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RESEARCH ARTICLE

# The role of remnant forest patches for habitat restoration in degraded areas of Palau

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**To be successful, prescriptions for tropical forest restoration should facilitate natural recovery while also being easy to implement and inexpensive. In the Lake Ngardok Nature Reserve, Palau, we monitored native forest patches (4–275 m$^2$) over 3 years to assess the influence of several low-cost restoration methods on patch expansion, growth of naturally established tree saplings, density of naturally establishing tree seedlings, growth of planted tree seedlings, flower and fruit production, and bird and flying fox visitations. Treatments included fertilization, trimming of surrounding herbaceous vegetation, mulching of patch perimeters, and planting native tree seedlings. Fertilized patches expanded faster and were associated with higher growth rates of perimeter saplings, higher fruit and flower production and growth of adjacent planted *Acacia auriculiformis* trees. Trimming perimeter vegetation led to higher tree seedling densities and species diversity, but both trimming and fertilizer effects on patch perimeter measures decreased over time. *Pterocarpus indicus*, a high value native legume, was the fastest growing planted tree species. The most common visitors were small, omnivorous, predominately endemic bird species. Visitations to fertilized patches were more frequent than to non-fertilized patches. The strongest predictors of visitation frequency were patch area, mean number of total fruits, and mean height of nearest neighboring trees. We conclude that forest succession can be accelerated by applying small amounts of fertilizer (approximately 22.5 g/m$^2$ per application) to enhance tree growth and increase visitation rates of native pollinators and dispersers.**

**Key words:** assisted regeneration, Babeldaob, birds, flying fox, nucleation, Pacific Islands

### Implications for Practice

- Small, periodic applications of fertilizer to forest patch interiors on Babeldaob Island can help increase the rate of forest patch expansion and visitation by native birds, while avoiding potentially damaging nutrient run-off.
- Native tree seedlings planted on the perimeter of forest patches with lime and compost soil amendments have high survivorship but do not increase non-fertilized patch expansion.

## Introduction

Tropical forest clearing, followed by intensive agriculture and especially periodic burning, can lead to the formation of degraded grassland or fernland plant communities (Cohen et al. 1995). Forest restoration is a common management goal in these anthropogenic systems, particularly where biodiversity is valued. Numerous prescriptions have been proposed and tested to restore forest to degraded areas, with plantations of nitrogen-fixing trees being one of the most common. This approach can be expensive, with success depending on complex site variables (Bradshaw 1989; Parker 1997). An alternative is to plant trees in or near existing forest patches, mimicking the natural process of forest nucleation, which in some cases promotes tree seed dispersal and establishment of other plant species (Holl 2002; Zahawi & Augspurger 2006; Benayas & Bullock 2008; Schlawin & Zahawi 2008; Cole 2009; Corbin & Holl 2012). A patch-focused restoration approach may be more cost-effective if tree survivorship and growth are maximized (Zahawi et al. 2013).

On many Pacific islands, a century of agriculture, abandonment, and anthropogenic fire regimes have greatly expanded the area of degraded land and the need for forest restoration has been repeatedly identified in regional assessments (e.g. DeBell & Whitesell 1993). In the Republic of Palau, *Acacia auriculiformis* (Fabaceae) plantations have been attempted, to increase

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forest cover in several degraded areas. As these plantations have largely failed, due to nutrient poor soils, interest in identifying successful low-cost alternatives is substantial. No attempts have been made at patch-focused restoration in Palau, so we initiated a study of small forest patches, commonly found in and surrounded by nonforest vegetation.

The term "savanna" has been used to describe several subtypes of dry land nonforest vegetation in Palau including bare land, grassland, fernland, shrub, and abandoned agriculture (Cole 1987). Archeological and botanical studies indicate that Palauan savanna is anthropogenic (Costion & Lorence 2012). Furthermore, historical aerial photos show that savannas adjacent to intact forest naturally revert to native forest (Endress & Chinea 2001). However, isolated forest patches seem to expand very slowly, if at all, possibly due to periodic fires. Most savanna areas in Palau are mosaics of plant species and ages resulting from patchy fires. Frequent fires arrest forest recovery by reducing seed availability, shifting competitive advantage from tree seedlings to fire adapted grasses and ferns, creating unfavorable microclimatic conditions for tree growth, and reducing soil fertility (D'Antonio & Vitousek 1992; Aide & Cavelier 1994; D'Antonio et al. 2011). Even if fire is prevented, patch size, proximity of patches to remnant forest, and availability of pollinators and seed dispersers also affect forest recovery (Holl 2007; Cole et al. 2010).

Natural forest regeneration in Palau is facilitated by diverse, largely intact communities of pollinators and seed dispersers, both vertebrate and invertebrate. Palau's fauna includes three frugivorous bird species and a large population of flying foxes, known to feed on the fruits of greater than 50 tree species and the flowers of greater than 25 tree species (Wiles et al. 1997). Fleshy fruited tree species maximize frugivore visitation rates by providing both food and perch sites (Robinson & Handel 2000). Numerous studies have documented higher seed rain under remnant trees and shrubs compared with open pasture (Guevara & Laborde 1993; Estrada et al. 2000; Slocum & Horvitz 2000; Holl 2002). However, increasing disperser visitation alone may not be sufficient to facilitate forest restoration. Site preparation and substrate manipulation may be required to provide favorable sites for seed germination and subsequent seedling establishment of native forest tree species (Urbanska 1997).

