



## Litterfall and nutrient dynamics shift in tropical forest restoration sites after a decade of recovery

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### ABSTRACT

Multi-year studies comparing changes in litterfall biomass and nutrient inputs in sites under different restoration practices are lacking. We evaluated litterfall dynamics and nutrient inputs at 5 yr and after a decade of recovery in four treatments (natural regeneration—no planting, plantation—entire area planted, tree islands—planting in patches, and reference forest) at multiple sites in an agricultural landscape in southern Costa Rica. We inter-planted two native species (*Terminalia amazonia* and *Vochysia guatemalensis*) and two naturalized N-fixing species (*Inga edulis* and *Erythrina poeppigiana*) in plantation and island treatments. Although litterfall N was higher in plantations in the first sampling period, litter production and overall inputs of C, N, Ca, Mg, P, Cu, Mn, and Fe did not differ between island, plantation, or reference forest after a decade; however, all were greater than in natural regeneration. Potassium inputs were lower in the natural regeneration, intermediate in island and plantation, and greater in reference forest. The percentage of litterfall comprised by the N-fixing planted species declined by nearly two-thirds in both plantations and islands between sampling periods, while the percentage of *V. guatemalensis* more than doubled, and the percentage from naturally regenerated species increased from 27 to 47 percent in islands. Island and plantation treatments were equally effective at restoring litterfall and nutrient inputs to levels similar to the reference system. The nutrient input changed substantially over the 7-yr interval between measurements, reflecting shifts in vegetation composition and demonstrating how rapidly nutrient cycling dynamics can change in recovering forests.

Abstract in Spanish is available with online material.

**Key words:** active restoration; applied nucleation; Costa Rica; litter production; nutrient cycling; plantations; tropical forests.

TROPICAL FORESTS PLAY AN IMPORTANT ROLE IN THE CYCLING OF CARBON AND OTHER NUTRIENTS at both local and global scales (Dixon *et al.* 1994, Lewis 2006). Although a vast amount of tropical forests have been cleared globally (FAO 2015) with a significant disruption of the nutrient cycling services they provide (Reiners *et al.* 1994, Guariguata & Ostertag 2001), cover of tropical secondary forests has increased in some regions as a result of changing land uses (Aide *et al.* 2013, Chazdon 2014), and there has been a dramatic increase in large-scale forest restoration (Chazdon *et al.* 2017). Whereas many past studies have measured nutrient inputs in naturally recovering tropical forests (*e.g.*, Ewel 1976, Lugo 1992, Ostertag *et al.* 2008) and tree plantations (*e.g.*, Cuevas & Lugo 1998, Parrotta 1999, Goma-Tchimbakala & Bernhard-Reversat 2006), few have evaluated such changes over time (Marín-Spiotta *et al.* 2008), and we know of no studies

directly comparing nutrient inputs under different forest restoration strategies.

In many cases, former agricultural lands regenerate rapidly without human intervention when the disturbance impeding recovery (*e.g.*, grazing) is stopped (Aide *et al.* 1996, Chazdon & Guariguata 2016). But in sites that have a long history of intensive land use, and where sources of floral and faunal propagules are lacking, recovery can be slow (Holl 2012). In these circumstances, the most widespread approach to accelerate forest recovery is to establish tree plantations, which can attract seed dispersing animals and shade out ferns and pasture grasses (Holl 2012, Lamb 2014) and reestablish nutrient cycling processes. But, plantation-style planting is resource intensive and the species chosen can strongly affect nutrient cycling (Firn *et al.* 2007, Siddique *et al.* 2008, Celentano *et al.* 2011, Holl *et al.* 2013).

Increasingly, alternative tropical forest restoration approaches are being tested that are less resource intensive and better simulate the natural recovery process. One such approach is applied nucleation, where trees are planted in patches or 'islands' (Corbin

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& Holl 2012). This approach is based on nucleation theory (Yarranton & Morrison 1974), a natural recovery process where pioneer shrubs and trees establish patchily and facilitate recruitment via enhanced seed dispersal and improved establishment conditions; patches spread outward clonally and/or by facilitating the colonization of later-successional species. Research to date shows that applied nucleation is equally effective in enhancing seed dispersal and seedling establishment of tropical forest trees, as more intensive plantation style planting methods (Reid *et al.* 2015, Holl *et al.* 2017), but at least in the short-term results in less above-ground biomass (Holl & Zahawi 2014).

