Low-cost agricultural waste accelerates tropical forest regeneration

Timothy L. H. Treuer¹,², Jonathan J. Choi¹, Daniel H. Janzen³, Winnie Hallwachs³, Daniel Pérez-Aviles⁴, Andrew P. Dobson¹, Jennifer S. Powers⁴, Laura C. Shanks⁵, Leland K. Werden⁶, David S. Wilcove¹,⁷

Lower-cost tropical forest restoration methods, particularly those framed as win–win business-protected area partnerships, could dramatically increase the scale of tropical forest restoration activities, thereby providing a variety of societal and ecosystem benefits, including slowing both global biodiversity loss and climate change. Here we describe the long-term regenerative effects of a direct application of agricultural waste on tropical dry forest. In 1998, as part of an innovative agricultural waste disposal service contract, an estimated 12,000 Mg of processed orange peels and pulp were applied to a 3 ha portion of a former cattle pasture with compacted, rocky, nutrient-poor soils characteristic of prolonged fire-based land management and overgrazing in Área de Conservación Guanacaste, northwestern Costa Rica. After 16 years, the experimental plot showed a threefold increase in woody plant species richness, a tripling of tree species evenness (Shannon Index), and a 176% increase in aboveground woody biomass over an adjacent control plot. Hemispheric photography showed significant increases in canopy closure in the area where orange waste was applied relative to control. Orange waste deposition significantly elevated levels of soil macronutrients and important micronutrients in samples taken 2 and 16 years after initial orange waste application. Our results point to promising opportunities for valuable synergisms between agricultural waste disposal and tropical forest restoration and carbon sequestration.

Key words: Área de Conservación Guanacaste, carbon sequestration, Citrus, Costa Rica, ecological restoration, fertilization, invasive grass, reforestation

Implications for Practice

- Agroindustry and other sectors in the tropics often produce large quantities of nutrient-rich by-products or waste streams, which in some cases require high net-cost disposal or processing.
- In countries with strong waste disposal laws, cost-negative “win–win” restoration projects through creative partnerships between the private sector and restoration ecologists can be achieved.
- Such initiatives also potentially result in significantly accelerated carbon sequestration.
- Documentation of the history as well as restoration and carbon benefits of one such initiative using orange waste are provided as a model for future undertakings.
- While aggressive safeguards should be taken to mitigate unintended consequences, at least in the case discussed here, concerns over negative environmental impacts associated with agricultural waste use proved unfounded.

Introduction

Improved methods for restoring tropical forests are important for meeting global conservation (Possingham et al. 2015) and climate change amelioration goals (Locatelli et al. 2015), given the capacity of second growth forests to support biodiversity (Dunn 2004; Bowen et al. 2007; Chazdon et al. 2009), and to sequester atmospheric carbon dioxide (Poorter et al. 2016). Tropical forest area is declining (Asner et al. 2009; Hansen et al. 2013) and calls have been made for large-scale reforestation of degraded lands (Janzen 1988a, 1988b; Dobson 1997; Lamb et al. 2005; Chazdon 2008, 2014). Tropical forest restoration, however, is often expensive (Lamb et al. 2005), particularly...
when land use has resulted in increased soil compaction, decreased soil organic carbon, and decreased nutrient-storing capacity (Hamza & Anderson 2005; Ohsowski et al. 2012), and when native tree saplings and seedlings must compete intensively with invasive plants (Holl et al. 2000; D’Antonio & Meyerson 2002). To date, however, few studies have considered the possibility that large-scale application of agrowaste can catalyze successional processes on degraded lands through amelioration of the abiotic conditions and/or competition that prevents woody seedling establishment. A Web of Science search with the terms “forest restoration” and “agricultural waste” or “agricultural by-product” or “crop residue” yielded results related only to the use of municipal solid wastes and/or sewage sludge (Shiralipour et al. 1992; Cellier et al. 2012), various forms of biochar derived from agricultural sources (Thomas & Gale 2015), and “Bokashi” (fermented agricultural by-products: Jaramillo-López et al. 2015). Additional gray literature reports of the use of composts, biosolids, and sewage sludge for soil remediation or forest restoration also exist (Rathinavelu & Graziosi 2005; U.S. EPA 2007), but the authors could not find well-documented examples of the use of direct application of agricultural waste products for forest restoration.

However, a lack of peer-reviewed studies data based on Web of Science or other readily accessible gray literature does not imply that trials or experiments on the use of direct application of agricultural waste for forest restoration have not been conducted.