We therefore assessed the impact of four low-input forest restoration methods: interior patch fertilization, outer patch perimeter mulching, outer patch perimeter trimming, and planting native tree seedlings. We replicated these treatments across a wide range of patch sizes, and examined six indicators of ecological recovery. These forest patches were found in a Palauan savanna recovering from fire, due to long-term (>15 years) fire prevention efforts, where plantation-style restoration with *A. auriculiformis* had previously failed. The forest patches, composed of native tree species, are situated within a matrix of mostly dead or stunted *A. auriculiformis* trees. The ecological indicators were as follows: (1) Patch expansion; (2) Growth rates of naturally occurring native tree saplings in patch perimeters; (3) Growth rates of native tree seedlings planted in outer patch perimeters; (4) Density and species diversity of naturally establishing tree seedlings in patch perimeters; (5) Fruit and flower production of native patch tree species; and (6) Patch visitation frequency by birds and flying foxes. We predicted that: (1) Interior patch fertilizer application accelerates patch expansion, increases tree fruit and flower production, and increases patch visitation frequency; (2) Outer patch perimeter mulch application increases growth rates of naturally occurring saplings and planted native tree seedlings; (3) Outer patch perimeter trimming of herbaceous vegetation changes density and species diversity of naturally establishing native tree seedlings; (4) Patch visitation by birds and flying foxes is most influenced by patch size, fruit production, and distance to forest edge; and (5) Increasing patch size is correlated with higher survival and growth rates of native tree seedlings planted in outer patch perimeters.

## Methods

### Study Site

Lake Ngardok Nature Reserve (LNNR) is a 650 ha terrestrial reserve in the State of Melekeok, east central Babeldaob, which is Palau's largest island (approximately 134.6°E, approximately 7.5°N; Fig. 1). The LNNR comprises a mosaic of diverse habitats, including upland volcanic forest (73%), savanna and bare areas (23%) as well as a lake, river, and marsh (4%). Mean annual rainfall is approximately 3,600 mm, with a mild dry season from February to April (averaging approximately 229 mm/month). Mean annual temperature is approximately 27°C (USDA 2009). The site has undulating to steep complex slopes and multiple-facing aspects. All soils are very deep and well drained, derived from very old, weathered volcanic material, highly acidic, and generally fall into two soil series: Babelthuap—very fine, ferruginous, isohyperthermic Typic Kandiperox under ferns; and Aimeliik—very fine, halloysitic, isohyperthermic Typic Kandiperox under forest (USDA 2009). Both soil series exhibit decreased fertility with depth, but have significantly different properties in the top 10 cm. Top soils under ferns exhibit on average 3% organic matter content, 1.2 effective cation exchange capacity (ECEC), 0.5 cmol/kg nutrients (Ca, Mg, and K), 4.9 pH, and 60% Al saturation, while those under forest exhibit on average 17% organic matter, 15 ECEC, 15 cmol/kg nutrients, 5.3 pH, and 1% Al saturation (Smith & Babik 1988). Common native herbaceous species include the fern, *Dicranopteris linearis* (Gleicheniaceae), club mosses of the genus *Lycopodiella* (Lycopodiaceae), and the insectivorous angiosperm *Nepenthes mirablis* (Nepenthaceae) (a pitcher plant), indicative of poor soils. Common native tree species include *Commersonia bartramia* (Malvaceae), *Symplocos racemosa* (Symplocaceae)*, Timonius subauritus* (Rubiaceae), *Trichospermum ledermannii* (Malvaceae), *Alphitonia carolinensis* (Rhamnaceae), *Calophyllum inophyllum* var. wakamatsui (Clusiaceae), *Dracaena multiflora* (Asparagaceae), *Garcinia matsudai* (Clusiaceae), *Planchonella obovata* (Sapotaceae), and *Rhus taetensis* (Anacardiaceae). Common native shrubs include *Decaspermum parviflorum* (Myrtaceae), *Eurya japonica* (Theaceae), *Hedyotis korrorensis*

