Bryophyte Species Diversity in Secondary Forests Dominated by the Introduced Species *Spathodea campanulata* Beauv. in Puerto Rico

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ABSTRACT

The introduced tree species *Spathodea campanulata* (Bignoniaceae) forms novel forests in Puerto Rico, these having emerged after the abandonment of fields in the mid-20th century and resulting in forests with a new species composition. We assessed bryophyte species richness in these novel forests and sought correlations with geological substrate, past land use, forest edge and patch area, forest structure, elevation, microhabitat diversity, tree species richness, and microclimatic conditions. Transects were established (edge and forest interior) in nine moist forest patches dominated by *Spathodea* in north-central Puerto Rico. These *Spathodea* forest patches ranged from 0.6 to 9 ha. ANOVA, Chi-square, correlation, and cluster analyses were used in data analyses. We found 57 bryophyte species. There was a significant difference in bryophyte richness among patches. Those on karst exhibited highest bryophyte richness due to microhabitat diversity, past land use, and shorter hydroperiods. Alluvial sites scored lowest in bryophyte species richness, and forest structure was important for bryophyte communities on these sites. Significant differences in temperature, relative humidity, and light intensity were observed between edge and forest interior. These appeared important for establishing bryophyte species cover but not richness and composition. Microhabitat diversity, patch area, and forest age were more related to bryophyte species richness than elevation, exposed edge, and tree species richness, regardless of geologic substrate. Collectively, *Spathodea* patches were similar to mature forests on the Island with respect to bryophyte species richness and composition. Novel *Spathodea* forests have conservation value due to their habitat suitability for bryophyte communities.

Abstract in Spanish is available in the online version of this article.

Key words: bryophyte ecology; bryophyte richness; introduced species; microhabitats; novel forests.

SECONDARY FORESTS ARE UBIQUITOUS IN THE TROPICS and a subset of these forests is characterized by the presence of introduced species. Occurring on degraded lands, these secondary forest subsets have been defined as novel, new, or emerging based on their exhibiting species combinations that have previously not been observed (Lugo & Helmer 2004, Hobbs *et al.* 2006). According to Ellis *et al.* (2010), most of the tropical evergreen and deciduous woodland in Latin America and the Caribbean will eventually become predominantly novel forest. On this point, Lugo (2009) has labeled the establishment of these forests as 'the new era of novel tropical forests'. Nevertheless, ecologists have underestimated the importance of these new ecosystems with respect to function, services, and their conservation and restoration potential (Lugo 2009).

A process of socioeconomic change that began in Puerto Rico in the 1940s stimulated the abandonment of agriculture areas (Ramos González 2001, Grau *et al.* 2003). In turn, this promoted the natural succession of secondary forests dominated by non-native species, such as *Spathodea campanulata* Beauv. The tree plant species richness, physiognomy, and structural features of

these novel forests are similar to those of native stands. Still, an important difference is found in the lower number of native tree species (Lugo & Helmer 2004, Abelleira Martínez *et al.* 2010). The regeneration of native tree species underneath the canopy of novel *Spathodea* forests, however, prevents the homogenization of forests on the island (Lugo 2009, Abelleira Martínez 2010). Although the structure of novel *Spathodea* forests has been studied, we do not know their importance as functional systems for harboring bryophyte species.

As Puerto Rico's novel *Spathodea* forests have a closed canopy, we expected that the environmental conditions are favorable for bryophyte establishment. A closed canopy reduces evaporation stress and promotes bryophyte growth (Beesby *et al.* 1978), factors which are likely to promote forest interior species (Hylander 2005). We addressed the following question: do these novel forests also foster bryophyte establishment? Our goal was to assess bryophyte diversity patterns within novel *Spathodea* forests on different geological substrates and in relation to other variables such as past land use, forest patch area and edge, forest structure, elevation, microhabitat diversity, tree species richness, and microclimatic conditions. As the structure of novel *S. campanulata* forests does not vary along elevation and substrate gradients in Puerto Rico (Abelleira Martínez *et al.* 2010), we hypothesized that bryophyte richness would be related to microhabitat diversity and microclimatic conditions. As the structure of

novel *Spathodea* forests is similar to that of mature native forests in Puerto Rico, we hypothesized that bryophyte species richness and composition of these novel forest patches would be similar to that of mature stands in Commonwealth Forests Reserves on the Island with respect to similar elevations and life zones (*e.g.,* Guajataca, Maricao, Carite, Toro Negro). Finally, we assessed the importance of novel *Spathodea* forests in terms of functional conservation importance for bryophytes.