Here we report on an orange waste biodegradation project in Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (Jimenez 1998, 1999; Escofet 2000; Janzen 2000; Daily & Ellison 2002) and document how this management project, conducted through an agricultural waste disposal service contract, has changed soil conditions and led to accelerated forest regeneration (in terms of woody biomass recovery and tree species accumulation) on heavily degraded, abandoned pasture characterized by compacted, rocky, nutrient-poor soils. The site was previously not allowed to regenerate for a century or more because of active grazing and prescribed burning prior to its incorporation into Guanacaste National Park in 1989 (later formally incorporated into the larger ACG in 1994 around which time all remaining cattle were fully removed from the park). These edaphic conditions combined with the continued presence of invasive jaragua (Hyparrhenia rufa) grass are thought to be the primary barriers to rapid natural regeneration in this area.

**Project History**

In 1991–1992, Del Oro S.A., an orange juice company, established thousands of hectares of orange (Citrus × sinensis) plantations near the town of Santa Cecilia, Guanacaste Province, in northwestern Costa Rica. These plantations abut ACG (http://www.acguanacaste.ac.cr) and occupy a once-forested ecosystem that is an interface between Costa Rican lowland rainforest and dry forest (Janzen & Hallwachs 2016). By 1995, the first juice oranges were available and D. Janzen (hereafter D.H.J.) asked Del Oro about the plans for disposing of the orange waste from its newly constructed extraction plant (Janzen 2000). The orange waste was a product of both machine-removal of juice as well as a second machine processing to remove most of the essential oils from the rind, a common step taken with citrus crops (Weiss 1997). The company replied it was going to construct a multimillion dollar drying and pelleting plant to make cattle feed of the waste (Daily & Ellison 2002). From the ACG viewpoint, the orange waste seemed to be an ideal food source for one or more of the estimated 375,000 species living in ACG (D. Janzen 2017, University of Pennsylvania, personal communication). Seeking win–win partnerships with surrounding landholders, D.H.J. offered a different plan for the orange waste: biodegrade it on recently incorporated degraded pastureland within ACG. In return for this agricultural waste management, Del Oro could donate its forested land at the margins of ACG that it had no intention of cultivating, and eventually provide cash payments. An experiment was born. No active planting or deliberate seeding of the site was planned as the necessary and sufficient justification for the collaboration was anticipated win–win biodegradation of agricultural waste; forest restoration was a secondary consideration albeit anticipated as a significant ancillary benefit.

On 14 May, 1996, at the beginning of the rainy season following the usual 5-month dry season, Del Oro donated 100 dump truckloads of orange processing waste (~1,200 Mg), which was spread on about 0.25 ha of centuries-old ACG pasture (termed “Modulo I”). At that time, it was densely covered with introduced and ungrazed African pasture grasses (primarily H. rufa) dotted with a few species of native shrubs. Eighteen months later, with no further treatment, the deposition had created a deep black loam soil, and all grasses (whose roots had presumably been killed by the anoxic conditions created by the orange waste) had been replaced by broad-leaved herbs (see Fig. S1, Supporting Information). The primary biodegraders of the orange waste were the larvae of three species of hoverflies (Syrrphidae, unknown species), an abundant soldier fly (Stratiomyidae, Hermetia illucens), and their accompanying fungi and microbes (Janzen personal observation; Jimenez 1998), all common members of the decomposition process for fallen wild fruit crops in the adjacent ACG forests.

With these experimental results of the pilot study in hand, ACG developed a formal contract with Del Oro to biodegrade 1,000 truckloads (~12,000 Mg) of processed orange waste per year for 20 years in exchange for 1,600 ha of intact primary forest land owned by Del Oro that lay contiguous with ACG forest at 400–700 m elevation on the slopes of Volcan Orosi and Orosilito (Janzen 2000; Daily & Ellison 2002). In the beginning of the 1998 dry season (January), the first 1,000 truckloads were delivered to a 3 ha patch of highly degraded ACG pasture (termed “Modulo II”), a few kilometers east of Modulo I. This patch was selected for its convenient accessibility to trucks carrying orange waste from a roughly 1 × 1–km (100 ha) extent of largely homogenous former pasture. The waste was left to biodegrade without further treatment. The project was terminated after this step due to a complex series of politicized events that took place over the following 3 years. These events began with a lawsuit filed by a competing orange processing company on the grounds that Del Oro and ACG staff had
sullied a national park (Escofet 2000). However, the anticipated biodegradation process at Modulo II continued and resulted in the disappearance of the orange waste. For additional historical details on the Modulo II site and its context within the history of ACG as a landscape-level forest restoration project, see Janzen (2000), Daily and Ellison (2002), and Allen (2001). While the orange waste project at Modulo II represents an unreplicated treatment, such uniqueness has famously not prevented deep insights from analogous ecological studies (e.g. Whittaker et al. 1989; Savchenko 1995; Silvertown et al. 2006). The treated area of Modulo II is in fact slightly larger than the entire Park Grass Experiment, arguably the longest-running and among the most important ecological experiments ever conducted (Silvertown et al. 2006).

