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Alien species affect the abundance and richness of native species in tropical forests: The role of adaptive strategies

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Abstract

Understanding the role of alien species in forest communities, and how native and alien species interact to shape the composition and structure of contemporary forests, is of critical importance to invasion ecology and natural resource management. We used vegetation data collected over a 20-year period in 341 permanent plots representing remnants of closed-canopy forests and post-agricultural secondary forests across Puerto Rico to compare changes in the composition and abundance of native and alien woody species in plots with and without aliens across different forest types and to assess whether aliens and natives show divergence or convergence regarding functional roles and ecological strategies. We also tested the applicability of Grime's CSR (competitive, stress-tolerant, and ruderal strategies) theory to explain naturalization success. Species richness and abundance of natives are consistently lower in plots in which aliens are present compared with those without them. This negative association between aliens and natives has been consistent over the 20 years and across all forest types. Both native and total richness slightly increased over the 20 years, but the increase in native species richness was three times lower in plots with aliens relative to those without aliens. The CSR classification provided insight into the naturalization success of aliens. Corroborating the "join the locals" hypothesis, aliens use the same functional spaces as natives. The exception is in dry forests, where aliens and natives differ in the use of functional spaces, a result that corroborates the "try harder" hypothesis. Generally, aliens were better competitors compared with natives, and natives were more stress-tolerant than aliens. Our combined results suggest that alien species may inhibit population growth or even drive local changes in native plant communities by transforming the assembly and dynamics of tropical forests. Ultimately, modifications linked to invasive species may have significant implications for local forests, affecting their regeneration and productivity. More definitive conclusions require additional plot censuses, and analyses of disturbance regimes and stand-age structure to

reveal the long-term implications of alien species on regenerating tropical forests, including their vulnerability, resilience, and adaptive capacity to cope with various aspects of climate change.

INTRODUCTION

Human-mediated introduction of species in areas beyond their native distribution is a process that has been steadily increasing globally for the last few centuries and is projected to continue growing in the future (Seebens et al., 2017, 2021). These increases in the introduction and naturalization of alien species have been driven by globalization, the intensification of international trade and travel, and the modification of natural habitats (Ellis et al., 2013). Currently, over 13,000 species of vascular plants have become naturalized in areas outside their native range (Pyšek et al., 2017; van Kleunen et al., 2015). A subset of those have successfully overcome survival barriers and are actively spreading into new areas where they are identified as invasive species (sensu Blackburn et al., 2011). Ample evidence documents that some alien invaders can completely displace native vegetation and modify ecosystem functions by altering fire regimes, nutrient and hydrology cycles, biophysical dynamics, or community composition (e.g., D'Antonio, 2000; Ehrenfeld, 2003; Liao et al., 2008; Rojas-Sandoval et al., 2016; Yelenik & D'Antonio, 2013). Additionally, rates and trajectories of ecological succession in invaded areas may be altered by the continued persistence of invaders or by their eventual replacement by groups of species that differ substantially from those in pre-invasion communities (Cramer et al., 2008; D'Antonio et al., 2017; Walker & Smith, 1997). Neither of these outcomes is desirable for the conservation of natural ecosystems and their native biodiversity.

Attempts to identify plant traits that are associated with naturalization and invasion success show that there is not a unique set of attributes responsible for invasiveness but that considerations of functional traits and natural histories are crucial for understanding naturalization and invasion processes (Richardson & Pyšek, 2012). Traits such as rapid growth, early flowering, and wide native ranges are frequently associated with the invasiveness of alien plant species (Divíšek et al., 2018; Junaedi et al., 2021; van Kleunen et al., 2010). Additional evidence shows that invasive plants generally outcompete native and other alien species due to functional traits related to growth rate and resource acquisition and that these traits promote invasiveness under many circumstances (van Kleunen et al., 2010). Nevertheless, some studies have raised concerns regarding trait-based approaches and comparisons of "trait assemblages" between natives and aliens since trait patterns are complex and often context dependent (Funk et al., 2017; Hulme & Bernard-Verdier, 2018).

Invasions can also be evaluated by contrasting two opposing theories of how particular trait combinations related to resource economics (ability to capture and retain resources) can facilitate or prevent aliens from establishing and becoming invasive in a community. The first is the "join the locals" theory, which derives from the concept of habitat filtering (Keddy & Weiher, 1999). According to this theory, environmental filters, such as local climate, nutrient availability, or disturbance regimes, may limit the number of alien species that can successfully establish in a particular community. Under this theory, successful invaders should have similar traits to those of the local native species, especially the dominant ones (Leishman et al., 2007; Lodge et al., 2018; Tecco et al., 2010). Conversely, the "try harder" theory, which derives from the concept of limiting similarity (Crawley et al., 1996; Keddy & Weiher, 1999). According to this theory, successful invaders deal better with local conditions than natives. Therefore, alien species will more likely invade communities that lack species that are similar to them because aliens take advantage of underexploited resources or have resource acquisition strategies that are different from those of natives (Ordoñez et al., 2010; Tecco et al., 2010; van Kleunen et al., 2010).

Grime's CSR (competitive, stress-tolerant, and ruderal strategies) life-strategy scheme (Grime, 2001; Grime & Pierce, 2012) provides a practical approach for evaluating how functional traits facilitate naturalization or invasion success. This scheme represents a conceptual framework that uses two major selection pressures, such as stress (defined as constraints to growth, for example, shortage of resources) and disturbance (defined as biomass destruction or removal, for example, by herbivores or humans), to classify species into one of three functional categories: (1) competitors (C), which exploit low-stress

and low-disturbance conditions; (2) stress-tolerators (S), which adapt to high-stress and low-disturbance conditions; and (3) ruderals (R), which adapt to low-stress and high-disturbance conditions. Moreover, intermediate categories (e.g., CS, SR, and CR) are recognized. Using this classification, Pierce et al. (2017) developed "StrateFy," an ordination tool that calculates continuous quantitative CSR scores based on the trade-offs among three leaf traits (leaf area [LA], specific leaf area [SLA], and leaf dry matter content [LDMC]) that represent extremes of plant functional specialization. Previous studies using this approach at local and regional scales have shown that alien species generally exhibit C- and R-strategies (and their intermediates), whereas S-species are underrepresented (Dalle Fratte et al., 2019; Lambdon et al., 2008). Additionally, recent studies have effectively demonstrated the global applicability of this tool for explaining the naturalization success of alien plants. Using a global dataset of vascular plants, these studies have revealed that for alien species across different life-forms, high C- and R-scores are correlated positively with the probability of becoming naturalized, whereas high S-scores are negatively correlated with that probability (Guo et al., 2018, 2019). Although Grime's CSR model has limitations (Hulme & Bernard-Verdier, 2018), it is a useful approach for distinguishing strategies at different levels (i.e., from species to biomes), and its validity has been confirmed in several experiments and field studies (Dalle Fratte et al., 2019; Pierce et al., 2017; Rosado & de Mattos, 2017).

Herein, we leverage comprehensive data from Puerto Rico to evaluate interactions between native and alien woody species in different forest types and to assess whether alien and native species are divergent (indicating limiting similarity) or convergent (denoting habitat filtering) with respect to functional spaces or ecological strategies. Puerto Rican forests, like many other Caribbean forests, support plant communities that are characterized by high species richness and endemism while being subject to a hurricane-dominated disturbance regime (Lugo et al., 2000). Nonetheless, extensive anthropogenic disturbances, combined with the introduction of alien species, have modified successional processes and assemblages of local forests (Helmer et al., 2018; Lugo & Helmer, 2004). Currently, forests across Puerto Rico represent a mixture of alien and native species that is generally dominated by naturalized and invasive species (Lugo, 2004; Rojas-Sandoval & Acevedo-Rodríguez, 2015). Because of these environmental circumstances and the fact that Puerto Rican forests are among the best-studied in the Caribbean, with excellent availability of long-term data, the island is an exceptional place to understand the role of native and alien species in forest communities as well as how they interact to shape the composition and structure of contemporary forests. Although patterns and mechanisms of invasion have been widely studied in temperate forests, they are still poorly understood in tropical forests. While many patterns and mechanisms are expected to be quite general in applicability, we lack extensive empirical evidence for tropical regions to corroborate such expectations (Chong et al., 2021). This study partially addresses this knowledge gap.