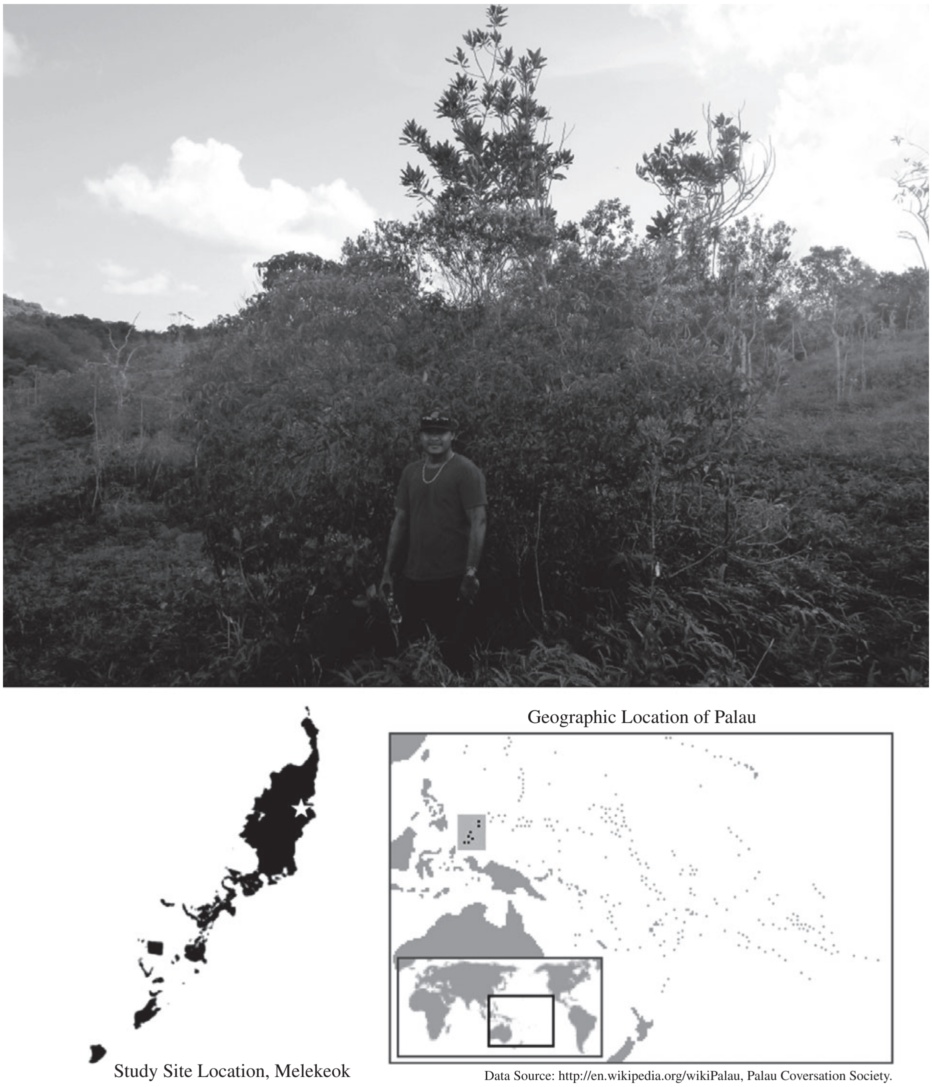


Figure 1. Study site—location of Republic of Palau, savanna study site within the LNNR, and picture of a forest patch with person for scale.

(Rubiaceae), *Melastoma malabathricum* (Melastomataceae), and *Wikstroemia elliptica* (Thymelaeaceae).

Parts of the LNNR were cleared for agriculture in the early 1900s but abandoned after WWII. The resulting vegetation was periodically burned, but this ended in 1997 when the reserve was created. The LNNR has received attention because it contains the largest freshwater lake in Micronesia, which is also the water source for two villages and the national capitol building, and is considered a hotspot for native, endemic plant and animal species. The LNNR's management plan calls for reforestation and maintenance of ecological integrity. Reforestation efforts starting in 1993 focused on planting *Acacia auriculiformis*, a non-native, nitrogen-fixing tree, with the goal of improving soil health, but nearly all the planted trees are stunted or dead because of the low nutrient status of the soils. Concerns about fertilizer run-off to the lake prevented more aggressive nutrition management of the *A. auriculiformis* plantings.

### Experimental Design

**Definitions.** Planted tree seedlings—native tree seedlings plucked from forest, raised in nursery and transplanted into study site; change in height used to compare planted tree species and gauge planting method.

Naturally establishing tree seedlings—less than 10-cm-high native trees germinating naturally along forest patch perimeters, generally growing underneath herbaceous vegetation; change in density used to gauge trimming and mulching methods.

Naturally occurring tree saplings—greater than 30 cm high, less than 3 cm diameter at breast height (DBH) native trees growing above herbaceous vegetation along forest patch perimeters; change in height used to gauge interior patch fertilization and mulching methods.

In 2009, we identified 32 forest patches, varying in size from 4 to 275 $m^2$. Patch area was defined by woody plant drip lines, and measured with a Topcon Hiper Pro DGPS system in

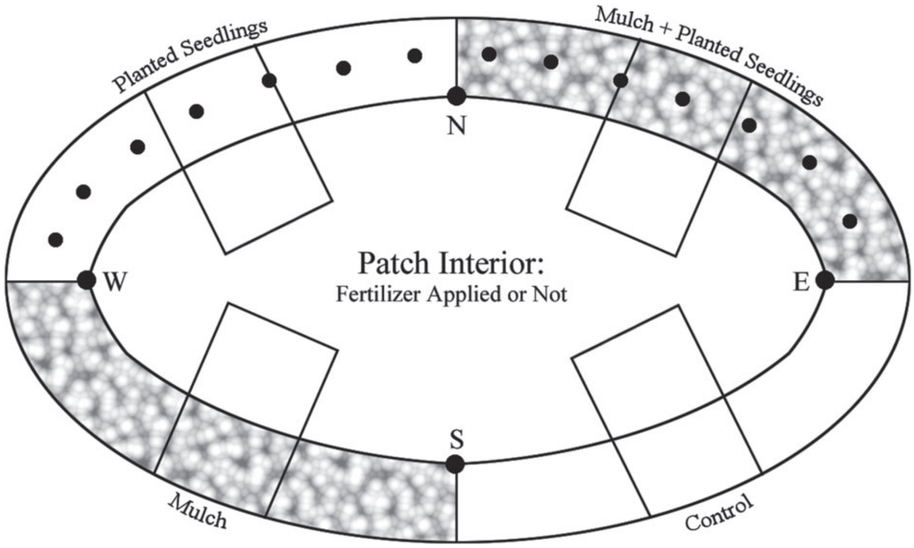


Figure 2. Forest patch treatment design—forest patch restoration split plot treatment design for the largest 16 of 32 total patches studied within the LNNR study site. Each patch received one of four treatments in each perimeter quadrant, and was paired by size for interior fertilization and control treatments. Directional markers are indicated with dots and letter abbreviations and quadrat placement for seedling density estimates is indicated with hollow boxes.

