

5-2019

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Brett T. Wolfe  
*University of Puerto Rico*

Raúl Macchiavelli  
*University of Puerto Rico*

Skip Van Bloem  
*Clemson University, skipvb@clemson.edu*

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### Recommended Citation

Wolfe, BT, Macchiavelli, R, Van Bloem, SJ. Seed rain along a gradient of degradation in Caribbean dry forest: Effects of dispersal limitation on the trajectory of forest recovery. *Appl Veg Sci*. 2019; 22: 423–434. <https://doi.org/10.1111/avsc.12444>

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# Seed rain along a gradient of degradation in Caribbean dry forest: Effects of dispersal limitation on the trajectory of forest recovery

Brett T. Wolfe<sup>1</sup>  | Raúl Macchiavelli<sup>1</sup>  | Skip J. Van Bloem<sup>1,2</sup> 

<sup>1</sup> University of Puerto Rico, Department of Agroenvironmental Sciences, Mayagüez, Puerto Rico

<sup>2</sup> Baruch Institute of Coastal Ecology and Forest Science, Clemson University, Georgetown, South Carolina

## Correspondence

Brett T. Wolfe, Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancon, Republic of Panama.  
Email: btwolfe@gmail.com

## Present Address

Brett T. Wolfe, Smithsonian Tropical Research Institute, Balboa, Ancon, Republic of Panama

## Funding information

USDA McIntire-Stennis grant PR00MS014 [SJV], Ford Motors José Berrocal Scholarship for Environmental Studies in Puerto Rico [BTW].

Co-ordinating Editor: Borja Jiménez-Alfaro

## Abstract

**Questions:** Tropical dry forests that experience severe disturbances (e.g., fires) often remain degraded for long time periods, during which non-native grasses and trees dominate. One barrier to native tree regeneration in degraded areas may be seed dispersal limitation. To better understand how dispersal limitation influences recovery from degradation, we tested whether the mode and rates of seed dispersal differed in degraded sites dominated either by the exotic tree *Leucaena leucocephala* or open areas dominated by introduced pasture grasses. We also tested whether *L. leucocephala* stands facilitate the recruitment of native trees by increasing their seed input compared to open grass areas.

**Location:** Guánica Commonwealth Forest, Puerto Rico.

**Methods:** Seed rain was measured for one year in traps located within five vegetation types that ranged in degree of forest degradation from open grass to intact native forest.

**Results:** In open grass areas, seed rain density was similarly low for *L. leucocephala* and abiotically dispersed native trees (mean [95% CI] = 50.9 [15.1–171.0] vs. 34.2 [10.3–113.5] seeds m<sup>-2</sup> year<sup>-1</sup>), whereas it was even lower for animal-dispersed native trees (0.14 [0.03–0.67] seeds m<sup>-2</sup> year<sup>-1</sup>). Compared to open grass areas, *L. leucocephala*-dominated stands, even those with grass understories, had higher seed rain density of animal-dispersed trees (43.0 [12.9–143.6] seeds m<sup>-2</sup> year<sup>-1</sup>), but not abiotically dispersed trees (20.8 [6.3–68.5] seeds m<sup>-2</sup> year<sup>-1</sup>).

**Conclusions:** The dominance of *L. leucocephala* in disturbed Caribbean dry forests does not appear to be mediated by disproportionate seed arrival in open areas compared to native tree seeds. Rather, subsequent factors such as seed and seedling survival likely favor *L. leucocephala* in highly degraded areas. Since *L. leucocephala* stands increase the seed rain of animal-dispersed native trees, retaining them in highly disturbed Caribbean dry forests may facilitate the regeneration of native forests.

## KEYWORDS

dispersal limitation, facilitation, fire, Guánica forest, introduced species, *Leucaena leucocephala*, recruitment, resilience, seasonally dry tropical forest, secondary succession, seed rain

## 1 | INTRODUCTION

When ecosystems are disturbed by human activities, such as burning or bulldozing, they often experience persistent compositional and structural changes relative to pre-disturbance conditions. These changes represent ecosystem degradation and are generally associated with negative societal consequences (Putz & Redford, 2010; Ghazoul, Burivalova, Garcia-Ulloa, & King, 2015). For example, ecosystem services such as carbon storage and biodiversity conservation are reduced in degraded areas. In tropical regions alone, it is estimated that >60% of forested area is currently degraded (Lamb, Erskine, & Parrotta, 2005; Chaturvedi, Raghubansi, & Singh, 2017). Improving the degradation status of forests in order to offset carbon dioxide emissions and conserve biodiversity has become a global interest, such as through REDD+ (Vargas, Paz, & de Jong, 2013). Therefore, it is imperative to understand the ecological factors that drive recovery from degradation in disturbed ecosystems.

Persistent exotic plant communities in degraded areas indicate a failure of native species to recruit. For example, when tropical forests are highly degraded, they are often converted to grasslands dominated by exotic species, where native trees rarely recruit (Murphy & Lugo, 1986a; Nepstad, Uhl, Pereira, & da Silva, 1996). Various causes of recruitment failure include dispersal limitation (i.e., a failure of seeds to arrive at all sites suitable for recruitment), environmental filtering, and competition for resources (Ghazoul et al., 2015). As such, in highly degraded areas, tropical forest regeneration can be very slow and grassland communities can become persistent alternative states (Uhl, Buschbacher, & Serrao, 1988; Aide, Zimmerman, Herrera, Rosario, & Serrano, 1995; De la Peña-Domene, Martínez-Garza, & Howe, 2013). However, when exotic tree species establish in these areas, they may help native tree species to re-establish by increasing seed arrival, ameliorating environmental conditions, and reducing competition with grasses (Lugo, 2004; Romero-Duque, Jaramillo, & Pérez-Jiménez, 2007).

In intact tropical forests, dispersal limitation contributes to species diversity by slowing competitive exclusion (Dalling, Muller-Landau, Wright, & Hubbell, 2002). However, in highly degraded sites, dispersal limitation can impede forest regeneration because few tree seeds arrive in areas beyond forest edges (Holl, 1999; Wijdeven & Kuzee, 2000). Early colonizing trees reduce dispersal limitation in degraded areas by attracting seed-dispersing birds and bats (Wunderle, 1997). However, when early colonizing trees are exotic, they may lack features that attract dispersers, such as canopies adequate for perching or nutritious fruits and seeds. Furthermore, early colonizing trees may slow the input of ballistic and wind-dispersed seeds because they physically block their movement and reduce surface lift that carries these seeds long distances (Nathan & Katul, 2005). Nevertheless, exotic forests that displace exotic grassland communities may enhance native tree recruitment by ameliorating soil and microclimatic conditions and by suppressing grasses (Parrotta, Turnbull, & Jones, 1997; Lugo & Helmer, 2004).