We used plant data collected from more than 300 permanent plots from the USDA-Forest Service Forest Inventory and Analysis (FIA) Program established across Puerto Rican forests to: (1) characterize the species richness, abundance, and occurrence of alien and native woody species; (2) evaluate whether the presence of aliens is associated with changes in the richness and abundance of native species; (3) assess whether alien and native species occupy different or similar functional spaces within Grime's CSR scheme; and (4) evaluate whether naturalization success is related to high C- and R-strategies. The availability of highly replicated, fine-grain data on species occurrence and abundance across plots that differ in their original plant species composition and richness, as well as in the surrounding landscape conditions, provided a unique opportunity to examine potential interactions between natives and aliens in tropical forests. By evaluating such interactions, we expect to determine whether the richness and abundance of natives vary over time in association with the presence or abundance of aliens, and if such relationships are independent of forest type. Moreover, because recent studies suggest that naturalization success of alien plant species is linked to C- and R-strategies (Dalle Fratte et al., 2019; Guo et al., 2018, 2019), we expect CSR scores to differ between natives and aliens as a result of their different strategies of resource acquisition.

MATERIALS AND METHODS

Study site

The archipelago of Puerto Rico comprises the islands of Puerto Rico (8740 km^2), Culebra (25 km^2), Vieques (125 km^2), and other smaller islands in the Caribbean Sea. These islands occupy the Puerto Rican Bank, the easternmost extension of the Greater Antilles. The climate is tropical and predominantly maritime, with mean annual temperatures ranging from 19 to 26°C and annual rainfall ranging from 800 to >4000 mm. Elevation ranges from sea level to 1338 m, including a wide variety of habitats and substrates (alluvial, limestone, volcanic, serpentine, and karst). Vegetation ranges

from dry forests in the lowlands, to wet-rainforests, including cloud forests, at higher elevations (Daly et al., 2003; Ewel & Whitmore, 1973; Helmer et al., 2018). Contrary to the trend in many tropical countries, forest cover in Puerto Rico has steadily increased over the past 70 years due to socioeconomic changes. Puerto Rico's economy has switched from being essentially an agricultural system to being a more industrialized system, with an emphasis on manufacturing, services, and tourism (Grau et al., 2003; Parés-Ramos et al., 2008). As agricultural production declined, forest cover in Puerto Rico increased from less than 6% in 1930–1950 to more than 55% in 2014 (Marcano-Vega, 2017). Natural succession on abandoned agricultural fields and pastures rather than active restoration has led to forest recovery on the island (Grau et al., 2003; Zimmerman et al., 2007). Consequently, contemporary forests throughout Puerto Rico are a mixture of native and alien species, generally dominated by naturalized and invasive alien taxa (Lugo, 2004; Rojas-Sandoval & Acevedo-Rodríguez, 2015).

Data compilation

We used vegetation data for 341 permanent plots that were established across the islands of Puerto Rico, Vieques, and Culebra as part of the USDA-Forest Service FIA Program. These permanent plots are arranged in a hexagonal grid and are systematically spaced every 24 km^2 on Puerto Rico, and every 2 km^2 on Culebra and Vieques, covering all the ecological life zones that characterize these islands. For plots to be included in FIA surveys, they must be characterized by at least 10% of forest canopy cover from trees with height $\geq$30 cm. Consequently, plots range from representing young secondary forest to old closed-canopy forest. Each permanent plot comprises four adjacent circular (7.3 m radius) subplots with a cumulative area of 0.067 ha. Every five years, these plots are surveyed to identify (at species level) and measure all woody plants with dbh $\geq$ 2.5 cm. Detailed information on methodology, plot descriptions, and other collected data is at the USDA Forest Service's FIA website (https://www.fia.fs.fed.us/).

We used vegetation data from each of four FIA surveys (2001–2004, 2006–2009, 2011–2014, and 2016–2019) covering a period of almost 20 years. First, species names were standardized using the R package *taxonstand* (Cayuela et al., 2021), and then species were classified as native or alien following Acevedo-Rodríguez et al. (2012). In each plot, we used these data to separately calculate the species richness and abundances of natives and aliens. Because the methodology designated by FIA requires canopy cover in a subplot to be at least 10% for

it to be measured, and because the identity and configuration of the four subplots are never altered, plots in which one or more subplots did not have the minimum 10% of canopy cover at the time of each survey were "partially sampled." Species richness would be underestimated, and abundances of species would be less accurate in such partially sampled plots. Therefore, to avoid sampling bias in the analyses, for each survey, we only retained plots in which all four constituent subplots were sampled.

Using the map of forest life zones for Puerto Rico (Ewel & Whitmore, 1973; Appendix S1: Figure S1), plots were classified according to the forest type as follows: (1) dry forest, (2) moist forest, (3) wet forest, (4) rainforest, or (5) lower montane forest. Because rainforest is a small and restricted life zone, occurring only in the Luquillo Mountains where it is surrounded by wet forest, and because these two forest types are physiognomically and floristically similar (Ewel & Whitmore, 1973), plots that occurred in wet forest or rainforest were classified as a single category, hereafter "wet-rainforest." Finally, plots that occurred in the lower montane forest were excluded from the analyses because the FIA sampling design captures few plots in this forest type. Plot sample sizes in each forest type are shown in Table 1. The number of plots differed among forest types due to their different areal extents in Puerto Rico (Appendix S1: Figure S1).

Data analysis

We performed analyses by considering all plots regardless of forest type (hereafter "all forest types"), as well as by considering plots separately for each forest type. To evaluate if the presence of aliens is associated with changes in the abundance or richness of natives, we estimated the mean species richness (number of species) and mean abundance of natives in plots with and without aliens for all forest types pooled and for each forest type separately for each survey. Generalized linear mixed-effects models (GLMMs) were used to analyze the dependence of species richness or abundance of natives on three predictor variables: (1) the presence of aliens; (2) time (survey year as a categorical factor with four levels); and (3) forest type. We used GLMMs with Poisson error terms and a canonical log-link function for species richness and Gaussian error terms and the identity-link function for species abundance. Plot identity was included as a random factor to account for repeated measures. Abundance was transformed as $\log_{10}(x + 1)$. The R function *glmer* from the package *lme4* was used to fit the GLMMs (Bates et al., 2015).

We quantified temporal changes in species richness of a plot as the difference between the number of species between the last survey (2016–2019) and the first survey

TABLE 1 Summary of the total number of alien and native species as well as the number of plots with 100% of their area sampled for all forest types pooled and for each forest type independently.

Metric	2001–2004	2006–2009	2011–2014	2016–2019
All forest types				
No. species	246	250	253	249
Alien species	48	45	45	42
Native species	198	205	208	207
No. plots	174	183	189	183
Plots with aliens (%)	77	79	79	77
Moist forest				
No. species	167	172	169	167
Alien species	36	36	38	32
Native species	131	136	131	135
No. plots	85	85	85	82
Plots with aliens (%)	79	84	84	82
Dry forest				
No. species	66	72	66	68
Alien species	9	9	9	9
Native species	57	63	57	59
No. plots	28	36	44	42
Plots with aliens (%)	75	75	80	75
Wet-rainforest				
No. species	144	132	143	143
Alien species	29	23	25	23
Native species	115	109	118	120
No. plots	61	61	60	58
Plots with aliens (%)	78	80	77	76

Note: This characterization is provided for each of four Puerto Rico-Forest Inventory and Analysis surveys covering almost 20 years.

(2001–2004) and did so separately for native species only as well as for all species (aliens + natives, hereafter "total richness"). To evaluate the effect of the presence of alien species on temporal changes in richness, we categorized plots into: (1) those with aliens during both surveys and (2) those without aliens during both surveys. Plots in which the incidence of aliens changed over time (from present to absent or absent to present) were excluded from consideration. Thereafter, for native richness as well as for total richness separately, we used a two-way ANOVA with an alien incidence as a fixed factor (aliens present vs. aliens absent) and time as a repeated measure to evaluate the effects of time, alien incidence, and their interaction. The same approach was used to quantify temporal changes in native abundance and total abundance.

Linear models were used to assess the relationship between: (1) the species richness of natives and the abundance of all alien species and (2) the species richness of alien and the abundance of all alien species. For these analyses, we only included plots with the presence of aliens or

plots where either *Leucaena leucocephala*, *Spathodea campanulata*, or *Syzygium jambos* occurred (hereafter *Leucaena*, *Spathodea*, and *Syzygium*). We focus on these three alien species because they are the most widespread aliens across Puerto Rico and potentially have the greatest impact of any woody invaders. Moreover, selecting these three species reduces the phylogenetic variance caused by multiple invasive woody species (see *Results* and Table 2). For each of these alien species and for all alien species pooled, we evaluated the relationship between the richness of natives or aliens and the abundance of aliens across all plots where they occurred. For these analyses, abundance was log-transformed to improve symmetry and linearity and to stabilize variances.