Here, we explore the current outcome of the Modulo II biodegradation project in terms of impacts on soil chemistry, specifically concentration and bulk density of nutrients, and forest recovery, specifically species richness and evenness of trees, canopy closure, aboveground biomass, and numbers of saplings. Our point of comparison is adjacent untreated, abandoned pasture. We choose to compare the Modulo II site to adjacent untreated pasture rather than old-growth forest (by using compositional similarity or other metrics benchmarked against old-growth forest) given the lack of suitable, nonriparian old-growth forest to serve as a baseline of comparison. Moreover, we feel this comparison best reflects the actual opportunities that may arise if orange waste is found to benefit reforestation. We evaluate three hypotheses: deposition of orange waste, careful monitoring did not document any fires at either the control or treatment sites.

Methods

Study Site and Biodegradation

The study site Modulo II is located on the former La Guitarra ranchland at the east end of ACG’s Sector El Hacha (11.028°N, 85.523°W; 290 m above sea level). The site is located at the northwestern base of Volcan Orosí and at the eastern edge of the ACG dry forest where it begins to intergrade with the ACG rainforest. Species composition of the forest fragments in the surrounding landscape shows a transition between dry forest and rainforest flora (Janzen & Jimenez unpublished data). The ranchland of La Guitarra occupied approximately 1,000 ha and is believed to have been cleared in the 1600s or 1700s, and with the exception of stream buffers, remained unrestored until the advent of this project. Modulo II was located in the northeast corner of an approximately 100 ha block of contiguous former pasture within La Guitarra. Before application of orange mulch in 1998, the site was covered primarily by Hyparrhenia rufa, and dotted with occasional shrubby trees, primarily Curatella americana and Byrsonima crassifolia. No differences in vegetation structure or composition were noted between the treatment area and the approximately 100 ha of pasture surrounding Modulo II prior to application of orange waste (D. Janzen 2017, University of Pennsylvania, personal communication).

In 1998, 1,000 truckloads of orange waste (described above) were applied to a 3 ha plot (hereafter “orange waste treatment”) on the eastern side of a single-track dirt access road running alongside Modulo II. The organic material was spread into a layer approximately 0.1–0.5 m thick by Del Oro using heavy machinery (Mata 1998), with an estimated weight at the time of application of approximately 400 kg/m² of which 320 kg/m² was water, and 80 kg/m² was organic waste (Universidad Nacional 1999), though D.H.J. believes the true mass of orange waste was about half that value (D. Janzen 2017, University of Pennsylvania, personal communication). Chemical analyses determined that the organic waste was 13% cellulose, 8% protein, 68% carbohydrate, 4% fats, and 5% ash (Universidad Nacional 1999). Nutrient surveys of the orange waste found 14.0 g Ca, 9.7 g K, 0.9 g Mg, and 1.2 g P per 1.0 kg of dry orange waste (Del Oro 1998).

Four months after initial deposition, there was still a layer of 0.1–0.2 m of organic matter at the site (Janzen, personal observation; Mata 1998). At no point were seedlings planted or attempts made to increase seed rain at the site, though the orange waste was anticipated to remove grasses believed to be competing with seedlings. For all variables, we compare measurements made within the 3 ha site receiving agrowaste to the adjacent untreated abandoned pasture (hereafter “control”). Only the 3 ha closest to the treatment site were surveyed, despite the 100 ha extent of the largely homogenous untreated former pasture contiguous with the treatment site. In the years following the application of orange waste, careful monitoring did not document any fires at either the control or treatment sites.

