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Planting position and shade enhance native seedling performance in forest restoration for an endangered malagasy plant

Cyprien Miandrimanana [a], J. Leighton Reid [b], Tahiry Rivoharison [a], Chris Birkinshaw [a, *]

[a] *Missouri Botanical Garden, Madagascar Research and Conservation Program, BP3391, Antananarivo 101, Madagascar*
[b] *Center for Conservation and Sustainable Development, Missouri Botanical Garden, 4344 Shaw Boulevard, St Louis, MO 63110, USA*

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A B S T R A C T

The critically endangered tree *Schizolaena tampoketsana* is confined to a few diminished and degraded forest fragments on the Malagasy highlands. This habitat is vulnerable to loss due to frequent fires in the surrounding grassland that threaten to spread into the forest. One of these fragments is the focus a conservation project and here the managers aim to conserve *S. tampoketsana* by restoring its forest habitat to its former extent as evidenced by remnant woody plants. To inform this activity the survival and early-stage growth of seedlings of four locally native tree species were compared under contrasting conditions of proximity to the remaining forest and shade. After 12 months, seedlings of three species (*Baronia taratana*, *Eugenia pluricymosa*, *Uapaca densifolia*) survived better and experienced improved growth in height in grassland close to the existing forest rather than distant from it, and two survived better with shade rather than unshaded. A number of mechanisms could explain these results including reduced exposure to desiccating sunlight and winds and better soil and greater water availability close to the forest. The seedlings of one species (*Nuxia capitata*) survived well under all conditions. This study suggests that reforestation in these dry highlands is most feasible adjacent to remnant forest fragments and in microhabitats that minimize water loss, though young plants of some tree species may be capable of surviving in harsher conditions.

1. Introduction

Today the vegetation in most of Madagascar's central highlands consists of vast expanses of frequently burnt, almost treeless grasslands with small and increasingly rare evergreen forest in valleys (Burney et al., 2003; Bond et al., 2008). In living memory, areas of forest occurred in most of the valleys of this highly dissected landscape, but much of this vegetation has been degraded, diminished or entirely lost in recent times due to selective exploitation of large trees often followed by charcoal production using the remaining woody plants, and then burning by grassland fires that can easily penetrate the degraded forest (pers. obs.). Although small and degraded, the remaining evergreen forests of the Malagasy central highlands are of conservation significance because they provide testament to the previous natural vegetation of parts of this zone and also because they provide habitat for a diverse flora and fauna including threatened, locally endemic species. It is now urgent to conserve a representative sample of this neglected vegetation before it is lost entirely. In many cases effective long term conservation of such vegetation will require restoring the target forest to its former extent in the recent past which can be determined from relict forest trees now lying some distance from the forest edge as well as from local memory and old aerial photos.

One such conservation endeavour is at the Ankafobe Forest on the Tampoketsa of Ankazobe (Fig. 1), a complex of three adjacent, valley-bottom forest patches diminished from their extent in the recent past and now totalling just 33 ha. Staff from Missouri Botanical Garden have promoted the community-based conservation of this site since the tree *Schizolaena tampoketsana* Lowry, G.E. Schatz, J.-F. Leroy & A.-E. Wolf was rediscovered here 40 years after its last previous sighting by a scientist in 1967. *S. tampoketsana* is classified in the plant family Sarcolaenaceae, which is endemic to

* Corresponding author.
E-mail addresses: cyprien.miandrimanana@bongolavamaintso.mg (C. Miandrimanana), leighton.reid@mobot.org (J.L. Reid), voisohisika@gmail.com (T. Rivoharison), chris.birkinshaw@mobot-mg.org (C. Birkinshaw).