MATERIALS AND METHODS

STUDY AREA.—We selected *S. campanulata* forest patches such that there were three each of alluvial, karst, and volcanic geological substrates in the north-central region of Puerto Rico (Table 1; Fig. 1). For each of these three substrate types, two of the patches were categorized as old sites (25–41 yr) and one as a young forest (<25 yr; Table 1). All sites, which ranged from 0.6 to 9 ha, were dominated by *Spathodea* (Table 1). In addition, forest structure was similar among geological substrates and along elevation gradient (Abelleira Martínez *et al.* 2010). The other tree species that were present included the following: *Albizia procera* (Roxb.) Benth., *Spondias mombin* L., and *Terminalia catappa* L. on alluvial substrate; *Tetrazygia eleagnoides* (Sw.) DC., *Guarea guidonia* (L.) Sleumer, *Vitex divaricata* Sw., *Andira inermis* (W. Wright) Kunth ex DC., *Chrysophyllum argenteum* Jacq., *Citharexylum fruticosum* L., and *Musa* x *paradisiaca* L. on karst substrate; and *Syzygium jambos* (L.) Alston, *Tetragastris balsamifera* Oken, *Roystonea borinquena* O. F. Cook, and *G. guidonea* on volcanic substrate (Table 1; Abelleira Martínez *et al.* 2010). With the exception of young patches and the La Curva old site, the *Spathodea* forest patches were the same as those identified in Abelleira Martínez *et al.* (2010), for which forest structure (dbh and basal area), tree species richness, and composition data were available. For the other sites, these data were not available.

ECOLOGICAL INVENTORY.—To efficiently determine bryophyte species diversity, we followed the suggestions of the Floristic Habitat Sampling (FHS) of Newmaster *et al.* (2005). According to this method, all dominant and restricted mesohabitats are identified and sampled; in addition, different types of microhabitats (*e.g.,* logs, roots, rocks) potentially colonized by bryophytes are recorded. In our study, the dominant mesohabitats are the *Spathodea* forest patches while the restricted ones are forest edge and interior. Forest edges were *Spathodea* forest patch areas in proximity to a trail or in contact with the matrix surrounding the *Spathodea* forest (*e.g.,* native or other type secondary forest). By contrast, the forest interior was 20 m from the identified edge. In each of the old sites we sampled, the only two restricted mesohabitats available were forest edge and forest interior (this being 20 m from the edge). As young sites in general have a higher percentage of exposed forest edge (Table 1) and are more homogenous, we did not find restricted mesohabitats. Therefore, we randomly placed two transects within young sites.

In old sites, we located transects perpendicular to each restricted mesohabitat and divided them into 1-m² subunits. Spe-
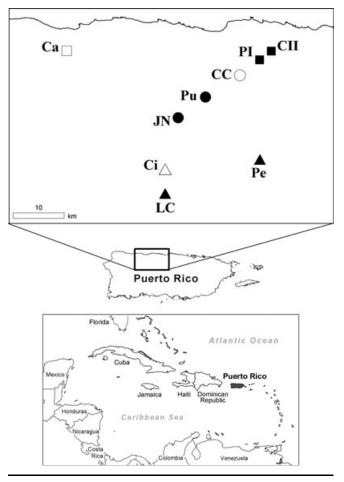

FIGURE 1. Map showing inset of Puerto Rico and selected study sites dominated by *Spathodea campanulata* forests in north-central Puerto Rico. Empty symbols denote young sites and dark symbols denote old sites (Table 1). Squares denote alluvial, circles denote karst, and triangles denote volcanic substrate sites (Table 1). Site labels correspond to Ca, Cambalache; CII, Cibuco II; PI, Paso del Indio; CC, Cuatro Caminos; Pu, Pugnado; JN, Juan Nieves; Ci, Cialitos; LC, La Curva; and Pe, Perchas (Table 1).