Soil Sampling

We used two sets of soil samples to quantify initial and persistent changes in soil chemistry resulting from orange waste deposition. The first set of samples was collected and analyzed in 2000 by L.C.S. and the second set was collected in 2014 by J.J.C. Samples were analyzed using different but comparable methods. In 2000, six composite samples of 20 subsamples each were taken from the orange waste treatment site. Six composite control samples of 20 subsamples each were then taken from untreated pasture to the north and east of the orange waste treatment plot (see Appendix S1 for details on the exact sampling scheme). pH, organic matter, and concentrations of extractable Al³⁺, P, Ca, Mg, K, Cu, Fe, and Zn were measured for each sample from control and treatment plots. Sampling protocol details can be found in Appendix S1. Data from control and treatment samples were compared using single-tailed Student’s t-tests in Statgraphics (Rockville, MD, U.S.A.).

A different soil sampling protocol was implemented in July 2014 by J.J.C. and J.S.P. because they were unaware of the 2000 soil sample collection. Because only some of the exact boundaries of the orange waste treatment area were clearly demarcated in 2014, soil samples were taken from a 50 × 50 m grid within the central core of the orange waste treatment area. An identical grid was created on the opposite side of the access...
road in the control to create a sampling design that captured a similar amount of landscape heterogeneity.

As opposed to 12 composite samples of 20 subsamples from 2000, in 2014, 18 composite soil samples were taken of 9 subsamples each. These 2014 subsamples were collected to a depth of 0.1 m within a 1-m² area next to each of nine equidistant points in the grid mentioned above (see Appendix S1 for additional details). Soils were analyzed for percent carbon, nitrogen, and Mehlich III-extractable elements at the Research Analytical Laboratory at the University of Minnesota, Minneapolis, MN, U.S.A. Welch’s unequal variance t-tests and Wilcoxon rank-sum tests were used to compare the data depending on the normality. As a drying oven was not available in 2014, the sampling grids were revisited in July 2016 and 12 additional soil samples were taken (six from the orange waste treatment site and six from the control) using a 0.1 m tall, 0.07 m diameter soil core ring, and oven-dried at 100°C for 24 hours prior to weighing to determine bulk density. Bulk densities were used to estimate total nutrient pools for each nutrient in the top 0.1 m of the treatment and control sites (see Appendix S1 for additional details).

Vegetation
To quantify changes in vegetation structure and composition resulting from the orange waste deposition, three 100 x 6–m transects were established within the orange waste treatment area at a distance 50, 75, and 100 m from the access road dividing the control and orange waste treatment plots in June 2014. An equivalent set of transects was established in the control pasture on the opposite side of the road. Vegetation was sampled following the approach of Powers et al. (2009). All trees larger than 5 cm diameter at breast height (dbh) and taller than 1.3 m within 3 m of the centerline of each transect were tagged, dbh was measured, and identified to species by J.J.C., D.P.A., and T.L.H.T. All saplings <5 cm dbh and taller than 1.3 m that were growing within 3 m of the centerline of each transect were measured for dbh, but were not tagged or identified, to account for their aboveground biomass. All size measurements were completed during the first 2 weeks of July 2014. Individual-based rarefaction curves were constructed to quantify differences in species richness of trees.

Aboveground biomass was calculated for control and orange waste treatment sites from transect dbh data using allometric scaling equations from van Breugel et al. (2011) and wood density measurements from Powers and Tiffin (2010) and the Dryad Wood Density Database (Dryad, Durban, NC, U.S.A.) (Chave et al. 2009). Owing to the unreplicated nature of the Modulo II management application, we used the data available to calculate the probability that one would observe a difference in aboveground biomass as great as was actually observed assuming the trees at the site were randomly distributed. This was done by constructing a null model, wherein the estimated biomass of each measured tree was randomly assigned to “orange waste treatment” and “control” populations with 50% probability. We conducted 1,000,000 such trials and ranked our observed difference by percentile as a nonparametric test of significance.

To further determine the degree to which orange waste deposition resulted in forest regeneration after 16 years, solar radiation indices, percent of visible sky, and leaf area indices were determined using HemiView software (Delta-T Devices Ltd, Cambridge, UK) and images taken with a fisheye lens on 11 July, 2014 (Rich et al. 1999). Photos (n = 66) were taken 1.3 m off the ground every 10 m along each transect within each set of three transects in both the waste application plot and the control plot. A tripod was used for stabilization and a spherical level was used to ensure that the camera was level. The photos were taken during the late morning and early afternoon at times when the sky was deeply overcast to reduce glare in the photos. Wilcoxon rank-sum tests were used to compare data.

