



Patterns in understory woody diversity and soil nitrogen across native- and non-native-urban tropical forests



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ABSTRACT

Urban expansion is accelerating in the tropics, and may promote the spread of introduced plant species into urban-proximate forests. For example, soil disturbance can deplete the naturally high soil nitrogen pools in wet tropical soils, favoring introduced species with nitrogen-fixing capabilities. Also, forest fragmentation and canopy disturbance are likely to favor high-light species over shade-adapted rainforest species. We measured understory woody diversity, the abundance of introduced species, and soil nitrogen and carbon in urban, suburban, and rural secondary forests in Puerto Rico with canopies dominated by (1) native species, (2) introduced Fabaceae (potential nitrogen-fixers), and (3) introduced non-Fabaceae species. We hypothesized that forest stands with introduced Fabaceae in the canopy have higher soil nitrogen levels than stands with other introduced canopy species, and that this higher nitrogen is linked to increased native woody species diversity in the understory. We also predicted that more open canopies and smaller fragment sizes would be positively related with introduced species in the understory, and negatively related with total understory diversity. We found that stands with introduced Fabaceae in the canopy had significantly higher soil nitrogen levels than stands with other non-nitrogen fixing introduced species, and understory woody diversity in Fabaceae stands approached similar diversity levels as stands with native-dominated canopies. As predicted, aboveground stand structure and fragment size were also significantly associated with understory woody diversity across stands. These results suggest that introduced nitrogen-fixing trees may improve recruitment of native woody species in degraded tropical sites where native soil nitrogen is naturally high, particularly as Fabaceae stands mature and canopies close.

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1. Introduction

Urban expansion is occurring rapidly in tropical regions (Lambin et al., 2003), with significant potential to affect urban-proximate forests (Kaye et al., 2006; Martinelli et al., 2006), particularly via the spread of introduced plant species (Chytry et al., 2008). Biological invasions are a major driver of global environmental change, endangering native species populations and potentially altering ecosystem structure and function (Vitousek et al., 1996, 1997). Introduced plants may spread from urban centers into nearby forests (Cowie and Werner, 1993; McKinney, 2002, 2008), particularly where unmanaged afforestation is occurring such as on abandoned agricultural sites across Latin America (Lugo, 2004; Grau and Aide, 2008). Investigation of landscape- and ecosystem-scale factors that promote regeneration of native diversity in tropical urban forest fragments has received little attention, despite widespread concern about biodiversity in tropical forests.

Changes in soil properties with urban activity may contribute to the spread of introduced species. For example, localized soil compaction and topsoil removal (e.g. erosion) can increase soil bulk density and decrease the availability of nitrogen (N) and other nutrients in surface soils (Woodward, 1996), contributing to high variability in soil N levels among nearby urban forest stands (Cusack, 2013). Soil N loss in tropical forests can have a negative effect on the establishment of native tropical forest plants (Reiners et al., 1994), likely because native plants are adapted to the relatively high background N availability in highly weathered tropical soils (Walker and Syers, 1976; Chestnut et al., 1999; Martinelli et al., 1999; Hedin et al., 2009). Thus, soil disturbances that deplete naturally high N pools in highly weathered tropical soils can favor introduced species adapted to low soil N (Funk and Vitousek, 2007). This relationship is in contrast to patterns observed in some Northern sites, where N deposition in urban-proximate forests increases N availability in naturally N-poor soils, and can favor the spread of introduced plants that are competitive at higher soil N (Howard et al., 2004). Thus, N depleted soils in urban-proximate tropical forests are likely to promote loss of native plant species,

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and the spread of introduced species that have a competitive advantage at low N.

Plants with N-fixing capabilities in the Fabaceae family are highly likely to be successful invaders in N-poor soils (Binggeli, 1996; Pysek, 1998). In tropical areas where native Fabaceae are rare or absent (Allen and Allen, 1981), they can be particularly successful invaders in degraded areas, with the capacity to increase local soil N levels over time via N-fixation (Vitousek et al., 1987). Because of their positive effect on soil N, mature stands of introduced Fabaceae may eventually promote restoration of native understory growth, as has been seen in a dry subtropical forest (Parrotta, 1993). Thus, soil disturbance in urban-proximate tropical forests may deplete N and favor introduced N-fixing species, but these may in turn restore naturally high soil N levels over time.

In addition to soil disturbance, forest fragmentation and canopy disturbance are common in tropical forests (McGrath et al., 2001; Geist and Lambin, 2002; Sodhi et al., 2010), particularly around urban areas (Huston, 2005), and are also linked to the spread of introduced plants (Cowie and Werner, 1993; Charbonneau and Fahrig, 2004; Groffman et al., 2006). For example, forest fragmentation in Brazil decreased species number and stem abundance (Benítez-Malvido and Martínez-Ramos, 2003), with urban fragments particularly susceptible to establishment of introduced plants (da Fonseca and Carvalho, 2012). Increased canopy openness has been linked to the success of shade intolerant introduced plants, particularly in wet tropical forests where mature forest canopies are dense and native understory plants are adapted to low light (Murphy et al., 2008; Siddique et al., 2008). Introduced Fabaceae can have a strong competitive advantage where disturbed canopies create high light understory conditions (Wolfe and Van Bloem, 2012). Thus, disturbances to both soil and aboveground forest structure in urbanized tropical areas are likely to favor the spread of introduced Fabaceae species.

Colonization of disturbed urban-proximate forests by introduced species could alter successional pathways. First, if introduced plants are established as successful invaders reaching the canopy, they may persist and dominate species assemblages in the long-term, especially if they are shade tolerant with high survival and growth under the canopy (Murphy et al., 2008). Alter-

nately, initial cohorts of introduced plants may facilitate the regeneration of native species if they improve site conditions, resulting in novel species assemblages (Lugo and Helmer, 2004), or restoration of native species compositions eventually.