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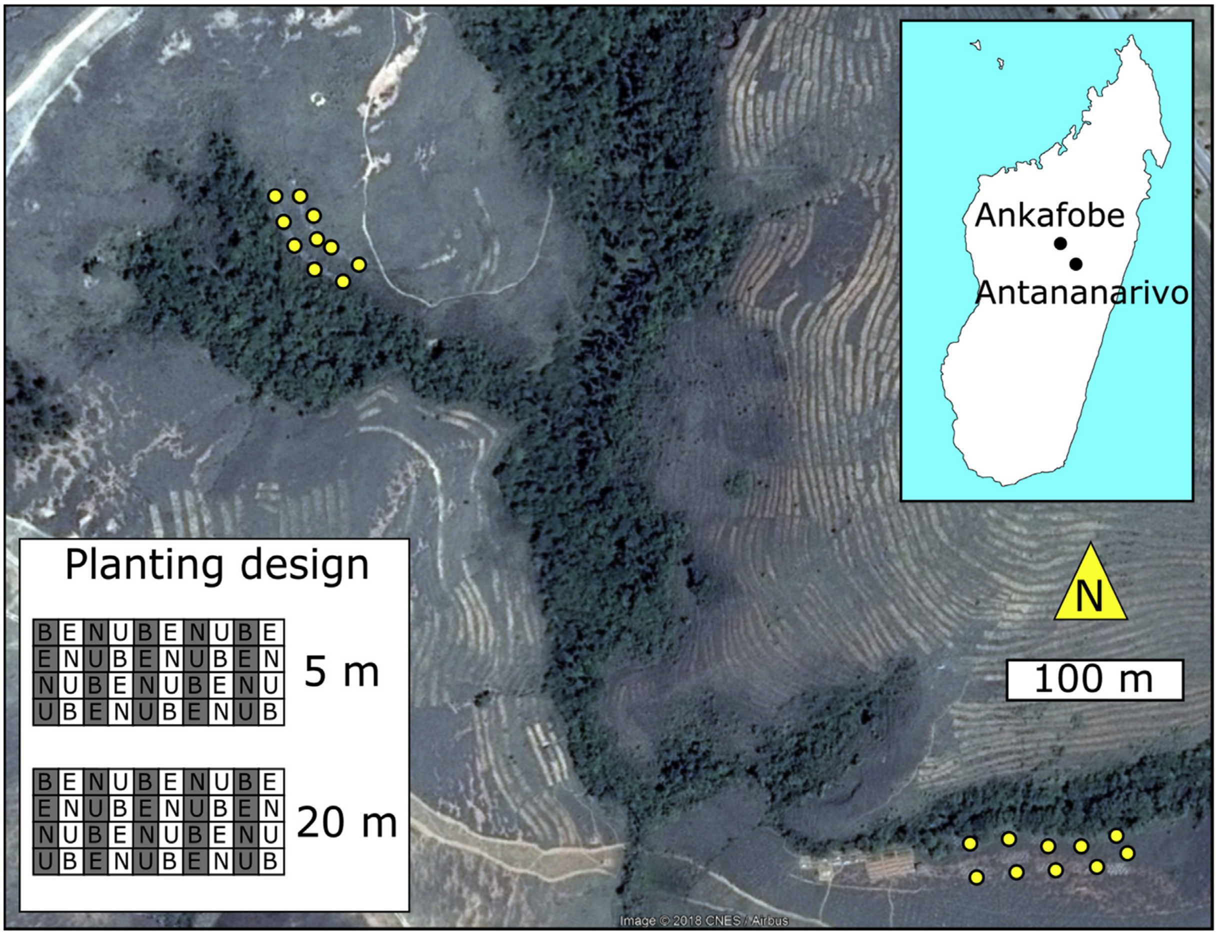

Fig. 1. Location of the Ankafobe Forest and replicates (shown as yellow dots), and experimental design (B = *Baronia taratana*, E = *Eugenia pluricymosa*, N= *Nuxia capitata*, U = *Uapaca densifolia;* shaded cells are shaded plants).

Madagascar, and the species is now considered to be critically endangered (Members of the IUCN SSC Madagascar Plant Specialist Group, 2016).