Results
Soils
The application of orange waste led to dramatic differences in soil available nutrients in both 2000 and 2014 as reflected in the differences between orange waste treatment and control samples (Table S1; Fig. S3). In 2000, soils in the orange waste treatment site showed increases in pH relative to the control (Student’s one-tail t-test, n = 6, p < 0.01, 10.9% increase), and significantly higher concentrations, relative to the control, of extractable K, Ca, Cu, Fe, and Zn (Table S1). The initial increases in nutrient availability were largely maintained 14 years later (Table S1). Moreover, orange waste deposition resulted in significant increases in the macronutrients N (Welch t-test, n = 18, p < 0.001, 28.3% increase) and Mehlich III extractable P (Wilcoxon, p < 0.001, 157.8% increase), and micronutrients Mg (Welch, p = 0.002, 62.9% increase) and Mn (Welch, p = 0.012, 77.0% increase). Finally, orange peel deposition resulted in a decreased C:N ratio (Welch, p < 0.001, 17.4% decrease), when comparing 2014 orange waste treatment and control samples.

Bulk density was significantly higher in the control than in the treatment (Welch, p = 0.022, 14.0%, Table S1). However, even when correcting for the reduced mass in the top 0.1 m of soil at the control and orange waste treatment sites, the significant disparities in individual nutrients noted above persisted, albeit the magnitude of the difference was reduced (see Table S2).

Vegetation
Deposition of orange peels resulted in differences in vegetation cover 16 years later that were readily visible to the naked eye (Fig. 1). Within the total surveyed area of 1,800 m² in the control site, we found 149 trees with a dbh greater than 5 cm from 8 different species from 7 different families, compared to 133 trees, representing 24 species from 20 families in the equivalent area of the treatment (see Table S3 for full species lists). These 133 trees along the treatment transects solely consist of new arrivals to the plot, as post-orange waste deposition monitoring documented a die-off of all trees present at the time of deposition, presumably through asphyxiation of roots. Of the 149 control plot trees, 134 (89.9%) were either Curatella americana or Byrsonima crassifolia (Table S3; Fig. 2) both species are associated with heavily degraded cattle.
Regenerating tropical forest with orange waste

Figure 1. Aerial imagery of orange peel fertilized treatment area (mosaic of >10 m trees and dense mats of herbaceous shrubs and vines to right of dirt road) and unfertilized control (rocky expanse of grass with scattered approximately 2 m tall trees to left of dirt road) taken by quadcopter drone in July 2015.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Species</td>
</tr>
<tr>
<td>Apeiba tibourbou</td>
<td>Apeiba tibourbou</td>
</tr>
<tr>
<td>Ardisia revoluta</td>
<td>Ardisia revoluta</td>
</tr>
<tr>
<td>Bursera simaruba</td>
<td>Bursera simaruba</td>
</tr>
<tr>
<td>Byrsonima crassifolia</td>
<td>Byrsonima crassifolia</td>
</tr>
<tr>
<td>Cecropia peltata</td>
<td>Cecropia peltata</td>
</tr>
<tr>
<td>Cochlospermum vitifolium</td>
<td>Cochlospermum vitifolium</td>
</tr>
<tr>
<td>Cordia alliodora</td>
<td>Cordia alliodora</td>
</tr>
<tr>
<td>Cordia panamensis</td>
<td>Cordia panamensis</td>
</tr>
<tr>
<td>Curatella americana</td>
<td>Curatella americana</td>
</tr>
<tr>
<td>Ficus spp 1</td>
<td>Ficus spp 1</td>
</tr>
<tr>
<td>Ficus spp 2</td>
<td>Ficus spp 2</td>
</tr>
<tr>
<td>Genipa americana</td>
<td>Genipa americana</td>
</tr>
<tr>
<td>Gliricidea sepium</td>
<td>Gliricidea sepium</td>
</tr>
<tr>
<td>Guazuma ulmifolia</td>
<td>Guazuma ulmifolia</td>
</tr>
<tr>
<td>Luehea seemannii</td>
<td>Luehea seemannii</td>
</tr>
<tr>
<td>Muntingia calabura</td>
<td>Muntingia calabura</td>
</tr>
<tr>
<td>Piper spp</td>
<td>Piper spp</td>
</tr>
<tr>
<td>Sapum glandulosum</td>
<td>Sapum glandulosum</td>
</tr>
<tr>
<td>Schefflera morototoni</td>
<td>Schefflera morototoni</td>
</tr>
<tr>
<td>Simaruba glauca</td>
<td>Simaruba glauca</td>
</tr>
<tr>
<td>Spondias mombin</td>
<td>Spondias mombin</td>
</tr>
<tr>
<td>Tabebuia rosea</td>
<td>Tabebuia rosea</td>
</tr>
<tr>
<td>Trichilia martiana</td>
<td>Trichilia martiana</td>
</tr>
<tr>
<td>Vachellia collinsii</td>
<td>Vachellia collinsii</td>
</tr>
<tr>
<td>Vernonia patens</td>
<td>Vernonia patens</td>
</tr>
<tr>
<td>Xylopia frutescens</td>
<td>Xylopia frutescens</td>
</tr>
</tbody>
</table>

