

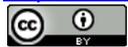
Moss Propagules Banks in a Secondary Subtropical Moist Forest in Puerto Rico: A First Description

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Abstract

A bryophyte propagule bank serves as a source for population maintenance and survival, and many factors can influence these propagules' germination. However, it is unknown how soil depths affect propagules banks, their diversity and abundance overtime in a Neotropical forest. To understand such a paradigm, soil samples were obtained from different depths (0 - 5 cm, 5 - 10 cm, and 10 - 15 cm) at Guajataca State Forest, Puerto Rico; then, they were transferred to the laboratory, cultured, and the amount of gametophytes from propagules present over a seven-month period were measured. Forest soil depth did affect the density of gametophytes. Gametophytes densities augmented overtime for almost all species. Two species mainly influenced the propagule production over time. Also, propagules can have a long-term germination potential for some species.

Keywords

Bryophytes; Soil Propagule Banks; Neotropical Forest; Propagule Survival

1. Introduction

Bryophytes use different strategies for survival, among them we can find the development and maintenance of soil-buried propagules banks [1]. These banks function as a reservoir of previous generation genetic material [2], which could be produced by spores or/and asexual propagules (*i.e.* gametophyte fragments, gemmae, etc.). They are similar to a vascular plant's seed banks by: enabling species to survive environmental stressors, rapid colonization when a disturbance occurs, and influencing the species composition and occurrence after a disturbance [3]. Until favorable conditions arise and propagules germinate, the persistence of this bank will depend on the

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ability of the propagules to: disperse to the bank, withstand predation, and be influenced by depth deposition and/or microhabitat conditions [4]-[7].

Soil banks persistence has been observed in ferns and its propagules' viability has been shown to diminish by depth [8] [9]. Yet, propagule bank persistence could be linked to the amount of propagules produced and deposited, and also its viability may be related to species' life strategy [1] [10] [11]. In *Sphagnum* spp. banks, spore longevity and dormancy period were affected by weather; under adequate conditions, *Sphagnum*'s spores may retain mean viability up to five years [12]. Although for some species longevity or viability is known for soil banks, it is unknown how many germinated modules from buried propagules can be produced overtime for a given soil sample.

In Puerto Rico, extensive agriculture deforested and affected forest diversity, species composition, and soil qualities. Then Puerto Rico's economy changed to an industrial, which aided in the reestablishment and emergence of secondary forests [13]. Such disturbance was observed in the Guajataca Commonwealth Forest and could have affected its propagule bank. In this forest, we find areas that contain new forest and relatively old forest sinkholes and haystacks hills [14]. This heterogeneous habitat could influence what is found in these soils. Especially since forest and soil type can have different topographic conditions [7] that may alter the propagule bank.

Hock *et al.* [15] demonstrated that bryophytes of open grassland on dolomite rock can affect temporal variability of stored propagules for *Bryum argenteum* Hedw., *Bryum erythrocarpum* Schwägr, and *Weissia controversa* Hedw. However, in Atlantic Rain Forest, diaspore dynamics was influenced by species traits and microhabitat characteristics [16]. Also, the soil layer can alter species presence and frequency [17]. Nevertheless, it is unknown how secondary moist forest in Puerto Rico may affect the propagules and spore bank frequency, species composition, and the interactions between these factors and depth. If propagule assemblage is affected by these parameters then forest depth will change the propagule species occurrence. Therefore, we are interested in studying how in a secondary forest, soil depth affects: the species, propagule frequency, and abundance over time.