Most studies of tropical forest restoration focus on the first few years (Shoo & Catterall 2013), despite the fact that recovery is a long-term process and past studies show that nutrient cycling in particular changes substantially over time, especially in tropical forests (Macedo *et al.* 2008, Ostertag *et al.* 2008). Litterfall represents a key process in the long-term maintenance of nutrient cycling in tropical forests (Vitousek & Sanford 1986, Paudel *et al.* 2015). Accordingly, our goals in this study were to: (1) compare litterfall biomass and nutrient inputs per unit area after a decade of recovery across three treatments—natural regeneration (no planting), plantation (systematic tree planting), and tree islands (planting trees in patches); (2) determine whether treatments had achieved levels comparable to mature reference forests; and (3) assess whether litterfall patterns had changed in the 7 yr since a prior set of measurements.

Between 2008 and 2009, Celentano *et al.* (2011) collected data on nutrient cycling in the same experimental restoration sites 5 yr after treatment establishment and found that: (1) litterfall biomass was much higher in plantations than in island or natural regeneration treatments; and (2) there was a strong effect of the two planted, N-fixing species on nutrient cycling in the plantation, with marginally higher N inputs, equivalent C, but significantly lower Mg, Ca, and K as compared to adjacent 7- to 9-yr-old secondary forests. We predicted that litterfall biomass differences in the island and plantation treatments would diminish between the two sampling periods due to the establishment of naturally recruiting trees in the island treatment (Holl *et al.* 2017). We also anticipated that there would still be substantial differences in plantation nutrient inputs, as compared to the island treatment and reference forests, given that the majority of the woody biomass in plantations is comprised of the four planted tree species (Holl & Zahawi 2014), two of which fix nitrogen.

## METHODS

**STUDY SITE.**—We conducted the study at sites located between the Las Cruces Biological Station (8°47'7" N; 82°57'32" W) and the town of Agua Buena (8°44'42" N; 82°56'53" W) in Coto Brus county, southern Costa Rica. The forests in this region are at the borderline between Tropical Premontane Wet and Rain Forest zones (Holdridge *et al.* 1971). A large proportion of these forests were cleared in the last century, with cover reduced from 98.2 percent in 1947 to approximately 27.9 percent by 2014 (Zahawi *et al.* 2015). Most forest loss (>90%) occurred between

1947 and 1980. The study sites cover an elevation range from 1000 to 1300 m asl. Mean annual temperature is 21°C with minimal variation during the year, and mean annual rainfall ranges between 3000 and 4000 mm with a marked dry season from December to March. Soils are primarily volcanic in origin and fertile. For more detailed information on sites, see Holl *et al.* (2011).

**EXPERIMENTAL DESIGN.**—Restoration sites were established in degraded agricultural lands between June 2004 and July 2006. At each of 16 sites, three 50 × 50 m treatments were established: Natural Regeneration (no planting); Plantation (entire area planted); and Islands (six patches or 'islands' of trees planted with two of each of three sizes: 4 × 4 m, 8 × 8 m, and 12 × 12 m). Restoration treatments thus had a gradient of intervention from no planting, to 344 trees/ha and 1252 trees/ha in the natural regeneration, island, and plantation treatments, respectively.

Plantation and island treatments were each planted with a mix of four species: two native species *Terminalia amazonia* (JF Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae) intermixed with two naturalized fast growing N-fixing species *Erythrina poeppigiana* (Walp.) O. F. Cook, and *Inga edulis* Mart. (both Fabaceae). Seedlings were planted in alternating rows of *Vochysia/Terminalia* and *Inga/Erythrina* and were separated by 4 m within rows and by 2.8 m across rows. All plots were cleared with machetes for 2.5 yr after planting to allow tree growth to overtop grasses (Holl *et al.* 2011). Within sites, treatments were separated by ≥5 m; restoration sites were separated by 1–10 km.

