Island biogeography of native and alien plant species: Contrasting drivers of diversity across the Lesser Antilles

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Abstract
Aim: Understanding the factors driving the diversity of alien and native species on islands is crucial for predicting the spread of alien species and for proposing management practices to protect the unique native biodiversity that often occurs in insular ecosystems. The main objective of this study was to evaluate whether native and alien plant species respond similarly to natural biogeographic and human-related drivers.

Location: Lesser Antilles, Caribbean.

Methods: We compiled a dataset with the verified status of native and alien plant species occurring on 15 islands across the Lesser Antilles. We assessed the relationship of native and alien plant species richness and identified the biogeographic and socio-economic variables that best explain the diversity patterns of both alien and native species on these islands by combining correlation analysis and generalized linear models.

Results: The final dataset comprises a total of 2,438 plant species with 1,825 native species and 613 alien species. For the 15 islands analysed, native and alien species richness is strongly and positively correlated, but different variables explained their diversity patterns. We found that biogeographic drivers such as island area, elevation and distance to the mainland best explain patterns of native species richness. On the other hand, alien species richness was well predicted by a combination of geographic and socio-economic variables, with per capita gross domestic product (GDP) and island area having the strongest effect. Species composition of alien floras is also significantly influenced by the historical colonial identity of these islands.

Main conclusions: While native species are clearly associated with biogeographic variables, alien species are strongly influenced by variables related to human activities and therefore anthropogenic disturbance processes. Modification of natural areas by human activities can result in high alien species richness even on islands with high native species richness.

Keywords
Caribbean islands, diversity patterns, invasive plant species, phytogeography, spermatophytes
1 | INTRODUCTION

The theory of island biogeography predicts that species diversity on islands will be the result of a dynamic balance between three main processes: immigration, speciation and extinction (MacArthur & Wilson, 1967). According to this theory, species richness on insular ecosystems is expected to follow positive species-area relationships and negative species-isolation relationships. Since the postulation of this theory, a large number of studies accounting for these patterns on oceanic islands have been published (Whittaker & Fernandez-Palacios, 2007; Kreft, Jetz, Mutke, Kier, & Barthlott, 2008; Matthews et al., 2016; Matthews, Rigal, Triantis, & Whittaker, 2019; Triantis, Guilhaumon, & Whittaker, 2012; Whittaker, Triantis, & Ladle, 2008). However, only until more recently have studies begun to distinguish between native and alien species and consider biogeographic models involving the role of human interactions (Sax & Gaines, 2006; Carboni, Thuiller, Izza, & Acosta, 2010; Blackburn, Cassey, & Lockwood, 2008; Helmus, Mahler, & Losos, 2014; Blackburn, Delean, Pyšek, & Cassey, 2016; Ackerman, Tremblay, Rojas-Sandoval, & Hernández-Fig ueroa, 2017; Silva-Rocha, Salvi, Carretero & Ficetola, 2019). Whether alien and native species on islands respond similarly to biogeographic and human-related drivers still remains an open question (Buckley & Catford, 2016; Burns, 2015; Capinha, Essl, Seebens, Moser, & Pereira, 2015). Understanding the factors driving the diversity of alien and native species is a first step to guide data collection for better predicting the spread of alien species and implementing management strategies to protect the unique native biodiversity that often occurs on insular ecosystems (Simberloff, 2000; Sax & Gaines, 2008; Blackburn et al., 2016; Rojas-Sandoval, Tremblay, Acevedo-Rodríguez & Díaz-Soltero, 2017).

Globalization and the intensification of international trade and travel have been transgressing the natural barriers to dispersal (Levine & D’Antonio, 2003; Hulme, 2009) and are leading to an unprecedented increase in the rates of introduction and naturalization of alien species (Seebens et al., 2017). Ultimately, this may cause the breakdown of the "classical" biogeographic theory and the emergence of new biogeographic arrangements determined primarily by environmental factors and by patterns in human activity (Burns, 2015; Capinha et al., 2015; Dawson et al., 2017; Essl et al., 2019). On islands, the introduction of alien species circumvents natural geographical barriers (isolation), which may lead to increases in the numbers and distribution of naturalized species. These events can potentially amplify negative impacts on native species with important implications for conservation of insular ecosystems (Moser et al., 2018; Russell, Meyer, Holmes, & Pagad, 2017; Sax & Gaines, 2008; Simberloff, 2000). In fact, previous studies have shown that alien diversity on islands is strongly and positively influenced by human-related factors, such as economy and market size, human population density and exchange and transportation rates (Blackburn et al., 2016; Dawson et al., 2017; Denslow, Space, & Thomas, 2009; Kueffer et al., 2010; Rojas-Sandoval, Tremblay, Acevedo-Rodríguez, & Díaz-Soltero, 2017).