2. Materials and Methods

2.1. Study Site

Moss propagule banks were studied for three forest stands in the Guajataca Commonwealth Forest (18°24.480N, 066°58.406W), Puerto Rico. Two of the stands were in sinkholes and another was located on a haystack hill. These stands contained an Old Forest, which was designated as a moist forest that was present in Puerto Rico in 1936. This forest stand was identified from a shape file superimposed on a digital topographic map (Anonymous, US Geological Survey) of the Guajataca State Forest using Arc Map (ArcGIS software (digital file) (J. D. Chi-nea, unpublished data)). Forest stands that did not exist in 1936 were identified and classified as young (New Forest-A and New Forest-B). Forest stands were located in the field using an eTrex® GPS from Garmin and USGS topographic maps showing the location of the selected forest stands. Coordinates were entered into the GPS instrument and the Puerto Rico Datum was selected.

Guajataca Commonwealth Forest is a subtropical moist forest [18] that encompasses an area of 926 hectares and elevations from 150 to 300 m. This secondary forest is located in the municipality of Isabela, northwest Puerto Rico. Also, the forest was established in 1943 and is characterized by its combination of haystack hills and sinkholes typical of a karst topography formation [14].

2.2. Sampling and Culture

Three soil samples were obtained from random points, five random points in total per transect. Each point is equal to an area of 1 m²; points were selected from a 10-meter transect placed on each type of forest strand (n = 15, for each forest stand). Samples were removed with a soil borer for three depth categories (0 - 5 cm, 5 - 10 cm, and 10 - 15 cm; volume of 57 cm³, respectively) from each point, and then separated into small bags. Soil samples were later used for propagule bank culture held in the laboratory. Soil samples were taken to the University of Puerto Rico-Mayagüez Campus (Tropical Bryology Laboratory) and each sample spread on a petri dish and later put on shelves illuminated with 2200 lux and maintained with light/dark periods of 12/12 at 17.65 ± 12.92°C (Kestrel 4500-0845). Samples were wet with non-chlorinated water once every week; germinated plants were then counted, removed, and identified [19] [20] bi-weekly to monthly for a seven-month period.

2.3. Statistical Analysis

Moss species that were not present among all forest and had low abundance were removed from the data due to their statistical insignificance (list of species; [Appendix 1](#)). Species used to observe propagule germination patterns included: *Anoetangium aestivum* (Hedw.) Kindb., *Callicostella depressa* (Hedw.) A. Jaeger, *Fissidens palmatus* Hedw., *Fissidens zollingeri* Mont., *Funaria hygrometrica* var. *calvescens* Schwägr., *Philonotis uncinata*, (Schwägr.) Brid., and *Vesicularia vesicularis* var. *portoricensis*. (Brid.).

Data were tested for normality and homoscedasticity. Even after it was transformed, it showed non-normality and heteroscedasticity. A Kruskal-Wallis (pairwise post hoc test, $\alpha = 0.05$) was used to estimate means similarities or difference for propagule abundance with species and/or depth of sampling; also, richness and soil depth. A Pearson's correlation coefficients (r) and coefficients of determination (R^2) were used to observe the relationship and dependence between richness and depth, and changes in abundance according to number of days. Statistical analyses were carried out on Infostat [21]. The Simpson, Evenness, Dominance, and Chao diversity indices were calculated via PAST [22].

3. Results

In the soil propagule bank of the Guajataca Moist Forest, we found 10 moss species from 8 genera distributed in 7 families ([Appendix 1](#)). The Fissidentaceae had the most species (3), followed by the Hypnaceae (2), and the other families had one species each. Acrocarpous mosses dominated this soil bank (60%) in comparison to pleurocarpous mosses (40%).

The propagule bank produced a great amount of gametophytes in the Guajataca Moist Forest. Gametophyte overall abundance was different in each stand; New Forest-A had the highest module quantity (12,268), subsequently followed by Old Forest (9403), and New Forest-B (94). From the pooled data, we found 5070, 6466, and 964 modules from 0 - 5 cm, 5 - 10 cm, and 10 - 15 cm, respectively. In these soils, *F. palmatus* had the highest gametophyte relative frequency, followed by *F. hygrometrica* var. *calvescens* (74% and 24%, respectively). However, *C. depressa* and *A. aestivum* relative frequency was low (1%); but *F. zollingeri* and *V. vesicularis* var. *portoricensis* had the lowest (less than 1%).