The experimental design for the two studies differed slightly due to circumstances beyond our control. For Celentano *et al.* (2011), we measured litterfall at six restoration sites 5 yr after site establishment (September 2008 to August 2009), and compared values to litterfall in three nearby 7- to 9-yr-old secondary forests (hereafter 'first sampling period'). Comparable measurements were collected 7 yr later (October 2015 to September 2016) in three of the six restoration sites that were used in the first sampling period; unfortunately, by this time the remaining three sites used in the first study had been converted to other uses by the land owners. Accordingly, we added two additional restoration sites, one each established in 2005 and 2006, for a total of five restoration sites sampled 10–12 yr after establishment (hereafter 'second sampling period'). Although these sites were established in subsequent years, by 2012 there was no effect of planting years on above-ground tree biomass (Holl & Zahawi 2014). In the second sampling period, we also measured litterfall in adjacent mature remnant forest patches at three sites. We describe the details for the second sampling period below.

**LITTERFALL.**—In each treatment, we placed twelve 0.25 m<sup>2</sup> litterfall traps elevated to 0.60 m above the ground. In plantation and control treatments, traps were placed in four groups of three traps to facilitate comparisons with permanent vegetation plots and seed rain sampling; in island, treatments traps were distributed proportionally to island interior, edge, and unplanted areas (Fig. S1, Reid *et al.* 2015).

Litterfall was collected twice monthly for 12 mo beginning in October 2015. All samples were dried at 65°C for 72 h and then separated into the following components: leaves, woody tissue (<1 cm diameter), reproductive parts (flowers), and miscellaneous (uncategorized plant material). We also determined the litterfall contribution made by each of the four planted species, grasses, and other dicots. All litterfall collected in reference forest plots was classified as ‘other dicot’ due to the difficulty in identification and the near absence of grasses or any of the planted tree species.

**DETERMINATION OF LITTERFALL NUTRIENT CONTENT.**—We analyzed the concentration (%) of total C and N, Ca, Mg, K, P, and the mg/kg of Cu, Zn, Mn, Fe for all litterfall components combined and for three time periods (December 2015–February 2016, March–May 2016, June–August 2016) using a combined sample for each treatment at each site ( $N = 54$ ). Total C and N were determined by combustion using an autoanalyzer (ThermoFinnigan FlashEA 1112). Nutrient concentration of Ca, Mg, K, Cu, Zn, Mn, and Fe was determined from a subsample of litterfall that was ground and sieved (1 mm; 18/ASTM) (Díaz-Romeu & Hunter 1978, Association of Official Agricultural Chemists 1984, Mills & Jones 1996) and analyzed for atomic absorption using an AAnalysis 100 (PerkinElmer) after wet digestion. Phosphorus was determined by the colorimetric method developing blue molybdenum, and read through a UV/V Spectrophotometer at 660 nm.

**CANOPY CLOSURE AND TREE GROWTH.**—We determined percent canopy closure directly above each litterfall trap using a densiometer at two time intervals (January–February and April–May 2016) and averaged the two values. Survival and diameter at breast height (dbh) were measured for each planted tree in June–July 2009 and in May–June 2016 and used to calculate total basal area.

**DATA ANALYSES.**—We compared nutrient concentrations among treatments using the mean value of the three time periods. We estimated nutrient inputs of litterfall to the forest floor by multiplying the nutrient concentration determined for each time period by the total litter production (kg/ha) for that same period and then summing all values; the biomass for the first 2 mo and final month (when nutrient concentrations were not quantified) were included with the biomass for the adjacent sampling period.

To compare litterfall biomass per unit area and nutrient concentrations and inputs from the second sampling period across the restoration treatments and reference forest, we conducted analysis of variance using linear mixed models and an incomplete block design (as the reference forest treatment was only replicated at three of five study sites). Litterfall biomass was analyzed using a repeated-measure ANOVA with treatment and time of collection as fixed factors and site as a random blocking factor; we compared differences in monthly litter production across treatments using planned contrasts. For all other analyses, variables were summed (biomass of component plant parts, planted

species, nutrient inputs) or averaged (nutrient concentrations) over the entire year. The dependent variables were litterfall (total production, components, and the contribution of the four planted species), litterfall chemistry, and nutrient inputs to the soil, and the independent variables were treatment (fixed factor) and site (random blocking factor); when treatment had a significant effect in the full model we used Fisher’s least significant difference (LSD) to compare specific treatments ( $P < 0.05$ ).