Globally, island ecosystems are under severe threat due to habitat loss and climate change and are areas particularly susceptible to biological invasions (Caujapé-Castells et al., 2010; Denslow, 2003; Pyšek & Richardson, 2006; Rejmánek, 1996; Russell et al., 2017; Taylor & Kumar, 2016). Islands are recognized as hotspot of alien species (Dawson et al., 2017; Essl et al., 2019), and in the case of plants, the number of naturalized alien species on islands is almost twice the number of those recorded in similar sized patches on the mainland with approximately the same number of native species (Sax, Gaines, & Brown, 2002).

The Caribbean region is a hotspot of biodiversity with high priority for conservation due to its remarkable biological richness and high levels of endemism (>70% for Caribbean flowering plants; Acevedo-Rodríguez & Strong, 2012; Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000; Roncal, Nieto-Blázquez, Cardona, & Bacon, 2020; Santiago-Valentin & Olmstead, 2004). Historically, Caribbean islands have played a crucial role as crossroads between continental America, Europe and Africa, resulting in multiple introductions of alien species over centuries as well as changes in land use and biota composition (Lugo, 2004; Rojas-Sandoval et al., 2017). Additionally, the flora of the Lesser Antilles is among the best documented for tropical archipelagos; comprehensive and updated botanical inventories are available providing the information needed for this study. Owing to these unique circumstances, the Lesser Antilles is an excellent place to study the biogeography of alien and native plant species and to evaluate whether alien species follow the same biogeographic patterns as native species, and under which circumstances human-related activities could lead to a failure of the traditional biogeographic rules.

In this study, we address the following questions: (1) What is the relationship between native and alien species richness in the Lesser Antilles, (2) what are the biogeographic and human-related predictor variables driving native and alien plant species richness on these islands and (3) are these variables exerting the same effects on native species as for alien species? To address these questions, we compiled a dataset with the verified status of native and alien plant species occurring on 15 islands across the Lesser Antilles. We hypothesized that if natural biogeographic variables exert the same effects on alien species as they do on native species (Whittaker & Fernandez-Palacios, 2007, Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017), then we would expect biogeographic and biotic variables to be dominant drivers of both alien and native species richness on these islands (e.g. alien species would be more frequent and abundant on large islands as these can support a higher number of species). On the other hand, if the effects of human activities overshadow natural processes, then we would expect the alien species richness to be dominated by human-related variables (e.g. alien species would be more frequent and abundant on islands with larger human populations and higher economic development).

2 | METHODS

2.1 | Study site

We used plant diversity of native and alien species from 15 islands in the Lesser Antilles ranging from Anguilla in the north
### TABLE 1  Summary of the biogeographic, socio-economic and historical variables compiled for 15 islands in the Lesser Antilles