Figure 2. Relative abundance of tree species in orange waste fertilized (treatment) and unfertilized (control) transects.

pastures in this region (Condit et al. 2011). In comparison, six treatment plot species had more than 10 individuals and a maximum abundance of just 16 individuals and included two species (Table S3; Fig. 2), *Trichilia martiana* (12 individuals) and *Xylopia frutescens* (11 individuals) that are associated with advanced secondary growth or mature forest (Condit et al. 2011). The other four most common treatment trees were *Cercropia peltata* (16 individuals), *Guazuma ulmifolia* (15 individuals), *Cochlospermum vitifolium* (13 individuals), and *C. americana* (11 individuals) (Table S3; Fig. 2). The Shannon Index value for transects in the orange waste treatment area was roughly triple the value of the control transects (Table 1), and differences in species richness were taken to be statistically significant ($p < 0.05$) based on nonoverlapping 95% confidence intervals of rarefaction curves (Fig. 3). There were 820 saplings in the treatment compared to 353 in the control.

Despite containing 10% fewer total stems >5 cm dbh, the estimated aboveground woody biomass of trees and saplings within the orange waste treatment was nearly triple.
Regenerating tropical forest with orange waste

Table 1. Comparison of species richness, diversity, and evenness indicators for tree species in control and treatment in 2014.

<table>
<thead>
<tr>
<th>Index</th>
<th>Control</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td>8</td>
<td>24</td>
</tr>
<tr>
<td>Unique species</td>
<td>3</td>
<td>19</td>
</tr>
<tr>
<td>Shannon Index</td>
<td>0.96</td>
<td>2.82</td>
</tr>
<tr>
<td>Gini-Simpson Index</td>
<td>0.47</td>
<td>0.93</td>
</tr>
<tr>
<td>Inverse Simpson Index</td>
<td>1.89</td>
<td>13.70</td>
</tr>
<tr>
<td>Chao species richness</td>
<td>12.5</td>
<td>30</td>
</tr>
<tr>
<td>Singletons</td>
<td>3</td>
<td>6</td>
</tr>
</tbody>
</table>

Figure 3. Individual-based rarefaction and extrapolation of tree species richness in treatment (pink) and control (blue). Shaded area indicates the 95% confidence interval for the extrapolated or interpolated species richness.

(73.69 Mg/ha) that of the control (26.73 Mg/ha). This observed difference in biomass (46.96 Mg/ha) was higher than the difference observed in 99.87% of null model trials (Fig. 4). The difference in biomass remained significant after removing an outlier tree from the treatment dataset and rerunning the model (Fig. S5).

Canopy variables indicated a higher degree of canopy closure in the treatment transects than in the control transects (Fig. 5). Leaf area index (LAI) and percent visible sky calculated from hemispherical photography along the treatment transects (mean ± standard error: 2.184 ± 0.996 and 17.2 ±11.3%, respectively) were significantly higher (Wilcoxon, p < 0.001) than LAI and percent visible sky along control transects (0.355 ± 0.367 and 59.2 ±15.9%, respectively).