Autotopo mode (1 second recording interval); three nearby base stations were used for control points (accuracy approximately 1.2 m) and imported into ArcMap™. Patch edge at the drip line was marked at the four cardinal directions with PVC pipe. In each patch, all woody plants of stem DBH greater than 1 cm were identified to species level with (Kitalong et al. 2008) and their DBH recorded. Point quantum sensors (LI-190, Li-Cor Inc., Lincoln, NE, U.S.A.) in a subset of eight patches of varying sizes (4–220 $m^2$) were used to measure transmitted photosynthetically active radiation (μmol photons $m^{-2} s^{-1}$; TPAR = understory PAR/above canopy PAR). Patch air temperature was also measured over 7 days, using centrally placed HOBO H8 Pro series temperature and humidity sensors (Onset Computer Corp., Pocasset, MA, U.S.A.).

The 32 patches were paired by size and each member of each pair was then randomly assigned to control and fertilization treatments ($n = 16$ pairs), to control for the known influence of patch size on biophysical factors. In fertilizer-treatment patches, 22.5 g/$m^2$ of 16 : 8 : 12 NPK formula solid fertilizer (3.6 g/$m^2$ N, 0.79 g/$m^2$ P, and 2.2 g/$m^2$ K) was uniformly applied, by hand, across the entire patch in March, June, and September of 2010. This rate scales to approximately 100 kg N per hectare, on the low end of the range for short-rotation tropical forestry (Goncalves et al. 1997). Following patch remeasurement in May 2013, we detected a decline in the growth rate of naturally occurring saplings, and so an additional 22.5 g/$m^2$ of fertilizer was applied to fertilizer-treatment patches only in September 2013.

In June 2010, tree seedlings were planted and mulch was applied along the perimeters of the 16 largest patches (eight fertilized and eight controls), organized into a split-plot design (Fig. 2). Mulch was produced from shredded branches and leaves pruned from *A. auriculiformis* trees outside of the study area and applied by hand to achieve a 2-cm deep and 1-m wide layer along 50% of patch perimeters. Seedlings of five common native tree species (*Pterocarpus indicus* [Fabaceae], *R. taetensis*, *Macaranga carolinensis* [Euphorbiaceae], *Campnosperma brevipetiolata* [Anacardiaceae], and *P. obovata*) were selected based on seedling availability and common occurrence in savanna or forest edge habitats. Seedlings and potting soil were obtained from upland volcanic forest near the Nekken Forestry Station in Aimeliik State and were acclimated to full sun approximately 3 months before outplanting. Each seedling (10–102 cm) was planted into a tree hole with collected soil as well as 1 L of agricultural compost and 0.25 L of calcium oxide (NRCS 1999). The seedlings were planted 1 m apart and 0.5 m outside the patch drip line, and received no supplementary water. At least one seedling of each species was planted in two quadrants of the 16 patches, while controlling for aspect within pairs of fertilized and control patches. Immediately after planting and again in June 2012, seedling height was measured from root collar to highest meristem.

#### Pre- and Post-Treatment Measurements

We estimated naturally establishing native tree seedling density and species diversity by counting all seedlings in 2 $m^2$ quadrats for all but the four smallest patches in which 1 $m^2$ quadrats were used. Quadrats were placed straddling the drip line with half inside and half outside, halfway between directional markers, with four subsamples per patch (Fig. 2). Seedlings were counted in June 2010, immediately prior to trimming of herbaceous vegetation, in December 2010, and again in June 2012. The trimming (mostly *D. linearis*) was done with machete to ground level in a 1-m band surrounding each patch.

We measured naturally occurring native tree sapling growth along patch perimeters to measure effect of fertilization on sapling height change and patch expansion. The directional markers were used as reference points for random sampling of saplings within 2-m-wide belt transects, spanning 1 m on each side of the drip line. Proceeding clockwise from directional markers, the first 10 woody saplings greater than 30 cm in height, but less than 3 cm DBH were tagged and measured for height from root collar to highest meristem. Tagged saplings were remeasured in December 2010 and June 2012. Directional markers were used to measure mean patch expansion in August 2014.

In addition, we counted flowers and fruits in forest patches to measure the effect of fertilization on flower and fruit production. Flower and fruit counts of all trees within all 32 forest patches were recorded before and after treatment applications. Flower and fruit production, and presence or absence of new leaves of all patch trees were monitored twice monthly (with binoculars where necessary) from July to December 2010. For each monitoring period, the total number of fruits and total flowers per patch, number of fruiting and flowering native tree species per patch, and number of tree species producing new leaves per patch were summed for comparison between paired fertilized and non-fertilized patches.