| Island   | Diversity | Biogeographic | Biotic | Socio-economic | Historical |
|----------|-----------|---------------|--------|----------------|------------|
|          | Nativea   | Alienb        | Totalc | Forest cover (%)d | Agriculture cover (%)e | Human population | Paved roads (km)f | GDP (US$g) | Number of touristsih | Colonial identity |
|          | Area (km²) | Age (my)b     | Elevation (m) | Latitude (°N) | Distance to mainlandc | (km) | (km) | (US$) | (billion) | (millions) |
| Anguilla | 256       | 149           | 405     | 73             | 18.219     | 838 | 61.1 | 0  | 17,422 | 82       | 0.175 | 151,000 | UK     |
| Antigua  | 711       | 222           | 933     | 402            | 17.075     | 706 | 22.3 | 20.5  | 95,882 | 386     | 2.393 | 247,000 | UK     |
| Barbados | 539       | 301           | 840     | 336            | 13.194     | 395 | 19.4 | 32.6  | 293,131 | 1,700   | 5.218 | 1,350,000 | UK     |
| Dominica | 980       | 244           | 1,224   | 1,447          | 15.415     | 517 | 59.2 | 34.7  | 74,027 | 762     | 0.783 | 71,000  | UK     |
| Grenada  | 751       | 199           | 950     | 840            | 12.117     | 157 | 50   | 32.3  | 112,207 | 902     | 1.634 | 168,000 | UK     |
| Guadeloupe | 1,182  | 333           | 1,515   | 1,457          | 16.265     | 591 | 47.3 | 15     | 448,713 | 1,742   | 3.513 | 650,000 | France |
| Martinique | 1,205  | 401           | 1,606   | 1,397          | 14.642     | 441 | 43.4 | 20     | 429,510 | 1,579   | 6.117 | 536,000 | France |
| Montserrat | 595    | 198           | 793     | 1,050          | 16.743     | 668 | 25   | 30     | 5,315   | 227     | 0.167 | 9,000   | UK     |
| Nevis    | 207       | 38            | 245     | 985            | 17.155     | 716 | 42.3 | 23.1  | 11,108  | 163     | 1.528 | 115,000 | UK     |
| Saba     | 363       | 147           | 510     | 888            | 17.636     | 779 | 32   | 6.3   | 1,991   | 19      | 0.048 | 13,200  | NL     |
| St Eustatius | 322    | 103           | 425     | 602            | 17.489     | 759 | 38   | 5.3   | 3,393   | 18      | 0.102 | 10,500  | NL     |
| St Kitts | 491       | 133           | 624     | 1,156          | 17.358     | 738 | 42.3 | 23.1  | 34,983  | 163     | 1.528 | 115,000 | UK     |
| St Lucia | 985       | 333           | 1,318   | 948            | 13.909     | 370 | 77   | 17.4  | 165,510 | 847     | 2.542 | 386,000 | UK     |
| St Martin | 389    | 112           | 501     | 424            | 18.071     | 820 | 18.4 | 1     | 74,961   | 900     | 0.927 | 402,000 | NL     |
| St Vincent | 893   | 244           | 1,137   | 1,234          | 13.251     | 298 | 68.7 | 25.6  | 102,089 | 580     | 1.265 | 76,000  | UK     |

*aNumber of species including only spermatophytes.  
*bGeological age in million years.  
*cDistance in km to the nearest continental mainland.  
*dPercentage of total land area cover by forest. Forest area is land spanning more than 0.5 hectare with trees higher than 5m and a canopy cover of more than 10% to include windbreaks, shelterbelts and corridors of trees greater than 0.5 hectare and at least 20 m wide.  
*ePercentage of total land area cover by agriculture, permanent crops and active pastures.  
*fTotal length of the paved road network.  
*gGross domestic product per capita on purchasing power parity in billion US dollars.  
*hNumber of international tourist arrivals.  
*iLast European territory ruling the island. UK: United Kingdom; NL: Netherlands.
to Grenada in the south (Figure S1). These 15 islands may be divided into two major groups based on their geological histories and elevation. The first group comprises an inner arc of islands (including Grenada, St. Vincent, St. Lucia, Martinique, Dominica, Montserrat, Nevis, St. Kitts, St. Eustatius and Saba) with volcanic origin, elevations over 500 m and a wide range of habitats, including dry thickets, mountain and rain forests, seasonal forests and high-altitude forests. The second group comprises an outer arc of islands (including Anguilla, St. Martin, Antigua and Barbados), which are mostly composed of marine sediments (limestone), have elevations below 500 m and vegetation dominated by lowland dry forests and coastal shrublands (Bouysse, 1984; Donnelly, 1989; Joseph, 2012, 2013; Ricklefs & Lovette, 1999). Guadeloupe is a dual island, with a mountainous volcanic portion to the west separated by mangroves and a narrow channel from a lowland limestone island to the east. Most of the islands in the Lesser Antilles have been in their current positions for at least 10 million years, are surrounded by deep water and have had no connection to other islands or to the mainland. Exceptions to this include three groups of islands that currently occupy shallow banks and that were inter-connected during the Pleistocene when sea level was lower. These three island groups correspond to Nevis and St. Kitts, Antigua and Barbuda, and Grenada and the Grenadines (Ricklefs & Lovette, 1999).