There were significant differences in the interaction between gametophyte abundance with species and depth of sampling (Kruskal-Wallis, $df = 2$, $H = 7.58$, $p < 0.0001$) in this karst region ([Table 1](#)). Species and soil depth separated themselves according to the ranked abundance and this difference was variable. In soil depth, 0 - 5 cm showed similarity in gametophyte ranked abundance with 5 - 10 cm and 10 - 15 cm abundance; yet, 5 - 10 cm and 10 - 15 cm ranked abundance differed from one another (Kruskal-Wallis, $df = 17$, $H = 31.41$, $p = 0.0006$). For species, gametophyte abundance was divided in two groups, high and low relative abundance; where *F. hygrometrica* var. *calvescens*, *F. palmatus*, and *C. depressa*, had the highest gametophyte abundance (Kruskal-Wallis, $df = 5$, $H = 20.50$, $p < 0.0001$). In contrast, *C. depressa* shared a similarity in abundance with those that produced fewer gametophyte.

Among soil depth, there were differences in moss richness (Kruskal-Wallis, $df = 2$, $H = 4.69$, $p = 0.07$). Where, 5 - 10 cm had the highest richness (1.80 ± 1.61) but was similar to 0 - 5 cm (1.20 ± 1.21); in contrast, 10 - 15 cm had the lowest richness (0.60 ± 0.99) and was similar to 0 - 5 cm. However, no relationship or dependence was found between moss richness and soil depth ($R^2 = 0.03$, $r = 0.18$; $df = 1$, $F = 1.48$, $p = 0.23$).

Chao's index shows that we obtained the estimated moss species for each depth ([Table 2](#)). In addition, 5 - 10 cm had the highest estimated richness, followed by 0 - 5 cm, and then 10 - 15 cm. But, 0 - 5 cm had higher diversity than 5 - 10 and 10 - 15 cm. Though, 10 - 15 cm depth had more dominant species, while 0 - 5 cm had the lowest dominance of the three depths. Also, 10 - 15 cm showed the highest evenness, whereas 5 - 10 and 10 - 15 cm were low (32% - 50%).

Bryophyte gametophyte abundance from propagules augmented as time increased. We found a positive linear relationship between days and gametophyte' abundance, and dependence among those variables ($r = 0.88$, $R^2 = 0.78$; $df = 1$, $F = 38.81$, $P < 0.001$). The species that seemed to influence this propagule bank tendency was *F. palmatus* (the most frequent species). *F. palmatus* showed a very strong linear relationship and dependence ($r = 0.89$, $R^2 = 0.79$; $df = 1$, $F = 41.26$, $P < 0.001$) between days and gametophyte production. *F. hygrometrica* var. *calvescens*, *C. depressa*, *F. zollingeri*, and *A. aestivum* demonstrated a strong linear relationship ([Table 3](#)); all of these, except *C. depressa*, had a dependence between variables. *V. vesicularis* var. *portoricensis*, had a low abundance and no pattern was observed for this species.

Table 1. Pair-wise comparison ($\alpha = 0.05$) of rank abundance means for the interaction between soil depth (cm) and species. Means with common letter are not significantly different.