In an attempt to reduce the vulnerability of this diminished forest due to burning, the site managers at Ankafobe at first tried to promote forest expansion into the adjacent fire-prone grassland, by installing firebreaks along the ridgetops surrounding the forest in the expectation that, in the absence of fire, the forest would naturally colonise the grassland to attain its area of occupation in the recent past. Forest encroachment into grassland following fire suppression has been widely reported in the tropics (Hoffmann et al., 2012; Stevens et al., 2017). However, paralleling the situation reported by Duncan and Duncan (2000) in Uganda, after a decade during which the grassland adjacent to this forest did not burn, forest trees had not naturally seeded into the adjacent grassland. Consequently, the managers decided to propagate and plant young plants of native tree species in this vegetation. The first endeavours resulted in high seedling mortality but also the realisation that some locations in the landscape were much more conducive to the survival and growth of tree seedlings than other locations some short distance away. Cheesman et al. (2018) has already demonstrated the importance in forest restoration of considering how different species perform in the often-challenging and heterogeneous biophysical environments of degraded landscapes. To explore how seedling survival and growth varied at a local scale in the landscape and thereby inform our restoration work, the research described below was conducted to identify if, where, and how microsites in the grass-dominated hillsides could facilitate restoration of this Malagasy Highland Forest. Specifically, this experiment tested the effects of proximity to forest and shade on the early-stage survival and growth of young plants of four native tree species. Given that the site experiences a 7-month dry season, and based on results from a prior study at the nearby forest remnant of Ambohitantely (Pareliussen et al., 2006) as well as research elsewhere in the tropics listed by Duncan and Duncan (2000) and the more recent study by Charles et al. (2018), it was expected that seedlings planted close to the forest edge would demonstrate higher rates of survival and grow faster given that they may experience reduced sunlight due to the shade of the adjacent trees and that the soil may have been less disturbed than soil farther from the forest edge (i.e., it was expected that soils near forest would have experienced fewer fires and perhaps less compaction, leaching and erosion). The shade structures were used to elucidate one possible mechanism for seedling survival and growth by reducing direct sunlight.

2. Materials and methods

2.1. Study site

This research was conducted in the grasslands surrounding the Ankafobe Forest (18° 6′18″S, 47°11′17″E, elevation 1475 m) on the Tampoketsa of Ankazobe, 30 km northwest of Ankazobe, at PK 132, in Ankazobe Commune (Fig. 1).

According to Cornet (1974), the climate at Ankafobe Forest can be classified as sub-humid with mists. Two distinct seasons occur; wet and hot between December and April, and dry and cool between May and November. Total average annual precipitation is 1850 mm, with 85% falling during the 5-month wet season. The highest average monthly temperature (23.7 °C) occurs in November, and the lowest (13.5 °C) in August. Fogs are particularly frequent in the dry and cool season (Ratsirarson and Goodman, 2000; Pareliussen et al., 2006).

The soil at Ankafobe Forest is an acid red laterite. In this study it was described using an array of parameters proposed by United States Department of Agriculture (2001), with replicated sampling sites within the grassland and also within the forest (Table 1). Compared to forest soil, the soil in the grassland has a higher bulk density, lower porosity, lower water-filled pore space and, related to these attributes, much lower permeability to water. The grassland soil is also more nutrient poor and has fewer earthworms. Although the mean annual precipitation at this site is quite high, most of the rain is received on a few days during the relatively short wet season and the low permeability of the grassland soils means that much of the precipitation is lost as run-off.

The Ankafobe Forest is species-diverse, evergreen forest (Moat and Smith, 2007). Four 0.1-ha forest plots were established by the site-mangers in 2013 and have been monitored annually since (unpublished data, VOI-Sohisika). In 2016, tree stem density (diameter at breast height or dbh $\geq$ 5 cm) ranged from 27.8 m^2 to 37.1 m^2 per hectare and the number of stems from 2350 to 2850. The number of tree species per 0.1 ha plot ranged from 59 to 87, and the species most represented in terms of number of stems included *Suregada gaultherifolia* (Euphorbiaceae), *Baronia taratana* (Anacardiaceae), *Tambourissa purpurea* (Monimiaceae), *Syzygium parkeri* (Myrtaceae), *Ixora regalis* (Rubiaceae), *Ficus soreciodes* (Moraceae), *Dracaena reflexa* (Asparagaceae), *Macaranga alnifolia* (Euphorbiaceae), *Grewia speciosa* (Malvaceae), and *Stephanodaphne germinata* (Thymelaeaceae).

The forest is surrounded by grassland dominated by *Loudetia simplex*, an African grass that is also found in Madagascar. This tightly caespitose, around 1 m tall, perennial grass forms short, woody rhizomes just below ground level which are surrounded by cumulative layers of leaf sheath bases. These sheaths protect the rhizome meristems from grassland fires, so after each fire this grass regrows rapidly (pers. comm., Maria Vorontsova). The second most common species is *Schizachyrium sanguineum*. Other grass species include *Aristida rufescens, Aristida tenuissima, Panicum luridum, Eragrostis lateritica* and *Schizachyrium brevifolium.* Wetter areas towards the valley bottoms support *Andropogon trichozygus, Setaria sphacelata, Trichopteryx dregeana*, and *Hyparrhenia schimperi* (pers. comm., Maria Vorontsova).