cies data were recorded from ground level up to 2 m in height. In each subunit, we recorded microhabitat heterogeneity by counting substrates that potentially can be colonized by bryophytes. In addition, we measured their cover percentage using a ranking scale (1 = 25%, 2 = 25–50%, 3 = 50–75%, and 4 = 75–100%). Subsequently, we collected the bryophytes and scored their microhabitat type and cover within each microhabitat using the same ranking scale described above. This process was repeated for each subsequent 1-m² subunit until no new species were found, and the species accumulation curve had therefore reached a plateau. Species that appeared more than once were collected only if the microhabitat was different from the ones scored previously. Some of the microhabitats observed and scored for *S. campanulata* forest patches were as follows: organic soil, mineral soil, rock, snag, twig, tree trunk, shrub trunk, logs and their determined decay class (*i.e.,* D1–D5; Sastre-De Jesús 1992), fern, herbs, and roots, among others. Moss specimens

TABLE 1. *Age substrate land-use history and spatial properties of Spathodea campanulata forests sampled in this study. Age since abandonment corresponds to young (<25 yr old) and old (25–41 yr old) sites. Land-use history corresponds to sugar cane (SC), pastures (P), coffee (C), and subsistence agriculture (SA). Forest patch area was estimated from digital aerial photography (ESRI 1999). The percentage of exposed edge corresponds to forest edges with a distance >30 m perpendicular to the nearest forest cover, which is an accepted threshold for dispersal limitation (Holl 1999, Zimmerman et al. 2000, Abelleira Martínez 2010).*

Site	Forest patch age	Geological substrate	Elevation (m)	Land-use history	Forest patch area (ha)	Exposed edge (%)
Cambalache	Young	Alluvial	5	SC, P	0.6	90
Cuatro Caminos	Young	Karst	160	P	4.3	67
Cialitos	Young	Volcanic	560	C, P	5.7	62
Cibuco II[*]	Old	Alluvial	10	SC	1.1	61
Paso del Indio[*]	Old	Alluvial	10	SC, P	4.0	69
Juan Nieves[*]	Old	Karst	30	SA, P	4.2	5
Pugnado[*]	Old	Karst	170	SA, P	0.9	50
Perchas[*]	Old	Volcanic	200	C, P	9.0	36
La Curva	Old	Volcanic	540	C, P	3.0	5

Notes: An asterisk denotes sites whose tree structure and vascular species composition was described by Abelleira Martínez *et al.* 2010.

were identified using the pleurocarpous guide for the West Indies (Buck 1998). For acrocarpous mosses, we used the floras from Central America (Allen 1994, 2002) and Mexico (Sharp *et al.* 1994a, b). For liverworts, we used the keys published by Gradstein (1989) and Gradstein and Pinheiro da Costa (2003). In this study, we collected 314 bryophyte specimens that were deposited in the Herbarium (MAPR) of the University of Puerto Rico at Mayagüez.

MICROCLIMATE MONITORING.—Environmental data were recorded on three *Spathodea* forest sites: Pugnado, Paso del Indio, and Cibuco II (Table 1). On each site, we assessed and measured relative humidity and temperature (RH/T) with a U23–001 data logger (Onset, Bourne, Massachusetts, U.S.A.) at four distances from the edge toward the forest interior (0, 10, 20, and 30 m). To measure light intensity, we installed one data logger (model UA-002–64; Onset) at 0 m (edge) and 20 m (forest interior) points. As *Spathodea* forest patches on karst and alluvial substrate are susceptible to flooding during rainy periods, we measured water level using a data logger model U-20–001 (Onset), which records water level as absolute pressure. Using readings of the Barometric Compensation Assistant in Hoboware Pro (Anonymous 2006), we converted these values to meters. All data loggers were programmed to read environmental conditions at intervals of 15 min between February and June 2010 (dry to wet season).

BRYOPHYTE SPECIES ANALYSIS.—To analyze species richness and cover values, we used InfoStat 2009 version (Di Rienzo *et al.* 2009). An ANOVA with a 95% confidence interval and Tukey pairwise comparisons were run to identify differences in species and microhabitat richness among *Spathodea* forest patches and other variables, including the following: forest age, edge effect, and past land use. As we did not have enough samples to represent forest age, edge effect, and past land use per *Spathodea* forest patch, we characterized these variables as treatments, using geological substrate as a classification variable and both bryophyte

species and microhabitat richness as dependent variables. Because cover percentages were categorical data, we ran a χ^2 test with a 95% confidence interval to assess bryophyte species and microhabitat cover percentages with both forest age and edge effect.