Here, we examined distributions of introduced Fabaceae, introduced non-Fabaceae, and native trees in the canopies and understories of eight forest stands in an urban-suburban watershed, and three stands in a rural watershed in subtropical secondary forests in Puerto Rico. We explored relationships for understory woody plant diversity with soil and aboveground characteristics to address the following hypotheses: (1) forest stands with introduced Fabaceae in the canopy have higher soil N levels than stands with non-Fabaceae introduced canopy species, approaching the high background soil N levels found in native tropical forests; (2) stands with Fabaceae in the canopy have greater native understory plant diversity than stands with non-Fabaceae introduced canopy species, indicating improved recruitment of native species in high N soils; (3) disturbances that allow more light into the understory are negatively associated with total native woody species diversity, and positively associated with the abundance of introduced plants in the understory.

2. Materials and methods

2.1. Study sites

The main site for this study was an urban-suburban watershed in Puerto Rico, with additional sites in a rural watershed (Fig. 1). Eight urban and suburban forest stands were located in the Río Piedras watershed within the San Juan Urban Long Term Research Area (ULTRA-Ex). The 8 stands represented the major forested areas of the urban-suburban (hereafter “urban”) watershed, spanning from the low-elevation urban core, to higher elevation suburban areas (Table 1). The urban watershed is in the subtropical moist forest life zone (sensu Holdridge et al., 1971), ranges in elevation from 0 to 220 m above sea level (masl), has mean annual precipitation (MAP) of 1750 mm, and mean annual temperature (MAT) of 25.7 °C. Rural sites were located in secondary forests in the USFS Cubuy Annex (18°16'N, 65°52'W), which is also in the

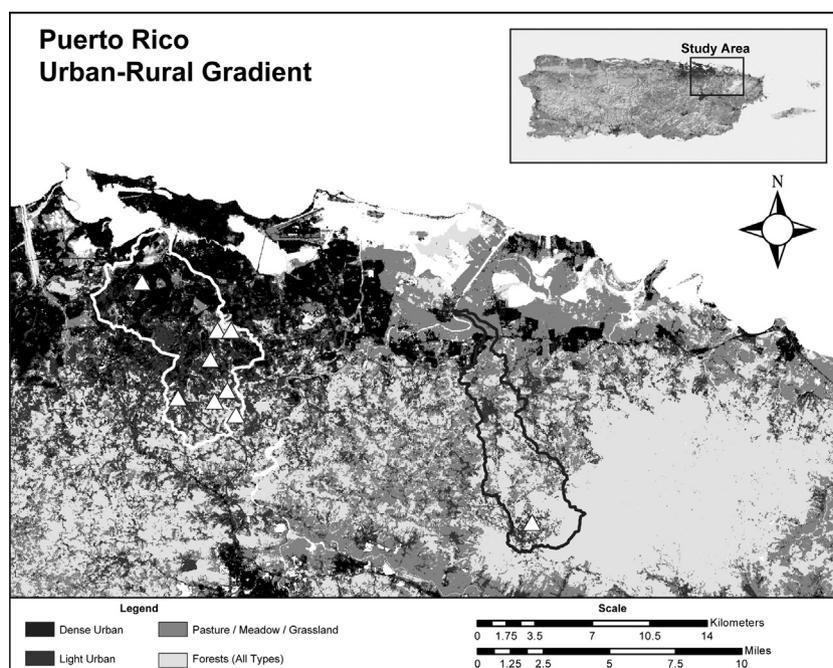


Fig. 1. Map showing the locations of 8 forest fragments (white triangles) within the urban Río Piedras watershed in Puerto Rico (white outline), and three sites in a rural forest watershed (black line) within the USFS Cubuy Annex (white triangle). Cover types have been modified from (Kennaway and Helmer, 2007).

Table 1

Site information and understory species number and stem abundance are shown for eight urban forest stands (U) and rural forest stands (R) in Puerto Rico. Data are shown for forest stands within six urban sub-watersheds (1–6) feeding the main stem (0) of the Río Piedras river. The second digit designates the tertiary tributary (e.g. 0.5). Urban stands are ordered from lowest elevation and closest proximity to the urban center (0), to highest elevation and farthest from the urban center (6). Introduced tree species in the canopy are shown as a percent of total basal area (mean \pm 1 SE, $n = 3$).