Here, we explore the role of dispersal limitation in the successional patterns of highly degraded Caribbean dry forests. These areas are dominated by exotic forage grasses (e.g., *Pennisetum ciliare* (L.) Link, *Bothriochloa pertusa* (L.) A.Camus, and *Urochloa maxima* (Jacq.)

R.D.Webster) that are maintained as grassland-savannas by anthropogenic fires (Ewel & Whitmore, 1973; Francis & Parrotta, 2006; Wolfe & Van Bloem, 2012). Given sufficient time without burning, the exotic tree species *Leucaena leucocephala* (Lam.) de Wit (Fabaceae-Mimosoideae) commonly establishes in these grassland-savannas and dominates for >50 years (Ray & Brown, 1994; Molina Colón & Lugo, 2006; Pérez Martínez, 2007). *Leucaena leucocephala* is recognized as one of the most invasive tree species throughout the tropics (Richardson & Rejmanek, 2011), yet it may catalyze the regeneration of native Caribbean dry forests by serving as a nurse tree for native tree species (Santiago-García, Colón, Sollins, & Van Bloem, 2008).

Caribbean dry forests generally have depauperate seedbanks (Castilleja, 1991; Ray & Brown, 1994; Murphy & Lugo, 1995), so forest regeneration in areas cleared of rootstocks, either mechanically or through burning, is largely dependent on propagule input from outside the affected area. As such, seed rain is sequentially the first factor that limits forest recovery, while factors such as seed predation, seed germination, seedling survival and growth act subsequently to determine successional plant communities. However, few studies have tracked seed rain in tropical dry forests, let alone degraded areas, so the relative importance of propagule input versus subsequent factors in structuring secondary dry forests is not well understood.

In order to better understand how *L. leucocephala* comes to dominate degraded dry forest areas and how its dominance affects the capacity for native tree species to regenerate, we measured seed rain in stands with differing canopy and understorey compositions (i.e., native-tree canopies with woody understories, native-tree canopies with grass understories, *L. leucocephala* canopies with woody understories, *L. leucocephala* canopies with grass understories, and open grass areas). The stands formed a gradient of forest degradation (sensu Ghazoul et al., 2015), in that they ranged in their similarity to the reference state of undisturbed, intact forest. Various disturbances degraded the stands (Table 1), yet the stands also differed in their recovery rates, such that arrested succession resulted in non-equilibrium stable states with differing canopy and understorey compositions. Thus, our sampling design was able to assess the role that dispersal limitation plays in shaping regime shifts of alternative states of degraded forests.

Specifically, we tested the following hypotheses: (a) in the absence of fire, open grass areas become dominated by *L. leucocephala* trees because their seed input outnumbers that of native trees; and (b) *L. leucocephala* forests facilitate native tree regeneration by increasing the density and diversity of animal-dispersed tree seeds compared to open grass areas. Since there are few studies of seed rain in tropical dry forest (Derroire, Tigabu, Odén, & Healey, 2016), an additional goal was to compare seed rain density in a tropical dry forest to that of wetter tropical forests.

## 2 | METHODS

### 2.1 | Study Site

This study was conducted in the Guánica Commonwealth Forest, located within the dry forest zone of southwestern Puerto Rico

**TABLE 1** Characteristics of the vegetation and land-use history at each of the study sites

| Site     | Vegetation type (Canopy/Understorey) | Tree density (m <sup>-2</sup> ) | Percent <i>L. leucocephala</i> | Percent grass cover | Land-use history   |
|----------|--------------------------------------|---------------------------------|--------------------------------|---------------------|--|
| Cuevas   | Native/Woody                         | 0.59 (0.25)                     | 0 (0)                          | 0 (0)               | Selective cutting and goat grazing ca. 80 years prior                          |
|          | Native/Grass                         | 0.19 (0.06)                     | 0 (0)                          | 36 (24)             | Selective cutting and goat grazing ca. 80 years prior, wildfire 25 years prior |
|          | <i>L. leucocephala</i> /Woody        | 0.48 (0.31)                     | 44 (11)                        | 0 (0)               | Cattle grazing and agriculture ca. 80 years prior                              |
|          | <i>L. leucocephala</i> /Grass        | 0.37 (0.15)                     | 86 (17)                        | 30 (25)             | Cattle grazing and agriculture ca. 80 years prior                              |
|          | Open/Grass                           | 0.06 (0.02)                     | 2 (4)                          | 58 (21)             | Selective cutting and goat grazing ca. 80 years prior, wildfire 25 years prior |
| Ensenada | Native/Woody                         | 0.26 (0.06)                     | 8 (4)                          | 0 (0)               | Selective cutting prior  |
|          | Native/Grass                         | 0.27 (0.10)                     | 25 (17)                        | 33 (15)             | Selective cutting prior, grazing?  |
|          | <i>L. leucocephala</i> /Woody        | 0.45 (0.38)                     | 56 (22)                        | 0 (1)               | Cattle grazing, bulldozed ca. 20 years prior                                   |
|          | <i>L. leucocephala</i> /Grass        | 0.24 (0.13)                     | 64 (18)                        | 45 (21)             | Cattle grazing, bulldozed ca. 20 years prior                                   |
|          | Open/Grass                           | 0.06 (0.03)                     | 42 (19)                        | 83 (10)             | Cattle grazing, bulldozed ca. 20 years prior, wildfire?                        |
| La Hoya  | Native/Woody                         | 0.37 (0.12)                     | 8 (11)                         | 0 (0)               | Selective cutting and goat grazing ca. 80 years prior                          |
|          | Native/Grass                         | 0.11 (0.04)                     | 40 (10)                        | 23 (21)             | Selective cutting and goat grazing ca. 80 years prior, wildfire 8 years prior  |
|          | <i>L. leucocephala</i> /Woody        | 0.43 (0.20)                     | 70 (25)                        | 0 (0)               | Selective cutting and goat grazing ca. 80 years prior, wildfire 8 years prior  |
|          | <i>L. leucocephala</i> /Grass        | 0.54 (0.27)                     | 82 (16)                        | 37 (18)             | Selective cutting and goat grazing ca. 80 years prior, wildfire 8 years prior  |
|          | Open/Grass                           | 0.11 (0.04)                     | 76 (11)                        | 42 (25)             | Selective cutting and goat grazing ca. 80 years prior, wildfire 8 years prior  |
| Pitirre  | Native/Woody                         | 0.68 (0.67)                     | 7 (16)                         | 0 (0)               | Selective cutting and goat grazing ca. 80 years prior                          |
|          | Native/Grass                         | 0.19 (0.06)                     | 0 (0)                          | 28 (14)             | Selective cutting and goat grazing ca. 80 years prior, wildfire?               |
|          | <i>L. leucocephala</i> /Woody        | 0.79 (0.72)                     | 100 (0)                        | 2 (2)               | Agriculture ca. 20 years prior   |
|          | <i>L. leucocephala</i> /Grass        | 0.20 (0.05)                     | 100 (0)                        | 49 (20)             | Agriculture ca. 20 years prior   |
|          | Open/Grass                           | 0.04 (0.01)                     | 72 (41)                        | 61 (40)             | Selective cutting and goat grazing ca. 80 years prior, repeatedly burned       |

Notes: Values are means and standard deviation for the five traps in each vegetation type at each site. Tree density and percent *Leucaena leucocephala* were calculated using the ten trees nearest each trap.