To evaluate whether or not aliens and natives use different or similar functional strategies, we calculated CSR scores using the CSR calculator tool "StrateFy" (Pierce et al., 2017) based on LA, SLA, and LDMC data that were obtained from the literature (Appendix S1: Table S2 provides a list of all the references consulted) and from the

TABLE 2 The 10 most widespread woody species in each of the three forest types and in all forests combined.

Species	Native or alien	Occurrence (%)	Abundance (no. trees/ha)
All forest types			
Guarea guidonia	Native	31.7	495 ± 40
Spathodea campanulata	Alien*	28.5	612 ± 129
Andira inermis	Native	26.7	167 ± 16
Cecropia schreberiana	Native	22.6	117 ± 20
Tabebuia heterophylla	Native	17.5	411 ± 53
Casearia guianensis	Native	16.8	720 ± 44
Bursera simaruba	Native	16.3	171 ± 7
Ocotea leucoxylon	Native	16.2	222 ± 37
Leucaena leucocephala	Alien*	15.9	1220 ± 235
Syzygium jambos	Alien*	14.6	337 ± 69
Moist forest			
A. inermis	Native	36.8	211 ± 21
S. campanulata	Alien*	36	759 ± 150
G. guidonia	Native	30.4	537 ± 42
C. guianensis	Native	26.3	805 ± 75
T. heterophylla	Native	22.3	346 ± 49
Citharexylum spinosum	Native	20	172 ± 15
B. simaruba	Native	19.8	208 ± 14
Casearia sylvestri	Native	18	805 ± 75
Guapira fragrans	Native	18	235 ± 35
Zanthoxylum martinicense	Native	15.4	83 ± 9
Dry forest			
L. leucocephala	Alien*	46.4	1695 ± 400
Prosopis pallida	Alien*	35.4	669 ± 85
B. simaruba	Native	31.6	104 ± 16
Bourreria succulenta	Native	20.1	687 ± 173
G. fragrans	Native	16.7	357 ± 16
Bucida buceras	Native	15.8	295 ± 135
Vachellia farnesiana	Alien*	15.3	723 ± 61
Exostema caribaeum	Native	14.4	500 ± 77
Pictetia aculeata	Native	12	870 ± 50
Randia aculeata	Native	11.5	425 ± 94

(Continues)

TABLE 2 (Continued)

Species	Native or alien	Occurrence (%)	Abundance (no. trees/ha)
Wet-rainforest			
G. guidonia	Native	57.6	455 ± 50
C. schreberiana	Native	51.9	100 ± 19
O. leucoxylon	Native	43.9	242 ± 37
Inga vera	Native	37.3	133 ± 18
S. campanulata	Alien*	36.3	413 ± 109
S. jambos	Alien*	35	336 ± 40
Schefflera morototoni	Native	30.9	93 ± 21
Cordia sulcata	Native	26.8	90 ± 14
Inga laurina	Native	25.5	118 ± 8
A. inermis	Native	23.9	63 ± 9

Note: Occurrence is the percentage of the plots at which a species occurs. Abundance is the number of trees per hectare (mean ± SE) for the plots at which a species occurs. Species are ranked by occurrence. An asterisk (*) indicates alien species regarded as invasive in Puerto Rico (following Rojas-Sandoval & Acevedo-Rodríguez, 2015).

TRY database (Kattge et al., 2011; https://www.try-db.org/TryWeb/Home.php). Of the 356 woody species in our plots (see *Results*), we found measurements for all three traits (SLA, LA, and LDMC) for 147 species (109 natives and 38 aliens). C-, S-, and R-adaptive strategy scores were estimated for these 147 species, and this information was used to create and analyze ternary plots. For each species, the CSR scores generated by StrateFy indicate the proportion of each strategy (C:S:R) along each axis in Grime's triangular plot (Grime, 2001; Grime & Pierce, 2012; Pierce et al., 2017). We used the *R* package *ggtern* (Hamilton, 2015) to visualize the triangular plot of the C-, S-, and R-scores of the native and alien species for all plots and for each forest type separately, and then we deployed a multivariate analysis of variance to compare the adaptive strategies of aliens and natives based on those three scores. Finally, to assess whether naturalization success of aliens is related to higher C-, S-, or R-scores, we computed a one-way ANOVA for each axis (C, S, and R) separately. These analyses were conducted for all plots regardless of forest type, and for each forest type separately. All analyses were performed in *R* (R Core Team, 2021).

RESULTS

A total of 356 woody species (288 natives and 77 aliens) were recorded over the course of the four surveys. In general, aliens represent 27% of all species, with averages

ranging from 15% in dry forest to 20% in wet-rainforest and 25% in moist forest. The percentage of plots with aliens was similar across all forest types (ranging from 75% to 84%) and varied little over time (Table 1). Only minor changes (<9%) in the percentage of plots with aliens were detected over the 20-year study period (Table 1). By individually comparing the status of plots (with or without aliens) in the last survey (2016–2019) to their status in the first survey (2001–2004), we found that 11% of the plots changed from "pure native" to having aliens present, while 8% experienced the opposite transition (Appendix S1: Figure S2). The 10 most widespread species in plots regardless of forest type, measured by their frequency of occurrence, included three alien species (Table 2). *S. campanulata* is the only alien ranked among the 10 most frequent species in the moist and wet-rainforest types. In contrast, 3 of the 10 most frequent species in dry forest are aliens (i.e., *L. leucocephala*, *Prosopis pallida*, and *Vachellia farnesiana*), none of which are frequent in the other two forest types (Table 2).

Species richness and abundance of natives in the presence of aliens

Native species richness depends significantly on the three factors evaluated: alien presence, forest type, and survey year. The mean species richness of natives was significantly higher in plots without aliens than in plots with them based on all plots regardless of forest type. This pattern was consistent across all the surveys and for the three forest types analyzed separately (Table 3; Figure 1a–d). Interaction terms between predictor variables were included in the models but were not significant. The largest differences in native species richness were observed in the dry forest, where the number of native species in plots with aliens was on average more than three times lower than in plots without aliens (Figure 1b). A similar trend was detected for total richness (Appendix S1: Table S2). Significantly lower total richness was observed in plots with aliens for dry forest and for wet-rainforest, whereas no significant differences were detected for all plots pooled or for moist forest (Appendix S1: Figure S3). Again, the largest differences in total richness were detected in dry forest (Appendix S1: Figure S3b).

Significant temporal changes in species richness between the last survey (2016–2019) and the first survey (2001–2004) were detected for all species and for natives in plots with and without aliens (Figure 2). For native species and for all species, the absence of a significant interaction indicates that the differences in species richness between time periods were consistent regardless of alien incidence and the differences in species richness between plots with or without aliens were consistent regardless of time (native species—alien incidence [$F_{1,115} = 12.46$, $p < 0.001$], time [$F_{1,115} = 44.17$, $p < 0.001$], and interaction [$F = 2.05$, $p = 0.155$]; all species—alien incidence [$F_{1,115} = 4.72$, $p = 0.032$], time [$F_{1,115} = 34.33$, $p < 0.001$], and interaction [$F = 3.91$, $p = 0.551$]). After 20 years, both native and total richness slightly increased in plots with and without aliens. In plots with aliens, the average richness of natives increased by approximately one species, whereas total richness increased by approximately two species. In contrast, in plots without aliens, the average richness of natives increased by approximately three species (Figure 2).

TABLE 3 Generalized linear mixed effects models (GLMMs) assessing the response of species richness or abundance of native species against three predictor variables (presence of aliens, time, and forest type).