Watershed	Site ID	Elevation (masl)	Latitude N	Longitude W	Forest frag size (km ²)	Distance to urban center (km)	Shortest distance to major road (km)	Basal area (m ² ha ⁻¹)	% Canopy total non-natives (of basal area) ^a	% Canopy Fabaceae (of area)	% Canopy openness	Total # of understory species/10 m ²	Total # of understory stems/10 m ²	Seedling: sapling ratio	% Fabaceae of understory stems	Shannon diversity index ^b
Urban	0.5	20	18.4079	-66.0934	0.27	3.6	0.6	38 \pm 1	83 \pm 3	83 \pm 3	8 \pm 1	4.7 \pm 1.7	33 \pm 26	7.1 \pm 6.6	27 \pm 27	0.37 \pm 0.04
Urban	3.0	40	18.3831	-66.0496	1.79	6.8	2.1	30 \pm 2	10 \pm 3	10 \pm 3	7 \pm 0.3	4.3 \pm 0.2	183 \pm 59	39.8 \pm 33.7	27 \pm 24	0.27 \pm 0.09
Urban	2.6	50	18.3813	-66.0420	1.79	7.4	1.4	29 \pm 2	3 \pm 3	3 \pm 3	10 \pm 2	5.3 \pm 0.3	204 \pm 20	1.7 \pm 0.3	0	0.45 \pm 0.05
Urban	3.4	80	18.3662	-66.0539	0.08	8.3	1.6	14 \pm 2	85 \pm 7	85 \pm 7	23 \pm 5	2.7 \pm 0.3	10 \pm 2	0.3 \pm 0.04	35 \pm 16	0.32 \pm 0.02
Urban	6.0	88	18.3453	-66.0718	0.07	10.3	0.2	33 \pm 3	92 \pm 5	0	3 \pm 1	7.3 \pm 0.3	97 \pm 40	2.1 \pm 1.1	0	0.49 \pm 0.10
Urban	4.3	100	18.3483	-66.0444	0.21	10.5	2.6	20 \pm 3	11 \pm 11	11 \pm 11	7 \pm 1	6.0 \pm 0.6	32 \pm 21	1.1 \pm 0.5	7 \pm 2	0.57 \pm 0.11
Urban	5.1	120	18.3425	-66.0517	0.06	10.9	1.3	37 \pm 9	67 \pm 2	0	6 \pm 1	5.0 \pm 0.6	113 \pm 65	11.0 \pm 4.5	1 \pm 1	0.22 \pm 0.08
Urban	5.0	160	18.3349	-66.0394	0.56	12.1	1.2	29 \pm 6	86 \pm 9	0	8 \pm 2	4.0 \pm 0.6	82 \pm 34	8.9 \pm 8.4	0	0.28 \pm 0.05
Rural	R	490	18.2767	-65.8690	0.67	28.3	4.6	37 \pm 1	6 \pm 1	6 \pm 1	5 \pm 1	13.3 \pm 0.3	100 \pm 32	1.6 \pm 0.3	7 \pm 1	1.0 \pm 0.004

^a Canopy non-native species here include Fabaceae and non-Fabaceae (primarily *Spathodea campanulata*) individuals.

^b The Shannon diversity index (H') was calculated as: $H' = -\sum P_i \ln P_i$, where P_i is the proportional abundance of each species (Mueller et al., 2004).

subtropical moist forest life zone, has elevation from 300 to 500 masl, MAP of 2500 mm, and MAT of 26 °C (Silver et al., 2004). The rural site had a smaller sample size because of limited access to private land in the rural watershed. Three forest stands in a rural watershed were used to explore the landscape-scale spread of introduced Fabaceae. Soils at all sites were volcaniclastic Ultisols (Boccheciamp, 1978).

All forest stands were secondary regeneration following widespread agricultural abandonment in Puerto Rico starting in the 1930s (Kennaway and Helmer, 2007). The rural Cubuy forest has been held by the US Forest Service since the 1930s and has areas of natural regeneration on pastureland (Marrero, 1947). Two larger forest fragments in the mid-urban watershed (stands 2.6 and 3.0, Table 1) are in the Bosque Estatal del Nuevo Milenio managed by the Puerto Rico Department of Natural Resources and the Environment (DNRE), and the Jardín Botánico of the University of Puerto Rico, respectively. Plots in both of these stands were in areas that have had natural forest regeneration since the 1930s following agricultural activity, similar to the rural site (Lugo et al., 2005). Site 0.5 is in the Bosque San Patricio, also managed by the DNRE, and is forest regeneration following agricultural abandonment in the 1930s, although part of the forest was used as US military housing until the 1960s (DNRE, 2003). Site 4.3 was a private coffee plantation and was allowed to reforest starting in the 1930–40s. Stands 3.4, 5.1 and 6.0 are on unprotected government land with natural regeneration of unknown age at a roadside, near Las Curias Reservoir, and surrounding a power station, respectively. Site 5.0 is on private land belonging to the Betancourt family and is natural regeneration.

The same most common secondary woody species (native and introduced) are present across the urban and rural sites (Aide et al., 2000). In native forests of Puerto Rico, Fabaceae woody species are rare or absent (Little and Wadsworth, 1964). The urban Río Piedras forests contain a mixture of native and non-native species with introduced trees of the Fabaceae family as canopy trees (Helmer, 2004; Lugo, 2004; Kennaway and Helmer, 2007), including *Albizia procera* (Roxb.) Benth., and *Adenantha pavonina* L. The species *A. procera* is particularly widespread in degraded areas such as roadsides, abandoned land, and waste places (Rivera, 1992). The most common introduced non-Fabaceae in these secondary Puerto Rican forests is *Spathodea campanulata* P. Beauv. (Lugo, 2004) which is light-demanding, shade intolerant, and wind dispersed (Rivera and Aide, 1998; Marciano-Vega et al., 2002; Lugo, 2004).

Landscape-scale urban factors were measured to characterize each forest fragment. Forest fragment sizes, distance to the urban center, and distance to the nearest major road were measured for each forest stand using Arc GIS 10 with a land-cover classification map for the area (Kennaway and Helmer, 2007). Forest fragments were defined as areas of continuous forest, and were generally bounded by roads, grass sites or urban cover. Urban forest stands were assigned to three size classes that roughly divided the number of sites evenly: class 1 < 0.2 km²; class 2 = 0.2–1.8 km²; class 3 > 1.8 km².

2.2. Understory and canopy surveys

Understory surveys of seedlings and saplings were conducted in July 2011 in the urban and rural forest stands. Three 2 m \times 5 m plots were randomly located in the core area of each forest stand, avoiding edges, and all understory woody individuals under 150 cm were counted and identified to species or genus. Individuals < 25 cm tall were categorized as seedlings, and individuals 25–150 cm were saplings. Using species numbers and stem abundances in each plot, we calculated Shannon's diversity index (Mueller et al., 2004) for comparison among sites (Table 1). The

Simpson's diversity index was also calculated, and showed the same patterns as the Shannon index, so is not reported here.

