



Antigonon leptopus invasion is associated with plant community disassembly in a Caribbean island ecosystem

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Abstract Invasions by non-native plant species are widely recognized as a major driver of biodiversity loss. Globally, (sub-)tropical islands form important components of biodiversity hotspots, while being particularly susceptible to invasions by plants in general and vines in particular. We studied the impact of the invasive vine *A. leptopus* on the diversity and structure of recipient plant communities on the northern Caribbean island St. Eustatius. We used a paired-plot design to study differences in species richness, evenness and community structure under *A. leptopus*-invaded and uninvaded conditions. Community structure was studied through species co-occurrence patterns. We found that in plots invaded by *A. leptopus*, species richness was 40–50% lower, and these plots also exhibited lower evenness. The magnitude of these negative impacts increased with increasing cover of *A. leptopus*. Invaded plots also showed higher degrees of homogeneity in species

composition. Species co-occurrence patterns indicated that plant communities in uninvaded plots were characterized by segregation, whereas recipient plant communities in invaded plots exhibited random co-occurrence patterns. These observations suggest that invasion of *A. leptopus* is not only associated with reduced species richness and evenness of recipient communities in invaded sites, but also with a community disassembly process that may reduce diversity between sites. Given that *A. leptopus* is a successful invader of (sub-)tropical islands around the globe, these impacts on plant community structure highlight that this invasive species could be a particular conservation concern for these systems.

Keywords Biodiversity impacts · C-score analysis · Community diversity · Evenness · Exotic plant invasion · Species richness

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Introduction

Invasions by non-native plant species represent an important ecological driver of ecosystem change, exerting profound impacts on biodiversity, ecosystem services and human well-being (Olson 2006; Pejchar and Mooney 2009; Vilà et al. 2011; Bellard et al. 2016; Shackleton et al. 2019). These impacts can result from a range of mechanisms, including the direct exclusion of native species (Reed et al. 2005; Molinari and

D'Antonio 2014; Bradley et al. 2019; De la Riva et al. 2019), and biotic homogenization at the expense of endemic species (McKinney and Lockwood 1999; Olden et al. 2004; Sax and Gaines 2008; Santos et al. 2011; Khanna et al. 2012; Kortz and Magurran 2019; Galán-Díaz et al. 2020). The latter mechanism is of particular concern for (sub-)tropical island archipelagos. These islands are characterized by high levels of endemism due to unique evolutionary histories (Myers et al. 2000; Brown and Sax 2004; Sloan et al. 2014). Moreover, (sub-)tropical islands have experienced the highest numbers of non-native plant invasions (Essl et al. 2019). While the impacts of invasive plant species on the diversity of recipient plant communities have been well documented in general (Vilà et al. 2011; Mollot et al. 2017; Pyšek et al. 2017; Peng et al. 2019), the specific impacts of invasive plant species in (sub-)tropical island ecosystems have been studied less in comparison (Pyšek et al. 2008; Sax and Gaines 2008; Lowry et al. 2013; Jeschke et al. 2018; Peng et al. 2019).

A straightforward way to assess the impact of non-native invasive plants on recipient communities is to compare species richness and evenness in pre- and post-invasion conditions (e.g. Heard et al. 2012). Through this approach, one can demonstrate that invasive species establish and expand at the expense of a decline in (native) species richness (Diekmann et al. 2016). However, in cases where space-for-time substitutions are used instead of longitudinal studies, it becomes more challenging to determine whether invasive species are driving or responding to variation in (native) species diversity (MacDougall and Turkington 2005; Bauer 2012; Cassini 2020). Moreover, the magnitude of invasive plant species' impacts may depend on contextual factors such as climate, habitat, land use and land cover characteristics (Gaertner et al. 2009; Vilà et al. 2011; Casado et al. 2015; Martín-Forés et al. 2015, 2017; Diekmann et al. 2016; Mollot et al. 2017; Pyšek et al. 2017). Specifically, previous studies have shown how recipient plant community richness in urbanized landscapes may be more negatively impacted by invasive species than recipient plant communities in more natural landscapes (González-Moreno et al. 2017; Gutiérrez-Cánovas et al. 2020; but see Martín-Forés et al. 2017).