To assess whether litterfall biomass, contributions of different species, and nutrient inputs had changed in the 7 yr between the two sampling periods, we conducted a repeated-measures ANOVA using the three restoration sites that were assessed in both sampling periods. The model included site (as a random blocking factor), treatment, sample period, and a treatment  $\times$  sample period interaction, followed by a Fisher’s LSD to compare treatment  $\times$  yr combinations. All analyses and graphics were performed using InfoStat 2016 (Di Rienzo *et al.* 2015) and R 3.2.1 (R Core Development Team 2016), and we report means  $\pm 1$  SE throughout.

## RESULTS

**LITTERFALL PRODUCTION AND COMPOSITION.**—Total litterfall biomass, as well as biomass of leaves and woody tissues, were similar in islands (IS), plantation (PL), and reference forest (RF) in the second sampling period; all were significantly higher than natural regeneration (NR) ( $N = 216$ ;  $F = 4.5$ ;  $P < 0.0001$ , Fig. 1, Table S1). Leaves constituted more than 87 percent of litterfall in all treatments (Table S1).

Litterfall was highest between December and March (dry season) with a peak in February (Fig. 1); 50.4 percent of litter for the entire sampling period was produced during these 4 mo. Litter production across all treatments was positively correlated with canopy closure ( $r = 0.73$ ,  $P = 0.0005$ ), which was significantly lower ( $N = 54$ ;  $F = 12.4$ ;  $P < 0.0001$ ) in natural regeneration plots as compared to other treatments (NR =  $74.2 \pm 8.7\%$ , IS =  $94.8 \pm 0.8\%$ , PL =  $99.0 \pm 0.3\%$ , RF =  $99.4 \pm 0.2\%$ ).

Total litterfall biomass increased significantly between the two sampling periods, which was primarily due to the island treatment ( $F = 6.8$ ,  $P = 0.0263$ , Fig. 2); however, litterfall species composition changed dramatically in all treatments. The vast majority of litterfall in plantations came from planted species in both sampling periods (first: 94.7%, second: 89.7%), whereas planted species made up 69.0 percent and 52.6 percent of litterfall in islands in the first and second sampling periods, respectively (Fig. 2). Litterfall from unplanted dicots increased substantially in the second sampling period in both island (first: 27.2%, second: 47.4%), and natural regeneration plots (first: 71%, second: 94%), but remained a small percentage of litterfall in plantations (first: 4.7%, second: 10.3%). Of the planted species, *V. guatemalensis* and *I. edulis* contributed most of the litter production in plantations and islands in the second survey (Fig. 2). There was also a marked shift in the makeup of planted species litter production; percent litterfall comprised by *V. guatemalensis* more than doubled in the islands and increased

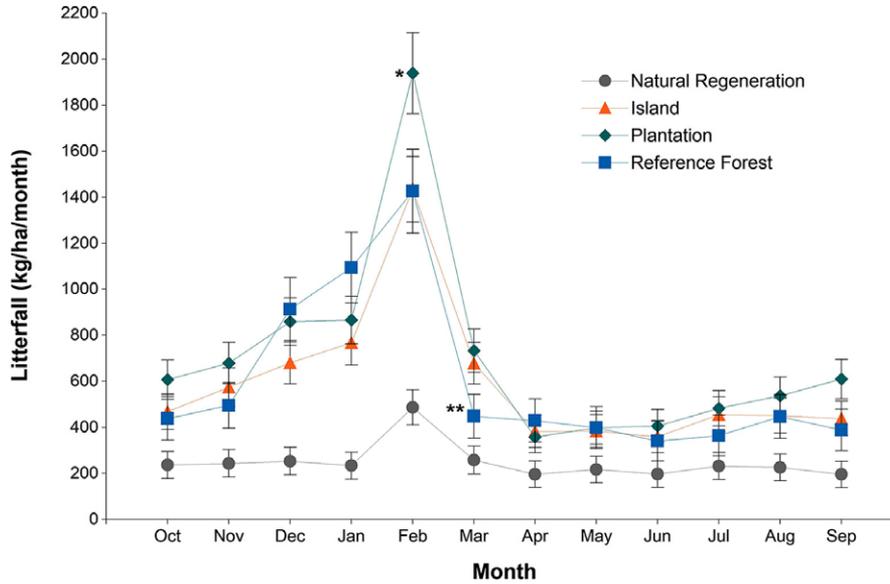


FIGURE 1. Mean monthly litterfall production (kg/ha/mo ± 1 SE) in the natural regeneration, island, plantation, and reference forest treatments during the second sampling period. Natural regeneration differed significantly from the other treatments in all months. \*Indicates month when litterfall in plantation differed from island and reference forest using planned contrasts. \*\*Indicates month when island differed from plantation and reference forest.

sixfold in the plantations ( $F = 14.5$ ,  $P = 0.0088$ , Fig. 2), whereas the percent litterfall comprised by *I. edulis* in the second sampling period was approximately a quarter of the value registered in the first sampling period for both islands and plantations ( $F = 33.8$ ,  $P = 0.0002$ ).