Forest stand basal area and the percent of introduced trees in the canopy were measured from three points in each site using a handheld bottle-opener dendrometer (JIM-GEM Cruz-all, Forestry Suppliers, Jackson, MS), noting the proportion of basal area belonging to introduced Fabaceae or *S. campanulata* (Table 1). Canopy openness was measured as the percent of open versus foliage-covered area using a hand-held spherical crown densitometer (Forestry Suppliers, Jackson, MS).

2.3. Soil collection and analysis

Soils were collected from 0 to 10 cm using a 2.5 cm diameter soil probe. At each site soils were collected from three 20 m transects ($n = 3$) near seedling plots. Four soil cores were collected at each of four points along each transect (total of 16 cores per transect), and then pooled to give one representative sample per transect. Bulk density was measured from 0 to 10 cm back from the undisturbed face of a 20-cm deep pit in each forest stand using a 6.5 cm inner-diameter corer as described in Cusack (2013).

For soil nutrient analyses, fresh soils were extracted using 2 M potassium chloride (KCl) for ammonium (NH_4^+), nitrate (NO_3^-), dissolved organic C (DOC), and total dissolved N (TDN) on the day of collection in Puerto Rico to minimize storage effects on mineral N pools (Turner and Romero, 2009) as described in Cusack (2013). Frozen extract samples were shipped for analysis to the University of California – Los Angeles. Extractable NH_4^+ and NO_3^- were analyzed using standard colorimetric techniques in 96-well plates (Rhine et al., 1998; Doane and Horwath, 2003). Analyses included standard curves, check standards, and four analytical replicates per sample. Mineral N levels were measured on a BioTek Instruments Inc., Synergy HT absorbance spectrometer. Extracted DOC and TDN were measured in duplicate together with standard curves and check standards on a Shimadzu TOC-L CSH, with a TNM-L unit for TN detection. Separate soil subsamples were air-dried and ground using a mortar and pestle for total C and N analyses, which were measured on a Costech Elemental Analyzer using atropine and acetanilide as standards.

2.4. Statistical analysis

We assessed site-level differences and ecosystem drivers of understory diversity and the abundance of introduced species for: (1) comparisons among the eight urban forest stands ($n = 3$ plots per stand), and (2) relationships of ecosystem factors (e.g. soil and canopy characteristics) with understory plant species compositions within the urban watershed ($n = 24$ plots for regression analyses), (3) comparisons between urban forests stands ($n = 8$) and rural forest stands ($n = 3$). We used analysis of covariance (ANCOVA) to test predictors of understory woody species numbers, stem abundance, proportion of Fabaceae, and diversity index values. ANCOVA were built using forward stepwise models. Predictors included: forest fragment size class, basal area, canopy openness, % introduced (Fabaceae and non-Fabaceae) canopy basal area, and soil characteristics (bulk density, pH, %N, %C, C:N, mineral N levels, DOC, and TDN). We also included urban landscape factors (distance to the urban center, shortest distance to a major road) as covariates for predicting understory species compositions. Because there were a large number of stands with no Fabaceae, data were also transformed into presence/absence for further statistical analysis, and chi-square tests were used to determine correspondence between presence/absence in the canopy and in the understory.

Additional analyses were done to explore patterns and similarities among the forest stands using multivariate analysis of variance (MANOVA), with post hoc *t*-tests to assess significant

differences in specific ecosystem characteristics. We used Ward Hierarchical Cluster Analysis to explore similarities in understory species number and stem abundance among forest stands. Seedlings and saplings were assessed both pooled and separately as an indication of survivorship. Continuous variables were log transformed where necessary to meet assumptions of normality. Means are reported \pm one standard error, and significance levels are $p < 0.05$ unless otherwise noted.

3. Results

3.1. Introduced canopy trees and soil characteristics

Introduced Fabaceae were present in the canopies of 44% of the plots. In general, stands with introduced trees in the canopy had native species plus either Fabaceae or *S. campanulata*, without mixtures of these two introduced groups of species (Table 1). Addressing our first hypothesis, forest stands with canopy Fabaceae had the highest soil N concentrations ($0.32 \pm 0.02\%$), stands with introduced non-Fabaceae had the lowest soil N ($0.22 \pm 0.02\%$), and stands with all-native canopies were intermediate and not significantly different ($0.29 \pm 0.03\%$, Fig. 2). Using bulk density for each site, these concentrations represent N stocks to a depth of 10 cm of $3.1 \pm 0.1 \text{ mg N/cm}^3$ in Fabaceae stands, and $3.1 \pm 0.5 \text{ mg N/cm}^3$ in all-native stands, which were both significantly higher than stands with non-Fabaceae introduced canopy species ($2.3 \pm 0.1 \text{ mg N/cm}^3$). Similarly, soil C concentrations were significantly higher under canopies with Fabaceae present ($4 \pm 0.3\%$), versus stands with introduced non-Fabaceae in the canopy ($2.5 \pm 0.2\%$), and values were not significantly different under all-native stands ($3.5 \pm 0.3\%$).

As with canopy trees, the presence of introduced Fabaceae in urban forest understories corresponded to soil properties. Soil bulk density was significantly lower where understory Fabaceae were present versus absent, indicating less compacted soils (Table 2). Soil % N, % C, and C:N ratios were all significantly higher in stands with understory Fabaceae present versus absent (Table 2). Bulk density was negatively correlated with soil % N ($R^2 = 0.31$, $p < 0.05$), such that less compact soils had higher soil N, and more understory Fabaceae. There were also trends of higher soil TDN, total mineral N, and NH_4^+ in stands with understory Fabaceae present versus absent ($p = 0.08$). The first axis in MANOVA explained nearly all of the variability in presence versus absence of Fabaceae in the understory (96%), with soil % N and bulk density having by far the highest loadings on this axis (score of 7 each), followed by NH_4^+ and canopy openness (score of 1.5 each). Soil factors were more closely related to the presence of Fabaceae in the understory than were aboveground forest structure or landscape-scale factors. In general, Fabaceae in both the canopy and understory tended to correspond to improved soil conditions.