Variable	Considering forest effect				All forests combined (no forest effect)			
	Estimate	SE	z	p	Estimate	SE	z	p
Species richness								
Intercept	1.094	0.160	6.445	<0.001	1.652	0.078	20.968	<0.001
Presence of aliens	−0.154	0.066	−2.298	0.022	−0.137	0.067	−2.046	0.041
Time	0.081	0.012	6.496	<0.001	0.080	0.012	6.469	<0.001
Forest type	0.255	0.066	3.812	<0.001				
Abundance								
Intercept	6.092	0.396	15.361	<0.001	6.643	0.197	33.554	<0.001
Presence of aliens	−0.462	0.178	−2.596	0.009	−0.451	0.178	−2.533	0.012
Time	0.174	0.037	4.686	<0.001	0.172	0.037	4.662	<0.001
Forest type	0.249	0.155	1.608	0.109				

Note: GLMMs were performed by considering plots separately for each forest type, as well as considering all plots together regardless of forest type. Only plots with 100% of their area sampled were considered ($n = 234$ plots).
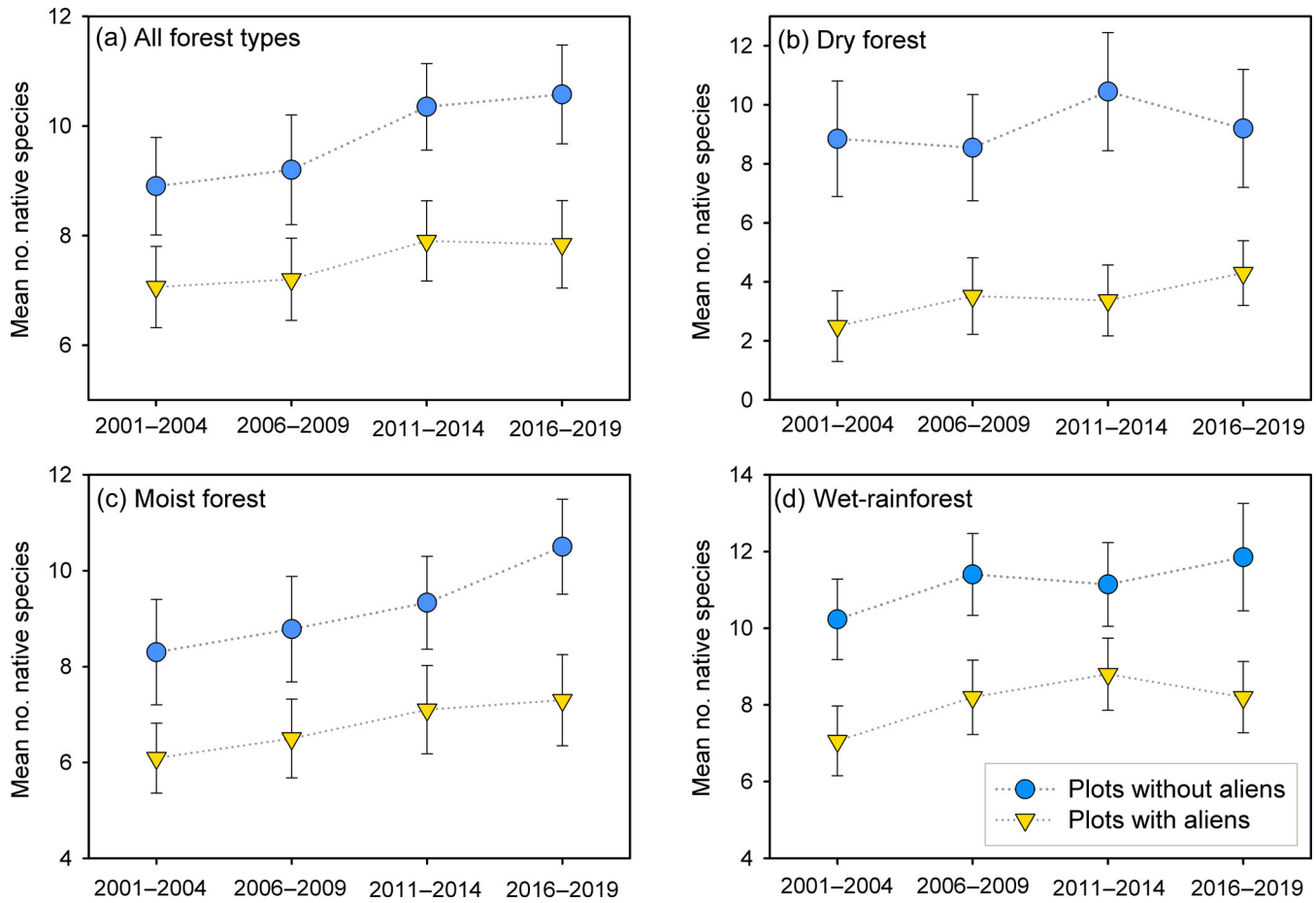
FIGURE 1 Mean number of native species in plots with and without alien species based on Puerto Rico-Forest Inventory and Analysis surveys. Means ± SE are shown as symbols (circles and triangles) and vertical bars, respectively.
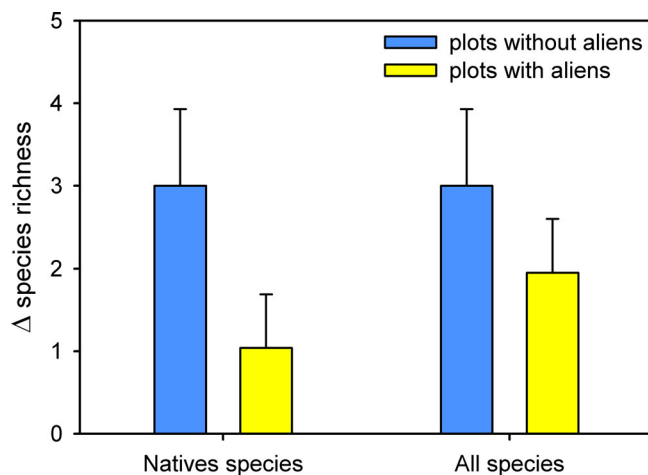

FIGURE 2 Mean change in species richness (Δ species richness) in plots with alien species versus those without alien species between the last survey (2016–2019) and the first survey (2001–2004). Analyses were conducted separately for changes in native species richness and for changes in total species richness (all species). Vertical lines represent 1 SE of the mean.

The abundance of natives was significantly higher in plots without aliens than in plots with aliens when data from all forest types were combined. This pattern was consistent across all the surveys (Table 3; Figure 3a–d). For analyses restricted to a single forest type, significant differences were detected only for the dry and moist forests, but not for the wet-rainforests. Again, interaction terms between predictor variables were included in the models but were not significant. The largest differences in native abundances were observed in the dry forest, where the mean abundance of native species in plots with aliens was four times lower than in plots without aliens (Figure 3b).