2.2 | Data collection

We compiled a dataset with information on the presence/occurrence of plant species (including only spermatophyte species) for each of the 15 islands included in this study (see Appendix S1 in Supporting Information for a list of the references consulted). Each species was classified as either native or alien for each island. For this study, only naturalized alien species were considered and species with unreliable records (e.g. listed as both native and alien) were excluded. We built a second dataset comprising 15 biogeographic, biotic and human-related factors (i.e. socio-economic and historical variables) of each island that we suspected to be drivers of plant diversity (Table 1). Most of these data were obtained in May 2019 from the World Factbook (https://www.cia.gov/library/publications/the-world-factbook/) and some local and international websites (see Appendix S2 for a complete list of the sources consulted). Distances to the nearest mainland (hereafter “distance to mainland”) were calculated using the Google Maps Distance Measurement Tool as the distance in kilometres from the centre of each island to the coastline of the nearest continental mainland (Weigelt & Kreft, 2013). Data for biogeographic, biotic and socio-economic variables for the Dutch and French parts of St. Martin were combined and reported as actual or mean values depending on the variable type.

2.3 | Statistical analyses

Generalized linear models (GLMs) were used to assess potential relationships between native and alien species richness and biogeographic, biotic and socio-economic variables. Given the high number of variables (Table 1) and the potential collinearity problems that this might cause on multiple regression models, we first performed pairwise correlations to identify potential drivers of plant diversity on these islands (Figure S2). The variables evaluated as predictors were as follows: island area, elevation, distance to mainland, human population size, kilometres of paved roads, per capita GDP (hereafter GDP) and percentage of area covered by agriculture and forest (Table 1). Latitude and number of tourists were not included in subsequent analyses owing to their strong pairwise correlations with other less intercorrelated variables that are at least as relevant based on ecological theory and our hypotheses (Figure S2). Predictor variables island area, human population size and kilometres of paved roads were log-transformed to reduce heteroscedasticity. As species richness is count data, we first tested different GLMs with Poisson and negative binomial families. However, we decided to use GLMs of the Gaussian family because they consistently outperformed GLMs with Poisson and negative binomial in terms of model fit and model diagnostics (Crawley, 2007; Weigelt & Kreft, 2013). We also inspected the homoscedasticity and normality of the residuals with Q-Q plots obtaining similar results (Quinn & Keough, 2002). GLMs were fitted using linear or second-order polynomials, and models including predictor variables with strong pairwise correlation (r > 0.7; Figure S2) were removed from the list of plausible models to ensure that collinearity did not affect our results (Dormann et al., 2013). Models were ranked according to the corrected Akaike’s information criterion (AICc), and the model with the lowest AICc is considered the best-fit model (Akaike, 1974; Sugiura, 1978). Those models with AICc differences < 2 relative to the best-fit model were also considered as plausible (Arnold, 2010). All models evaluated are included in Appendix S3 and S4. The importance of each predictor variable was evaluated by summing the AICweight over all the models in which the selected predictor variable appeared, normalized by the total weight of all plausible models. The predictor variable with the highest AICweight (closest to 1) is considered as the most important for explaining the response variable, while the predictor variable with the smallest AICweight (closest to 0) is considered the least important (Giam & Olden, 2016; Silva-Rocha et al., 2019). All GLM analyses were performed in R (R Development Core Team, 2013) using the MASS package (Venables & Ripley, 2002) and the dredge function in the MuMIn package (Bartón, 2019) for comparing all models. Finally, non-metric multidimensional scaling (NMDS) ordination was used to evaluate whether the composition of alien plant species could be nested among islands grouped by their shared historical colonial identities. For this analysis, islands were classified as British, French or Dutch based on historical records referring to the last European
country ruling each island (Table 1). NMDS ordination was based on Euclidean distance measure and was computed on PC-ORD version 5.0 (McCune & Mefford, 1999).