Similarly, the species that comprised the majority of the basal area in the second sampling period were *V. guatemalensis* and

*I. edulis* in the islands and the plantation (Table 1). Indeed, *V. guatemalensis* was the species with greatest increase in basal area in both plantations and islands with mean increases of 14.1 and 4.4 m<sup>2</sup>/ha in the two treatments, respectively, over the 7-yr interval; both *I. edulis* (both treatments) and *E. poeppigiana* (plantation only) had ≥30 percent mortality in planted treatments during the 7-yr interval, which reduced the basal area of each species (Table 1).

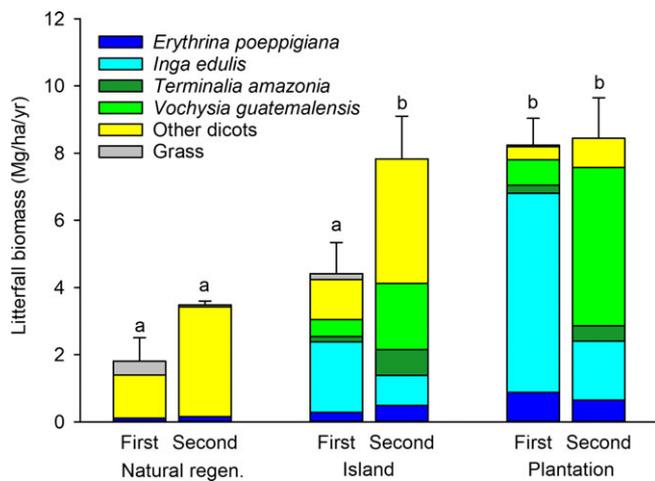


FIGURE 2. Comparison of annual litterfall production (Mg/ha/yr) of natural regeneration, island, and plantation treatments in the first and second sampling periods. Values are means of total litterfall biomass (±1 SE) for the three sites measured in both sampling periods. Mean total litterfall biomass values with the same letters are not significantly different ( $P < 0.05$ ) using Fisher's LSD.

LITTERFALL NUTRIENT CONTENT AND INPUTS.—Percent C and N in litterfall did not differ among treatments in the second sampling period, despite the fact that N-fixing species were planted in plantation and island treatments and percent C and N in litterfall was higher in islands and plantations in the first sampling period (Celentano *et al.* 2011). However, plantation litterfall had significantly lower percentages of Ca, K, P, and Zn (Table S2).

Total litterfall nutrient (kg/ha/yr) inputs of C, N, Ca, Mg, P, Cu, or Fe did not differ between the island, plantation, and reference forest treatments in the second sampling period; however, all were significantly greater than in natural regeneration (Table 2). This contrasts sharply with the first sampling period where nutrient inputs varied considerably and were generally highest in young secondary forest (Celentano *et al.* 2011). Potassium inputs were lower in the natural regeneration, intermediate in island and plantation, and greatest in reference forest. As anticipated, C, P, Ca, Mg, and K litterfall input increased overall between the two sampling periods ( $F > 5.5$  and  $P < 0.05$  in all cases) and most strongly in the applied nucleation treatment (Fig. S2). Litterfall N input, however, did not increase significantly over time ( $F = 3.2$ ,  $P = 0.1025$ ).

TABLE 1. Percent survival and total basal area of four planted tree species in island and plantation treatments. Values are means  $\pm$  1 SE for N = 3 sites measured in both sampling periods.