For native species and for all species, the significant interactions in the two-way ANOVAs indicate that differences in abundance between time periods depend on alien incidence and the differences in abundance between plots with and without aliens depend on time (native species—alien incidence [$F_{1,115} = 10.98$, $p = 0.001$], time [$F_{1,115} = 6.64$, $p = 0.011$], and interaction [$F = 4.72$, $p = 0.032$]; all species—alien incidence
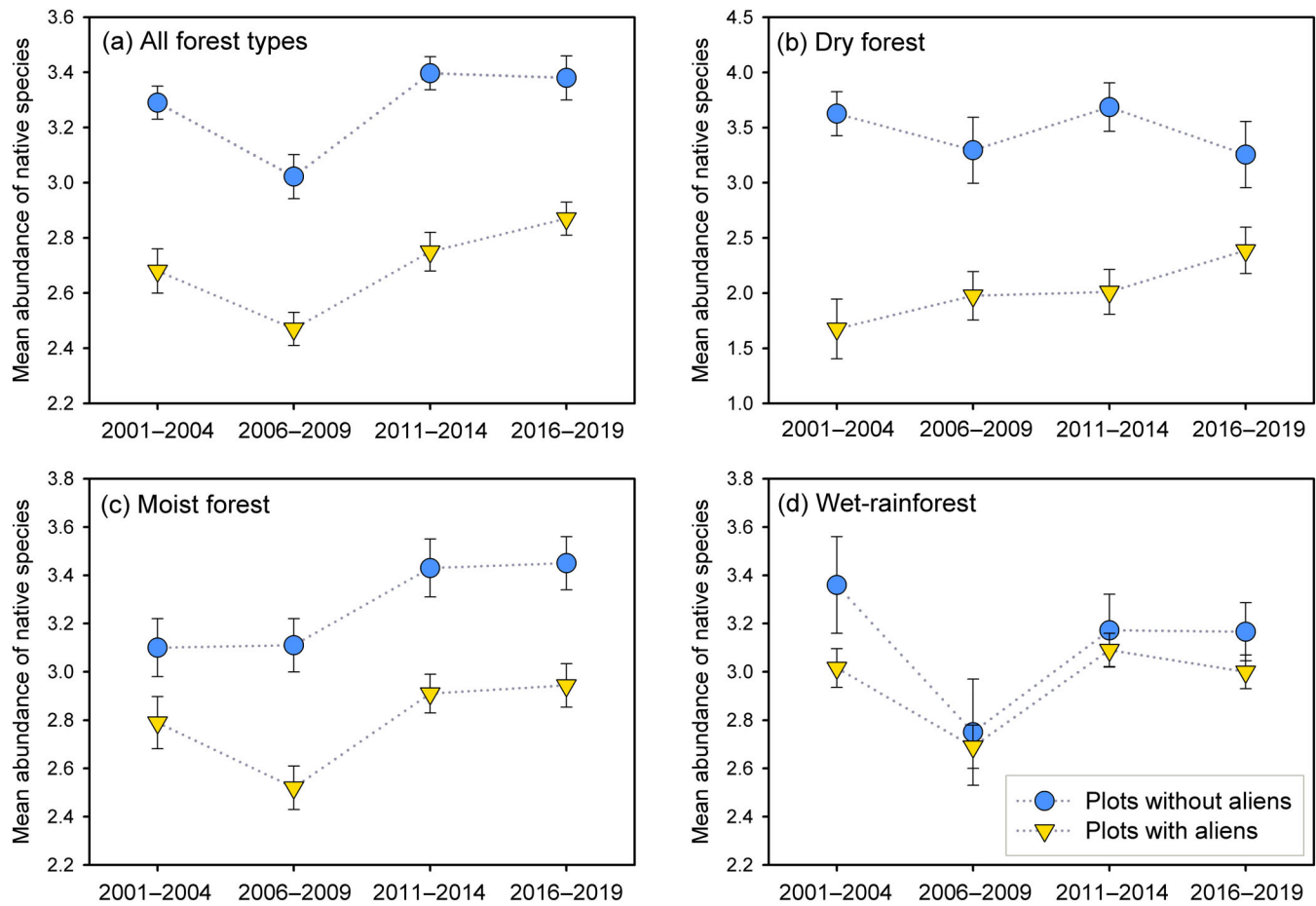
FIGURE 3 Mean log-abundance (in trees per hectare) of native species in plots with and without alien species based on Puerto Rico-Forest Inventory and Analysis surveys. Means $\pm$ SE are shown as symbols (circles and triangles) and vertical bars, respectively.

$[F_{1,115} = 2.56,\ p = 0.112]$, time $[F_{1,115} = 1.68,\ p = 0.197]$, and interaction $[F = 7.42,\ p = 0.007]$). After 20 years, the abundance of natives increased on average by 475 individuals in plots without aliens, a value seven times higher than that in plots with aliens. A similar pattern was detected for the total abundance, which showed an increase that was approximately twice as large in plots without aliens compared with plots with aliens (Appendix S1: Figure S4).

Relationship between species richness and abundance of aliens

For all plots, regardless of forest type, native species richness decreased as the abundance of aliens increased (Figure 4a). Although the relationship was weak ($R^2 = 0.08$), with considerable variation in native richness when alien abundance was low, the slope was sufficiently large to result in a highly significant relationship ($y_1 = -1.89$, df = 545, $p < 0.001$; Figure 4a). Moreover, native richness also declined with the

increasing abundance of each of the three most frequent invaders. The declines were significant for *Leucaena* ($R^2 = 0.11$, df = 132, $p < 0.001$; Figure 4b) and *Spathodea* ($R^2 = 0.16$, df = 205, $p < 0.001$; Figure 4c) and approached significance for *Syzygium* ($R^2 = 0.03$, df = 124, $p = 0.07$; Figure 4d). In contrast, alien richness significantly increased with the increasing abundance of aliens ($R^2 = 0.14$, df = 545, $p < 0.001$; Figure 4e), suggesting that some alien species may benefit from the presence of other aliens. However, no significant relationships were detected between alien richness and the abundances of *Leucaena* ($R^2 = 0.003$, df = 132, $p = 0.54$; Figure 4f), *Spathodea* ($R^2 = 0.003$, df = 205, $p = 0.43$; Figure 4g) or *Syzygium* ($R^2 = 0.008$, df = 124, $p = 0.32$; Figure 4h) when considered separately.

Adaptive strategies

Regardless of forest type, mean C-, S-, and R-scores ($\pm$SD) for natives (C = 37 $\pm$ 15%, S = 52 $\pm$ 20%, R = 11 $\pm$ 6%) and aliens (C = 44 $\pm$ 18%, S = 43 $\pm$ 17%, R = 13 $\pm$ 7%)
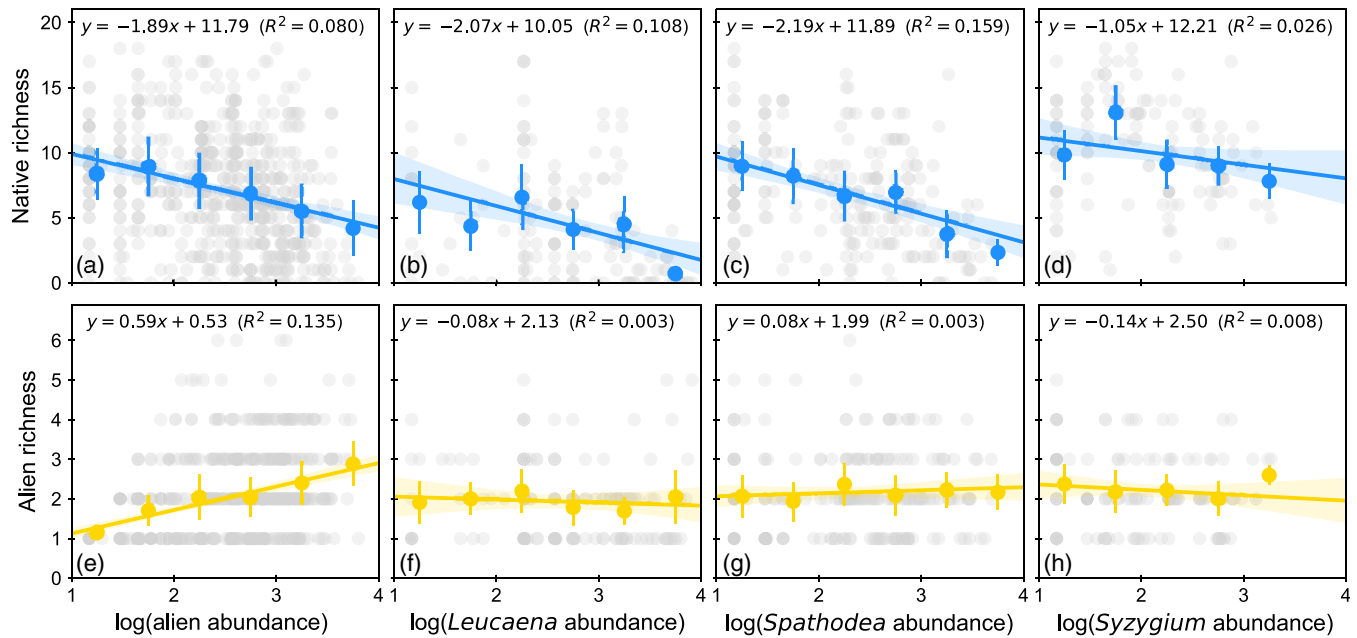
FIGURE 4   Relationship between native species richness (a–d) or alien species richness (e–h) and log-abundance of all alien species (a, e), log-abundance of *Leucaena leucocephala* (b, c), log-abundance of *Spathodea campanulata* (c, g), or log-abundance of *Syzygium jambos* (d, h). Gray points correspond to individual plots, whereas colored points with error bars indicate mean ± SE within evenly spaced logarithmic bins. Solid lines and shaded regions indicate least squares regressions and 95% confidence intervals, respectively.

were clustered around the CS-adaptive strategy with low R-scores (Figure 5). Indeed, alien species did not diverge significantly from native species when considering all forest types together (Wilks = 0.944, $F_{1,145}$ = 2.83, p = 0.09; Figure 5a), as well as when considering only moist forest (Wilks = 0.978, $F_{1,120}$ = 2.86, p = 0.09; Figure 5c) or only wet-rainforest (Wilks = 0.972, $F_{1,96}$ = 0.96, p = 0.55; Figure 5d). In contrast, significant differences were detected between alien and native species within dry forest (Wilks = 0.964, $F_{1,55}$ = 6.49, p = 0.01; Figure 5b). For all forest types together, for the moist forest, and for the wet-rainforest, natives and aliens occupy indistinguishable functional spaces, whereas in dry forest, aliens and natives diverge in the use of functional spaces. In dry forests, aliens cluster toward C-space while natives cluster toward S-space (Figure 5b).