To correlate bryophyte species richness with microhabitat diversity, forest patch area, exposed edge, and elevation variables, we used one matrix that included all the patches (young and older ones). We used a second matrix that included bryophyte species richness based on exclusive use of old patches as well as forest structure and tree species richness. As we used the identical old *Spathodea* forest patches as in Abelleira Martínez *et al.* (2010), we excluded the La Curva old site from the second matrix because we did not have forest structure and tree species richness data for this site. With each matrix, we ran a correlation analysis using Pearson coefficient and $P = 0.05$.

SPATHODEA AND COMMONWEALTH FORESTS.—As liverworts species are little known in Puerto Rico, we compared only moss species richness and composition of the *S. campanulata* forests with mosses species lists and distribution published by the following authors: Sastre-De Jesús and Buck (1993), Reyes-Colón and Sastre-De Jesús (2000), and Pérez and Sastre-De Jesús (2009). A presence/absence matrix was used to compare species composition of *S. campanulata* forest patches with Commonwealth Forests and Federal Forest Reserve in Puerto Rico (Fig. S1). Data were analyzed with PC-Ord (McCune & Mefford 1999) for cluster analysis through use of Euclidean (Pythagorean) distance measures and Ward's group linkage.

MICROCLIMATE DATA ANALYSIS.—To analyze these data, we used InfoStat 2009 version (Di Rienzo *et al.* 2009). An ANOVA with a 95% confidence interval and a Tukey *post-hoc* test were run to identify the forest edge effect on microclimatic variables (T, LI, and RH). For each variable, we used stand and distance as classification variables. The water level data did not comply with the normality assumption and a Kruskal–Wallis analysis was used with $P = 0.05$ to identify significant differences among sites.

RESULTS

BRYOPHYTE SPECIES RICHNESS AND COVER PATTERNS.—We found 57 bryophyte species in our study area (Appendix S1). Of these, 20 species are liverworts in six families, and 37 species are mosses in 15 families. Within liverworts, Lejeuneaceae is the family that contains the highest number of species with 11. Aneuraceae, Geocalycaceae, and Jubulaceae had one species each. For mosses, Hypnaceae and Fissidentaceae had the highest number of species with six species each. Other moss families had one species each. These included Bartramiaceae, Leskeaceae, Leucobryaceae, Myriniaceae, Neckeraceae, Pseudocryphaeaceae, and Stereophyllaceae.

When all *Spathodea* forest patches studied were taken into account, significant differences in bryophyte species were observed among geological substrate. Patches on karst had higher bryophyte species richness than those on volcanic and alluvial substrates ($P < 0.05$). Significant differences were observed within patches (edge vs. interior) and across patches due to site and land-use history (Table 2A). Significant differences in bryophyte and microhabitat cover percentage was identified between young and old forest and between edge and forest interior (Table 2A). At the substrate scale, a significant difference in bryophyte species richness was identified for forest age only (Table 2B). On volcanic patches, forest age showed significant difference for both liverwort and moss species richness, whereas on karst sites, the difference was significant for liverworts only (Table 2B). For microhabitat species richness, the difference was significant only on karst sites (Table 2B).

Sites used for subsistence agriculture and pasture had significantly higher species richness than those used for sugar cane cultivation and pasture ($P < 0.05$, Table 1). This pattern was significant for bryophytes ($P < 0.05$), mosses ($P = 0.05$), liverworts ($P = 0.05$), and microhabitat richness ($P < 0.05$). The

Spathodea patches used for coffee plantation and pasture had similar bryophyte richness to patches used for subsistence agriculture and pasture. The overall species richness for *S. campanulata* forest patches was positively correlated with microhabitat diversity, forest patch area, forest age, and structure, and negatively correlated with forest edge exposure, tree species richness, and elevation (Table 3).

SPATHODEA FORESTS AND COMMONWEALTH FOREST.—Among geological substrate types, *Spathodea* forest patches on karst had the highest bryophyte species richness with 40 species followed by volcanic forest patches with 37 species. Alluvial sites had the lowest species richness with 15 species. The total moss species composition of *S. campanulata* forest patches is similar to species found in Commonwealth Forests on karst, these being from Guajataca and Río Abajo. The group formed by karst reserves and *Spathodea* forest patches shared more species with the Guilarte and Carite Commonwealth Forests (both on volcanic substrates) than with dry sites as Guánica, Mona Island, and Caja de Muertos, which are on limestone substrate. Luquillo, Toro Negro, and Maricao reserves, however, formed a distinct cluster (Fig. S1); the first two are on volcanic substrate and the latter on serpentine.