#### Bird and Flying Fox Visitation and Movement

We counted visits of all bird species and *Pteropus mariannus pelewensis* (Palau Flying Fox) to patches from 06:00 to 08:00 and 16:00 to 18:00 hours, for 7 days, twice monthly, from July to December 2010. For every 2-hour monitoring period, we recorded start and stop time, cloud cover, and estimated wind strength. Monitoring was not conducted if we encountered rain stronger than a drizzle, or wind exceeding Beaufort Force 3. To standardize the total observation time along line transects for each patch, we used 10-minute intervals to pace observer movement. We recorded the species of visitors and the species of individual trees visited within patches, as well as flybys and flyovers. In addition, flying fox flyovers were counted from a stationary position near the highest point of the study area for 30–60 minutes after sunset, depending on visibility and weather conditions. Flights directly over the savanna area and visits to forest patches were recorded.

#### Analyses

We used simple linear regression to analyze relationships between patch size (log transformed to improve normality) and height of tallest patch tree, tree species richness, basal area, and daily temperature fluctuations. Two-sample *t* tests were used to compare initial seedling density, sapling number, and mean sapling height differences between areas inside and outside of patch drip lines. Paired two-sample *t* tests were used to compare pre- and post-trimming of naturally establishing seedling density, growth of naturally occurring saplings, patch expansion with and without fertilizer applications, bird visits to fertilized and control patches, and flower and fruit productions in fertilized and control patches. We used one-way analysis of variance (ANOVA) to compare treatment effects on naturally establishing seedlings, naturally occurring saplings, and planted seedlings in patch perimeters (four levels—four treatments) and to compare the growth of the five native tree species planted in patch perimeters (five levels—five species). We used Minitab Statistical Software™ version 16 for all analyses. We used a standard Akaike Information Criteria (AIC) method to evaluate the significance of models containing the following variables: patch area, maximum tree height, distance to forest edge, species richness, mean total fruits, mean tree species in fruit, mean total flowers, mean tree species in flower, mean tree species with new leaves, mean distance to nearest neighbor trees, and mean height of four nearest neighbor trees. This last variable is defined as those trees closest to patch directional markers whose size and proximity to the forest patches could influence patch visitation. Significant predictor variables were brought into an ordinary least squares (OLS) regression (ArcMap™ 10.0), except where autocorrelation exceeded 0.7. Response and predictor variables were log transformed when needed.

## Results

#### Forest Patch Characteristics

Tree species richness ($R^2 = 0.816$, $p < 0.001$), height of tallest patch tree ($R^2 = 0.672$, $p < 0.001$), and basal area ($R^2 = 0.832$, $p < 0.01$) all increased with patch area, while daily temperature fluctuations and light transmittance into patch interiors decreased with patch size (data not shown). Dominant species of trees greater than 1 cm DBH were *C. inophyllum*, *Maranthes corymbosa* (Chrysobalanaceae), *Symplocos racemosa*, *Planchonella obovata*, and *Alphitonia carolinensis* (Table S1, Supporting Information). Six of the 22 species of naturally occurring saplings measured in patch perimeters are endemic to Palau and two are endemic to Palau and Yap (Table S2).

Fertilizer application accelerated patch expansion. Four years after initiation of treatments, the mean lateral expansion of fertilized forest patches ($52 \pm 11$ cm) was greater than that of non-fertilized patches ($9 \pm 6$ cm; paired *t* test, $n = 16$, $p < 0.001$; Table S4).

#### Patch Production Ecology

Application of fertilizer significantly increased flower, fruit, and new leaf production (Table 1). In fertilized patches, more tree species per patch flowered, more species per patch fruited, and more species per patch flushed new leaves than in non-fertilized patches. Summed together, all producing trees in fertilized patches displayed more flowers and fruits per patch than unfertilized patches.

#### Naturally Establishing Tree Seedling Responses

Fertilizer application had no effect on naturally establishing tree seedling density, but the native tree seedling planting treatment had increased it after 6 months of planting. After 6 months of trimming of perimeter vegetation, there were $2.7 \pm 0.4$ seedlings per $m^2$ outside and $1.7 \pm 0.3$ inside of patch drip lines,

**Table 1.** Comparison of mean native tree flower and fruit production ecology values between fertilized and non-fertilized forest patches in the LNNR savanna study site, from June to December 2010.

| | # Flowers | # Fruits | # Flowering spp. | # Fruiting spp. | # spp. with New Leaves |
|---|---|---|---|---|---|
| Fertilized patches | $45.1 \pm 6.9$ | $137.2 \pm 27.0$ | $1.4 \pm 0.8$ | $1.7 \pm 0.1$ | $5.0 \pm 0.2$ |
| Non-fertilized patches | $17.4 \pm 4.3$ | $72.5 \pm 21.1$ | $0.9 \pm 08$ | $1.1 \pm 0.1$ | $4.0 \pm 0.2$ |
| Difference | $27.7 \pm 8.3$ | $64.7 \pm 34.7$ | $0.5 \pm 0.1$ | $0.5 \pm 0.1$ | $2.9 \pm 0.2$ |
| $p$ Value | <0.001 | <0.05 | <0.001 | <0.001 | <0.001 |