Is naturalization success related to higher C- and R-scores? We analyzed CSR axis scores as independent variables and found that aliens had significantly higher C-scores, whereas native species had significantly higher S-scores. In contrast, R-scores were indistinguishable for aliens and natives (Figure 6). This pattern was consistent for analyses for all forest types combined (C-axis, $F_{1,145}$ = 4.59, p = 0.03; S-axis, $F_{1,145}$ = 4.25, p = 0.04; R-axis, $F_{1,145}$ = 0.21, p = 0.64; Figure 6a), and for analyses restricted to dry forest (C-axis, $F_{1,55}$ = 10.12, p = 0.001; S-axis, $F_{1,55}$ = 6.04, p = 0.01; R-axis, $F_{1,55}$ = 0.04 p = 0.97; Figure 6b) or restricted to moist

forest (C-axis, $F_{1,120}$ = 4.87, p = 0.02; S-axis, $F_{1,120}$ = 3.95, p = 0.04; R-axis, $F_{1,120}$ = 0.50, p = 0.48; Figure 6c). However, no significant differences between natives and aliens were detected in wet-rainforest (C-axis, $F_{1,96}$ = 0.71, p = 0.40; S-axis, $F_{1,96}$ = 0.36, p = 0.54; R-axis, $F_{1,96}$ = 0.02, p = 0.96; Figure 6d). In general, aliens are better competitors than natives; natives are more stress-tolerant than aliens; and both share similar ruderal strategies.

DISCUSSION

Analyses of forest dynamics in temperate regions have revealed negative relationships between native woody species and invasive plants (e.g., Collins et al., 2020; Huebner et al., 2009; Lázaro-Lobo et al., 2021). Do these patterns apply to tropical forests? While some tropical plant invasions have had dire consequences to native forest processes (e.g., Asner et al., 2008; Bempah et al., 2021; Rothstein et al., 2004), other studies suggest that they may be beneficial to the reestablishment of native species in degraded lands (e.g., Abelleira Martínez et al., 2010; Aide et al., 2000; Lugo, 2004). We leveraged one of the largest and more comprehensive regional vegetation datasets to quantify the richness, abundance, and functional traits of native and alien species that occupy contemporary tropical forests, one of the forest types where our understanding of interactions between native and
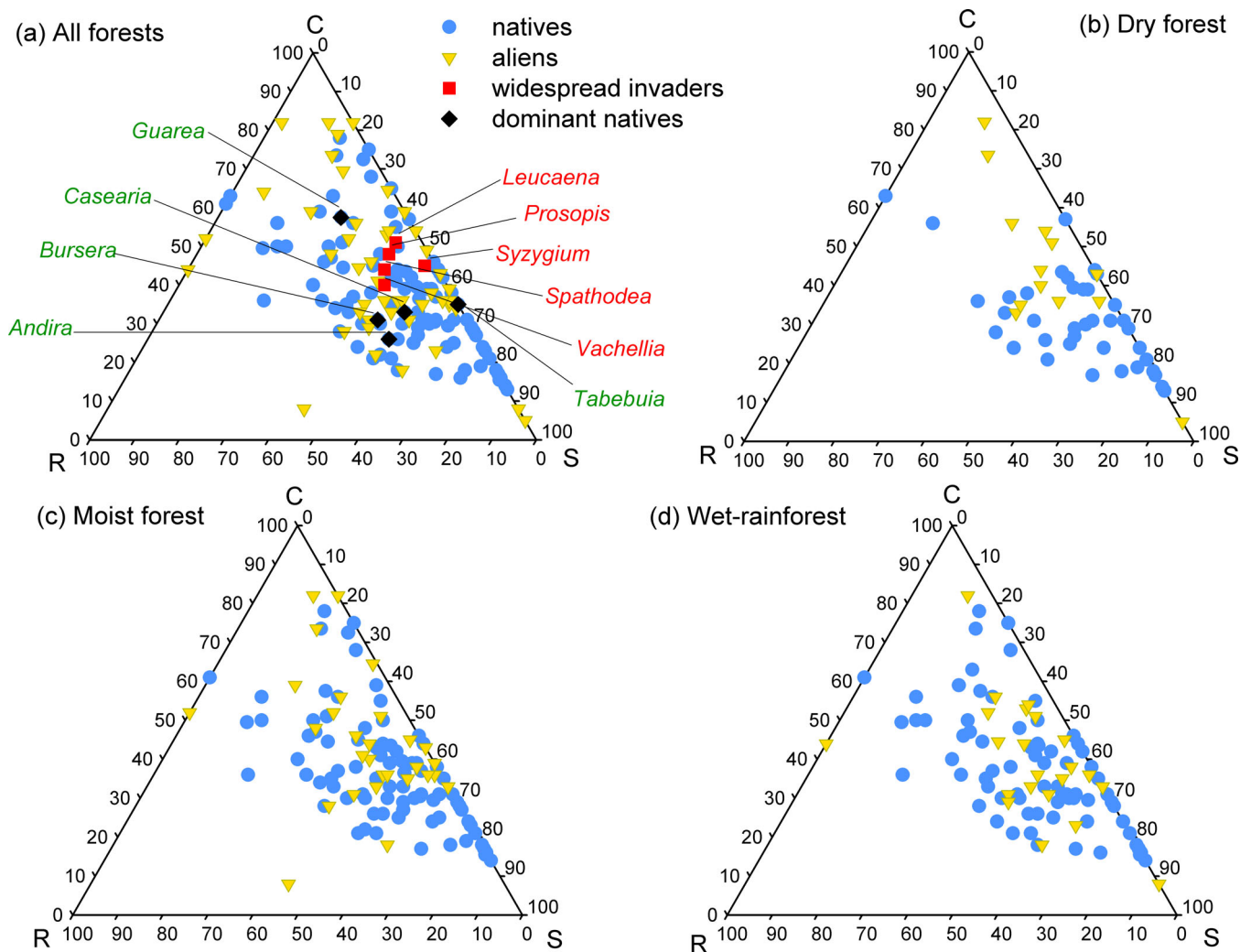
FIGURE 5 Position of native and alien species within the CSR-adaptive strategies triangles. For each triangle, each axis represents the relative contribution of C (competitor), S (stress-tolerant), and R (ruderal) components to the overall CSR score of each species.

alien species is scant. Generally, our results highlight the potential detrimental impact that woody invaders have on native species across major forest types in Puerto Rico. The species richness and the abundance of natives are consistently lower in plots with aliens compared with plots without aliens across all forest types. This negative association has been consistent for nearly 20 years. Alien species are likely major drivers of change in the community composition and assembly of Puerto Rican forests. These findings agree with previous studies that have also reported negative impacts of invasive aliens on species richness and abundance of natives in invaded forests (Asner et al., 2008; Hejda et al., 2009; Mollot et al., 2017; Wolfe & Van Bloem, 2012). Frequently, this negative relationship between native and invasive species has been attributed to the superior colonizing ability of the latter, which is achieved through various mechanisms, including effective dispersal, high growth rates, and multiple reproductive pathways (Bempah et al., 2021;

Junaedi et al., 2021; Liebhold et al., 2017; van Kleunen et al., 2010).