3.2. Introduced canopy trees and understory woody diversity

Understory diversity and Fabaceae presence varied among stands with all-native versus introduced canopy species. Addressing our second hypothesis, the Shannon diversity index was significantly higher under all-native canopies than under canopies with introduced non-Fabaceae in urban forests, and intermediate (i.e., not significantly different) under canopies with Fabaceae (Fig. 2). Thus, forest stands with introduced Fabaceae canopy trees had the highest levels of soil N but intermediate understory woody diversity, whereas stands with introduced non-Fabaceae had the lowest soil N levels and the lowest understory diversity.

Overall, the presence of Fabaceae in the canopy tended to correspond to the presence of Fabaceae in the understory ($p = 0.08$),

with the proportion of Fabaceae in the understory ranging from 0% to $35 \pm 16\%$. The abundance and proportion of understory Fabaceae in urban forests were both significantly higher in stands with canopy Fabaceae present (31 ± 23 Fabaceae-stems/10 m², $25 \pm 10\%$ of stems) versus introduced non-Fabaceae (0.1 ± 0.1 Fabaceae-stems/10 m², $0.01 \pm 0.01\%$ of stems), and not significantly different in all-native stands (0.3 ± 0.3 Fabaceae-stems/10 m², $3 \pm 2\%$ of stems). Interestingly, understory Fabaceae as a proportion of stems was not significantly different between rural versus urban forest stands ($7 \pm 1\%$ in rural versus $12 \pm 5\%$ in urban forests), unlike trends for canopy Fabaceae, suggesting increased survivorship or spread of Fabaceae seedlings into the rural sites.

3.3. Aboveground characteristics and understory diversity

Addressing our third hypothesis, the strongest single predictor of understory species number in the urban forests was canopy openness ($R^2 = 0.35$, $p < 0.05$), with the lowest species numbers under more open canopies. Similarly, the abundance of understory stems was related to both canopy openness (negative relationship, $R^2 = 0.21$, $p < 0.05$), and forest fragment size, with more stems per area in the largest forest fragments (Fig. 3). In contrast, the presence of understory Fabaceae corresponded to somewhat more open canopies ($11.5 \pm 2.8\%$ open where Fabaceae were present, versus $7.2 \pm 0.9\%$ open where Fabaceae were absent, $p = 0.08$). Similarly, stands with Fabaceae canopies had significantly greater canopy openness than introduced non-Fabaceae stands, while native-dominated canopies were not significantly different (Fig. 2). Thus, stands with Fabaceae in the canopy had the highest levels of soil N, but also greater canopy openness, both of which appear to play a role driving understory diversity, potentially explaining the intermediate understory diversity in these stands.

3.4. Landscape patterns in understory diversity and stem abundance

Overall, we identified 40 understory woody species from 18 plant families across stands (Appendix), with 8 families and 8 species common to both urban and rural stands. In the urban stands the Flacourtiaceae and Meliaceae families accounted for >50% of understory stems, and Fabaceae accounted for 17%. The most abundant species in the urban stands were *Guarea guidonia* (30.4% of stems), *Calophyllum calaba* (13.5% of stems), and *Casearia decandra* (13.1% of stems). Fabaceae species identified included *A. pavonina*, *A. procerca*, *Andira inermis*, and *Inga laurina*. Of the Fabaceae identified, *I. laurina* and *A. inermis* are native to Puerto Rico, but these species accounted for only 5 of 399 total understory Fabaceae individuals observed (Appendix). The rural forest understories were dominated by woody species in the Bignoniaceae, Chrysobalanaceae, and Myrtaceae, with these families accounting for >50% of all stems present, and Fabaceae accounting for 9.5%. The most abundant understory species in the rural stands were *Prestoea montana* (16.3% of stems), *Tabebuia heterophylla* (16% of stems), and *Hirtella rugosa* (14.7% of stems). *T. heterophylla* was one of the few wind dispersed species found, and *H. rugosa* is endemic to Puerto Rico (Appendix). No understory *S. campanulata* were found in any site.

There were significantly more understory woody species and higher diversity index values in the rural versus urban forests, whereas stem abundance was not significantly different (100 ± 32 stems/10 m² in rural forests, versus 94 ± 25 stems/10 m² in urban forests). The rural forests had an average of 13 ± 0.3 understory species/10 m², whereas the urban forests had 5 ± 0.5 species/10 m², and the Shannon diversity index was 1.0 ± 0.004 in the rural forests, versus 0.37 ± 0.04 across urban stands. There was strong patchiness in species dominance among the eight urban forest stands despite their relatively close proximity (Fig. 1, Appendix). Understory species number among the 8 urban stands ranged from