**Table 2.** Growth summary from 2010 to 2013 (cm/yr) of five native tree species, planted along forest patch perimeters (0.5 m from dripline, 1 m between plantings) in the LNNR savanna study site.

| *Planted Tree Species* | *Sample Size* | *Absolute Growth* | *SE* | *Relative Growth (% per yr)* |
|---|---|---|---|---|
| *Campnosperma brevipetiolata* | 52 | 11.0 | 0.9 | 11.6 |
| *Macaranga carolinensis* | 50 | 15.9 | 2.0 | 15.3 |
| *Pterocarpus indicus* | 48 | 43.8 | 4.8 | 56.9 |
| *Planchonella obovata* | 56 | 11.3 | 1.1 | 15.2 |
| *Rhus taetensis* | 38 | 8.3 | 1.5 | 6.5 |

and $2.7 \pm 0.3$ seedling species per $m^2$ inside drip lines, with $1.2 \pm 0.2$ seedling species outside. Fertilizer application had no impact on perimeter seedling density or diversity in the first 6 months ($p = 0.51$). Naturally establishing tree seedling density in the planted tree seedling quarters of the plots increased by $3.1 \pm 3.2$ seedlings per $m^2$ compared with control sections ($F = 3.15$, $df = 63$, $p < 0.05$). Two years after plot establishment, seedling density had increased by $7.7 \pm 2.6$ seedlings per $m^2$ ($T = 3.0$, $n = 32$, $p < 0.01$) while diversity had increased by $1.8 \pm 0.35$ species per $m^2$ ($T = 5.3$, $n = 32$, $p < 0.001$). The most common of 23 total seedling species were the shrubs *Hedyotis korrorensis* and *Melastoma malabathricum*. The endemic *H. korrorensis* comprised 351 of 559 total seedlings (63%) before trimming and 354 of 820 total seedlings (43%) 2 years after trimming.

### Naturally Occurring Sapling Responses

Fertilizer application increased growth of naturally occurring saplings. Saplings were initially on average 9.7 cm taller outside than inside patch drip lines (95% CI = 2.8–16.7, $p < 0.05$). Sapling density inside the drip lines was nearly double that found outside drip lines, and species diversity was 27% higher inside compared with outside. Absolute mean sapling growth was 18.2 cm (SE $\pm$ 0.8) over 2 years and perimeter sapling growth in fertilized patches was 6.1 cm greater than in non-fertilized patches ($T = 3.58$, $df = 599$, $p < 0.001$). Relative mean growth of saplings was 4.9%/year. The effects of mulch and planted saplings on naturally established sapling growth were nonsignificant ($F = 1.05$, $df = 157$, $p = 0.37$).

### Planted Seedling Responses

Mortality rate for the planted seedlings (2010–2013) was 9% (*Rhus taetensis*, 16%; *Macaranga carolinensis*, 16%; *Campnosperma brevipetiolata*, 10%; *Pterocarpus indicus*, 4%; and *P. obovata*, 2%). Planted seedling mortality was lower for the northwest (NW) (3%) and northeast (NE) (6%) aspects compared with southeast (SE) (10%) and southwest (SW) (14%) aspects. Differences in growth among the five species planted were significant (Table 2), with *P. indicus* growing fastest ($F = 34.27$, $n = 244$, $p < 0.001$). Mulching did not influence growth of the planted seedlings. We found no correlation between patch size and planted seedling growth or mortality.

### Avian Visitation Responses

From July to December 2010, the three species that most frequently visited forest patches were *Zoterops finschii* (Dusky White Eye), *Aplonis opaca orii* (Micronesian Starling), and *Coracina tenuirostris monacha* (Palau Cicadabird) (Table 3). The best predictors of visitation included log of patch area ($p < 0.001$), log of mean total fruits ($p < 0.05$), and mean height of four nearest neighbor trees ($p < 0.01$), which combined into the following equation for visitation: *log number of total patch visits* $= -1.14 + (0.18 \times$ *mean neighbor tree height*$) + (0.45 \times$ *log patch area*$) + (0.08 \times$ *log total fruits*$)$ ($R^2 = 0.84$; Joint $F < 0.0001$; Fig. 3). High autocorrelation precluded the use of height of tallest tree and species richness in combination with patch area and more than one production ecology variable. Of the total observed visits, 24% were exclusive to one individual trees or tree species, with 3% including fruit, seed, or flower eating. The two tallest tree species (*M. corymbosa* and *C. inophyllum*; Table S1) accounted for 69% of the total exclusive tree visits to the marked patches. The diversity of bird species visiting patches increased with patch size ($R^2 = 0.757$, $p < 0.001$), and there were $1.5 \pm 0.6$ more bird visits per monitoring period to fertilized patches than to non-fertilized patches (paired $t$ test, $p < 0.05$).

