedling performance. In the shaded understorey, growth is light limited (Valladares et al., 2016), which could explain the small predictive power of the leaf traits studied on seedling growth in this environment.

Initial seedling height had apparently little influence on survival, which is contrary to that found in previous reports (Charles et al., 2018; Comita et al., 2009). Indeed, height at time of planting had no effect on survival in pastures when considering LMA, and made only a small contribution to explaining survival in secondary and logged forests. The seedlings might have been tall enough to overcome the limiting factors in the studied sites, but we did not further explore the effect of height since the seedlings were all within a small range of this parameter. These results also suggest that other factors are more determinant for the outcome, and support the predictive nature of LMA for tree seedling performance.

4.3 | Implications for restoration

An overarching goal in ecological restoration is to re-establish biodiversity and ecological functions, for which the achievement of

more successful and predictable outcomes is essential. Due to the high tree diversity in tropical forests and their specific requirements for establishment, the selection of species matching conditions of disturbance is necessary in order to implement effective interventions. Our results show that LMA is a reliable predictor of species responses to environmental variation within the shade tolerant guild, and can therefore be used to guide restoration practices.

The overall high survival found in all of the environments supports the use of shade tolerant species of high LMA values in cloud forest restoration efforts. The characteristics of shade tolerant species with a conservative strategy favour their establishment in the secondary and logged forest understories. Their successful establishment in these environments indicates that enrichment plantings with shade cloud forest species can be a viable strategy to assist the regeneration of diminishing populations. While high LMA remained linked to higher survival in the pastures, it involved such low growth rates that some species with these characteristics could fail to establish. Despite the lower survival and growth recorded in the pastures compared to the other environments, our results show notable exceptions for *M. vovidesii*, *Q. germana*, *Q. sartorii* and *U. mexicana*, which could be effectively incorporated into mixed species plantings to generate restored forests. Since initial successional communities are determinant in successional pathways, management interventions at early stages could help to enhance recovery rates and manipulate successional trajectories (Jakovac et al., 2021). Overcoming the domination of pioneer trees in regeneration sites by assisting the establishment of shade tolerant species where their seed availability is limiting may contribute to accelerated succession and mitigation of species loss.

Restoration of TMCF is urgently required due to the alarming loss and degradation caused by deforestation, logging and climate change, which increasingly threaten the extraordinary biodiversity and endemism of these ecosystems (Aide et al., 2011). Particular attention to assistance of the regeneration of shade tolerant, typically late-successional and often animal-dispersed species is crucial in order to safeguard biodiversity across tropical montane cloud forest landscapes. Some rare and endangered species, as well as their associated interactions, may not recover unless targeted efforts are made. These efforts can be made more efficient by the establishment of screening trials of several native species exhibiting high LMA values in degraded areas in order to identify other potential barriers and determine long-term restoration success.

ACKNOWLEDGEMENTS

This study was funded by CONACYT (CB2014-01/238831) and Instituto de Ecología A.C. (20030-11218). We are grateful to the owners of the study sites: R. Macías, Y. Perroni, C. Gallardo, R. Hernández, A. SanGabriel, F. SanGabriel, G. Cervantes and G. Valencia. We thank Victor Vásquez, M.A. García-Hernández, Claudia Gallardo, Javier Tolome, Marichu Peralta, Martín SanGabriel, Carlos Iglesias, Karina Osorio and Carlos Flores for

their help in the field, and Graciela Sánchez for format edition. Rosario Landgrave calculated temperature and precipitation for the study sites and produced graphics for the figures. K. Macmillan edited the text. We thank the anonymous reviewers for their suggestions to a previous version.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

T.T.-A. led the writing of the manuscript; T.T.-A., M.B.-M. and F.L.-B. collected the data; T.T.-A. and V.J.S. analysed data. All authors contributed to the ideas in the manuscript and revision of drafts, and all gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital repository <https://doi.org/10.5061/dryad.q2bvq83mj> (Toledo-Aceves et al., 2022).