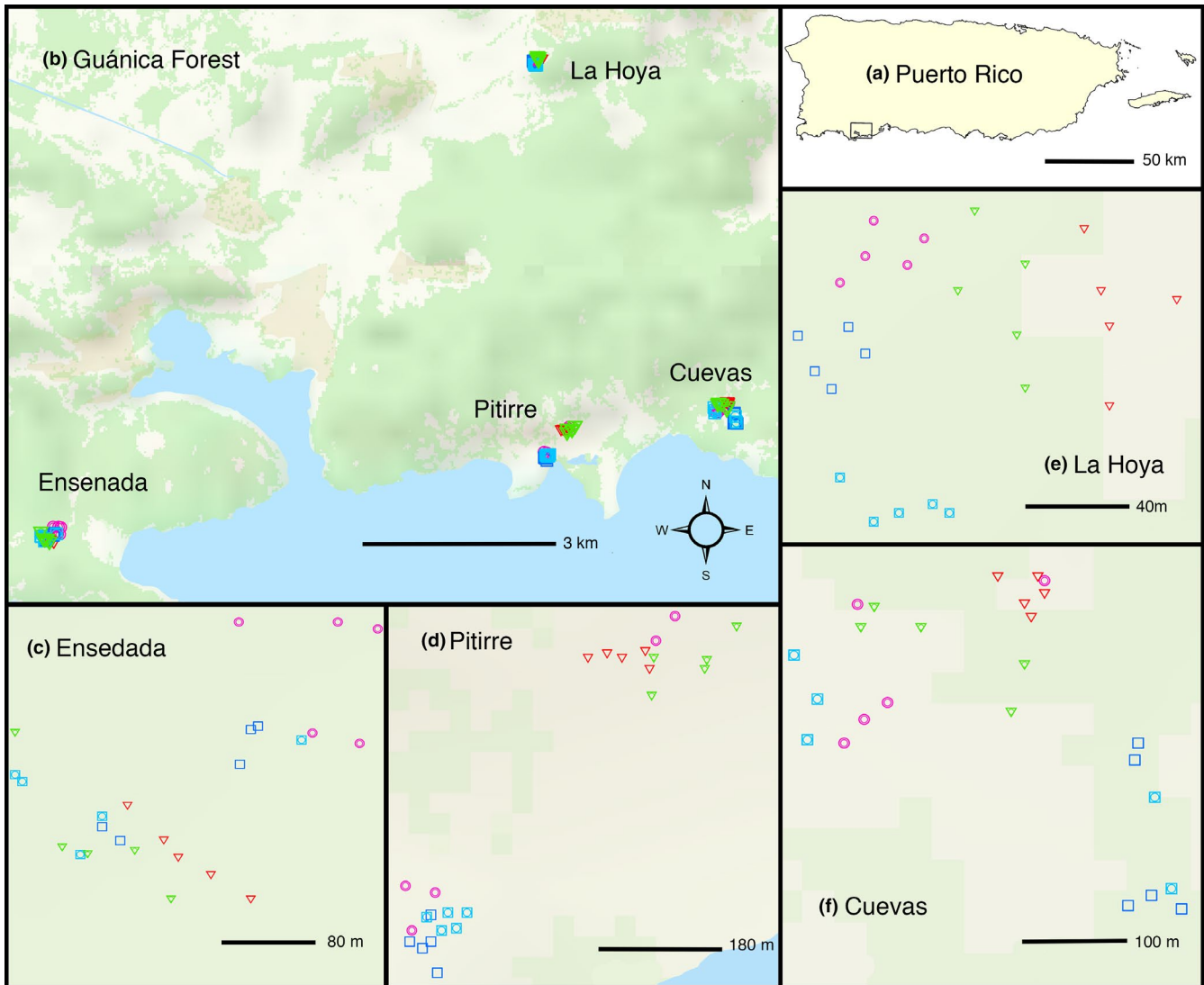
(17°58' N, 66°55' W). The forest is on limestone substrate and receives an average of 824 mm of rainfall annually (1931–2018; www.sercc.com and www.wrcc.dri.edu). Rainfall is irregular but largely distributed between minor and major wet seasons in April–May and August–November, respectively (Murphy & Lugo, 1986b). Guánica forest is a 4,500 ha protected area that is considered one of the most intact remnants of Caribbean dry forest (Ewel & Whitmore, 1973). However, sites within the forest have been subject to various perturbations, such as agriculture, tree plantations, cutting for charcoal production, and fire (Molina Colón & Lugo, 2006). The protected area is surrounded by urban and agricultural land uses (Figure 1).

Four sites within Guánica Forest were selected for this study based on their local disturbance histories that resulted in the close proximity of stand-level patches with varying degrees of plant-community degradation (M. Canals, Retired Forest Management Officer, personal communication, July 2006). The areas were spread throughout the forest, but three of the four sites were located near

its borders, where the majority of fires have occurred (Figure 1). Three of these sites experienced isolated fires 1–25 years prior to the study and the fourth site was bulldozed ca. 20 years prior (Table 1). Within each site, five vegetation types were identified based on the dominance of *L. leucocephala* or native tree species in the canopy and the presence or absence of exotic grasses in the understorey: open grass areas, *L. leucocephala* forests with grass understoreys, *L. leucocephala* forests with woody understoreys, native forests with grass understoreys, and native forests with woody understoreys (Table 1).