3 | RESULTS

The final dataset comprises a total of 2,438 plant species of which 1,825 are native species and 613 (25%) are alien species. We found that alien and native species richness is strongly and positively correlated (Kendall correlation = 0.92; p < .001; Figure 1), but different variables explained their diversity patterns. Our combined results showed that across the Lesser Antilles, both native and alien species are not distributed evenly among islands. As expected, small islands are sustaining smaller numbers of both native and alien species, while large islands are sustaining larger numbers of native and alien species (Figure 1). For most islands, the number of native and alien species also varied with distance to the mainland (Figure 2a). The highest species richness for both groups occurred at the middle point of the maximum distance from the continent. A significant reduction in the number of both native and alien species occurs as we move away from the mainland, with a more significant reduction in the number of native species on islands located further away from the continent (Figure 2a). We also detected a positive correlation between elevation and number of native and alien species, but the magnitude of the slope is steeper for native species than for alien species (Figure 2b). A similar pattern emerged for native species of the six most species-rich plant families (Orchidaceae, Poaceae, Fabaceae, Rubiaceae, Cyperaceae and Asteraceae), for which we detected a strong and significant increment in the number of native species as elevation is increased (Figure S3).

Pairwise correlation analyses showed strong correlations between island area, human population and kilometres of paved roads and between GDP, human population and kilometres of paved roads (r > .7 in all cases; Figure S2). Therefore, models including any pair of these correlated variables were removed from the GLM analyses to avoid collinearity (Dormann et al., 2013). For native species, the best-fit model (AICc < 2) includes three variables: island area, elevation and distance to mainland (Table 2; Appendix S3). The sum of the AICweight across all plausible models showed that island area (AICweight = 0.85) is the most important factor explaining native species richness followed by elevation (AICweight = 0.71) and distance to the mainland (AICweight = 0.69; Figure 3a). The relative importance of all the remaining variables was very low (AICweight ≤ 0.2 in all cases), indicating that they have negligible effect on models predicting native species richness (Figure 3a). The best-fit model suggested that the number of native species increased with island area and elevation and mostly decreased as we moved away from the mainland (Figure 2). Overall, our combined models showed that native species richness is strongly driven by biogeographic variables, whereas biotic and socio-economic variables play a minor role (Figure 3a).

For alien species, the AICc ranking identified three equivalent models (differences in AICc < 2) that are good predictors of alien species richness (Table 2; Appendix S4). The top two models included only one variable each: the best-fit model had the socio-economic variable, GDP, while the next best model included the biogeographic variable, island area. The third model included a combination of human population size and distance to the mainland (Table 2). The sum of the AICweight across all plausible models confirmed that GDP (AICweight = 0.63) and island area (AICweight = 0.67) are notably the most important predictors of alien species richness (Figure 3b). Our models reveal that while the number of alien species is positively correlated with island area (Figure 2), GDP is also having a significant positive effect on alien species richness (Figure 2; Figure 3b). Models also showed that the number of alien species increased with human population size and generally decreased as we move away from the mainland (Figure 3b). For the Lesser Antilles, our combined results support the hypothesis that human-related activities are strongly influencing and facilitating the introduction and establishment of alien species on these islands.

The best solution of the NMDS ordination included two dimensions and explained 91% of the variance (Axis 1: coefficient

**FIGURE 1** Relationship between native and alien plant species richness for the Lesser Antilles. The size of each circle is proportional to the island area in km². The grey area corresponds to the 95% confidence interval.
of determination \( r^2 = .32 \), Axis 2: coefficient of determination \( r^2 = 0.69, p < .01 \) in both cases). Using Pearson’s correlation analyses, we found that axis 1 is primarily correlated with distance to the mainland \( r = -.67, \ p = .001 \), whereas axis 2 is primarily correlated with island area \( r = -.89, \ p < .001 \), elevation \( r = -.74, \ p = .003 \) and human population size \( r = -.65; \ p = .001 \). The distribution of islands in the multidimensional space shows that there are strong differences in the composition of alien plant species among islands that can be explained (at least partially) by their historical colonial identity. The French islands of Martinique and Guadeloupe and the Dutch islands of St. Martin, Saba and St Eustatius form clearly distinct groups (Figure 4).