Without exception (i.e., for dry forest, moist forest, wet-rainforest, and all forests combined), lower mean species richness and lower mean abundance of natives characterized plots with aliens compared with plots without aliens. From a conservation perspective, these results raise alarm, as Puerto Rican forests, like many other Caribbean forests, are among the least protected and more highly exploited and degraded forests in the tropics (Lugo et al., 2000; Maunder et al., 2008). The expansion of alien species across Caribbean forests threatens these already endangered habitats, making them even more vulnerable to the impact of future biological invasions (Rojas-Sandoval et al., 2017, 2020). The elimination or reduction in the abundance of native species within natural forests can result in a plethora of cascading effects on many biotic components of the forest community as well as on trophic interactions that
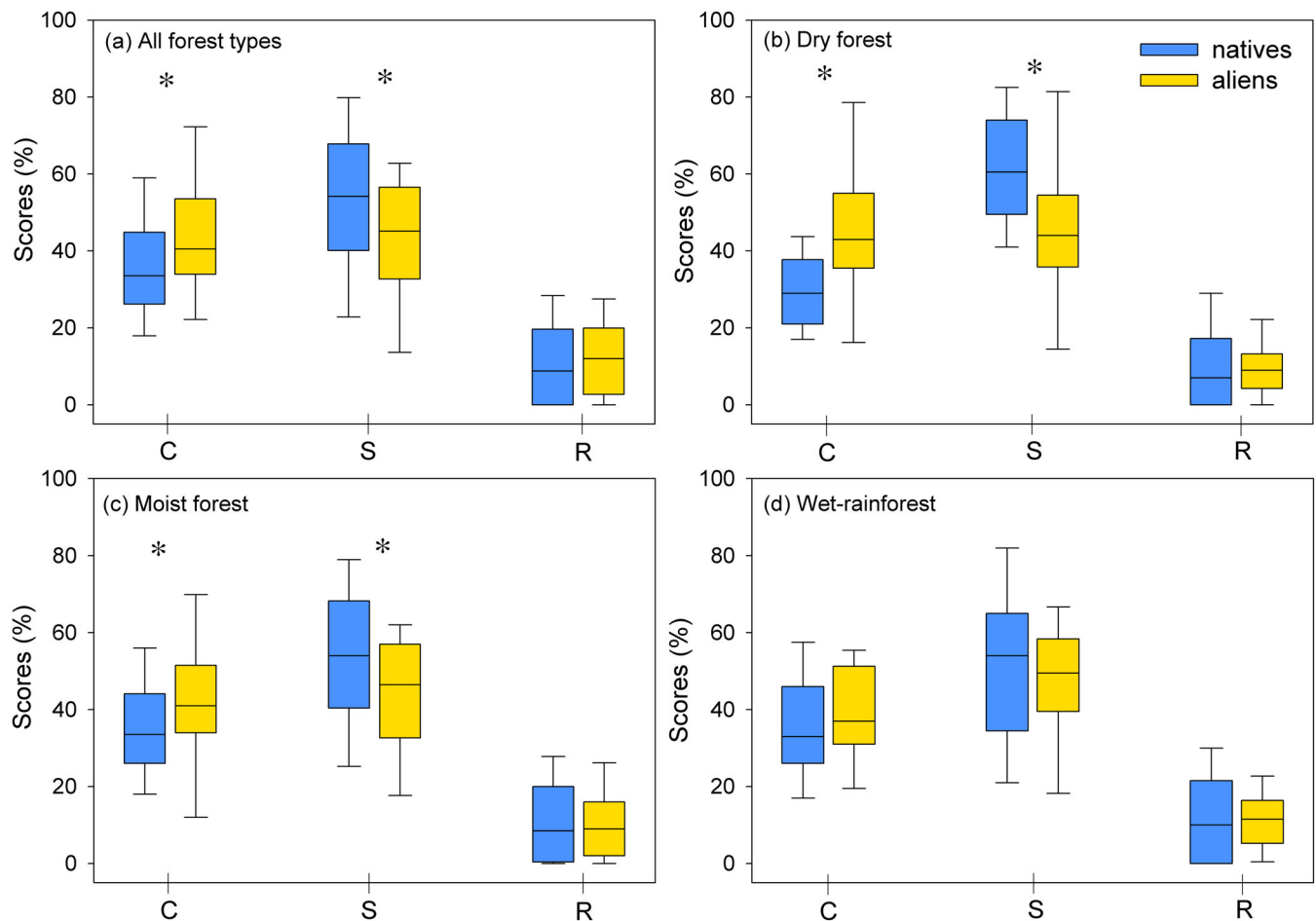
FIGURE 6 Boxplots for the C-, S-, and R-adaptive strategy scores for native and alien species. Boxes indicate the 25th to 75th percentiles, the middle horizontal line is the median, and the maximum length of the whiskers is 1.5 times the interquartile range. Asterisks (*) denote significant differences between natives and aliens ($p \leq 0.05$).

affect food web stability (Simberloff et al., 2013). For example, plant invasions may negatively impact the biodiversity of invertebrate and vertebrate species that utilize native plants as host resources (Gandhi & Herms, 2010; Hejda et al., 2017) and can also alter local biotas by increasing habitat homogeneity (Downey & Richardson, 2016; Tews et al., 2004). Moreover, invasive species are diminishing the richness and abundance of native trees, likely affecting forest resilience to extreme climate change and large-scale disturbances such as drought, tropical storms, and hurricanes (Paudel & Battaglia, 2021).

We also asked whether higher abundances of aliens could suppress native richness or facilitate the establishment of other alien species. Regardless of forest type, native richness is negatively correlated with the abundance of aliens (including *Leucaena* and *Spathodea*). Consequently, aliens may be displacing native species, which is consistent with previous studies in which increasing dominance by aliens negatively affected native

biodiversity (Bernard-Verdier & Hulme, 2015; Hejda et al., 2009). Such negative relationships may be due to direct or indirect competition for resources such as water, nutrients, or light (Liebhold et al., 2017). Conversely, a positive relationship was detected between alien richness and the abundance of alien species. This suggests that some alien species may be responding similarly to salient environmental gradients or that some alien species may benefit from the presence of other aliens. Such positive feedback loops could lead to a scenario of "invasional meltdown," triggering increased establishment rates of aliens or their magnified impact on natives (Simberloff, 2006; Simberloff & Von Holle, 1999). Overall, our findings suggest that the presence and higher abundance of alien species may negatively affect native communities rather than facilitate the recruitment and recovery of native species, as has been suggested for forests in Puerto Rico (Abelleira Martínez et al., 2010; Aide et al., 2000; Lugo, 2004). After 20 years, our data show a small increase in the importance of native species in plots with

aliens, a result diverging from what would be expected if the function of novel forests could extend beyond the scenario of degraded or abandoned agricultural land (see below).

Contemporary forests in Puerto Rico are the result of natural regeneration after agriculture and pasture lands were abandoned in the 1950s. Currently, forests on the island are a combination of aliens and natives that are frequently dominated by invasive species (Lugo & Helmer, 2004). Previous studies of abandoned agricultural and pasture lands at different successional stages (from 5 to >80 years) have shown that after 30–40 years, total species richness and the structural characteristics of plant communities return to levels comparable to those in older, closed canopy forests (Lugo, 2004; Zimmerman et al., 2007). Many of the species leading the recovery of such "regenerated forests" (also known as "novel forests") are pioneer aliens that are shade-intolerant. Consequently, as these aliens decline in abundance with stand age (canopies close during secondary succession), they could facilitate the recruitment and establishment of native species that could eventually replace them (Abelleira Martínez et al., 2010; Aide et al., 2000; Lugo, 2004). However, our results comparing plots with and without aliens suggest a plausible alternative scenario: alien species may suppress the diversity of native species rather than facilitate their recovery. The nature of disturbance prior to the establishment of these plots is likely variable in age, extent, and intensity, yet the negative alien-native relationships reported here are sufficiently strong as to be unobscured by such variability. Critically, such negative relationships characterize all forest types and persist over time. Meanwhile, alien richness is associated positively with the presence and higher abundance of alien species. Correlation is not causation, but the fact that native species recruitment over 20 years has been three times lower in plots with aliens compared with plots without aliens provides further support for this alternative scenario. None of the expectations of facilitation between natives and aliens is corroborated in analyses of these long-term plots.

Alternatively, alien species in regenerated forests may interrupt successional dynamics and create novel forests that are caught in a persistent degraded state in which aliens have been able to establish persistent communities that prevent (and resist) the colonization by native species (Cramer et al., 2008; D'Antonio et al., 2017; Kulmatiski, 2006). Areas that have been dominated by alien species for decades or more could be in an alternative stable state that is maintained through pervasive landscape alterations that arise from anthropogenic disturbances. Therein, native species' ability to assemble is limited by altered soil and microhabitat conditions, poor seed dispersal, and competition with alien species. As a result, recovery is constrained by intrinsic habitat factors that favor the continued dominance of alien species (Cramer et al., 2008; Kulmatiski, 2006). Although novel forests can provide valued ecosystem services (Evers et al., 2018), they enhance biotic homogenization through the loss and reduction of native biodiversity, potentially undermining the function, stability, and productivity of ecosystems (Olden et al., 2004; Wang et al., 2021).