ORCID

Tarin Toledo-Aceves  <https://orcid.org/0000-0001-6069-468X>
 Martha Bonilla-Moheno  <https://orcid.org/0000-0002-2403-2002>
 Vinicio J. Sosa  <https://orcid.org/0000-0002-4712-3900>
 Fabiola López-Barrera  <https://orcid.org/0000-0002-6092-6230>
 Guadalupe Williams-Linera  <https://orcid.org/0000-0001-6341-6570>

REFERENCES

- Agyeman, V. K., Swaine, M. D., & Thompson, J. (1999). Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology*, 87, 815–827. <https://doi.org/10.1046/j.1365-2745.1999.00400.x>
- Aide, T., Ruiz-Jaen, M., & Grau, H. (2011). What is the state of tropical montane cloud forest restoration. In L. Bruijnzeel, F. Scatena, & L. Hamilton (Eds.), *Tropical montane cloud forests: Science for conservation and management* (pp. 101–109). Cambridge University Press.
- Alameda, D., & Villar, R. (2008). Moderate soil compaction: Implications on growth and architecture in seedlings of 17 woody plant species. *Soil and Tillage Research*, 103, 325–331. <https://doi.org/10.1016/j.still.2008.10.029>
- Alvarez-Aquino, C., Williams-Linera, G., & Newton, A. C. (2004). Experimental native tree seedling establishment for the restoration of a Mexican cloud forest. *Restoration Ecology*, 12, 412–418. <https://doi.org/10.1111/j.1061-2971.2004.00398.x>
- Avendaño-Yanez, M. D., Sánchez-Velásquez, L. R., Meave, J. A., & Pineda-Lopez, M. D. (2016). Can Pinus plantations facilitate re-introduction of endangered cloud forest species? *Landscape and Ecological Engineering*, 12, 99–104. <https://doi.org/10.1007/s11355-015-0277-z>
- Bazzaz, F. A., & Pickett, S. T. A. (1980). Physiological ecology of tropical succession: A comparative review. *Annual Review of Ecology and Systematics*, 11(1), 287–310.
- Benítez-Malvido, J., Martínez-Ramos, M. M., Camargo, J. L. C., & Ferraz, I. D. K. (2005). Responses of seedling transplants to environmental variations in contrasting habitats of Central Amazonia. *Journal of Tropical Ecology*, 21, 397–406. <https://doi.org/10.1017/s0266467405002439>
- Brown, S., & Lugo, A. E. (1990). Tropical secondary forests. *Journal of Tropical Ecology*, 6(1), 1–32.