treatment (soil depth cm: species)	rank	difference in means			
0 - 5: <i>V. vesicularis</i> var. <i>portoricensis</i>	107	A			
10 - 15: <i>C. depressa</i>	107	A			
10 - 15: <i>F. zolingerii</i>	107	A			
10 - 15: <i>V. vesicularis</i> var. <i>portoricensis</i>	107	A			
0 - 5: <i>F. zolingerii</i>	107	A			
0 - 5: <i>A. aestivum</i>	114.83	A	B		
5 - 10: <i>V. vesicularis</i> var. <i>portoricensis</i>	122.63	A	B	C	
10 - 15: <i>A. aestivum</i>	123.23	A	B	C	
5 - 10: <i>F. zolingerii</i>	123.47	A	B	C	
10 - 15: <i>F. palmatus</i>	132.4	A	B	C	D
5 - 10: <i>A. aestivum</i>	134.97	A	B	C	D
0 - 5: <i>C. depressa</i>	140.07	A	B	C	D
10 - 15: <i>F. hygrometrica</i> var. <i>calvescens</i>	144.43	A	B	C	D
0 - 5: <i>F. palmatus</i>	162.87	A	B	C	D
5 - 10: <i>C. depressa</i>	163.87		B	C	D
0 - 5: <i>F. hygrometrica</i> var. <i>calvescens</i>	173.27			C	D
5 - 10: <i>F. hygrometrica</i> var. <i>calvescens</i>	180.17				D
5 - 10: <i>F. palmatus</i>	187.8				D

Table 2. Diversity indices for the moss abundance present in Guajataca's Forest soil propagules bank from different soil depths (0 - 5 cm, 5 - 10 cm, 10 - 15 cm).

indices	soil depth		
	0 - 5 cm	5 - 10 cm	10 - 15 cm
Taxa_S	4	6	3
Dominance_D	0.569	0.6473	0.6642
Simpson_1-D	0.431	0.3527	0.3358
Evenness_e^H/S	0.4985	0.3168	0.616
Chao-1	4	6	3

Table 3. Pearson linear correlation (r) and coefficient of determination (R^2) of changes in abundance according to number of days. Response type can be positive or null. The magnitude of the correlation indicates species response intensity, and response quality is reflected by level of significance ("ns" indicates statistically non-significant, * $P < 0.05$, *** $P < 0.001$).

species	r	R2
<i>F. palmatus</i>	0.89***	0.79***
<i>F. hygrometrica</i> var. <i>calvescens</i>	0.65*	0.82*
<i>A. aestivum</i>	0.80*	0.61*
<i>C. depressa</i>	0.82*	ns
<i>F. zolingerii</i>	0.55*	0.24*
<i>V. vesicularis</i> var. <i>portoricensis</i>	ns	ns

Overall, species varied in the relative frequency per date (**Figure 1**). No gametophytes from propagules were observed on the first date, yet on the second date and onward these modules were present; especially for *F. palmatus*, *C. depressa* and *F. hygrometrica* var. *calvescens*. In *F. palmatus*, relative frequency was high and swung between 65% and 81%, and *F. hygrometrica* var. *calvescens* was 17% to 33%. However, *C. depressa* was less than 1% to 3%. Later on *A. aestivum* started to show-up and had a low relative frequency (up to 2%). *F. zolingerii* and *V. vesicularis* var. *portoricensis* were the last to produce visible modules and with a very low relative frequency, less than 1%.