MICROCLIMATE.—There were significant microclimatic differences among stands. Pugnado scored the highest values for relative humidity and light intensity, Cibuco II had the highest values for temperature, and Paso del Indio had the lowest values for light intensity (Table 4). The forest edge had higher temperature and light intensity compared with those in forest interior, whereas relative humidity was lower at the edge compared with the forest interior (Table 4). For temperature values, 0 and 10 m had the highest value, and these were significantly different from those scored at 20 and 30 m. There was a significant difference for light intensity between the edge and 20 m (Table 4). Water level was different among sites ($P < 0.001$) and Paso del Indio ranked highest. During the 4 mo monitored, three inundation periods occurred. The first was in February, the second between March and April, and the third and longest one was scored in May. The highest value was reported for Pugnado with 0.51 m, yet the average water level at Pugnado was the lower than at Paso del Indio and Cibuco II.

DISCUSSION

BRYOPHYTE SPECIES RICHNESS AND COVER PATTERNS.—Bryophyte species richness has been related to microhabitat heterogeneity (Gignac & Dale 2005, Locky & Bayley 2006, Sagar & Wilson 2009), vascular plant richness (Pharo *et al.* 1999), elevational gradient (Gradstein *et al.* 2000), and forest structure (Vanderpoorten & Egels 2002, Vanderpoorten *et al.* 2005). We found that the bryophyte species richness changed with geological substrate type and responded to different variables. On alluvial sites, for example, tree diameter at breast height (dbh) and basal area were positively correlated with bryophyte species richness. In contrast,

TABLE 2. *(A) Effect of forest patch age (N = 18) edge (N = 12) and land-use history (N = 18) on species and microhabitat richness and species and microhabitat cover percentages. (B) Spathodea patches by geological substrate as compared by forest age (N = 6). ANOVA, Tukey pairwise comparisons were run to identify differences in species richness, while for cover we used a χ^2 test (P = 0.05). When a slash sign is present, left and right P values are for richness and cover percentage, respectively.*

Variable	Bryophytes	Mosses	Liverworts	Microhabitat
(A) All *Spathodea* forest patches				
Forest age	0.633/0.001[*]	0.659	0.664	0.095/0.001[*]
Forest edge	0.146/ < 0.001[*]	0.102	0.596	0.235/ < 0.001[*]
Land-use history	0.002[*]	0.004[*]	0.004[*]	0.001[*]
(B) *Spathodea* patches by geological substrate				
Forest age				
Alluvial	0.061	0.135	0.092	0.124
Karst	0.005[*]	0.088	0.008[*]	0.001[*]
Volcanic	0.002[*]	0.036[*]	0.006[*]	0.335

[*]There was significant difference, $P < 0.05$.

TABLE 3. *Correlation analysis for bryophyte species richness in Spathodea campanulata forests in Puerto Rico. The values for karst (1, N = 2) and alluvial (2, N = 2) were from quantitative data obtained from Abelleira Martínez et al. (2010), while the values for 'all substrates' (3, N = 9) were based on the first matrix described in the analysis section. The analyses were run using a correlation analysis and Pearson coefficient with 95% confidence intervals.*

Source	Elevation (m)	Exposed edge (%)	Forest patch area (ha)	Micro-habitat	Forest patch age (yr)	Vascular species	Basal area (m²)	dbh (cm)
1. Karst								
Bryophytes	—	—	—	0.85	0.3	−0.98	−0.73	−0.81
Mosses	—	—	—	0.71	0.67	−0.82	−0.8	−0.84
Liverworts	—	—	—	0.82	−0.19	−0.93	−0.48	−0.59
Microhabitats	—	—	—	1	0	−0.92	−0.28	−0.39
2. Alluvial								
Bryophytes	—	—	—	0.87	0.58	−0.58	0.78	0.71
Mosses	—	—	—	0.67	0	−0.45	0.38	0.34
Liverworts	—	—	—	0	0.71	0	0.36	0.34
Microhabitats	—	—	—	1	0.3	−0.9	0.42	0.32
3. All substrates								
Bryophytes	−0.21	−0.47	0.51	0.91[*]	—	—	—	—
Mosses	−0.28	−0.38	0.44	0.90[*]	—	—	—	—
Liverworts	−0.12	−0.48	0.49	0.84[*]	—	—	—	—
Microhabitats	−0.41	−0.41	0.14	1	—	—	—	—

[*]There was significant correlation between variables, $P < 0.05$.