Adaptive strategies and naturalization success

Alien species do not significantly diverge from native species with respect to CSR-adaptive strategies. This is true for all plots regardless of forest type, as well as for moist and wet-rainforest forests, suggesting that natives and aliens are basically occupying the same functional spaces within these forest types. These findings support the "join the locals" hypothesis, suggesting that across moist forests and wet-rainforests, alien species are successful because they share traits that are similar to those of native species (Keddy & Weiher, 1999). These similarities in the CSR strategy between native and alien species highlight the relevance of filtering by environmental factors (such as local climate and disturbance regimes) in influencing the convergence between natives and aliens. Within moist forests and wet-rainforests, alien species mostly share strategies deployed by successful native species. As a result, both natives and aliens should have the same probability of establishing persistent populations that thrive under local environmental conditions (Dalle Fratte et al., 2019; Lodge et al., 2018; Tecco et al., 2010), with local-scale to broad-scale disturbances (which characterize the disturbance regimes of many Caribbean forests), decreasing the benefits to natives derived from priority effects (Fukami, 2015).

In contrast, alien and native species of dry forests diverge in their use of functional spaces. This is consistent with the "try harder" hypothesis, suggesting that within dry forests, successful aliens are dealing better with local environmental conditions than natives (Crawley et al., 1996; Keddy & Weiher, 1999). In dry forests, aliens are better competitors (with higher C-scores) than natives, and this allows aliens to take advantage of changes in resource availability to grow and spread faster than native species. This agrees with previous studies suggesting that invasive aliens are successful because they generally have growth and survival strategies that allow them to perform better than native species (Lamarque et al., 2011; Maron & Marler, 2008; van Kleunen et al., 2010). The "try harder"

hypothesis could also be viewed as a "try differently" hypothesis, indicating that successful alien species may have traits that are simply different from those of native species (Lodge et al., 2018). Caribbean dry forests are highly degraded and fragmented ecosystems, characterized by high levels of anthropogenic disturbance, marked seasonality, water stress, and nutrient limitation. Across Caribbean islands, secondary dry forests are generally dominated by alien legume trees (Fabaceae), and the dominance of these trees could be related to their ability to fix nitrogen, which gives them a competitive advantage, especially in harsh environments, facilitating their establishment in degraded sites and on infertile soils (Ramjohn et al., 2012; Wolfe & Van Bloem, 2012). Our results are consistent with this pattern. The dominant alien species in dry forests are woody legumes: *L. leucocephala*, *P. pallida*, and *V. farnesiana*. These three species are nitrogen-fixing, whereas none of the 10 most frequent native trees within this forest type has this attribute (Table 2).

Throughout Puerto Rico, alien species have higher C-scores whereas native species have higher S-scores, supporting the hypothesis that naturalized aliens are effective competitors (Dalle Fratte et al., 2019; Guo et al., 2018, 2019). Indeed, successful invaders in natural and semi-natural habitats are generally effective competitors for limiting resources (Bempah et al., 2021; Liebhold et al., 2017). Competitors are characterized by traits such as rapid growth, short leaf life-span, high flowering frequency, nutrient-rich leaves, and high photosynthetic rates (Reich, 2014; Wright et al., 2004), all characteristics that are generally associated with invasive species (Richardson & Pyšek, 2012; van Kleunen et al., 2010). In a global assessment, Guo et al. (2018, 2019) also found a positive correlation between high R-scores and alien naturalization success. However, such a correlation does not characterize the situation in Puerto Rico. Instead, Puerto Rican forests harbor a few R-selected aliens. This may be a consequence, at least in part, of a survey design focused only on woody species. Pierce et al. (2017) showed that different life-form categories exhibit variation in the CSR scores. Trees generally cluster around the CS strategy; the R-strategy is more common for herbs and small shrubs, and for early successional stages; and adult trees with high R-scores do not exist (Caccianiga et al., 2006; Pierce et al., 2013, 2017; Rejmanek & Richardson, 1996).

The high S-scores of native species categorize them as stress-tolerant. Contrary to their competitors, stress-tolerant species are generally long-lived taxa with robust leaves, slow growth, and small fruit and seed production (Grime & Pierce, 2012). Stress-tolerant species are adapted to survive and thrive in areas where productivity is chronically or seasonally limited (Pierce et al., 2017).

We interpret stress-tolerant strategies for native species in Puerto Rico as adaptations to episodic droughts, floods, and cyclonic storms, which are, in aggregate, common events across the Caribbean (Lugo et al., 2000).

Implications for restoration

If the goal is to restore forests across Puerto Rico and at the same time maintain the highest diversity of native species (i.e., maintaining species composition similar to that occurring in non-invaded closed canopy forests), then it will be necessary to assist natural regeneration. Passive regeneration with minimal human intervention may not be sufficient to preserve the integrity of Puerto Rican forests based on our results. In Puerto Rico, assisting natural regeneration by including supplementary planting of native species, control and reduction of alien species, as well as reduction of anthropogenic fires in dry habitats (Wolfe & Van Bloem, 2012) may be necessary to preserve the compositional integrity of native species in forests. Assisted natural regeneration is a simple and inexpensive approach for converting areas of degraded vegetation into productive forests that provide critical ecosystem services. This approach is most suitable for restoring areas where secondary succession is in progress (Shono et al., 2007). Nevertheless, if key interspecific interactions, such as pollination and seed dispersal, have been lost because of extinctions, or if sources of native propagules are highly fragmented or distant, then assisted natural recovery may not be sufficient to ensure the recovery and long-term ecological functioning of these forests (Arroyo-Rodríguez et al., 2017). Comprehensive studies to evaluate the status and viability of such key biotic interactions are highly recommended.

Caveats and future directions

Our combined results suggest that alien species may drive local changes in native plant communities by transforming the assembly and dynamics of recovering tropical forests. However, we recognize that more definitive conclusions require additional plot censuses, and detailed considerations of disturbance regimes, land-use legacies, and stand age structure. Although tropical forests have a strong capacity to regrow on abandoned lands (Poorter et al., 2021), our understanding of how native and alien species interact in recovering tropical forests is still limited. Secondary tropical forests may play crucial roles in biodiversity conservation, climate change mitigation, and landscape restoration, yet the long-term implications of the incidence and expansion of alien

species in those forests are still an unanswered question. Similarly, further research on how adaptive strategies (competitive, stress-tolerant, or ruderal) differ within and between alien and native species may improve our knowledge of tropical forest responses to climate change and successional processes.

CONCLUSIONS

Globally, the introduction of alien species as well as the expansion of invasive species will likely accelerate over time. This study highlights the potential negative impact that alien species may have across major tropical forest types, where they have been spreading and interacting with native species for many decades. Our findings suggest that alien species are transforming the assembly and dynamics of local forests, with potential future consequences for native biodiversity loss. Some of the most widespread invasive aliens (e.g., *Leucaena* and *Spathodea*) possess the capacity to rapidly spread and increase their cover in anthropogenically disturbed areas, making them potentially much more abundant than native species. Our combined results suggest that alien species could inhibit population growth or even drive local losses of native species. These consequences may have profound impacts on the future of natural forests by altering successional regeneration and productivity, as well as the vulnerability, resilience, and capacity of the biota to adapt to climate change and altered disturbance regimes in which large-scale, extreme events such as drought, tropical storms, and hurricanes are increasing. While well-conserved tropical forests may be resistant to invasions by vascular plants (e.g., Ackerman et al., 2017; Zimmerman et al., 2021), we and others have shown that anthropogenically disturbed tropical forests can be quite vulnerable to biological invasions (Asner et al., 2008; Bempah et al., 2021; Rothstein et al., 2004) and that invasive alien species have the potential to severely alter the composition of tropical forests across different successional stages and have a long-term impact on the abundance and richness of native species.

AUTHOR CONTRIBUTIONS

Julissa Rojas-Sandoval conceived the study. Julissa Rojas-Sandoval and Humfredo Marcano-Vega compiled the data. Julissa Rojas-Sandoval designed and performed the analyses, with major inputs from James D. Ackerman and Michael R. Willig. Julissa Rojas-Sandoval led the writing and all authors contributed critically to the manuscript and gave final approval for publication.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the US Forest Service FIA DataMart: https://apps.fs.usda.gov/fia/datamart/datamart_excel.html.

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SUPPORTING INFORMATION

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

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