Treatment	Species	Survival (%)		Basal area (m <sup>2</sup> /ha)	
		First	Second	First	Second
Island	<i>Erythrina poeppigiana</i>	90.5 $\pm$ 6.3	72.9 $\pm$ 10.0	0.6 $\pm$ 0.3	1.4 $\pm$ 0.4
	<i>Inga edulis</i>	95.4 $\pm$ 2.3	48.9 $\pm$ 8.3	2.0 $\pm$ 0.6	2.1 $\pm$ 1.2
	<i>Terminalia amazonia</i>	81.6 $\pm$ 16.7	78.2 $\pm$ 18.4	0.4 $\pm$ 0.2	1.5 $\pm$ 0.9
	<i>Vochysia guatemalensis</i>	77.0 $\pm$ 16.2	74.7 $\pm$ 15.5	0.8 $\pm$ 0.4	5.2 $\pm$ 2.1
Plantation	<i>Erythrina poeppigiana</i>	97.6 $\pm$ 0.5	68.0 $\pm$ 14.0	2.5 $\pm$ 0.5	4.7 $\pm$ 0.9
	<i>Inga edulis</i>	97.2 $\pm$ 0.8	66.3 $\pm$ 12.4	8.1 $\pm$ 1.4	7.7 $\pm$ 3.0
	<i>Terminalia amazonia</i>	90.5 $\pm$ 3.8	87.8 $\pm$ 5.8	0.9 $\pm$ 0.1	2.2 $\pm$ 0.1
	<i>Vochysia guatemalensis</i>	96.0 $\pm$ 3.4	92.5 $\pm$ 3.8	2.7 $\pm$ 0.7	16.8 $\pm$ 2.3

TABLE 2. Input of litterfall nutrients in natural regeneration, island, plantation (N = 5), and reference forests (N = 3) at the second sampling period. Values are means  $\pm$  1 SE and means with different letters denote significant differences according to LSD Fisher (P < 0.05).

	Natural regeneration	Island	Plantation	Reference forest	F	P
kg/ha/yr						
C	1422.9 $\pm$ 359.7 <sup>b</sup>	3267.2 $\pm$ 359.7 <sup>a</sup>	3907.0 $\pm$ 359.7 <sup>a</sup>	3479.1 $\pm$ 458.0 <sup>a</sup>	11.0	0.0017
N	56.6 $\pm$ 20.4 <sup>b</sup>	138.5 $\pm$ 20.4 <sup>a</sup>	170.9 $\pm$ 20.4 <sup>a</sup>	142.8 $\pm$ 25.4 <sup>a</sup>	8.2	0.0047
Ca	74.9 $\pm$ 20.5 <sup>b</sup>	138.8 $\pm$ 20.5 <sup>a</sup>	148.4 $\pm$ 20.5 <sup>a</sup>	166.3 $\pm$ 24.6 <sup>a</sup>	6.4	0.0111
Mg	11.8 $\pm$ 3.6 <sup>b</sup>	21.9 $\pm$ 3.6 <sup>a</sup>	24.8 $\pm$ 3.6 <sup>a</sup>	28.2 $\pm$ 4.3 <sup>a</sup>	6.4	0.0109
K	21.5 $\pm$ 7.9 <sup>c</sup>	39.8 $\pm$ 7.9 <sup>b</sup>	45.7 $\pm$ 7.9 <sup>b</sup>	64.4 $\pm$ 9.1 <sup>a</sup>	9.7	0.0026
P	4.0 $\pm$ 1.0 <sup>b</sup>	7.5 $\pm$ 1.3 <sup>a</sup>	8.0 $\pm$ 1.0 <sup>a</sup>	7.8 $\pm$ 1.2 <sup>a</sup>	6.6	0.0099
g/ha/yr						
Cu	40.4 $\pm$ 12.5 <sup>b</sup>	82.0 $\pm$ 12.5 <sup>a</sup>	99.3 $\pm$ 12.5 <sup>a</sup>	89.0 $\pm$ 15.5 <sup>a</sup>	6.1	0.0125
Zn	179.4 $\pm$ 36.1 <sup>b</sup>	250.2 $\pm$ 36.1 <sup>b</sup>	389.2 $\pm$ 43.8 <sup>a</sup>	214.0 $\pm$ 36.1 <sup>b</sup>	7.4	0.0066
Mn	922.8 $\pm$ 350.4 <sup>b</sup>	1830.6 $\pm$ 350.4 <sup>a</sup>	2447.4 $\pm$ 350.4 <sup>a</sup>	1456.9 $\pm$ 430.9 <sup>ab</sup>	5.2	0.0203
Fe	498.7 $\pm$ 129.4 <sup>b</sup>	1043.3 $\pm$ 129.4 <sup>a</sup>	1181.6 $\pm$ 129.4 <sup>a</sup>	1182.3 $\pm$ 160.9 <sup>a</sup>	8.6	0.0041