TABLE 4. *Microclimatic conditions of Spathodea campanulata forests in Puerto Rico. Environmental data were recorded from forest fragments on karst (Pugnado) and alluvial (Paso del Indio and Cibuco II) substrates. At each patch relative humidity, temperature and light intensity was recorded from edge to 30 m toward forest interior at intervals of 15 min between February and June 2010.*

Variable	df	F-value	RH (%)	T (°C)	LI (lum/ft²)
Stand	2	7616.98	*	*	*
	2	462.45			
	2	811.89			
Pugnado			99.29[a]	23.13[a]	309.35[a]
Paso del Indio			98.46[b]	24.04[b]	230.64[b]
Cibuco II			97.69[c]	24.48[c]	305.28[a]
Edge effect	3	139.35	*	*	*
	3	77.58			
	1	167.43			
0 m			98.06[a]	24.00[a]	291.53
10 m			98.66[b]	23.96[a]	—
20 m			98.74[b]	23.86[b]	266.30
30 m			98.78[b]	23.77[b]	—

[*]There was significant difference using $P = 0.05$.
Different letters mean significant differences among means using $P = 0.05$.

such correlation was not found on karst substrate (Table 3). Compared with alluvial sites, which scored the lowest species and microhabitat richness, *Spathodea* forest patches on karst substrate had the highest species and microhabitat richness. Therefore, our hypothesis is partially supported because forest structure plays an important role for bryophyte species richness when patches contain low microhabitat diversity. In addition, sites on karst sub-

strate scored the highest mean relative humidity (99.29%). Higher relative humidity was linked to the higher density and diversity of bryophytes in other Neotropical areas, such as lowland rain forests in Costa Rica (Sonnleitner *et al.* 2009).

In *Spathodea* forest patches on alluvial substrate, the low availability of microhabitats makes tree trunks the most abundant of these. Moreover, as discussed earlier, bryophyte species richness increases in proportion to tree trunk area (Snäll *et al.* 2003, Löbel *et al.* 2006). Another factor resulting in low bryophyte richness on alluvial sites could be periodic flooding, which can limit the establishment of flood-intolerant species. According to Pollock *et al.* (1998), flood frequency influences species richness. In our study, alluvial and karst sites had the highest and lowest water level and lowest and highest species richness, respectively. Alluvial sites are close to rivers that overflow during rainy periods, flooding the forests up to 1 m in depth. Moreover, alluvial sites have poor drainage, which prolongs the periods of flooding. For example, although the flooding period in Pugnado occurred at the same time as those of Cibuco II and Paso del Indio, the average water level was lower and the duration of flooding was shorter than in the other patches. Flood frequency also influences moss species richness in temperate zones (Pollock *et al.* 1998). In Neotropical zones, the same pattern was shown for vascular plants, where the number of species increased significantly from sites with both higher water level and long flooding periods to sites with both lower water level and short flooding periods (Valle Ferreira 1997).

In *Spathodea* forests, the bryophyte species richness was not related to tree plant species richness and elevational gradient. The lack of correlation between bryophyte and total tree plant richness is similar to that reported by Pharo *et al.* (1999) and Löbel *et al.* (2006) for temperate zones. When the vascular plants were evalu-

ated by guild, as ferns, the relationship turned positive (Pharo *et al.* 1999). Vascular epiphyte species, however, appear to be scarce or nil on lower *S. campanulata* tree trunks (M. Pérez, pers. obs.), yet we did not aim to evaluate this relationship in our study.

According to Bruun *et al.* (2006), the richness for both mosses and liverworts showed a significant increase with elevation, being quite significant for liverworts. Nevertheless, the elevation range evaluated by Bruun *et al.* (2006) was from 0 to 1200 m, considerably different from the range (0 to 561 m) that was evaluated in our study. Indeed, we determined that elevation gradient was not related with bryophyte species richness. This may be attributable to the study gradient having been too small to reveal a pattern. Thus, in the absence of an elevation effect, microhabitat diversity plays a more important role in bryophyte richness.