## 2.2 | Experimental design and field measurements

We collected seed rain in 0.5 m × 0.5 m traps constructed of PVC frames that were fitted with 1 mm mesh baskets and suspended 40 cm above the ground. This trap design reliably estimates seed rain with minimal seed loss due to wind, bouncing, or predation (Stevenson & Vargas, 2008). The trap height was chosen to conceal



**FIGURE 1** Study site and experimental design. (a) The study area is demarcated by the rectangle in southwestern Puerto Rico. (b) Expansion of the study area within the rectangle in panel a shows the four study sites within Guánica Forest. (c–f) Expansions of the four study sites show the spatial distribution of seed traps within various vegetation types. Traps located in open grass areas are represented by circles within circles; *Leucaena leucocephala* forests with grass understories, circles within squares; *L. leucocephala* forests with woody understories, squares; native forests with grass understories, circles within triangles; and native forests with woody understories, triangles

the traps within the grass and understorey shrubs to prevent vandalism by passersby as well as perching by birds, which could bias results. Vegetation that grew within or directly upon the traps, usually grass or vines, was cleared away monthly. Twenty-five traps were placed at each of the four sites in random locations such that they were at least 20 m away from each other and stratified among the five vegetation types. Since vegetation was heterogeneous within the stands, traps had varying degrees of *L. leucocephala* and grass in their vicinity (Table 1). Seeds were collected from the traps monthly from July 2007 to June 2008. During this time period, the 845 mm of rainfall in Guánica Forest was 3% greater than the long-term average (rainfall data collected within Guánica Forest by the Western Regional Climate Center, [www.sercc.com](http://www.sercc.com)). The summer dry season was 24% drier than the long-term average, while the other seasons

were 2–13% wetter. Although the low pressure system that became Hurricane Noel resulted in a 79% wetter October than average, and the late-season Hurricane Noel made December 2.5 times wetter than average, neither storm was particularly strong and neither month was in the top 10% wettest for that month historically.

Upon collection, seeds were brought to an air-conditioned laboratory where they were air dried and stored until they were sorted and counted 1–4 months later. Seeds were identified by comparison with field-collected vouchers and those of the University of Puerto Rico at Mayagüez herbarium.

In order to describe the vegetation around each trap, we identified and measured the distance to the ten nearest trees that were >2.5 cm diameter at breast height (130 cm height). We measured the understorey plant community around each trap in September 2008.

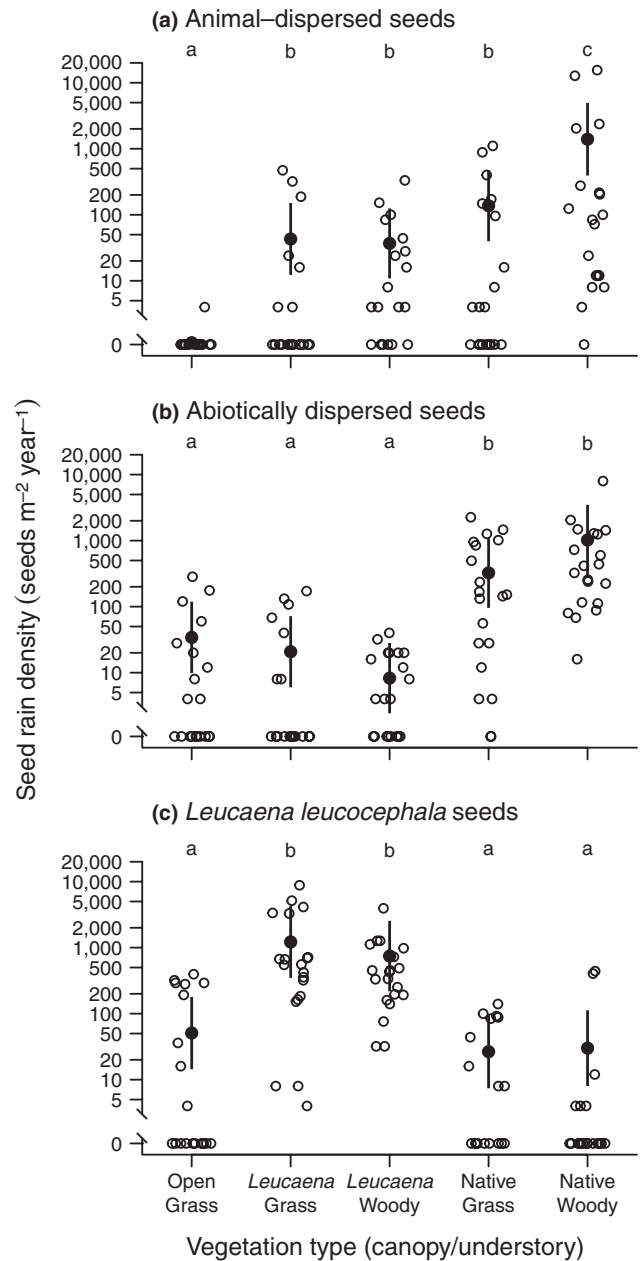
Three 0.5 m × 0.5 m plots were located 1 m from each trap in randomly selected, perpendicular directions. Within each plot, the grass cover was visually estimated to the nearest 5%.

### 2.3 | Data analysis

Seed counts for the 12 monthly collections were summed for each species within each trap and standardized to 1 m<sup>-2</sup> to calculate seed rain density (i.e., seeds m<sup>-2</sup> year<sup>-1</sup>). Species were classified according to their dispersal syndrome based on morphological characteristics as described by Little and Wadsworth (1964), Little, Woodbury, and Wadsworth (1974), and Castilleja (1991) for trees and Acevedo-Rodríguez (2005) for vines. Only counts of tree seeds were included in the statistical analyses, as tree regeneration was the focus of this study. Native tree seeds were grouped as animal- or abiotically dispersed. *Prosopis pallida* (Willd.) Kunth was the only exotic tree species other than *L. leucocephala* with seeds that were collected and identified in the traps. This species was included with the animal-dispersed species. *Bucida buceras* L. seeds have no apparent dispersal syndrome (Castilleja, 1991) and although they have been circumstantially reported to be dispersed by pigeons (Amadeo, 1888), we observed no evidence that they were dispersed by anything other than wind or gravity. This species was classified as abiotically dispersed for analyses. *Leucaena leucocephala* seeds are abiotically dispersed in this system (Molina Colón, Lugo, & Ramos González, 2011; Abelleira Martínez, Meléndez Ackerman, García Montiel, & Parrotta, 2015).