- Camacho-Cruz, A., González-Espinosa, M., Wolf, J. H. D., & De Jong, B. H. J. (2000). Germination and survival of tree species in disturbed forests of the highlands of Chiapas, Mexico. *Canadian Journal of Botany-Revue Canadienne De Botanique*, 78, 1309–1318. <https://doi.org/10.1139/b00-103>
- Charles, L. S., Dwyer, J. M., Smith, T. J., Connors, S., Marschner, P., & Mayfield, M. M. (2018). Seedling growth responses to species-, neighborhood-, and landscape-scale effects during tropical forest restoration. *Ecosphere*, 9(8), e02386. <https://doi.org/10.1002/ecs2.2386>
- Cole, R. J., Holl, K. D., Keene, C. L., & Zahawi, R. A. (2011). Direct seeding of late-successional trees to restore tropical montane forest. *Forest Ecology and Management*, 261, 1590–1597. <https://doi.org/10.1016/j.foreco.2010.06.038>
- Coley, P. D., & Barone, J. A. (1996). Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, 27, 305–335. <https://doi.org/10.1146/annurev.ecolsys.27.1.305>
- Comita, L. S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C. D., & Zimmerman, J. K. (2009). Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *Journal of Ecology*, 97(6), 1346–1359. <https://doi.org/10.1111/j.1365-2745.2009.01551.x>
- CONABIO. (2010). *El bosque mesófilo de montaña en México: Amenazas y oportunidades para su conservación y manejo sostenible*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.
- Crawley, M. J. (2013). *The R book*. John Wiley & Sons.
- Cuervo-Robayo, A. P., Tellez-Valdes, O., Gomez-Albores, M. A., Venegas-Barrera, C. S., Manjarrez, J., & Martínez-Meyer, E. (2014). An update of high-resolution monthly climate surfaces for Mexico. *International Journal of Climatology*, 34, 2427–2437. <https://doi.org/10.1002/joc.3848>
- Denslow, J. S. (1987). Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics*, 18, 431–451.
- Douterlungne, D., Ferguson, B. G., Siddique, I., Soto-Pinto, L., Jiménez-Ferrer, G., & Gavito, M. E. (2015). Microsite determinants of variability in seedling and cutting establishment in tropical forest restoration plantations. *Restoration Ecology*, 23, 861–871. <https://doi.org/10.1111/rec.12247>
- García-Orth, X., & Martínez-Ramos, M. (2011). Isolated trees and grass removal improve performance of transplanted *Trema micrantha* (L.) Blume (Ulmaceae) saplings in tropical pastures. *Restoration Ecology*, 19, 24–34. <https://doi.org/10.1111/j.1526-100X.2009.00536.x>
- González-Espinosa, M., Meave, J. A., Lorea-Hernández, F., Ibarra-Manriquez, G., & Newton, A. C. (2011). *The red list of Mexican cloud forest trees*. Fauna & Flora International.
- Gratani, L., Covone, F., & Larcher, W. (2006). Leaf plasticity in response to light of three evergreen species of the Mediterranean maquis. *Trees*, 20, 549–558.
- Holl, K. D., Loik, M. E., Lin, E. H. V., & Samuels, I. A. (2000). Tropical montane forest restoration in Costa Rica: Overcoming barriers to dispersal and establishment. *Restoration Ecology*, 8, 339–349. <https://doi.org/10.1046/j.1526-100x.2000.80049.x>
- Hooper, E., Condit, R., & Legendre, P. (2002). Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. *Ecological Applications*, 12, 1626–1641.
- Hunt, R. (1982). *Plant growth curves. The functional approach to plant growth analysis*. Edward Arnold Ltd.
- Jakovac, C. C., Junqueira, A. B., Crouzeilles, R., Peña-Claros, M., Mesquita, R. C., & Bongers, F. (2021). The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biological Reviews*, 96, 1114–1134. <https://doi.org/10.1111/brv.12694>
- Jantse-ten Klooster, S. H., Thomas, E. J. P., & Sterck, F. J. (2007). Explaining interspecific differences in sapling growth and shade tolerance in temperate forests. *Journal of Ecology*, 95, 1250–1260. <https://doi.org/10.1111/j.1365-2745.2007.01299.x>
- Kappelle, M., Geuze, T., Leal, M. E., & Cleef, A. M. (1996). Successional age and forest structure in a Costa Rican upper montane *Quercus* forest. *Journal of Tropical Ecology*, 12, 681–698. <https://doi.org/10.1017/s0266467400009871>