Discussion

Our results provide nuance and detail to what was overwhelmingly obvious during informal surveys in 1999 and 2003: depositing orange waste on this degraded and abandoned pastureland greatly accelerated the return of tropical forest, as measured by lasting increases in soil nutrient availability, tree biomass, tree species richness, and canopy closure. The clear implication is that deposition of agricultural waste could serve as a tool for effective, low-cost tropical forest restoration, with a particularly important potential role at low-fertility sites. As far as the authors are aware, this is the first demonstration in the scientific literature of the forest restoration potential of direct application of agricultural waste, without involving composting (Shiralipour et al. 1992; U.S. EPA 2007), pyrolyzation (Thomas & Gale 2015), or fermentation (Jaramillo-López et al. 2015). Direct application of agricultural waste, of course, assumes that conditions for forest recovery are otherwise suitable (e.g. nearby seed sources, protection from fires) and that fertilization with agrowaste is solving a disposal problem, rather than competing with some other more lucrative downstream use for the waste (e.g. Rathinavelu & Graziosi 2005), as well as a favorable socio-political environment. The degree to which non-orange agrowastes (or orange wastes with essential oils present) could be used to achieve similar results depends on the specific mechanisms by which forest recovery is accelerated (in particular, grass suppression versus fertilization versus a synergy of the two). It is also not clear from our study to what extent the removal of grazers and suppression of fire are required to achieve successful restoration using agricultural waste.

Soil Properties and Nutrients

The edaphic characteristics we measured showed dramatic changes toward increased fertility as a result of orange waste deposition. Key macro- and micronutrients (N, P, K, Ca, Mg,
Mn, Cu, Fe, Zn) showed significantly elevated concentrations in topsoil in the treatment site relative to the control 16 years after the initial orange waste deposition. The addition of nutrient rich organic material likely played an important role in accelerating the recovery of aboveground biomass and increasing the diversity of woody plants species in the orange waste treatment site relative to the control. However, the relative contributions of direct fertilization effects, indirect fertilization effects (e.g. attracting or enabling the presence of facilitating species), and nonfertilization effects (e.g. grass suppression) cannot easily be teased apart. Nonetheless, the soil sample results from 2000 and 2014 hold several important clues for how orange waste deposition may have improved soil conditions.

The reduction in soil acidity observed in 2000 in the treatment samples relative to control samples suggests that the incorporation of Ca$^{2+}$ and K$^+$ cations may have increased the pH of the soil by competing with H$^+$ ions for adsorption sites (Gardiner & Miller 2008). These two nutrients occur in high concentrations in biodegraded orange peels (Del Oro 1998) and were found at elevated levels in the topsoil in the treatment site in 2000 and 2014. The persistence of Ca$^{2+}$ and K$^+$ suggests that the cation exchange capacity of the fertilized soils was not a short-lived effect. This makes the addition of orange peels particularly beneficial for the dystrophic and acidic soils characteristic of both the Modulo II site and many cleared tropical forests around the world (Guariguata & Ostertag 2001).

One difference in macronutrients between orange waste treatment and control sites in the 2000 and 2014 surveys worthy of discussion is phosphorus. In 2014, there was 221.5% more P in the top 0.1 m of soil in the orange waste treatment site than in the control after correcting for bulk density differences. While the difference in P between the two sites is striking, the total additional amount of P in the top 0.1 m of soil at the treatment site is as little as 0.3% of the P originally present in the deposited orange waste, a much lower remaining proportion than for Ca, Mg, or even leaching-prone K. Combined with the dearth of nitrogen-fixing species common to young tropical forests (Batterman et al. 2013), this is suggestive of a P-limited system.

In summary, the effect of the orange peel deposition on edaphic conditions was dramatic and could serve as a reasonable partial explanation for the difference in tree species composition and aboveground biomass between orange waste treatment and control. Soil fertility showed dramatic signs of improvement both 2 years and 16 years after fertilization.

### Vegetation

A dramatic increase in species richness and evenness as a result of the orange waste deposition is unmistakable and would only further increase with the inclusion of woody shrubs (e.g. Vachellia spp.), vines, epiphytes, and understory herbaceous species, which we did not quantify. This expectation is supported by the presence of taller trees that are better able to support lianas, epiphytes, and shade-tolerant plants (Choi & Treuer unpublished data) within the orange waste treatment area.

When assessing secondary forests that are the product of restoration efforts, several authors have called for careful attention not just to the conditions following restoration, but also the trajectory that the forest is likely to follow, with respect to both flora (Brown & Lugo 1990; Chazdon et al. 2016) and fauna (Dent 2010). Orange waste application resulted in a considerable increase in the system’s fire resilience via suppression of highly inflammable grasses. Additionally, the more than doubling in sapling number in the treatment area relative to the control suggests that differences in aboveground biomass are likely to be maintained into the future. Finally, the presence of Cecropia peltata and Ficus sp. individuals in the treatment but not control area is important as both are known to provide important fruit resources to many forest dwelling animals (Fleming & Williams 1990).