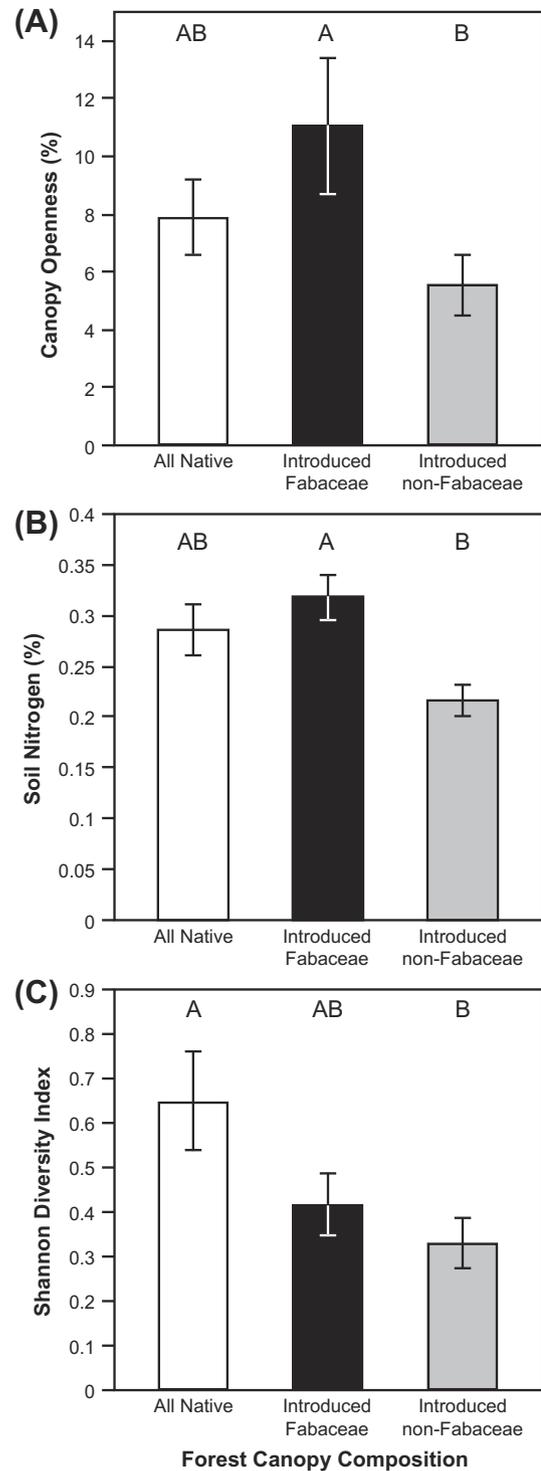


Fig. 2. Forest stands where canopy composition includes only native trees (All Native, $n = 6$), introduced Fabaceae ($n = 12$), or introduced non-Fabaceae ($n = 9$) are compared for: (2a) canopy openness (%); (2b) soil N concentrations (%); (2c) Shannon diversity index values. Introduced non-Fabaceae were predominantly *Spathodea campanulata*. Letters show differences using Fisher's Least Significant Difference test ($p < 0.05$).

2.6 ± 0.3 to 7.3 ± 0.3 species/10 m², understory stem abundance ranged from 9.6 ± 1.8 to 203.6 ± 20.3 stems/10 m², and the Shannon diversity index ranged from 0.22 ± 0.1 to 0.57 ± 0.1 (Table 1). The clustering analysis distance graph flattened after four clusters, such that the rural forest and the two largest urban forest fragments were each in their own cluster, and smaller forest fragments formed

Table 2

Comparison of soil characteristics for urban forest stands with introduced Fabaceae seedlings and saplings absent versus present in the understory.

Introduced Fabaceae seedlings and saplings	Absent	Present
Number of plots	14	10
Soil bulk density g/cm ³ (0–10 cm depth)**	1.14 ± 0.05	0.92 ± 0.05
Soil pH	6.3 ± 0.2	6.5 ± 0.3
Soil% N**	0.24 ± 0.01	0.33 ± 0.02
Soil% C**	2.81 ± 0.22	4.23 ± 0.38
Soil C:N**	11.79 ± 0.21	12.69 ± 0.39
NH ₄ ⁺ mg N/kg dry soil†	1.90 ± 0.24	2.77 ± 0.54
NO ₃ ⁻ mg N/kg dry soil	3.08 ± 0.43	3.72 ± 0.56
Total mineral N mg N/kg dry soil†	4.98 ± 0.52	6.49 ± 0.91
TDN mg N/kg dry soil†	15.2 ± 1.9	22.4 ± 4.6
DOC mg C/kg dry soil	70.6 ± 8.7	103.2 ± 30.9

** $p < 0.05$.
† $p < 0.1$.

smaller sub-clusters roughly in order of distance to the urban center (Fig. 4, Table 1).

The rural forest stands had significantly lower proportions of Fabaceae in the canopy ($6 \pm 6\%$ of basal area) compared with the urban forests ($24 \pm 7\%$ of basal area). For the urban stands, the percent of basal area occupied by total introduced species (Fabaceae plus non-Fabaceae) declined significantly with distance to a major road ($R^2 = 0.54$, $p < 0.05$), and the percent of basal area occupied by Fabaceae declined significantly with distance to the urban center ($R^2 = 0.41$, $p < 0.05$). Similarly, where understory Fabaceae were present ($n = 10$) the abundance of Fabaceae was negatively correlated with distance to the urban center ($R^2 = 0.56$, $p < 0.05$).

There were no differences in abundances of seedlings or saplings between the rural and urban forests, but the seedling:sapling ratio was significantly higher in urban (9.0 ± 4.5) versus rural (1.6 ± 0.3) stands (Table 1), possibly suggesting improved survivorship in the rural stands. The seedling:sapling ratio was not significantly different for total stems versus Fabaceae stems, suggesting no difference in survivorship for natives versus introduced species.