4 | DISCUSSION

Native and alien species richness of the Lesser Antilles is positively correlated, meaning that islands richer in native species are also hosting more alien species. This positive relationship between native and alien species diversity is counter to Elton’s biotic resistance hypothesis (Elton, 1958), which proposes that areas of high species richness should be resistant to biological invasions and assumes that niches are occupied, and native species are better competitors (Elton, 1958).
While this may be true at very small scales and certain vegetation types, it is difficult to find evidence for it in scales ranging from forest plots to regions (Ackerman et al., 2017; Kennedy et al., 2002; Stohlgren, Barnett, & Kartesz, 2003; Stohlgren, Jarnevich, Chong, & Evangelista, 2006). Nevertheless, local areas of high species richness within islands, such as forest reserves, can show a weaker relationship between native and alien species richness suggesting that somewhat permeable biotic resistance may occur (Ackerman et al., 2017). For the Lesser Antilles, this strong positive correlation detected between native and alien species richness implies that native diversity could be used as a good predictor for alien species richness. This correlation has been previously explained in terms of ecological processes including species interactions and comparable responses of both native and aliens to the same drivers, suggesting that ecological drivers that favour high number of native species may also increase niche opportunities for alien species (Fridley et al., 2007; Lonsdale, 1999; Sax et al., 2002; Stohlgren et al., 2003).

We also found that, as expected, larger islands are hosting more native species than smaller islands. This positive correlation observed between native diversity and island area is one of the core relationships proposed by the theory of island biogeography (MacArthur & Wilson, 1967; Whittaker & Fernandez-Palacios, 2007). However, we also detected that this relationship is not restricted to native species, and the number of alien species also increases with island area. These patterns observed in the Lesser Antilles are consistent with previous island biogeography studies (Blackburn et al., 2008, 2016; Denslow et al., 2009; Kueffer et al., 2010; Rojas-Sandoval et al., 2017). The theory predicts higher species diversity on large islands relative to small islands because populations are likely to be larger on big islands and thus less prone to stochastic extinction than on small islands (MacArthur & Wilson, 1967). Large islands are also more likely to have higher diversity of habitats than small islands, and like area, habitat heterogeneity is often positively correlated with species diversity (Hortal, Triantis, Meiri, Thébault, & Sfenthourakis, 2009; Patiño...
et al., 2013; Ricklefs & Lovette, 1999). The habitat heterogeneity hypothesis proposes that an increase in the number of habitats across a landscape leads to an increase in native species diversity because the number of partitionable niche dimensions expands (Crane & Willig, 2005). Consequently, large islands will not only have more available habitats for the evolution of native species but also have more habitats that may be colonized by alien species resulting in a higher number of both native and alien species (Jarnevich, Stohlgren, Barnett, & Kartesz, 2006). In the Lesser Antilles, islands with high topographic relief also have a broader range of temperatures and rainfall, and often support greater range of habitats and communities than islands with low relief (Ricklefs & Lovette, 1999; Ackerman, Trejo-Torres, & Crespo-Chuy, 2007; Joseph 2012; Joseph, 2013; Traxmandlová et al., 2017; Debrot, Madden, Becking, Rojer, & Miller, 2020). Not surprisingly, our data show that large islands with wide elevation ranges such as Guadeloupe and Martinique are hosting more species than small low islands such as Anguilla and St Martin.

The relationship between species richness in the Lesser Antilles and distance to mainland is not always as theory would predict, rather it can be taxon-dependent (Scott, 1972; Staats & Schall, 1996; Rodríguez-Durán & Kunz, 2001; Ricklefs & Bermingham, 2004). The largest islands of the Lesser Antilles are those in the middle of the island chain so that species richness actually increased with distance from continental mainland, and then dramatically dropped off in the northernmost part of the archipelago, where the islands all tend to be small. We therefore cannot clearly determine whether the decline in native species numbers in the northernmost part is due to reduced habitat diversity or distance to mainland; we suspect the former as species richness is related to island area (thus habitat diversity), and Guadeloupe, Martinique and Dominica are the largest islands and have the wider elevation ranges of the 15 islands included in our study. As was expected for alien species richness, distance to the mainland was less important than human-related activities (see below).

Historical colonial identity appears to have a legacy, but not with respect to species richness. Rather, it is associated with the species composition of alien floras in the Lesser Antilles. The clusters formed by the French (Martinique and Guadeloupe) and Dutch islands (Saba, St Eustatius and St Martin) imply that for these islands the composition of alien floras could be explained (at least in part) by their colonial identity and the political, cultural and economic connections that remain today (Fortune, 1984; Hall, 1982). These islands are dependencies of France and the Netherlands, meaning a closer connection, higher commercial and population exchange, and greater interdependence with these European countries than with other countries within the Caribbean region (Girvan, 2012; McElroy & De Albuquerque, 1995). The historical connection with these European countries and preferential trade with islands within the region sharing the same colonial identity appear to be influencing the pathways of introduction and producing unique clusters of alien species.