- Kitajima, K. (1994). Relative importance of photosynthetic traits and al-location patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, 98, 419–428. <https://doi.org/10.1007/bf00324232>
- Kursar, T. A., Engelbrecht, B. M. J., Burke, A., Tyree, M. T., El Omari, B., & Giraldo, J. P. (2009). Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology*, 23, 93–102. <https://doi.org/10.1111/j.1365-2435.2008.01483.x>
- Loik, M. E., & Holl, K. D. (1999). Photosynthetic responses to light for rainforest seedlings planted in abandoned pasture, Costa Rica. *Restoration Ecology*, 7, 382–391. <https://doi.org/10.1046/j.1526-100X.1999.72033.x>
- Lovelock, C. E., Jebb, M., & Osmond, C. B. (1994). Photoinhibition and recovery in tropical plant species: Response to disturbance. *Oecologia*, 97, 297–307. <https://doi.org/10.1007/bf00317318>
- Markestijn, L., Poorter, L., Paz, H., Sack, L., & Bongers, F. (2011). Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant Cell and Environment*, 34, 137–148. <https://doi.org/10.1111/j.1365-3040.2010.02231.x>
- Martínez-Garza, C., Bongers, F., & Poorter, L. (2013). Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *Forest Ecology and Management*, 303, 35–45. <https://doi.org/10.1016/j.foreco.2013.03.046>
- Martínez-Garza, C., & Howe, H. F. (2003). Restoring tropical diversity: Beating the time tax on species loss. *Journal of Applied Ecology*, 40, 423–429. <https://doi.org/10.1046/j.1365-2664.2003.00819.x>
- Martínez-Garza, C., Pena, V., Ricker, M., Campos, A., & Howe, H. F. (2005). Restoring tropical biodiversity: Leaf traits predict growth and survival of late-successional trees in early-successional environments. *Forest Ecology and Management*, 217, 365–379. <https://doi.org/10.1016/j.foreco.2005.07.001>
- Méndez-Alonso, R., Paz, H., Zuluaga, R. C., Rosell, J. A., & Olson, M. E. (2012). Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology*, 93, 2397–2406. <https://doi.org/10.1890/11-1213.1>
- Mulligan, M. (2011). Modelling the tropics-wide extent and distribution of cloud forest and cloud forest loss, with implications for conservation priority. In Bruijnzeel, L., Scatena, F., Hamilton, L. (Eds.), *Tropical montane cloud forests: Science for conservation and management* (pp. 16–38). Cambridge University Press.
- Muñiz-Castro, M. A., Williams-Linera, G., & Benítez-Malvido, J. (2015). Restoring montane cloud forest: Establishment of three Fagaceae species in the old fields of central Veracruz, Mexico. *Restoration Ecology*, 23, 26–33. <https://doi.org/10.1111/rec.12155>
- Muñiz-Castro, M. A., Williams-Linera, G., & Martínez-Ramos, M. (2012). Dispersal mode, shade tolerance, and phytogeographical affinity of tree species during secondary succession in tropical montane cloud forest. *Plant Ecology*, 213, 339–353. <https://doi.org/10.1007/s11258-011-9980-5>
- Ortiz-Colin, P., Toledo-Aceves, T., Lopez-Barrera, F., & Gerez-Fernández, P. (2017). Can traditional selective logging secure tree regeneration in cloud forest? *iForest-Biogeoecology and Forestry*, 10, 369–375. <https://doi.org/10.3832/ifer1937-009>
- Ostertag, R., Warman, L., Cordell, S., & Vitousek, P. M. (2015). Using plant functional traits to restore Hawaiian rainforest. *Journal of Applied Ecology*, 52, 805–809. <https://doi.org/10.1111/1365-2664.12413>
- Palma, A. C., & Laurance, S. G. W. (2015). A review of the use of direct seeding and seedling plantings in restoration: What do we know and where should we go? *Applied Vegetation Science*, 18, 561–568. <https://doi.org/10.1111/avsc.12173>
- Pedraza, R. A., & Williams-Linera, G. (2003). Evaluation of native tree species for the rehabilitation of deforested areas in a Mexican cloud forest. *New Forests*, 26(1), 83–99. <https://doi.org/10.1023/a:1024423511760>

- Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234. <https://doi.org/10.1071/bt12225>
- Poorter, L., & Bongers, F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, 87, 1733–1743. [https://doi.org/10.1890/0012-9658\(2006\)87\[1733:ltagpo\]2.0.co;2](https://doi.org/10.1890/0012-9658(2006)87[1733:ltagpo]2.0.co;2)
- Poorter, H., Niinemets, U., Ntagkas, N., Siebenkas, A., Maenpaa, M., Matsubara, S., & Pons, T. (2019). A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytologist*, 223, 1073–1105. <https://doi.org/10.1111/nph.15754>
- Poorter, H., Niinemets, U., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, 182, 565–588. <https://doi.org/10.1111/j.1469-8137.2009.02830.x>
- Prevedello, J. A., Almeida-Gomes, M., & Lindenmayer, D. B. (2018). The importance of scattered trees for biodiversity conservation: A global meta-analysis. *Journal of Applied Ecology*, 55, 205–214. <https://doi.org/10.1111/1365-2664.12943>
- Pywell, R. F., Bullock, J. M., Roy, D. B., Warman, L. I. Z., Walker, K. J., & Rothery, P. (2003). Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology*, 40, 65–77. <https://doi.org/10.1046/j.1365-2664.2003.00762.x>
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Ramírez-Marcial, N., González-Espinosa, M., & Williams-Linera, G. (2001). Anthropogenic disturbance and tree diversity in montane rain forests in Chiapas, Mexico. *Forest Ecology and Management*, 154, 311–326.
- Reich, P. B. (2014). The world-wide ‘fast-slow’ plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102, 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences*, 164, S143–S164. <https://doi.org/10.1086/374368>
- Rivers, M., Beech, E., Murphy, L., & Oldfield, S. (2016). *The red list of Magnoliaceae-revised and extended*. Flora & Fauna International.
- Rüger, N., Huth, A., Hubbell, S. P., & Condit, R. (2009). Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology*, 97, 1360–1368. <https://doi.org/10.1111/j.1365-2745.2009.01552.x>
- Rüger, N., Williams-Linera, G., Kissling, W. D., & Huth, A. (2008). Long-term impacts of fuelwood extraction on a tropical montane cloud forest. *Ecosystems*, 11(6), 868–881. <https://doi.org/10.1007/s10021-008-9166-8>
- Suganuma, M. S., & Durigan, G. (2015). Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. *Restoration Ecology*, 23, 238–251. <https://doi.org/10.1111/rec.12168>
- Swaine, M. D., & Whitmore, T. C. (1988). On the definition of ecological species groups in tropical rain forests. *Vegetatio*, 75, 81–86.
- Toledo-Aceves, T., Bonilla-Moheno, M., & López-Barrera, F. (2022). Data from: Tree seedlings leaf traits. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.q2bvq83mj>
- Toledo-Aceves, T., García-Hernández, M. D., & Paz, H. (2019). Leaf functional traits predict cloud forest tree seedling survival along an elevation gradient. *Annals of Forest Science*, 76, Article 111. <https://doi.org/10.1007/s13595-019-0900-5>
- Toledo-Aceves, T., López-Barrera, F., & Vásquez-Reyes, V. (2017). Preliminary analysis of functional traits in cloud forest tree seedlings. *Trees*, 31, 1253–1262. <https://doi.org/10.1007/s00468-017-1543-5>
- Toledo-Aceves, T., Trujillo-Miranda, A. L., & López-Barrera, F. (2021). Tree regeneration in active and passive cloud forest restoration: Functional groups and timber species. *Forest Ecology and Management*, 489, 119050.
- Trujillo-Miranda, A. L., Toledo-Aceves, T., López-Barrera, F., & Gerez-Fernandez, P. (2018). Active versus passive restoration: Recovery of cloud forest structure, diversity and soil condition in abandoned pastures. *Ecological Engineering*, 117, 50–61. <https://doi.org/10.1016/j.ecoleng.2018.03.011>
- Uhl, C., Clark, K., Dezzeo, N., & Maquirino, P. (1988). Vegetation dynamics in Amazonian treefall gaps. *Ecology*, 69, 751–763. <https://doi.org/10.2307/1941024>
- Valladares, F., Laanisto, L., Niinemets, U., & Zavala, M. A. (2016). Shedding light on shade: Ecological perspectives of understorey plant life. *Plant Ecology & Diversity*, 9, 237–251. <https://doi.org/10.1080/17550874.2016.1210262>
- Valladares, F., & Niinemets, U. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology and Systematics*, 39, 237–257. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173506>
- Veneklaas, E. J., & Poorter, L. (1998). Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. In H. Lambers, H. Poorter, & M. M. I. van Vuuren (Eds.), *Inherent variation in plant growth: Physiological mechanisms and ecological consequences* (pp. 337–361). Backhuys Publishers.
- Williams-Linera, G. (2002). Tree species richness complementarity, disturbance and fragmentation in a Mexican tropical montane cloud forest. *Biodiversity and Conservation*, 11, 1825–1843. <https://doi.org/10.1023/a:1020346519085>
- Williams-Linera, G., Dominguez-Gastelu, V., & García-Zurita, M. E. (1998). Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conservation Biology*, 12, 1091–1102. <https://doi.org/10.1046/j.1523-1739.1998.97262.x>
- Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Diaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2010). Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, 91, 3664–3674. <https://doi.org/10.1890/09-2335.1>
- Wright, S. J., Muller-Landau, H. C., Condit, R., & Hubbell, S. P. (2003). Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology*, 84, 3174–3185. <https://doi.org/10.1890/02-0038>
- Zirbel, C. R., Bassett, T., Grman, E., & Brudvig, L. A. (2017). Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *Journal of Applied Ecology*, 54, 1070–1079. <https://doi.org/10.1111/1365-2664.12885>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Toledo-Aceves, T., Bonilla-Moheno, M., Sosa, V. J., López-Barrera, F., & Williams-Linera, G. (2022). Leaf functional traits predict shade tolerant tree performance in cloud forest restoration plantings. *Journal of Applied Ecology*, 00, 1–13. <https://doi.org/10.1111/1365-2664.14128>