The extensive grasslands of the Tampoketsa of Ankazobe burn frequently, almost annually (Ratsirarson and Goodman, 2000). However, within the valleys, the forest is relatively sheltered from the strong winds that stoke these fires and, provided the canopy is intact, resists burning (pers. obs.). The former extent of forest in the recent past can be estimated by the occasional presence of species of forest tree surviving some distance from the current forest-grassland boundary. A minority of these plants are tall single-stemmed individuals but more numerous are multi-stemmed plants growing as a coppice from rootstocks. These species include *S. tampoketsana* (Sarcolaenanace), *Weinmannia rutenbergii* (Cunoniaceae), *Brachylaena merana* (Asteraceae), and *Albizia mainaea* (Fabaceae).

Table 1
Soil attributes within the grassland and forest at Ankafobe.

Mean values	Grassland mid-slope (N = 3)	Forest (N = 3)
Water infiltration (cm/hr)	4.29	201.93
Soil H_20 content (g/g)	0.15	0.28
Soil bulk density (g/cm^3)	0.95	0.73
Soil water-filled pore space (%)	0.22	0.28
Volumetric water content (g/cm^3)	0.14	0.20
Soil porosity (%)	64.14	72.58
Electrical conductivity (dS/m)	0.00	0.03
pH	5.53	6.40
Soil N03-N (kg N03-N/hectare)	0.00	4.05
No. earthworms (pit 30 cm × 30 cm)	0.00	2.00

2.2. Study species

Four species were chosen for this planting experiment, all of which were endemic to Madagascar, naturally present in the Ankafobe Forest, and popular with the local nurserymen because when seed samples are sown in the nursery they germinate reliably and the seedlings survive well and grow relatively rapidly. These species also represented contrasting niches:

- *B. taratana* Baker (Anacardiaceae) is a small pioneer tree that is occasional to frequent in degraded forest. Bond et al. (2008) lists this species as a heliophytic plant that is found along forest margins.
- *Nuxia capitata* Baker (Stilbaceae) is a small tree that is frequent on the upper slopes of forest and is resistant to burning with thick bark and a canopy that regrows after burning by epicormic sprouting - these functional traits are often associated with savannah trees according to Bond (2008). Ramananantoandro et al. (2016) reports that this species has a wood density of 0.9 g/cm^3 and is pioneer species.
- *Uapaca densifolia* Baker (Phyllanthaceae) is a small to medium tree that is locally frequent on upper slopes and ridges in forest on the Malagasy central highlands. Ramananantoandro et al. (2016) reports that this species has a wood density of 0.8 g/cm^3 and is semi-shade tolerant.
- *Eugenia pluricymosa* H. Perrier (Myrtaceae) is a medium tree of undisturbed forest in the central highlands and elsewhere in Madagascar.

2.3. Experimental design

The survival and early-stage growth of the young plants was evaluated in four combinations of two different environmental conditions: proximity to existing forest and shading. Two conditions were considered for proximity to existing forest: within 5 m of the forest edge (close to forest) and with a soil similar to “forest” soil as described in Table 1 versus 20 m from forest edge (far from forest) and with a soil similar to “grassland” soil. At 20 m from the forest edge the planted seedlings were never shaded by the forest trees and were outside their root zone. Two different conditions were considered for shading: covered with bamboo shade screen (= ca. 80% shade), 70 × 70 cm, suspended on posts 1 m above the young plant versus not covered. In total, there were ten replicates of each of the four treatments and five plants of each species were planted in each replicate. Thus, in total, 50 plants for each of the four species were planted under each of the four treatments, and a total of 800 plants were used in this experiment. Half of the replicates were located at each of two sites, one on the southern side of a valley and half on the northern side. The young plants used were 8–12 months old and had been propagated in a local nursery from locally collected seed. The experiment was established in February 2016, this month being typically the wettest during the year, at which time the young plants were planted in holes of dimensions 40 × 40 × 40 cm. The holes were necessary to plant the tree but their creation also removed competing grasses temporarily from the immediate vicinity of the young tree. Seedlings were planted ca. 2 m apart. At the time of planting the height of each seedling was measured as the vertical distance from the top of the soil to the apical meristem. The condition of the plant (whether dead or alive) was noted after 12 months and, for the living plants, their height was measured once again.