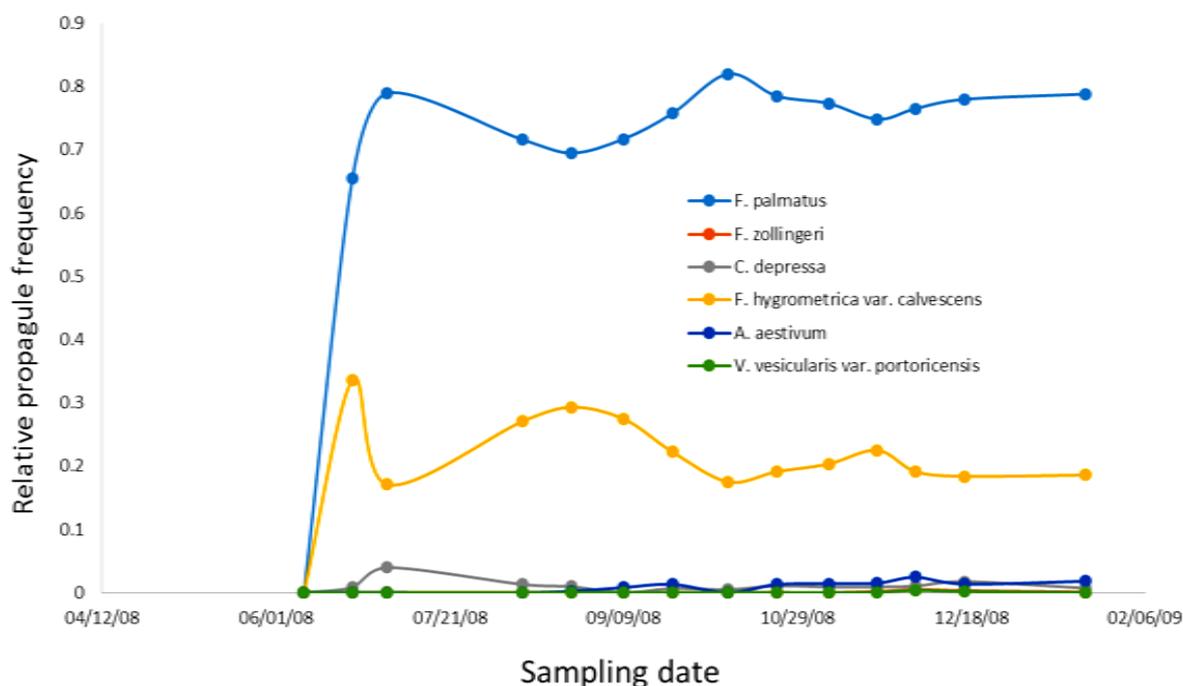


Figure 1. Overall relative frequency of germinated propagules for each moss species according to sampled date. Germinated propagules are from the soil banks from the Guajataca Commonwealth Forest, Puerto Rico.

4. Discussion

Guajataca State Forest has a propagule bank that is influenced by soil depth, and this bank can continuously produce modules. The source of these soil propagules is unknown (e.g. spores, gametophyte branches, bulbils, gemmae); but, germination may respond to a great amount of sexual and asexual propagules that could be disperse locally or from long range [23]. However, even though the amount of produced gametophytes varied between them, there is a prevalence in the production of these gametophytes from propagules among the different forest types (New Growth Forest-A, New Growth Forest-B, and Old Growth Forest). The type of forest and its soil micro-topographic condition may offer a refuge [7] and allow the survival of these propagules in the soil. The germination of propagules can depend on how these are subjected to environmental conditions and what enables them to grow; also, how disturbance allows these propagule banks to be exposed.

Soil propagule disturbance and exposure might occur by: a landslide, soil allocation by the uprooting of a tree moved by a strong wind, and by agriculture. Our study might have created a similar effect to these disturbances (animal activity, tree fall gaps; [16]) and enabled the moss module development. In this subtropical moist forest, there are about 50 species of moss [24]; the moss species found (11 species) only represent 22% of local flora. Six species are acrocarpic and the other four are pleurocarpic. Acrocarpic species may benefit from the disturbance that created this gap in vegetation and develop much faster than pleurocarpic species in these soils. Aside from species richness, acrocarpic species (*F. palmatus* and *F. hygrometrica* var. *calvescens*) produced the most amount of gametophyte from propagules in comparison to pleurocarpic species (*V. vesicularis* var. *portoricensis*). Edaphic conditions can affect species composition [25], and acrocarps may tolerate these initial soil conditions that might be limited in humidity. When bryophyte micro-canopy augments in complexity and cover, then moisture may be retained for longer periods of time and then pleurocarpic species abundance may augment. Esposito *et al.* [26] showed that in Mediterranean forest bryophyte coverage is low; even though, when fire disturbance occur the pioneer species that germinates are usually acrocarpic bryophytes.