The number of seeds that arrived at each trap was highly skewed. Many traps received no seeds of a particular type and a few traps received thousands (Figure 2), which is typical for seed rain data (Dalling et al., 2002). Therefore, to compare mean seed counts among vegetation types and dispersal syndromes, we used a generalized linear mixed model (GLMM) with a negative binomial distribution and a log-link function. This analysis was run with the glmer.nb function in the R package MASS (Venables & Ripley, 2002). Fixed effects were vegetation type, dispersal syndrome, and their interaction. Random site and trap within site effects were used on the intercept. We used four sets of contrasts to test our hypotheses. First, we tested whether seed rain density of the three dispersal syndromes (animal, abiotic, and *L. leucocephala*) differed in the open grass areas. Then, for each dispersal syndrome, we tested whether seed rain density differed among the five vegetation types. Contrasts were run in the R package multcomp (Hothorn, Bretz, & Westfall, 2008) with Bonferroni-corrected  $\alpha = 0.05$ .

To compare species richness and density among the five vegetation types, we constructed sample-based species rarefaction curves with EstimateS version 9.0 (Colwell & Elsensohn, 2014). Scaling rarefaction curves by the number of individuals sampled or the number of samples gives estimates of species richness and species density, respectively, which are two contrasting metrics of diversity (Gotelli & Colwell, 2001). We constructed both types of curves, combining sites for each of the vegetation types. Non-overlapping 95% confidence intervals were used as the criterion for significant differences among vegetation types.



**FIGURE 2** Seed rain densities in five vegetation types along a gradient of degradation within Guánica Forest, Puerto Rico, for (a) animal-dispersed tree seeds, (b) abiotically dispersed tree seeds, and (c) *Leucaena leucocephala* tree seeds. Open circles represent individual seed traps. Closed circles and bars represent GLMM-estimated means and 95% CIs, respectively. Note that the vertical axis is log-scaled with a break to show values of zero. Within seed type, vegetation types that share letters did not differ (Bonferroni-corrected  $\alpha = 0.05$ )

We compared whether the species composition of seed rain varied among the five vegetation types and four sites with non-metric multidimensional scaling (NMDS) with the quantitative Jaccard (i.e., Ružička) dissimilarity index using the metaMDS function in the R package vegan (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). We chose the quantitative Jaccard index because its rank-order is identical to the commonly



used Bray–Curtis index, but its metric properties are better suited for ecological data (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). We used a three-dimensional fit, which had a final stress of 0.14. Additionally, we tested whether the species composition of seed rain varied among vegetation types and sites using permutational multivariate analysis of variance (PERMANOVA) with the *adonis* function in *vegan*, using the quantitative Jaccard dissimilarity index. Separate PERMANOVA tests were run with site, canopy type (open, *L. leucocephala*, or native), and understorey (grass or woody) as factors. All analyses in R were performed with version 3.3.3 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

To compare seed rain density at our study site to that of other tropical forests, we conducted an extensive literature search in ISI Web of Science and in Google Scholar using the search terms “tropical” and “seed rain” or “seed fall”. We limited comparisons to papers that measured seed rain for a least one year in intact forest (i.e., not highly degraded sites or gaps) and that reported mean seed rain density. The compiled dataset included 11 sites located throughout the tropics (Table 2) and extended a similar dataset compiled previously (Moles, Wright, Pitman, Murray, & Westoby, 2009). To match our data handling with those in the literature, we calculated mean seed rain density for all non-graminoid seeds (in contrast to our analyses described above that include only tree seeds) for the traps located in the intact forest stands at our site, i.e., the native forests with woody understorey.

### 3 | RESULTS

The traps collected a total of 35,603 non-graminoid seeds from July 2007 to June 2008, of which 34,915 (98%) were identified to family, 34,870 to genera, and 34,271 to species (Appendix S1). Tree seeds accounted for 80.6% of the total, vines 15.4%, shrubs and forbs 1.5%, and epiphytes 0.5%. A total of 48 species and morphospecies were identified: 30 trees, 8 vines, 5 shrubs and herbs, and 1 epiphyte (Appendix S1). *L. leucocephala* was the most abundant species, with 11,582 seeds. *Pisonia albida* (Heimerl) Britton was the most abundant native species, with 7,065 seeds, of which 7,055 were collected in just two traps.

#### 3.1 | Do open grass areas receive more seed rain from *L. leucocephala* than native trees?

Overall, the seed rain in open grass areas was low. A total of 637 tree seeds were collected in these areas, 457 of which were *L. leucocephala* and 180 were native tree seeds (Appendix S1). Six of the 20 traps in open grass did not collect any tree seeds. In the GLMM of seed rain density, the mean seed rain densities of *L. leucocephala* and abiotically dispersed species did not differ (mean [95% CI] = 50.9 [15.1–171.0] vs. 34.2 [10.3–113.5] seeds m<sup>-2</sup> year<sup>-1</sup>), and both were higher than that of animal-dispersed species (0.14 [0.03–0.67] seeds m<sup>-2</sup> year<sup>-1</sup>; Figure 2).

**TABLE 2** Comparison of seed rain density among tropical forests

| Site                          | Forest type                     | Mean seed rain density (seeds m <sup>-2</sup> year <sup>-1</sup> ) | Mean annual rainfall (mm) | Reference   |
|-------------------------------|---------------------------------|--|---------------------------|---|
| Guánica, Puerto Rico          | Dry forest                      | 2,791  | 860                       | Present study   |
| Campinas, Brazil              | Semi-deciduous forest           | 442  | 1,425 <sup>f</sup>        | Grombone-Guaratini & Rodrigues (2002)                   |
| Dja Reserve, Cameroon         | Semi-deciduous forest           | 297  | 1,600                     | Hardesty & Parker (2003)                                |
| Hainan Island, China          | Montane rainforest              | 345  | 1,750 <sup>c</sup>        | Zang, Zhang, & Ding (2007)                              |
| Cairns, Australia             | Moist forest                    | 542  | 1,998 <sup>d</sup>        | Moles et al. (2009)                                     |
| Hawai'i, Hawaii               | Tropical forest                 | 5,658 <sup>f</sup>   | 2,000 <sup>f</sup>        | Drake (1998)  |
| Barro Colorado Island, Panama | Seasonally moist forest         | 740.4  | 2,600                     | Puerta-Piñero, Muller-Landau, Calderón, & Wright (2013) |
| Barro Colorado Island, Panama | Seasonally moist forest         | 965  | 2,600                     | Harms, Wright, Calderón, Hernández, and Herre (2000)    |
| Las Alturas, Costa Rica       | Seasonal pre-montane wet forest | 1,670  | 3,000                     | Holl (1999)   |
| Los Cruces, Costa Rica        | Premontane humid forest         | 1,017  | 3,500                     | Reid, Holl, & Zahawi (2015)                             |
| Los Tuxtlas, Mexico           | Rain forest                     | 781  | 4,825 <sup>f</sup>        | Martínez-Ramos and Soto-Castro (1993)                   |

<sup>a</sup>Mean annual rainfall not reported, datum from CEPAGRI-UNICAMP via Wikipedia (<https://en.wikipedia.org/wiki/Campinas>) Accessed 6 September 2018.