## Discussion

In Palau, excluding fire allows natural succession processes to proceed in anthropogenic savanna. However, low nutrient

**Table 3.** Total visits by species to marked forest patches in LNNR savanna study site from July to December 2010. Asterisks indicate species endemic to Palau. Bold type indicates potential seed dispersing species.

| *Species* | *Common Name* | *Total Island Visits* |
|---|---|---|
| ***Zoterops finschii**** | **Dusky White-Eye*** | 1,017 |
| ***Aplonis opaca orii*** | **Micronesian Starling** | 260 |
| ***Coracina tenuirostris monacha**** | **Palau Cicadabird*** | 163 |
| *Myzomela rubrata kobayashii* | Micronesian Myzomela | 109 |
| *Myiagra erythrops** | Palau Flycatcher* | 95 |
| *Rhipidura lepida** | Palau Fantail* | 75 |
| *Zosterops semperi semperi* | Citrine White-Eye | 38 |
| ***Ptilinopus pelewensis**** | **Palau Fruit Dove*** | 31 |
| *Todiramphus cinnamominus pelewensis** | Rusty-Capped Kingfisher* | 8 |
| *Rattus sp.* | RAT | 6 |
| *Camprimulgus indicus phalaena* | Gray Nightjar | 2 |
| ***Colluricincla tenebrosa**** | **Morningbird*** | 2 |
| *Cettia annae** | Palau Bush Warbler* | 1 |
| ***Pteropus mariannus pelewensis*** | **Palau Flying Fox** | 1 |
| *Gygis alba* | White Tern | 1 |
| Total visits | | 1,809 |

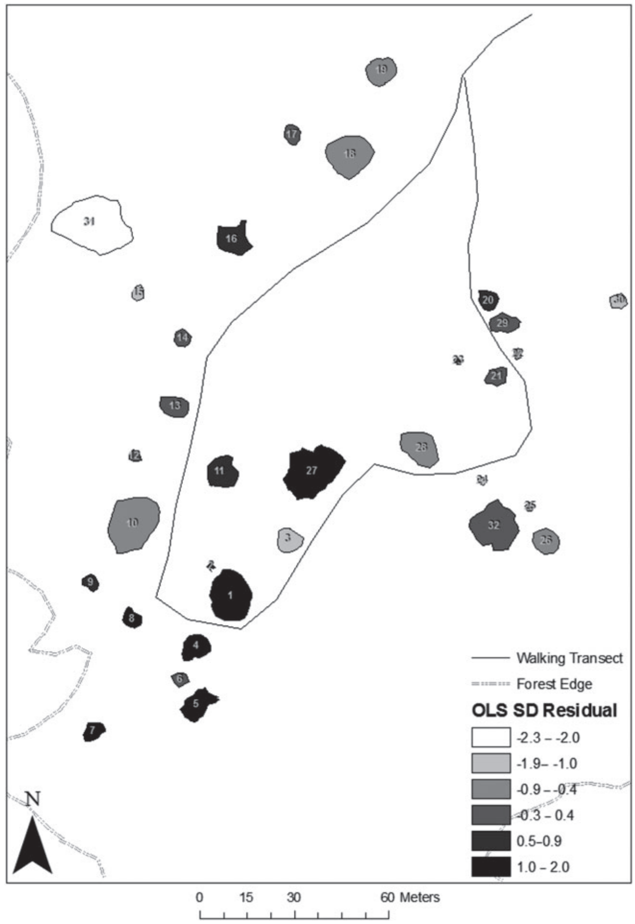


Figure 3. Patch visitation model—ArcMap™ OLS output showing standard distribution of residuals for each patch from the model predicting the log of total bird visits to patches (three predictors are log of island area, log of mean total number of fruits, and mean height of nearest neighbor trees). Values greater than ±2 indicate a significant deviation from the regression model prediction.

availability and competition with savanna vegetation constrain tree establishment and could therefore delay forest recovery for centuries (Dobson et al. 1997). While results of studies on fertilizer application and planting of leguminous trees in various degraded tropical forest sites have been mixed (Nichols et al. 2001; Ceccon et al. 2003; Davidson et al. 2004; Slocum et al. 2006), the presence of remnant trees, the planting of native tree seedlings, and the facilitation of naturally colonizing trees and shrubs have all been recognized as important in accelerating forest regeneration, through increased seed dispersal and improved soil quality and microclimate (Holl et al. 2000).

### Forest Patch Plant Growth and Expansion

Forest patch trees responded positively to fertilizer application, with effects extending into the patch perimeters. Naturally occurring sapling growth responses to fertilization decreased over 2 years, indicating that repeated applications of fertilizer are required to sustain high growth rates. The sapling community was more abundant and species rich inside forest patches, suggesting that patch interiors receive more dispersed seeds, and/or provide better conditions for seedling establishment than does the climatically and edaphically harsher savanna environment (Fig. S1; Smith & Babik 1988). However, saplings outside patch drip lines were taller, suggesting that the additional light and possibly reduced competition for nutrients allowed for faster growth. These results suggest that the perimeter may provide the most suitable location for tree planting.

Planted seedlings survived well after 2 years (91%), but for those species with higher mortality, different nursery preparation and additional or different amendments could improve survivorship. The substantially higher growth rate for the nitrogen-fixing *Pterocarpus indicus* and the fact that it produces high value timber and food for wildlife indicate consideration for further outplanting efforts. In areas with fertile soil and ideal growing conditions, *P. indicus* can be expected to grow up to 2 m/year, but in open savanna environments, they can grow 0.5–0.75 m/year and develop a multi-stemmed habit potentially useful for shading out competing nonforest vegetation (Thomson 2006).