Variation in gametophyte abundance and richness according to soil depth and species that produce the propagule may represent the strategies the plant utilizes to maintain its population or the propagule reservoir. Topsoil centimeters (0 - 5 cm) can show the highest diversity and it can be related to the direct dispersal from species of surrounding areas. However, propagules that fall in the first centimeter lower than the topsoil may retain viability until suitable condition arise and result in their germination. The intermediate area between the topsoil and

lower depth can be a buffer zone that creates an adequate storage for these modules; which in turn benefits species abundance and richness. However, the deeper the soil depth, the less likely it is for these modules to survive. Propagules survival according to depth can be ameliorated if the propagules deposited in lower depth are moved once again to higher depth by animal activity, like done by worms. During [27] demonstrated that spores buried less than 1 cm are more probable to germinate in comparison with the top centimeter. He also suggested that high mortality rate as a reason for the low production of gametophytes in the top centimeters can be caused by the constant exposition to desiccation, and the movement of propagules to deeper depth by water.

In this soil depth (0 - 5 cm, 5 - 10 cm, 10 - 15 cm), germinated propagules increased over time. The germinated abundance augmentation can be related to primary ecological succession (Figure 2). Some of the species would have more propagules in the soil, making them more dominant than others and even better competitors. Yet, this inter-specific competition could be suitable for a period of time until the primary edaphic habitat characteristics changed in response to the plant growing and making other nutrients available. Propagules germination can maintain overtime the current species population or develop different vegetation [28]. This temporal suitability for some species should provide enough time for their reproduction and dispersal of their progeny unto other soils banks or substrate that allows their “immediate” germination. Genetic material from these propagules at that specific depth may be the factor that aid in these modules survival or fitness [2]. If they fail to reproduce and disperse, then other species would take over and diminish the current moss population and favor another, thus creating a dynamic competition environment.

The continuous production and dominance of a species in the propagule bank may indicate species resilience. Such resilience may be due to the type of propagule released or that has fallen to the soil bank, and how long it stays in a biologically “inactive” state until soil conditions has met the requirement for germination. Sunberg and