<sup>b</sup>Mean annual rainfall reported as 1,500–2,000 mm.

<sup>c</sup>Mean annual rainfall not reported, datum from Australian Bureau of Meteorology ([http://www.bom.gov.au/climate/averages/tables/cw\\_031011.shtml](http://www.bom.gov.au/climate/averages/tables/cw_031011.shtml)) Accessed 6 September 2018.

<sup>d</sup>Excluding graminoid seeds.

<sup>e</sup>Median annual rainfall.

<sup>f</sup>Mean annual rainfall not reported, datum from De la Peña-Domene et al. (2013).

### 3.2 | Do *L. leucocephala* forests receive more native tree seeds than open grass areas?

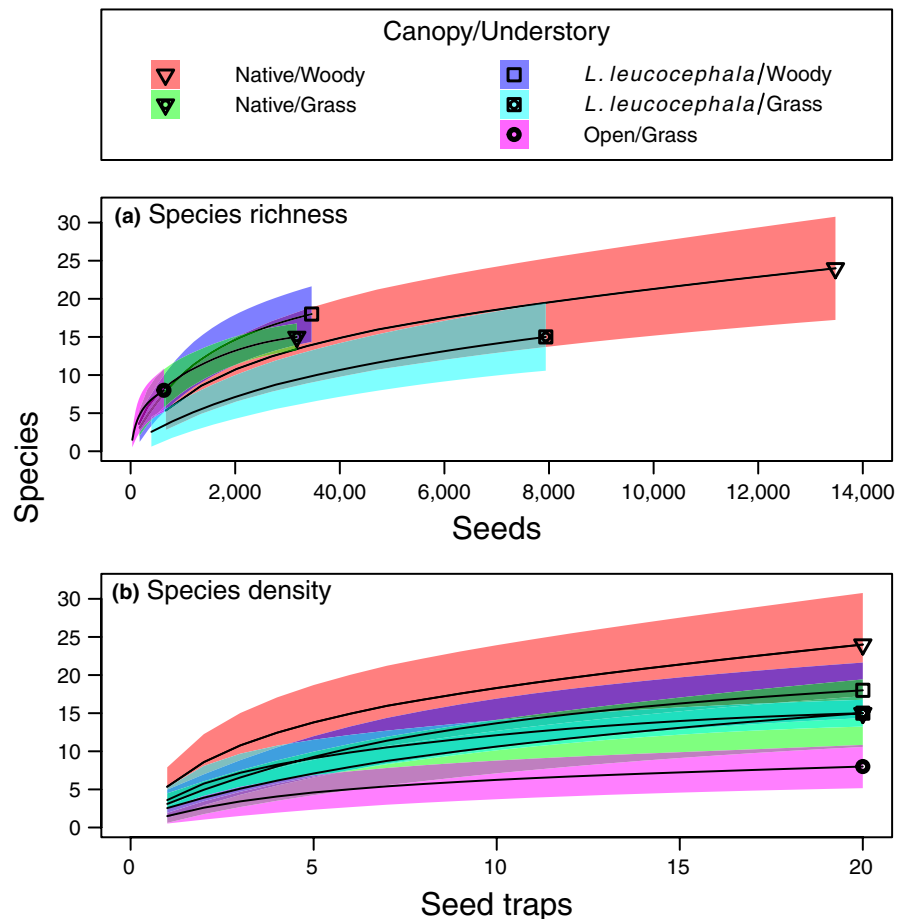
The traps in *L. leucocephala* forest stands (woody and grassy understorey combined) collected 11,406 tree seeds, of which 10,763 were *L. leucocephala*, 264 were from the non-native *Prosopis pallida*, and 379 were from native tree species. The GLMM showed that the three dispersal syndromes had contrasting patterns of seed rain density among the five vegetation types. Animal-dispersed seed rain density was >200-fold higher in *L. leucocephala* forests (both woody and grassy understorey) than in the open grass areas and still higher in the native forests (>700-fold higher, Figure 2a). Abiotically dispersed seed rain density did not differ between open grass areas and *L. leucocephala* forests and it was higher in native forests than in all other vegetation types (Figure 2b). *Leucaena leucocephala* seed rain density was higher in *L. leucocephala* forests than in open grass areas and native forests (Figure 3c).

### 3.3 | Species richness, density, and composition of seed rain along a degradation gradient

The total number of tree species collected in the seed rain ranged from eight species in open grass areas to 24 species in native forests with woody understoreys (Figure 3). When species rarefaction curves

were scaled to the number of seeds collected, the number of species in the five vegetation types had overlapping 95% confidence intervals at the maximum number of seeds at which all vegetation type could be compared (i.e., 637 seeds), indicating that species richness of tree seed rain is similar along the gradient of degradation (Figure 3a). When the rarefaction curves were scaled to the number of seed traps, at the maximum number of seed traps (i.e., 20 traps), the 95% confidence intervals did not overlap between open grass and the other vegetation types except slightly with *L. leucocephala* with grassy understorey, indicating that the species density of tree seed rain was lower in open grass areas than in less-degraded vegetation types (Figure 3b).

The NMDS plot showed clustering within canopy types and sites while understorey type was mixed within the plot (Figure 4). PERMANOVA analysis confirmed these visual trends; canopy type and site were highly significant factors (canopy type:  $df = 2$ , pseudo- $F = 6.4$ ,  $p < 0.001$ ; site:  $df = 3$ , pseudo- $F = 2.3$ ,  $p < 0.001$ ) while understorey type was not ( $df = 1$ , pseudo- $F = 0.9$ ,  $p = 0.5$ ). Given that our study design inherently skewed *L. leucocephala* seed rain among vegetation types (i.e., placing traps in *L. leucocephala*-dominated stands vs. native forest stands), we questioned to what extent the differences that we found in seed rain communities were driven by *L. leucocephala* seed rain alone. Therefore, we repeated the NMDS and PERMANOVA analyses with *L. leucocephala* seeds excluded. Similar to the full dataset, the NMDS plot showed clustering within canopy types and sites, but not understorey type (Appendix S2).



**FIGURE 3** Species rarefaction curves of seed rain in five vegetation types along a gradient of degradation in Guánica forest, Puerto Rico, scaled to (a) the number of seeds sampled and (b) the number of seed traps. Shading represents 95% CIs



Likewise, the PERMANOVA results were similar to those of the full dataset (canopy type:  $df = 2$ , pseudo- $F = 2.2$ ,  $p < 0.001$ ; site:  $df = 3$ , pseudo- $F = 1.8$ ,  $p < 0.001$ ; understorey type:  $df = 2$ , pseudo- $F = 0.9$ ,  $p = 0.7$ ).