In agreement with the theory of island biogeography, our GLM analyses showed that biogeographic variables including island area, elevation (surrogate for habitat and niche diversity) and distance to the mainland were the most important drivers of native species richness. In contrast, our models indicated that socio-economic variables played a key role in driving alien species richness. Our findings show that alien species are more frequent in large islands with greater socio-economic development. Island area influences the number of people that inhabit islands and consequently also the number of human-mediated introductions. Because aliens are defined as species introduced as a consequence of human activities, large and more populated islands are more likely to host a larger number of alien species than small, less populated islands. Therefore, larger islands with substantial human populations will not only generate more trade, economic activities and more transport interchange, but they will also have higher anthropogenic disturbance rates and thus more opportunities for accidental and deliberate introduction of alien species (Levine & D’Antonio, 2003; Catford et al., 2012; Hulme, 2009; Lockwood, Cassey, & Blackburn, 2009; Pyšek et al., 2010). In this regard, our results agree with previous studies (including studies performed in the Caribbean region) showing that human-related activities are key factors driving the introduction and establishment of alien species on islands (Ackerman et al., 2017; Dawson et al., 2017; Denslow et al., 2009; Helmus et al., 2014; Kueffer et al., 2010; Rojas-Sandoval & Acevedo-Rodríguez, 2015; Rojas-Sandoval et al., 2017).

### 4.1 Conservation perspective

Caribbean islands have been subjected to high levels of anthropogenic disturbance. Centuries of deforestation and land clearing first due to agriculture expansion and more recently due to urban and tourism development have resulted in the removal or alteration of much of the original vegetation and contributed to major changes to terrestrial habitats and a reduction in biodiversity (Dixon et al., 2001; Lugo, Helmer, & Valentín, 2012; Weaver, 2001). From a conservation perspective

**FIGURE 4** Non-metric multidimensional scaling (NMDS) ordination for the composition of alien plant species in the Lesser Antilles sorting out by the historical colonial identity of each island. Colonial identity: UK = United Kingdom, FR = France, NL = the Netherlands.
perspective, the results of this study may offer important guidance for the management and protection of native floras in the Lesser Antilles. First, there appears to be a strong conflict between human activities and the preservation of native plant diversity on these islands. Islands of the Lesser Antilles are exposed to huge residential and tourism pressures, and these activities are now primarily responsible for the reduction in forest cover and habitat degradation, but they are also the most relevant for the local economy of most islands (Dixon et al., 2001). More suitable and sustainable practices, as well as control in the expansion of urban and tourism activity, should be emphasized (Weaver, 2001). The preservation of areas of natural forests on these islands seems to be crucial not only for the conservation of their native diversity, but also for ecosystem services (e.g. water supply) most valued by humans (Anadón-Irizarry et al., 2012; Weaver, 2002). On the other hand, the remarkable importance of socio-economic variables driving alien plant richness observed in our results clearly emphasizes the vulnerability of large islands with high economic activity to the introduction and potential invasion of alien species. This link seems to be important to predict future trajectories of plant invasions on these islands, but also an opportunity to mitigate them. Finally, the implementation of more effective policies and management strategies to control the introduction and expansion of alien species should be a priority on these islands.

4.2 | Conclusions

As expected, biogeographic variables are the most important factors affecting diversity of native species. On the other hand, GDP and island area are the most important drivers of alien species richness. In the Lesser Antilles, as in other archipelagos, human activities (somewhat associated with historical and cultural affiliations) are having a deep impact on island floras and their distributions, reinforcing the importance of integrating human-related variables into biogeographic studies. Human-mediated dispersal is creating novel species assemblages on these islands and a profound biogeographic reorganization that is putting additional pressure on native floras. Additionally, the huge importance of socio-economic development (GDP) explaining alien species richness confirms the crucial role of human activities driving biological invasions. On these islands, modification of natural areas by human-related activities can result in high alien species richness even on islands with high native species diversity.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data used in this study can be found in Table 1.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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