4. Discussion

4.1. Introduced Fabaceae and soil conditions

Canopy Fabaceae were associated with higher soil N levels relative to stands with other introduced species in the canopy, sup-

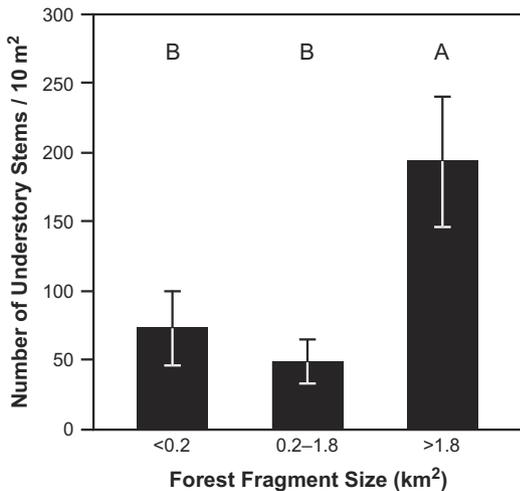


Fig. 3. Differences in the abundance of woody stems in the understory of urban forests are shown for three forest fragment size classes. Letters show differences using Fisher’s Least Significant Difference test ($p < 0.05$). Size class $< 0.2 \text{ km}^2$ has $n = 9$; class $0.2\text{--}1.8 \text{ km}^2$ has $n = 9$; class $> 1.8 \text{ km}^2$ has $n = 6$.

porting our first hypothesis. In managed restoration projects in the Neotropics, native or introduced Fabaceae have been planted because of their capacity to grow in disturbed soils and increase soil N and organic matter (Griscom and Ashton, 2011; Eaton et al., 2012). Similarly, native Fabaceae restored soil N during afforestation after pasture abandonment in Panamanian forests (Batterman et al., 2013), and introduced Fabaceae increased soil N in Hawai’i (Vitousek et al., 1987; Vitousek and Walker, 1989). In the absence of native Fabaceae in these Puerto Rican sites, it appears that introduced Fabaceae may have initially colonized disturbed, post-agricultural, N-depleted sites, and that N-fixation may have increased soil N to native levels in an unmanaged setting. Alternatively, Fabaceae could have increased soil N via inputs and accumulation of organic matter, which would also explain the higher soil C found in Fabaceae stands relative to stands with other introduced species. Or, increased N inputs from N fixation may have promoted soil C retention via formation of new organo-mineral associations (Cusack et al., 2011).

Regardless of the mechanism, improved soil conditions under introduced Fabaceae canopies appeared to favor regeneration of more native diversity than under other introduced species canopies, addressing our second hypothesis. Native species adapted to the high N availability typical of tropical forests on highly weathered soils (Walker and Syers, 1976; Chestnut et al., 1999; Martinelli et al., 1999; Hedin et al., 2009) may have benefited from the increased soil N under Fabaceae. Despite their apparent positive effect on understory diversity, Fabaceae stands did not reach diversity levels under all-native canopies, possibly because of their more open canopies. Greater canopy openness in these Fabaceae stands could indicate earlier successional stage than the native-dominated forest stands (Aide et al., 1996, 2000). Thus, Fabaceae stands may reach understory plant diversity levels equivalent to native stands as canopies close over time.

4.2. Canopy properties and understory diversity

Urban forest stands with 1–10% canopy openness had the highest understory woody species diversity, in part supporting our third hypothesis. A number of other studies in tropical forests have also found that high light conditions negatively correlate with understory native woody diversity and seedling abundance (Kuusi-palo et al., 1995; Parrotta et al., 1997; Powers et al., 1997; Cusack and Montagnini, 2004), likely because mature forest woody species

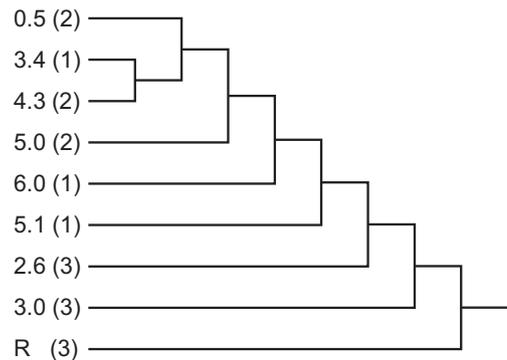


Fig. 4. Results from Ward Hierarchical Cluster Analysis using understory species number and stem abundance are shown for eight urban and one rural (R) forest stands. Forest stands were in six urban sub-watersheds (1–6) feeding the main stem (0) of the Río Piedras river. The second digit designates the tertiary tributary (e.g. 0.5). Urban stands are ordered from lowest elevation and closest proximity to the urban center (0), to highest elevation and farthest from the urban center (6). Parentheses following site numbers give forest fragment size classes, with class 1: $< 0.2 \text{ km}^2$; class 2: $0.2\text{--}1.8 \text{ km}^2$; class 3: $> 1.8 \text{ km}^2$. The distance graph for the analysis was relatively flat after 4 clusters, such that the largest fragments each had their own cluster.

Appendix A (continued)