FOREST EDGE, MICROCLIMATE, AND BRYOPHYTE SPECIES RICHNESS.—Differences in species composition are strongly related to microclimatic conditions (Goda Sporn *et al.* 2009, Oliveira *et al.* 2009). Relationships of species composition with microclimatic conditions, however, were not observed in this study. As in Belinchón *et al.* (2007) and Moen and Jonsson (2002), we found a relationship of bryophyte species percentage cover with distance from the forest edge. The same pattern was observed for bryophyte microhabitat percent cover. The relationship of cover percentage and microclimate was also previously reported for the Costa Rican tropical lowland rain forest, where relative humidity proved to be the most important factor (Sonnleitner *et al.* 2009). Our data suggest that microclimatic (temperature, light intensity, and relative humidity) variation from the forest edge to the interior affects bryophyte species cover, but not species richness and composition in novel *Spathodea* forest patches. Interior conditions of *Spathodea* patches, however, are apparently suitable for some species, such as the liverwort *Mastigolejeunea auriculata* (Wilson & Hook.) Schiffner, and the mosses *Vesicularia vesicularis* (Schwägr.) Broth. var. *portoricensis* (Brid.) W.R. Buck, *Sematophyllum subsimplex* (Hedw.) Mitt., and *Callicostella pallida* (Hornsch.) Ångström).

In Puerto Rico, most novel *S. campanulata* occur bordering on or near to other types of secondary forests. This precludes the possibility of finding forest patches that are totally isolated from any forest type (Abelleira Martínez 2010, O.J. Abelleira Martínez, unpubl. data). In addition, they can, at times, even be surrounded by them (Table 1). These surrounding forests can be novel or native primary to secondary in character, yet we do not have these data. Small (<1 ha) forest patches dominated by native trees, however, occur contiguous or very close to the old karst and volcanic sites, and <100 m from the alluvial sites in our study. On alluvial sites, the nearby native forests were atop surrounding karst ridges, not on alluvial flats. These nearby or surrounding native forests can be the sources of the bryophyte species we found on our sites. In turn, the *Spathodea* novel forests might be helping to decrease edge effects on these native forest patches by growing into the abandoned farmlands that surround them. Also *Spathodea* novel forests may be serving as link or corridor for bryophyte and other species dispersal between native and novel forest types.

LAND-USE HISTORY AND GEOLOGICAL SUBSTRATE VS. BRYOPHYTE SPECIES RICHNESS.—Species richness and composition of tree species in *S. campanulata* forest patches are influenced by human disturbance (Abelleira Martínez 2010, Abelleira Martínez *et al.* 2010). Most of these disturbances occurred on alluvial sites and on depressions on karst, leaving the drier, inaccessible, and less productive ridges and hilltops forested (Chinea 1980). Thus, higher species richness of large trees in karst and volcanic *Spathodea* forest patches result from the presence of these remnant fragments on hilltops and steep slopes, which is contrary to the alluvial sites where intensive sugar cultivation eliminated such remnants (Abelleira Martínez *et al.* 2010). Indirectly, past land use and substrate also influence bryophyte species richness. For example, the bryophyte communities previously established on tree remnants of hilltops or steep slopes possibly served as propagule sources during earlier forest development in the karst and volcanic patches. In addition, trees planted by farmers (*i.e., Persea americana* Mill.) and species used to shade coffee (*i.e., Inga vera* Willd., *I. laurina* (Sw.) Willd.) may have facilitated bryophyte establishment on tree trunks and acted as sources for bryophyte colonization after agriculture abandonment. On alluvial substrate, the cultivation of sugar cane (cane growth, harvesting, burning and regrowth, sometimes interspersed with fallow years) and periodic flooding events may have eliminated the possibility of bryophyte establishment (*i.e.,* spore bank, host trees). As suggested for tree species (Chinea 2002, Abelleira Martínez *et al.* 2010), bryophyte species colonization on alluvial substrate would necessarily involve dispersal from surrounding hills.