### Management and Policy Implications

When the contract between Del Oro and ACG was voided by the Costa Rican government Comptroller General in 1999 and ACG staff given an impossible-to-execute order by the Sala Cuarta to remove the orange waste that had long since degraded, substantive (as opposed to aesthetic) concerns with the biodegradation of the orange waste reportedly centered on the notion that the mulch would become a breeding ground for pests or pathogens or that there would be significant leaching of problematic compounds into surrounding waterways, most prominently the essential oil d-limonene, which was claimed to...
be a carcinogen (Escofet 2000). These concerns turned out to be baseless; an independent team of scientists dismissed concerns over pollution and threats to nearby producers as outlandish (Escofet 2000) and 1,2-limonene has been found not to be carcinogenic (Asamoto et al. 2002). Nevertheless, subsequent attempts to revive or establish similar restoration projects using agricultural waste have stalled due to the potential partners not wishing to risk highly politicized litigation again. These ameliorated concerns combined with the overwhelmingly positive results of orange waste application on forest restoration suggest that agricultural waste could have considerable potential as a management tool for forest restoration, though certainly careful consideration of social, political, and idiosyncratic environmental conditions (e.g. potential for harsh chemical or biohazardous runoff into local waterways) is warranted. The potential harm from pesticides or other problematic compounds in particular merit careful consideration and safeguards. Assuming these conditions can be met, further explorations of using agricultural wastes for restoration should be encouraged and potentially subsidized through existing or future payments for ecosystem services schemes, such as already exist in Costa Rica (Daily & Ellison 2002), rather than aggressively prohibited.

When agroindustry produces nutrient-rich, but costly-to-dispose-of waste streams (as in the case of oranges in Costa Rica), there is an opportunity for low-cost (or indeed, cost-negative), scalable, biodiversity-friendly, carbon-sequestering ecological restoration. Given that the scale of biodiversity-friendly restoration activities is typically limited by cost (Lamb et al. 2005) or by sociopolitical prohibitions as is the case described here, the results of this management project suggest that this general approach should be widely trialed in a variety of settings, using a variety of agricultural inputs. While the agroindustry may well be aware these wastes could serve to achieve biodiversity and climate mitigation goals via accelerated forest regeneration, as this study underscores, achieving positive outcomes requires outreach on the part of restoration ecologists as well as favorable regulatory regimes.

Acknowledgments

This paper benefited considerably from discussions with S. Pacala, L. Hedin, and J. Socolar. We also acknowledge the work of K. O’Malley, L. Sheridan, J. Rowlett, G. Funes, B. Waring, M. M. Chavarria, and R. B. Segura in support of this project, as well as financial support from the Princeton Environmental Institute (including support from the Walbridge Fund), the Princeton Department of Ecology and Evolutionary Biology, The Office of the Dean of the College at Princeton University, The High Meadows Foundation, Garden Society of America and Área de Conservación Guanacaste.

LITERATURE CITED

Del Oro (1998) Compendio de documentos relacionada con las actividades de carácter ambiental de Del Oro. Del Oro, Guanacaste, Costa Rica

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

Appendix S1. Additional descriptions of soil sample collection methods and sampling design.
Figure S1. Photographs from the orange waste deposition from (a) May 14, 1996—Initial deposition at Modulo I site. (b) 1997—Photo of Modulo I approximately 18 months after the initial deposition.
Figure S2. Sampling design of Modulo II and surrounding area (not drawn to scale).
Figure S3. Violin density plots illustrating the distribution of nutrient concentrations and water content in treatment and control samples from 2014.
Figure S4. The sole outlier tree in terms of dbh was an individual Ficus sp., growing along one of the treatment transects, that was 15 standard deviations above median treatment dbh.
Table S1. Soil properties from samples taken in 2000 and 2014.
Table S2. Comparison of estimated mass of individual soil nutrients from initially deposited orange waste and in top 0.1 m of soil at control and treatment sites in 2014.
Table S3. Comparison of species composition between control and treatment plots for trees >5 cm dbh in July 2014.

Received: 20 February, 2017; First decision: 22 April, 2017; Revised: 15 June, 2017; Accepted: 15 June, 2017

Coordinating Editor: J. Leighton Reid