2.4. Analysis

The effects of proximity to forest, shade, and species on seedling survival and growth were estimated using generalized linear mixed effects regression. Models estimating seedling survival used a binary error distribution and logit link, whereas seedling growth models used a Gaussian error distribution. The response variable for seedling growth was relative growth rate, i.e., the difference between seedling height at 12 months and seedling height at planting, divided by the seedling height at planting. To account for random differences between the two experimental sites and five replicates within each site (Fig. 1), we included a variable intercept for plot nested within site (1|plot/site).

For seedling survival, we compared a fully-specified model (including proximity to forest, shade, species, and all two-way interactions) to nested models using Akaike's information criterion (AICc; Burnham and Anderson, 1998). In a separate model, we also tested for an effect of initial seedling height on survival. For seedling growth, our sample was restricted by seedling mortality, and some combinations of predictors had insufficient replication. To account for this, we first fit a model with the fixed effects of proximity to forest, shade, and species, but we excluded all interactions. Next, we tested for potential interactions by comparing models using AIC_c, as above, but with the species comparison reduced to *N. capitata* versus all other species, reflecting the greater survivorship of *N. capitata*. One outlying seedling growth record (8.2 standard deviations from the mean, *N. capitata*) was removed prior to growth analysis. In both sets of model comparisons, survival and growth, models with $\Delta AIC_c < 2$ were taken to have equivalent support.

For all models, model fit was evaluated based on the adjusted R^2 from the regression between fitted and observed values. Models for seedling growth used F-tests with Saittherthwaite's approximation to calculate P-values for fixed effects (i.e., the effects of proximity to forest, shading, and species). Analyses were performed using the lme 4 package (Bates et al., 2015) in R version 3.4.0 (R Core Team, 2017), with F-tests for seedling growth models calculated using lmerTest (Kuznetsova et al., 2016) and AIC_c model comparison implemented with the AICcmodavg package (Mazerolle, 2016). Error was calculated and reported as one standard error of the mean. A cut-off for statistical significance was set at 0.05.

3. Results

After one year in the field, 76% of seedlings survived, with substantial variation among species and planting treatments (Fig. 2). The seedling species with the greatest survival was *N. capitata* (97.5 ± 1.1%), followed by *B. taratana* (84.0 ± 2.5%), *E. pluricymosa* (63.5 ± 3.4%), and *U. densifolia* (59.0 ± 2.6%). For all species except *N. capitata*, both proximity to remnant forest and shade structures increased seedling survival, by approximately 1.3 × and 1.2 × , respectively (Fig. 2). The effect of shade structures on seedling survival also tended to be ~1.2 × greater at 20 m from the forest edge compared to 5 m from the forest edge, and this interaction had some support from AIC model comparisons (Table S1), but the effect was non-significant ($P = 0.7$; Fig. S1). The initial height of seedlings planted did not affect their survival ($P = 0.8$; Fig. S2). Collectively, the interacting effects of species, proximity to forest, and shade explained 27% of the variation in seedling survival (Table S2).

Among 607 surviving seedlings, mean height after one year in the field was 91 ± 4% greater than the initial seedling height at planting. Relative growth rate (RGR) varied among species (Fig. 3), with the greatest increase in *B. taratana* (122 ± 10%) and *U. densifolia* (112 ± 11%) and lower increases in *N. capitata* (87 ± 6%) and *E. pluricymosa* (36 ± 6%). Regardless of species, seedlings planted 5 m from the forest edge grew 1.6× larger on average compared to seedlings planted 20 m from the forest edge. In contrast, shade structures made no difference (Table S3), nor did any interactions among predictors (Table S4). Collectively, the