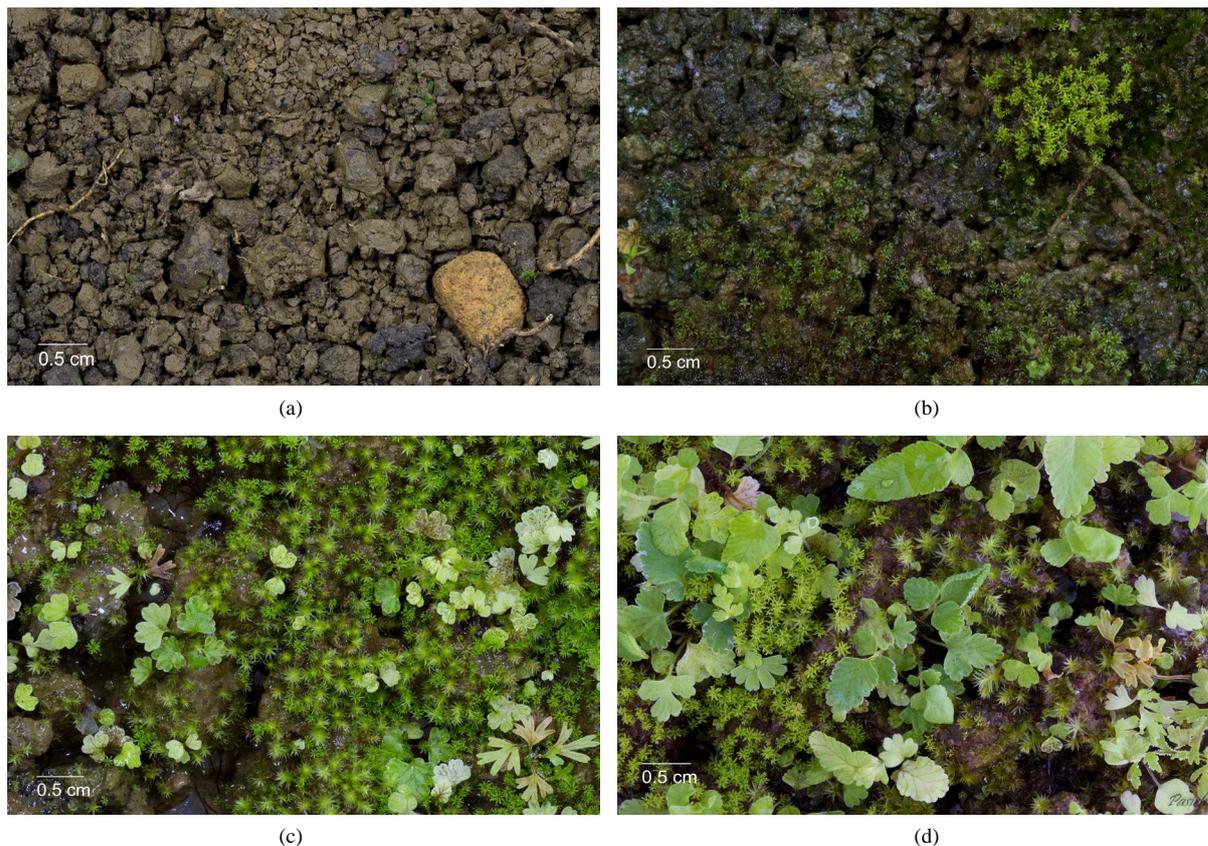


Figure 2. Changes in moss gametophyte abundance over time after a disturbance of soil extraction, exposition, and watering of propagules in the soil bank (a-d). Recently disturbed soil with no or little gametophyte cover (a), moss gametophyte and even fern abundance has augmented but cover and richness are low (b). Gametophyte abundance, richness, and cover increased but there is still soil without plant cover (c). Soil is almost completely covered by moss gametophyte (d). Bar = 0.5 cm.

Rydin [12] demonstrated that *Sphagnum spp.* spore could remain viable up to 20 years in soil banks. In vascular plants, *Vaccinium spp.* buried seed can have a mean longevity of 8.5 years [29], while *Artemisia tridentata* seed burial augments its short term longevity [30]. This longevity can explain the persistence of the bryophyte soil-buried propagule bank in the period studied. This soil bank propagule longevity potential can be taken advantage off to restore species in other areas that are facing extinction or are endangered.

We suggest that soil-buried propagule not only can have short-term germination potential [16] but also a long-term or continuous germination potential for at least some species. Species traits and soil depth according to the forest type offer different ways to maintain a population survival after a superficial or deep soil disturbance. Further studies can address how the soil qualities or edaphic conditions, light regimen, soil depth, and microtopography could affect the species density production and frequency over time for the Guajataca State Forest. This will coin the response of the soil propagules bank to other abiotic factors.

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Appendix 1. Species identified from propagule banks. Propagule banks germinated *ex situ* from transects on New Forest-A, New Forest-B, and Old Forest.

family	species
Bartramiaceae	<i>Philonotis uncinata</i> (Schwägr.) Brid.
Fissidentaceae	<i>Fissidens guianensis</i> var. <i>guianensis</i> Mont. <i>Fissidens palmatus</i> Hedw. <i>Fissidens zollingeri</i> Mont.
Funariaceae	<i>Funaria hygrometrica</i> var. <i>calvescens</i> Schwägr.
Hypnaceae	<i>Mittenothamnium reptans</i> (Hedw.) Cardot <i>Vesicularia vesicularis</i> var. <i>portoricensis</i> (Brid.)
Neckeraceae	<i>Neckeropsis disticha</i> (Hedw.) Kindb.
Pilothricaceae	<i>Callicostella depressa</i> (Hedw.) A. Jaeger
Pottiaceae	<i>Anoetangium aestivum</i> (Hedw.) Kindb