Family	Genus and species	Native to Puerto Rico? ^a	Dispersal mechanism ^b	Seedling or sapling	0.5	2.6	3.0	3.4	4.3	5.0	5.1	6.0	R
Chrysobalanaceae	<i>borinquensis</i> <i>Hirtella rugosa</i>	EN	Animal	Sapling									19
Chrysobalanaceae	<i>Hirtella rugosa</i>	EN	Animal	Seedling									25
Clusiaceae	<i>Calophyllum calaba</i>	N	Bird, bat, rodent	Sapling	8	138		1	47		1		
Clusiaceae	<i>Calophyllum calaba</i>	N	Bird, bat, rodent	Seedling	1	105			4				
Combretaceae	<i>Terminalia catappa</i>	I	Wind	Seedling		3					1		
Connaraceae	<i>Rourea surinamensis</i>	N	Bird	Sapling			9						6
Connaraceae	<i>Rourea surinamensis</i>	N	Bird	Seedling			9						13
Elaeocarpaceae	<i>Roystonea borinquena</i>	N	Animal	Sapling									3
Elaeocarpaceae	<i>Roystonea borinquena</i>	N	Animal	Seedling									2
Elaeocarpaceae	<i>Sloanea berteriana</i>	N	Bird, mammal	Sapling		31							
Elaeocarpaceae	<i>Sloanea berteriana</i>	N	Bird, mammal	Seedling		19			1		1		4
Fabaceae	<i>Adenanthera pavonina</i>	I	Bird	Sapling			29						
Fabaceae	<i>Adenanthera pavonina</i>	I	Bird	Seedling			264						
Fabaceae	<i>Albizia procera</i>	I	Pod/gravity	Sapling				7					1
Fabaceae	<i>Albizia procera</i>	I	Pod/gravity	Seedling	68			3					22
Fabaceae	<i>Andira inermis</i>	N	Bat	Sapling					3				
Fabaceae	<i>Andira inermis</i>	N	Bat	Seedling					1				
Fabaceae	<i>Inga laurina</i>	N	Mammal, large bird	Seedling							1		
Flacourtiaceae	<i>Casearia arborea</i>	N	Bird, mammal	Sapling									8
Flacourtiaceae	<i>Casearia arborea</i>	N	Bird, mammal	Seedling									1
Flacourtiaceae	<i>Casearia decandra</i>	N	Bird, mammal	Sapling		43							
Flacourtiaceae	<i>Casearia decandra</i>	N	Bird, mammal	Seedling		253							
Flacourtiaceae	<i>Homalium racemosum</i>	N	Animal	Sapling	1			4	1	50			
Flacourtiaceae	<i>Homalium racemosum</i>	N	Animal	Seedling				2	3	148			
Flacourtiaceae	<i>Samyda spinulosa</i>	N	Animal	Sapling									5
Flacourtiaceae	<i>Samyda spinulosa</i>	N	Animal	Seedling									15
Lauraceae	sp.	N	Animal	Sapling									6
Lauraceae	sp.	N	Animal	Seedling									3
Lauraceae	<i>Ocotea leucoxylon</i>	N	Bird, mammal	Sapling	1						5		8
Lauraceae	<i>Ocotea leucoxylon</i>	N	Bird, mammal	Seedling	1				5		1		3
Lauraceae	<i>Ocotea sintenisii</i>	N	Bird, mammal	Sapling							1		
Lauraceae	<i>Ocotea sintenisii</i>	N	Bird, mammal	Seedling						17			
Melastomataceae	<i>Miconia impetiolearis</i>	N	Bird, mammal	Sapling									6
Melastomataceae	<i>Miconia impetiolearis</i>	N	Bird, mammal	Seedling									9

(continued on next page)

Appendix A (continued)

Family	Genus and species	Native to Puerto Rico? ^a	Dispersal mechanism ^b	Seedling or sapling	0.5	2.6	3.0	3.4	4.3	5.0	5.1	6.0	R
Melastomataceae	<i>Miconia prasina</i>	N	Bird	Sapling		13						1	4
Melastomataceae	<i>Miconia prasina</i>	N	Bird	Seedling									10
Melastomataceae	<i>Miconia racemosa</i>	N	Bird	Sapling							6		
Meliaceae	<i>Guarea guidonia</i>	N	Mammal, large bird	Sapling				10	9	4	13	64	2
Meliaceae	<i>Guarea guidonia</i>	N	Mammal, large bird	Seedling			103	2	15	8	300	160	11
Moraceae	<i>Artocarpus altilis</i>	I	Animal	Sapling					3				1
Myrsinaceae	<i>Ardisia elliptica</i>	I	Bird, mammal	Sapling			13						6
Myrsinaceae	<i>Ardisia elliptica</i>	I	Bird, mammal	Seedling	1		27						13
Myrtaceae	<i>Eugenia monticola</i>	N	Bird, mammal	Sapling	1								
Myrtaceae	<i>Eugenia monticola</i>	N	Bird, mammal	Seedling	9								
Myrtaceae	<i>Eugenia</i> sp.	N	Animal	Seedling	1								
Myrtaceae	<i>Eugenia</i> sp.	N	Bird, mammal	Sapling	1								
Myrtaceae	<i>Eugenia stahlia</i>	EN	Bird, mammal	Sapling									25
Myrtaceae	<i>Eugenia stahlia</i>	EN	Bird, mammal	Seedling									7
Myrtaceae	<i>Myrcia</i> sp.	N	Bird, mammal	Seedling	2								12
Myrtaceae	<i>Syzygium jambos</i>	I	Mammal	Seedling			13						
Rubiaceae	<i>Gonzalagunia spicata</i>	N	Bird, mammal	Sapling						13	1		2
Rubiaceae	<i>Gonzalagunia spicata</i>	N	Bird, mammal	Seedling						3	1		
Rubiaceae	<i>Psychotria berteriana</i>	N	Bird	Sapling									2
Rubiaceae	sp.			Sapling				2		2			
Rubiaceae	sp.			Seedling				80					
Sapotaceae	<i>Chrysophyllum argenteum</i>	N	Mammal, large bird	Sapling				1					

^a Native to Puerto Rico: native (N), introduced (I), or endemic (EN).

^b Dispersal mechanisms compiled from the Smithsonian Tropical Research Institute (STRI) http://stri.si.edu/sites/esp/tesp/plant_search_quick.htm, the US Forest Service <http://www.fs.fed.us/database/feis/plants/index.html>, Invasive Species Specialist Group of the International Union for the Conservation of Nature (IUCN) <http://www.issg.org/>, and (Aide et al., 2000). In some cases “animal” is used if detailed information of bird, bat, or mammal dispersal was not available.

utary (e.g. 0.5). Urban sites are ordered from lowest elevation and closest proximity to the urban center (0), to highest elevation and farthest from the urban center (6). Native status, dispersal mechanism, and whether individuals were seedlings or saplings are specified.

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