### 3.4 | Pan-tropical comparison of seed rain density

The native forest with woody understorey (i.e., the intact forest) at our Caribbean dry forest site had higher mean seed rain density than 9 out of 10 other forests located throughout the tropics (range = 297–5,658 seeds  $m^{-2}$  year $^{-1}$ ; Table 2; Appendix S3), despite having the lowest mean annual rainfall among the sites (range = 860–4,825 mm/year; Table 2, Appendix S3). Indeed, we found no clear relationship between mean annual rainfall and seed rain density among forests (Appendix S3).

## 4 | DISCUSSION

We tracked seed rain in forest stands representing various states of degradation and disturbance recovery to test how dispersal limitation of native tree species is related to the development and

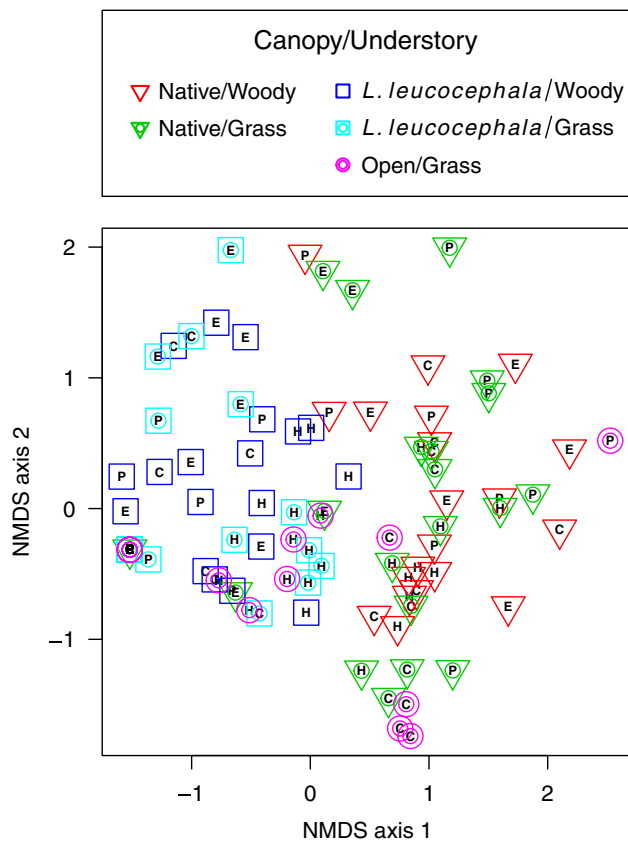
persistence of *Leucaena leucocephala*-dominated stands, which are widespread in degraded Caribbean dry forests. Overall, tree seed rain in open grass areas was very low, yet abiotically dispersed native tree species and *L. leucocephala* arrived in these areas at similar rates. This result does not support the hypothesis that high seed arrival drives *L. leucocephala* to dominate severely disturbed (i.e., cleared) sites. Rather, our results suggest that factors subsequent to dispersal limitation lead *L. leucocephala* to outperform native species in severely disturbed sites. The presence of *L. leucocephala* canopies increased the seed rain of animal-dispersed trees species >200-fold over open grass areas, suggesting that *L. leucocephala* forests encourage native forest regeneration by attracting seed dispersers. Below, we elaborate on these findings.

### 4.1 | The role of seed dispersal limitation in Caribbean dry forest regeneration

Few tree seeds arrived at open grass areas and those that did were nearly all *L. leucocephala* and abiotically dispersed native species (Figure 2). This suggests that *L. leucocephala* and abiotically dispersed native trees are similarly dispersal-limited in open grass areas, while animal-dispersed species are even more so. In Puerto Rico, *L. leucocephala* is described as wind-dispersed (Abelleira Martínez et al., 2015; Molina Colón et al., 2011), so it is reasonable that its seed rain density in open grass areas is similar to native abiotically dispersed species.

The dominance of *L. leucocephala* over native species (particularly abiotically dispersed native species) in forests that regenerate in open grass areas is likely due to demographic factors other than seed dispersal. Factors such as seed viability (Ray & Brown, 1994), seed predation, and germination may favor *L. leucocephala* recruitment. Indeed, relatively high germination rates among legume tree species may explain their high abundance in dry forests throughout the Neotropics (Vargas, Werden, & Powers, 2015). Additionally, *L. leucocephala* seedlings have higher survival and growth rates than native tree seedlings in open grass areas, where environmental conditions include degraded soils, grass competition, increased solar radiation, and anthropogenic fires (Wolfe & Van Bloem, 2012).

The seed rain density of animal-dispersed seeds was higher in *L. leucocephala* forests than in open grass areas (Figure 2a). In contrast, abiotically dispersed seed rain density was similar in open grass areas and *L. leucocephala* forests (Figure 2b). This suggests that *L. leucocephala* forests attract seed dispersers but have little effect on wind-dispersed seeds. Many studies in the tropics have shown that seed-dispersing birds and mammals avoid open grass areas and that a return to forest cover increases animal seed dispersal (reviewed by Wunderle, 1997). Although *L. leucocephala* does not produce fruits that attract frugivorous animals, it does increase the structural complexity when it establishes in open grass areas, providing perches and cover where dispersers may come to rest, nest, or traverse between better quality patches. During the project, we commonly noted insect larvae feeding on *L. leucocephala* seeds. It is possible that birds are attracted to *L. leucocephala* for the larvae,



**FIGURE 4** Nonmetric multidimensional scaling plot based on Jaccard dissimilarity in the species composition of seed rain along a gradient of forest degradation in four sites within Guánica Forest, Puerto Rico. Each symbol represents a seed trap. The first letter of each site (see Table 1) is indicated at the center of each symbol

although this tri-trophic interaction requires further study. Also, native tree seeds that arrive to *L. leucocephala* forests may have higher germination rates than those that fall from crowns, as mechanical scarification by birds has been shown to increase seed germination in many tree species native to the dry forest zone of Puerto Rico (Carvajal Velez, 2001).

Further evidence that *L. leucocephala* forests facilitate the dispersal and establishment of native trees was demonstrated by Pérez Martínez (2007). In nine *L. leucocephala* forest sites located throughout the dry forest zone of Puerto Rico, Pérez Martínez (2007) found that animal-dispersed tree species accounted for 83% (35 of 42) of the species of saplings encountered in the understorey. Animal-dispersed species had the highest importance value in the sapling category at four of the nine *L. leucocephala* sites. At three other sites an animal-dispersed species was second in importance only to *L. leucocephala*. The wind-dispersed shrub *Croton humilis* L. was more important at the two other sites.