## DISCUSSION

EFFICACY OF DIFFERENT STRATEGIES TO RESTORE LITTERFALL NUTRIENT INPUTS.—Annual litter production and inputs of all macronutrients except potassium did not differ between the island, plantation, and reference forest 10–12 yr after sites were established. Stated alternately, at this stage in recovery, the island treatment has similar litterfall biomass and nutrient inputs as a plantation or a mature remnant forest habitat even though we initially planted only a quarter of the number of trees in the island treatment. Data from this study support our earlier prediction (Celentano *et al.* 2011) that the much greater litterfall biomass and nutrient inputs noted in plantation compared to island treatments after 5 yr would diminish as forest recovery proceeded. Indeed, litterfall biomass and most nutrient inputs at least doubled in the island and natural regeneration treatments compared to the first study, whereas the increase in plantations was minimal. The lack of an increase in litterfall biomass in the plantations is driven in part by the high mortality of *I. edulis*, which comprised 70 percent of plantation litterfall in the first sampling

period, as well as the slow growth of naturally establishing recruits due to dense canopy closure and shade. That said, plantation values are similar to reference forest litterfall production and could thus be reaching an asymptote for this system.

Values for litterfall biomass in both the plantation and island treatments are in the mid-range of 10- to 16-yr-old plantations in the tropics, which are typically around 5–10 Mg/ha/yr (*e.g.*, Lugo & Fu 2003, Goma-Tchimbakala & Bernhard-Reversat 2006, Macedo *et al.* 2008, Marín-Spiotta *et al.* 2008, Castellanos Barliza & León Peláez 2010). Inputs of N and Ca in plantation and island treatments are similar to values from studies in secondary tropical forests that are <25 yr old reviewed in Vitousek (1984). Surprisingly, the P litterfall inputs are in the mid to upper range of values for tropical secondary forests that are <25 yr old, despite the fact that volcanic tropical soils are generally considered to be P limited (Uehara & Gillman 1981, Ewel 1986, Vitousek & Sanford 1986) and soil P levels in our sites are low (Holl & Zahawi 2014). Tree plantations typically increase in litterfall biomass and nutrients quickly within the first decade and then level out thereafter (Lugo 1992), but the rates are highly

dependent on the species planted (Lugo 1992, Parrotta 1999, Siddique *et al.* 2008).

Whereas litterfall biomass and nutrient inputs in naturally regenerating plots increased since the last study, values are at the lower end of those reported in the literature at this stage in recovery (Ewel 1976, Marín-Spiotta *et al.* 2008, Ostertag *et al.* 2008). This result is consistent with the limited woody recruitment and aboveground biomass quantified in these plots, which is most likely due to competition with pasture grasses (Holl & Zahawi 2014, Holl *et al.* 2017); a possible alternative is slower growth rates at our premontane wet forest sites. Brown and Lugo (1982) conclude that litterfall is highest at an intermediate ratio of temperature to precipitation; however, our sites have comparatively lower temperature to lowland sites where most tropical secondary forest litterfall studies have been conducted (*e.g.*, Ewel 1976, Ostertag *et al.* 2008) and relatively high rainfall (3–4 m/yr), which leads to a low ratio.

**LITTERFALL AND NUTRIENT DYNAMICS OVER TIME.**—We found a substantial shift in the litterfall contribution of the four planted species in just 7 yr. The most notable shift was a dramatic increase in the percentage of litterfall comprised by *V. guatemalensis* in islands and plantations. At the same time, the percentage of litterfall comprised by *I. edulis* was reduced to approximately a quarter of that reported in the earlier study. This shift reflects the substantial mortality of *E. poeppigiana* and *I. edulis* (Table 1) during this time interval. *Vochysia guatemalensis* was the species with the highest basal area increment during the same period and not surprisingly has been recommended for agroforestry systems because it grows quickly (Piotto *et al.* 2003, Redondo-Brenes 2007) and produces large amounts of litter that decompose fairly quickly (Byard *et al.* 1996).