The perimeter trimming applied to all forest patches appeared to increase naturally establishing tree seedling density and diversity, indicating that thick fern mats surrounding patches limit seedling establishment. Likely mechanisms include reduced light and/or nutrient availability, as reported in *Dicranopteris linearis* fernlands in Sri Lanka (Cohen et al. 1995). Two years after plot establishment, recolonizing ferns were growing over some outplants and natural saplings, which could explain the lack of significant differences in seedling density and sapling growth among the mulch, planted seedling, and combined treatments. From this, we speculate that higher rates of woody plant growth will require periodic perimeter trimming until restoration targets are achieved. Future experiments could investigate mulch quality and source, quantity, and timing of application in combination with more regular perimeter trimming.

Four years after establishment, fertilized patches had expanded about five times more than non-fertilized patches, with the mean baseline rate of unfertilized patch expansion a mere $2 \pm 1$ cm/year. This expansion appears to be due primarily to the growth of established trees rather than edge filling by newly established tree saplings and seedlings.

#### Forest Patch Size

Studies in Costa Rican montane pasture indicate that animal-dispersed tree species colonize larger forest nuclei, indicating that outplanting efforts should be directed to patches of at least 64 $m^2$ (Zahawi & Augspurger 2006; Cole et al. 2010). In line with these studies, we found more sapling species in larger forest patches, but because patch age could not be determined, it is difficult to distinguish age versus size effects. Our minimum-size outplanted patch was 35 $m^2$, but we found no correlation among patch size and the response size of any of our restoration treatments. Addressing the minimum size for outplanting in Palau will require additional study. However, five of the smallest patches in our study, including one that was fertilized, contracted over 4 years and the smallest seven patches had few observed bird visits over 6 months of monitoring. Taken together, it seems that patches of at least 15 $m^2$ or larger should be the focus of future work in Palauan savanna.

#### Forest Patch Composition

The tree species richness of smaller patches is comparable to secondary vegetation in early succession volcanic forests of Palau, while in larger patches richness is comparable to that found in late succession forests (Endress 2002). The large *M. corymbosa* and *C. inophyllum* trees in most of the larger patches suggest that these patches are refugia, which survived fires in this area (Kitalong et al. 2008). Most of the patch tree species either have some resistance to fire, or can resprout after fire (Author, J D 2015, personal observation), indicating the selective effects of fire on species composition of these forest fragments.

#### Bird and Flying Fox Visitation and Movements

The strongest predictor of patch visits was patch size and the visitation model suggests that frequency and diversity of visitors increase as patches become more like continuous forest, with taller and more species of trees and more diverse and abundant food resources. Distance to forest edge was not a significant factor in the model, but given the small area of the study site, we cannot rule distance out as a barrier to bird utilization. However, previous forest fragment and bird studies have also found distance to forest to be nonsignificant, with tree height and patch size being valuable predictors of bird species richness (Ferraz et al. 2007; Flaspohler et al. 2010).

Six of the top 10 patch visitors are endemic Palauan species, including the frugivorous *Ptilinopus pelewensis* (Palau Fruit Dove), indicating that endemic species may play important roles in the plant community dynamics of recovering savanna landscapes. Palau's other important frugivores—*Ducula oceanica* (Micronesian Imperial Pigeon) and *Caloenas nicobarica pelewensis* (Nicobar Pigeon)—rarely visited our savanna study site and in general tend to be observed in more intact forested landscapes. Despite only one patch visit by the Palau Flying Fox, we observed far more flyovers than for any other species observed in the study (Table S3). While numerous studies have attributed a large portion of seed rain to more numerous visits by seed dispersers (Estrada et al. 1993; Guevara & Laborde 1993; Da Silva et al. 1996; Estrada et al. 1997; Galindo-Gonzalez et al. 2000), dispersal studies will be required to understand the actual impact of these birds and bats on the ecology of Palauan savanna forest patches, because the logistics of capturing descending fecal or semi-eaten fruit material precluded inclusion in this study.

#### Research Impact

Our results for low-cost forest restoration methods on Babeldaob are promising, but the time, effort, and expense invested will be in vain if fire prevention is not effective. The effectiveness of these low cost prescriptions will thus be limited to areas protected from fire–on Babeldaob, or other sites with similar soils, vegetation, and management.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Inside and outside saplings—number of naturally occurring tree saplings by species growing inside and outside of forest patch drip lines (2010), in the Lake Ngardok Nature Reserve savanna study site.
**Table S1.** Characteristics of forest patches (2009) in the Lake Ngardok Nature Reserve savanna study site, Palau.
**Table S2.** Growth of naturally occurring tree saplings in forest patch perimeters in the Lake Ngardok savanna study site (June–December 2010). Bold type indicates species endemic to Palau, and asterisks indicate species endemic to Palau and Yap.
**Table S3.** Flybys and flyovers: bird and flying fox flybys (no observed forest patch or tree visit, flying below maximum tree height) and flyovers (flight above tallest trees and directly above savanna study site) from July to December 2010 in the Lake Ngardok Nature Reserve savanna study site. Bold type indicates potential seed disperser, and asterisks indicate species endemic to Palau.
**Table S4.** Woody vegetation dripline expansion (cm) of forest patches from 2010 to 2014 in the Lake Ngardok Nature Reserve savanna study site, measured from patch directional markers.

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