We found that understorey vegetation composition (i.e., grassy vs. woody) had no clear effect on the patterns of seed rain density or composition for any seed type (Figures 2–4; Appendix S2). While studies in Puerto Rico have shown that understorey vegetation in pine and mahogany plantations can affect habitat use by frugivorous birds (Cruz, 1987, 1988), the seed rain in this study was apparently unaffected by the dominance of grass in the understorey. However, another consideration is that grass tussocks may intercept falling seeds and trap them in their crowns, preventing seeds from reaching the soil. Seeds trapped in grass tussocks would have reduced chances of germinating and establishing, limiting tree regeneration. We cannot address this hypothesis because we continually cleared grass from the area directly above our seed traps, but it is potentially a factor that contributes to the persistence of open grass areas and grass understoreys in native and *L. leucocephala* forests.

## 4.2 | Comparing seed rain density among tropical forests

Our Caribbean dry forest site had higher overall seed rain density than most tropical forests despite having lower rainfall (Table 2; Appendix S3). This result is counter-intuitive since investment in reproduction is commonly considered a fixed fraction of net production (Moorcroft, Hurtt, & Pacala, 2001) and net production is lower in drier forests (Schoor, 2003). One possibility is that seeds in Caribbean dry forests are smaller (i.e., lower investment per seed) than those in other tropical forests, such that seed rain density is high despite relatively low reproductive investment. Forests also likely vary in the proportion of viable seeds in the seed rain. For example, in a Hawaiian forest, <10% of tree seeds that fell in traps contained embryos (Drake, 1998). Considering the depauperate seed bank in intact Caribbean dry forests (Castilleja, 1991; Ray & Brown, 1994; Murphy & Lugo, 1995), it is likely that much of the seed rain is composed of unviable seeds with relatively little investment per seed. However, low viability in our seed rain collection would

seem somewhat unlikely, as only 48% of the seeds that fell in native forest with woody understorey traps were scored as unviable due to damage or lacking embryos (data not shown). Still, more work is needed to compare seed rain among study sites; for one, there are few datasets (Table 2); secondly, seed rain can be highly variable interannually (Wright, Muller-Landau, Calderón, & Hernández, 2005) and most datasets are from single years; and thirdly, studies vary in their sampling design and data handling, making direct comparisons difficult.

## 4.3 | Management implications

Our results suggest that exotic forests dominated by *L. leucocephala* develop on abandoned farmlands and burned areas in the Caribbean dry forests due to factors subsequent to seed dispersal limitation. Although seeds of abiotically dispersed native tree species arrived to open grass areas at densities similar to seeds of *L. leucocephala*, native species rarely recruit to seedling and sapling stages in these areas (Francis & Parrotta, 2006). These results, combined with those of Ray and Brown (1995), who showed that native dry forest tree species have low germination and survival rates in open grass areas of the Virgin Islands, suggest that direct seeding with native tree species is impractical for reforesting highly degraded areas. Ray and Brown (1995) also showed that native species do not perform well when planted as seedlings in open grass areas and suggested the use of *L. leucocephala* as a nurse tree for plantings of native seedlings. In addition, our results show that the seed rain of animal-dispersed native trees is higher in *L. leucocephala*-dominated stands than in open grass areas. Thus, *L. leucocephala* may facilitate both the arrival and establishment of native tree species.

Unlike the main natural disturbance in Caribbean dry forests – hurricanes – anthropogenic disturbances such as fire and mechanical clearing create large open areas, eliminate roots and thick litter cover, and alter nutrient pools (Wolfe & Van Bloem, 2012). In contrast, hurricanes topple a small proportion of trees (~13%; Van Bloem et al., 2005), leaving stumps and roots for subsequent sprouting (Van Bloem, Lugo, & Murphy, 2006). Establishment of *L. leucocephala* stands appears to be a new successional step in recovering forest canopy, consistent with recent descriptions of the role of exotic species in the development of novel forests (Lugo, 2004; Lugo & Helmer, 2004). Indeed, because of its effects on seed arrival and subsequent establishment of native trees, *L. leucocephala* appears to make Caribbean dry forest more resilient to anthropogenic disturbances. Since *L. leucocephala* has low growth and survival in the understorey of native forests (Wolfe & Van Bloem, 2012; Van Bloem, unpublished data), passive management allowing *L. leucocephala* to grow in grass-dominated areas and preventing further burning may eventually allow recovery of native forests in highly degraded areas. However, these observations are restricted to Caribbean dry forests. Since *L. leucocephala* has been introduced widely throughout the tropics, management prescriptions should consider its interactions with the local environment (Costa, Fonseca, & Bianchini, 2015).

## ACKNOWLEDGEMENTS

We thank Miguel Canals Mora and the Puerto Rico Department of Natural Resources and Environment for facilitating research in Guánica Forest; Edwin Omar Sepulveda, Freddie O. Pérez Martínez, Katia Aviles, Ixia Aviles, and Ose Pauleus for help in the field; Ivonne Rosario for help in processing the seed collections; Gary J. Breckon for help in identifying seeds; and Brian Williams for help in producing Figure 1. Additional support for SJVB was provided by the USDA Forest Service International Institute of Tropical Forestry. Technical contribution 6,724 of the Clemson University Experimental Station.

## DATA AVAILABILITY

The data presented here are released under Creative Commons CC BY 4.0 “Attribution 4.0 International” (see: <https://creativecommons.org/licenses/by/4.0/>) and can be found at the Environmental Data Initiative (EDI) website <https://portal.edirepository.org> after August 2019. It is considered professional etiquette to provide attribution of the original work if this data package is shared in whole or as individual components. A citation is provided for this data package on the EDI website in the summary metadata page.

## ORCID

Brett T. Wolfe  <https://orcid.org/0000-0001-7535-045X>

Raúl Macchiavelli  <https://orcid.org/0000-0002-3727-6874>

Skip J. Van Bloem  <https://orcid.org/0000-0001-7165-6646>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1** Species counts of seeds collected during the study-

**Appendix S2** NMDS plot of seed rain excluding *L. leucocephala*

**Appendix S3** Mean seed rain density as a function of mean annual rainfall among tropical forests

**How to cite this article:** Wolfe BT, Macchiavelli R, Van Bloem SJ. Seed rain along a gradient of degradation in Caribbean dry forest: Effects of dispersal limitation on the trajectory of forest recovery. *Appl Veg Sci.* 2019;00:1-12. <https://doi.org/10.1111/avsc.12444>