SPATHODEA FORESTS AND COMMONWEALTH FOREST.—Novel *Spathodea* forests are important habitats for bryophytes in Puerto Rico. These forest patches harbor 13.4 and 8.4 percent of the diversity of mosses and liverworts reported for the Island, respectively (Gradstein 1989, Sastre-De Jesús & Buck 1993). The overall species richness in these novel forests is higher than that of some sinkholes that are considered centers of bryophyte diversity (Reyes-Colón & Sastre-De Jesús 2000). The nine *S. campanulata* study forests jointly rank seventh (from a list of 13 Commonwealth Forests) in moss diversity below those of the Guajataca, Carite, and Guilarte nature reserves (Pérez & Sastre-De Jesús 2009). The overall moss species composition of *S. campanulata* patches is similar to older native forest patches (Guajataca and Río Abajo) in the karst belt, this area being considered both the most intact forest cover and the least fragmented habitat left in Puerto Rico (Mujica-Ortiz & Day 2001). The species shared with those forests were *Chryso-hypnum diminutivum* (Hampe) W.R. Buck, *Crossomitrium patrisiae* (Brid.) Müll. Hal., *Ectropothecium leptochaeton* (Schwägr.) W.R. Buck, *Isopterygium tenerum* (Sw.) Mitt., *Neckeropsis disticha* (Hedw.) Kindb., *Octoblepharum albidum* Hedw., *Sematophyllum subsimplex* (Hedw.) Mitt., *Taxithelium planum* (Brid.) Mitt., and *Vesicularia vesicularis* (Schwägr.) Broth. var *rutilans* (Brid.) W.R. Buck. In the Caribbean, this group of species is typical of low elevation (Sastre-De Jesus *et al.* 2010). If we compare the *S. campanulata* patches with forests on karst topography, we found that the patches shared more species with moist sites (sinkholes,

SiKS) than dry areas (exposed stack hills, MKS; Fig. S1). Moist site conditions facilitate the establishment of species whose distribution is in cloud forests (Reyes-Colón & Sastre-De Jesús 2000). Two moss species were found in our study to occur outside their normal elevation range: *Fissidens serratus* var. *serratus* Müll. Hal. (500–2750 m) and *Rhynchostegium scariosum* (Taylor) A. Jaeger (usually above 1000 m). Our cluster analysis shows that overall moss species composition in *Spathodea* forests share more species with Commonwealth Forests on karst substrate than forests on volcanic and serpentine substrates. On the Island, the forests on volcanic and serpentine substrates have a bryophyte flora characteristic of lower montane areas, whereas the karts region represents a lowland flora.

NOVEL SPATHODEA FORESTS AND BRYOPHYTE SPECIES.—At the landscape level, novel *S. campanulata* forests can be considered being in a succession stage and thus moving toward higher dominance by native trees. This is a result of the invasion of native tree species through animal-mediated seed dispersal (Abelleira Martínez 2010). Such succession appears to be happening at the bryophyte microscale. For example, although a difference in bryophyte species richness was not detected at the landscape level, the total number of species was higher in older than in young *Spathodea* forests. Conversely, a difference was observed for species cover percentage where the highest percent occurred in younger patches. Thus, young patches have fewer species albeit higher cover. Some potential explanations for these observed patterns include the following: (1) the absence of host trees such as palms; (2) the absence of microhabitats (such as exposed roots and logs); and (3) the higher abundance of particular microhabitat, such as rocks and organic soil, that can result in the dominance of some early colonizing species. Rocks and organic soil microhabitats had the highest abundance within young patches with 30.3 and 47.6 percent, respectively. Older forest patches could be acting as propagule sources for colonization and establishment of bryophytes in abandoned sites and younger patches and could be serving as dispersal corridors and/or links between other novel and native primary or secondary forests present in the landscape.

Novel *Spathodea* forests could form the basis for a restoration program in which extirpated native tree species are added. The resulting deciduous canopy would favor juvenile tree species establishment and growth (Abelleira Martínez 2010, 2011). As for tree species, these novel forests facilitate bryophyte re-establishment and succession. Therefore, other vascular and non-vascular plants could be, through use of these novel Puerto Rican forests, incorporated in restoration plans. For example, in Carite Commonwealth Forest, Tremblay *et al.* (1998) found a correlation between moss carpets and the establishment of the rare orchid *Lepanthes caritensis* R.L. Tremblay & J.D. Ackerman. The same pattern was observed by the hemiepiphyte *Ficus stupenda* (Miq.) Miq. in a Bornean rain forest (Laman 1995). *In situ* experiments in these *Spathodea* forests can be carried out to assess the effect of bryophyte carpets on vascular epiphyte establishment, especially in karst forests where bryophyte cover is higher. Management of novel *Spathodea* forests can be aimed at promoting the redevelopment of tropical forest complexity, including both vascular epiphytes and bryophytes.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Bryophyte species composition patterns among *Spathodea campanulata* forests and Commonwealth Forests in Puerto Rico.

APPENDIX S1. Species list of mosses (Bryophyta) and liverworts (Marchantiophyta) reported for Spathodea forest patches in the north-central part of Puerto Rico.

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