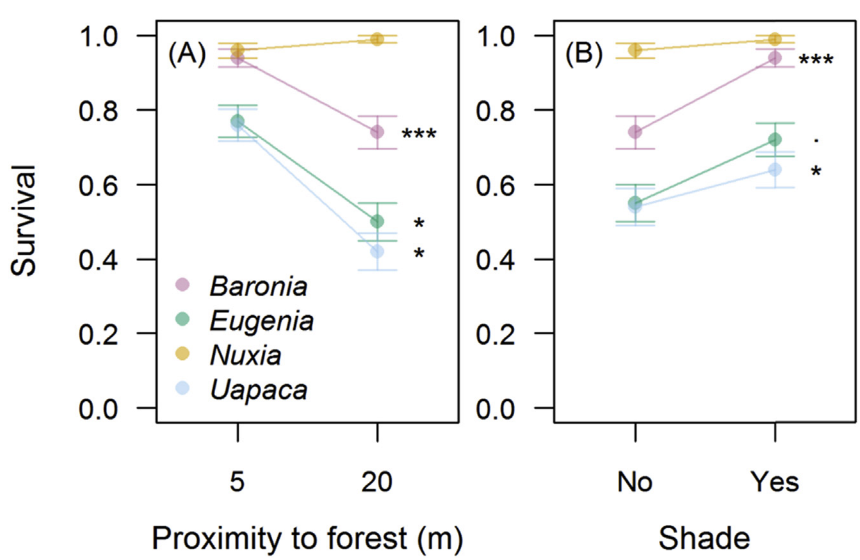

Fig. 2. Effects of proximity to remnant forest (A), shade structure (B), and their interactions with species on seedling survival one year after planting. Error bars represent one standard error. Significance levels are denoted as follows: $P < 0.001$ (***), $P < 0.01$ (**), $P < 0.05$ (*), $P < 0.1$ (.).

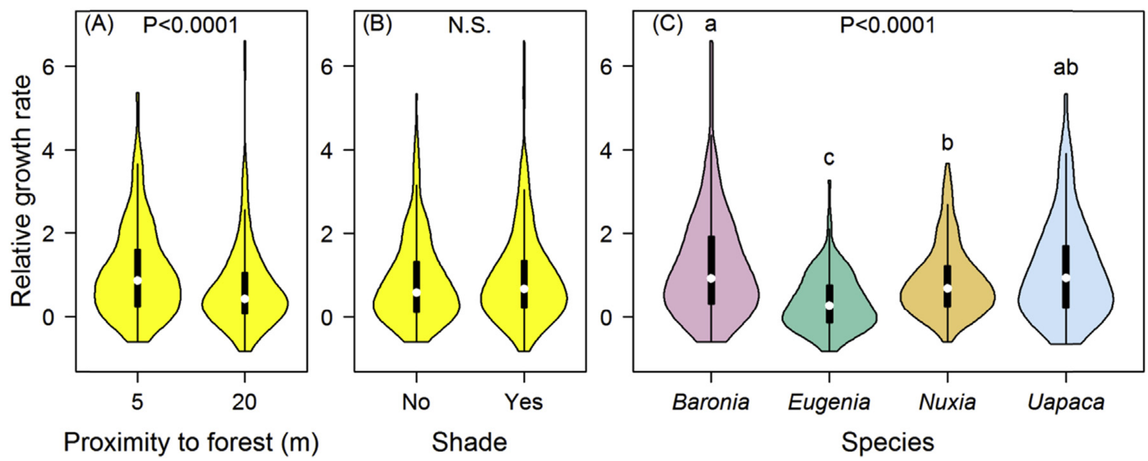

Fig. 3. Effects of proximity to remnant forest (A), shade structure (B), and seedling species (C) on the relative growth rates of native tree seedlings one year after planting. Lowercase letters denote significant differences (P < 0.05) from pairwise comparisons.

effects of planting position and seedling species accounted for 15% of variance in RGR.

4. Discussion

Forest degradation is outstripping forest recovery on the high Tampoketsa de Ankazobe due to slow natural recovery, even in places where forest was recently cleared. Here, we show that in the absence of fire, young trees of native species planted in degraded habitat adjacent to the Ankafobe forest can survive and grow. Presumably, the absence of natural recovery is due to limited propagule dissemination to the grassland or failure of propagules to germinate and grow due to predation, harsh environmental conditions, and competition with herbaceous plants, particularly grasses, for light, nutrients, and water. These causes have been identified elsewhere as reasons for slow colonization of tropical grassland by woody vegetation (e.g. Nepstad et al., 1996; Holl, 1999; Griscom et al., 2009; Gunaratne et al., 2010). Bond (2008) notes that grasses occupy the same root zone as young trees and are very competitive with them for both nutrients and water.