The shift in species composition drove substantial changes in relative nutrient inputs across treatments. We found higher N concentrations in islands and plantations than in the natural regeneration and the 7- to 9-yr-old secondary forests at the first sampling (Celentano *et al.* 2011), whereas there was no treatment-level difference for percent N concentrations after 10–12 yr. Indeed, foliar N concentration in the plantation decreased from 2.4 to 2.0 across the two sampling periods, reflecting the decreased dominance of litterfall by the two N-fixing species. The two N-fixing species likely played a critical role in the early successional phase by suppressing grass and herbaceous cover competition due to their rapid initial growth, canopy closure, and litter production, and by increasing N-availability (Siddique *et al.* 2008, Chaer *et al.* 2011, Batterman *et al.* 2013, Menge & Chazdon 2016); these effects decreased over time due to mortality, lessening the impact of planted, N-fixing trees on long-term successional trajectories. Similarly, Batterman *et al.* (2013) show that N-fixing tree species provided >50 percent of the N that fueled tree growth in the first 12 yr of a reforestation study in Panama, but that the nodulation rate declined in older sites.

Inputs of major cations (Ca, Mg, K), P, and most of the metals (Cu, Mn, and Fe) were typically highest in plantations, intermediate in islands, and lowest in plantations in the first sampling period. By

the second sampling period, inputs of all these nutrients had shifted so values for plantation and island treatments were similar and both were greater than natural regeneration. This shift largely reflects the substantial change in litterfall biomass over time, which overwhelms minor differences across treatments in litterfall nutrient concentrations, a number of which were slightly lower in the plantations at the second sampling period.

The contribution by unplanted dicots to overall litter production was substantially greater in islands than in plantations, suggesting greater biomass development of other species in this treatment. This supports the theory of applied nucleation, which predicts that islands should facilitate the colonization of naturally recruiting species (Yarranton & Morrison 1974). Islands attract seed dispersers (Fink *et al.* 2009), increasing the dispersal of zoochorous seeds, resulting in higher seed density and species richness as compared to open pastures (Zahawi & Augspurger 2006, Cole *et al.* 2010, Reid *et al.* 2015). In addition, islands increase spatial heterogeneity which likely facilitates the establishment and growth of new recruits and results in recruitment values that are greater than passive restoration and similar to those found in plantations, despite the fact that a much smaller area was planted initially (Holl *et al.* 2013, Zahawi *et al.* 2013). Similarly, Saha *et al.* (2013) found higher basal area of recruits in 10- to 26-yr-old *Quercus* spp. island as compared plantation plantings in Germany. The higher diversity of species represented in litterfall in islands could accelerate nutrient cycling (Lanuza 2016), particularly given that *I. edulis* litter decomposes fairly slowly due to the presence of polyphenolics (Palm & Sanchez 1990).

Our results demonstrate that restoration treatment effects on litterfall and nutrient inputs can change rapidly, underscoring the importance of not drawing conclusions based on short-term or single site studies. Inputs of the cations Ca, Mg, and K at least tripled in the island and natural regeneration treatments between the two sampling periods. The combined shift in the dominance of planted species (*i.e.*, decline of N-fixing species and increase in *V. guatemalensis*) and the increased recruitment of unplanted species means that a decade after treatment establishment islands has similar inputs of most nutrients as the plantation and reference forest. These results in turn support the idea that applied nucleation is a viable alternative restoration strategy to plantation-style planting that accelerates recovery of litterfall nutrient cycling and may promote a more diverse composition of litter over the long term, which could in turn affect the composition and diversity of soil invertebrates in our plots (Cole *et al.* 2016). Both the island and plantations treatments successfully restored most litterfall nutrient inputs level after a decade, but applied nucleation does so at a lower cost than a traditional plantation, as the cost of purchasing, planting, and clearing tree seedlings is scaled to the number of tree seedlings planted.

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## DATA AVAILABILITY

Data available from the Merritt Digital Repository: <http://n2t.net/ark:/13030/m5md3vvs>.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. Annual litter production separated by component (Mg/ha/yr) in natural regeneration, island, plantation ( $N = 5$ ), and reference forest treatments ( $N = 3$ ) measured in the second sampling period.

TABLE S2. Litterfall nutrient concentrations in the natural regeneration, island, plantation, and reference forest treatments in the second sampling period.

FIGURE S1. Experimental design showing litter traps.

FIGURE S2. Litterfall nutrient inputs in natural regeneration, island, and plantation treatments.

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