With the exception of *N. capitata*, tree seedlings survived and grew much better within a few meters of the forest edge compared to 20 m from it. Additionally, two of the four species survived better beneath shade structures (with a third, *E. pluricymosa*, trending in the same direction). Although forest proximity and shade structures had similar-magnitude effects on seedling survival, they did not interact significantly. This suggests that they may have improved seedling performance through different mechanisms. Shade structures clearly decreased irradiance, which likely reduced water loss and perhaps photo inhibition; and they would also have reduced exposure to wind. In contrast, forest proximity may have been associated with a diversity of beneficial conditions, possibly including greater soil moisture near the valley bottom, protection from desiccating winds (e.g., Nepstad et al., 1996), exposure to arbuscular mycorrhizal fungi spreading from nearby remnant forest soil, and greater soil macronutrient availability if prior fires were less common, less severe, or more recent than on the surrounding hillsides (pers. obs.). The likelihood of greater water and macronutrient availability near forest are supported by our soil comparisons between forest and mid-slopes (Table 1). The suggestion that mycorrhizae may be more prevalent near forest is speculative and requires testing.

These results confirm and extend those of Pareliussen et al. (2006) who compared survival of seedlings of five native tree and shrub species in grassland adjacent to the Ambohitantely Forest (some 10 km north-east of the Ankafobe forest) under a range of contrasting conditions. Among these conditions explored were proximity to the forest edge (where "near" was defined as 10 m distant and "far" as 50 m distant) and shading (seedling provided with shade screens or not). The experiment was conducted at three different locations. At one location the plants of all five species had a significantly better survival near to the forest compared to far; and at another location one of the study species (*B. taratana*) had significantly better survival near to the forest compared to far. The authors interpreted this result as being due to differences in microclimate and/or soil conditions (including nutrient composition) close to the forest compared to far. In Pareliussen et al. (2006) study the only significant effect of shade was discovered for one species *Dodonaea madagascariensis* at one of the sites, and in this case the provision of shade significantly reduced survival.

The similarities between our results and those of Pareliussen et al. (2006) offer two implications for forest restoration on the Tampoketsa de Ankazobe. First, tree planting generally will be most successful within a few meters of the edge of remnant forests. Although large areas of the Tampokesta are currently grassland, planting a thin buffer along remnant forest edges will result in higher seedling survival, and this strategy may also reduce edge effects, such as the influx of light, wind, and fire into remnant forest fragments (Metzger and Brancalion, 2017; Hill, 2018). This strategy is also precautionary. A significant risk in highland Madagascar and elsewhere is afforestation on native grasslands, which are often difficult to discern from degraded forest (Veldman et al., 2015). By focusing planting along forest edges, practitioners can reduce their risk of inadvertently contributing to native grassland conversion. Given the complete loss of many valley forests, a useful future research project would be to evaluate whether distance from the forest edge, per se, is important, or whether proximity to the moist valley bottom would suffice.

A second implication relates to species selection. Drawing on our results and those of Pareliussen et al. (2006), we find that *N. capitata* has the highest overall, one-year survival of any native species of the Tampoketsa tested thus far (98% on average). Of note, this species survives well in all tested conditions, including far from forest edge. In addition, it possesses thick bark and resprouts epicormically following fire, suggesting that it may be a savanna tree rather than a forest tree (as defined by Hoffmann et al., 2012). The runner-up for one-year survival is the forest edge or gap tree, *Baronia tarantana* (84%); six other species survived at rates of

40–64%. All of these survived better near forest edge in at least one trial. Given the high regional diversity, much more species screening is warranted, but these trials set a benchmark for expected growth and survival. As noted elsewhere, matching native trees to appropriate local site conditions will be critical for improving restoration efficiency (Vetaas, 1992; Park et al., 2010; Plath et al., 2011; Douterlungne et al., 2015). Good candidates to evaluate for forest or savanna restoration farther from the existing forest are the relictual trees already growing at such locations.

This study has several limitations, which highlight future directions for forest restoration research in highland Madagascar. One limitation is that we only observed change over one year. While this was probably the most significant period of mortality, it is likely that growth patterns would change over longer time periods. Second, we only replicated this study at a single site, though the similarity to Pareliussen et al. (2006) study lends credence to the modest generalization of our findings. As with any experiment, a variety of important factors were left unexamined here. Among these were planting configuration (e.g., plantation versus nuclei; Zahawi et al., 2013), density, diversity, and the stochastic effects of planting year (Stuble et al., 2017). Future experimentation in any of these areas will contribute to the conservation of Madagascar's unique biodiversity.

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Appendix Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2018.09.005.

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