In addition to negatively impacting the species richness of recipient plant communities, invasive species may exert more pervasive impacts as well,

including the disruption of plant-pollinator networks (Traveset and Richardson 2006; Vilà et al. 2009), abiotic habitat modification (Crooks 2002; Cuddington and Hastings 2004) and community disassembly (Sanders et al. 2003; Dostál 2011; Santoro et al. 2012). The latter refers to the process of non-random species losses and declines (*sensu* Zavaleta et al. 2009), and may generate additional changes in the structure of recipient plant communities (Sanders et al. 2003; Mangla et al. 2011; Santoro et al. 2012). To identify structure at the plant community level, species co-occurrence analyses can show whether species tend to segregate or aggregate (Stone and Roberts 1990; Gotelli 2000; Ulrich and Gotelli 2013). Species aggregation means that species tend to co-occur more often than expected from random co-occurrence, and may indicate the prevalence of facilitative interactions (Santoro et al. 2012; de Miguel et al. 2016). In contrast, species segregation means that species tend to co-occur less frequently than expected from random co-occurrence, and may indicate the prevalence of competitive interactions (Santoro et al. 2012; de Miguel et al. 2016; but see Ulrich et al. 2017). In addition to identifying patterns of species aggregation and segregation, co-occurrence analyses can also be used to infer the sign and magnitude of associations between particular pairs of species (Blois et al. 2013; Veech 2014; Verwijmeren et al. 2014; Lai et al. 2015; Li and Waller 2016; Waller et al. 2016). Within the context of plant invasion, a globally coordinated survey suggested that non-native plant species tend to aggregate in the non-native habitat, especially in patches with relatively high biomass and relatively small numbers of species (Stotz et al. 2020).

The Caribbean region includes multiple (sub-)tropical island archipelagos and is considered a global biodiversity hotspot, containing a large proportion of endemic species even when compared to other hotspots (Myers et al. 2000; Sloan et al. 2014). On Caribbean islands, lowland ecosystems are particularly susceptible to plant invasions (Kueffer et al. 2010), with climatic conditions favorable to the growth of lianas and vines (Schnitzer 2005; Schnitzer and Bongers 2011). These functional vegetation groups form a particular invasion concern, as they not only smother native vegetation, but also modify edaphic conditions (e.g. carbon and nitrogen dynamics, Bray et al. 2017; Ward et al. 2020) and micro-climatic conditions (e.g. humidity, Gordon 1998;

Horvitz et al. 1998). These processes may drive disproportionate ecosystem impacts as compared to invasive plant species of other growth forms that do not actively modify the environmental conditions for the recipient plant community (Crooks 2002; Cuddington and Hastings 2004; Harris et al. 2007; Kaproth et al. 2013; Gordon et al. 2017).

The aim of this study was to document the impact of invasion by the vine *Antigonon leptopus* on the Caribbean island of St. Eustatius. Specifically, we were interested in the impacts of *A. leptopus* on the diversity and structure of St. Eustatius' recipient plant communities. We addressed whether invasion by *A. leptopus*: (1) impacts the recipient plant communities' richness and evenness, and whether these impacts are mediated by land cover type; (2) leads to homogenization of recipient plant communities; (3) modifies species co-occurrence patterns; (4) differentially impacts native and non-native plant species. Based on general trends observed in the non-native plant invasion literature, we deduced the following hypotheses for our case study: (1) *A. leptopus* negatively impacts recipient plant community richness and evenness (Vilà et al. 2011; Mollot et al. 2017; Pyšek et al. 2017), and these effects are strongest in urban areas (González-Moreno et al. 2017; Gutiérrez-Cánovas et al. 2020). It is also hypothesized that these impacts increase linearly with increasing abundance of *A. leptopus* (Bradley et al. 2019); (2) Plant community composition in urban and semi-natural habitats is more homogeneous when these habitats have been invaded by *A. leptopus* (Huebner et al. 2012; Dar and Reshi 2015); (3) The sub-tropical lowland ecosystems of St. Eustatius are relatively benign habitats, and under such low stress conditions plant interactions may be dominated by competition (Maestre et al. 2009), which would be reflected in species segregation (Santoro et al. 2012; de Miguel et al. 2016). Invasion by *A. leptopus*, however, may disrupt these interactions and lead to a shift toward random co-occurrence patterns (Sanders et al. 2003; Santoro et al. 2012); and lastly 4) Non-native species co-occur more frequently with *A. leptopus* than native species (Stotz et al. 2020).

Material and methods

Study area

The research was conducted on St. Eustatius (17°28' N, 62°58' W), a northern Caribbean island that is part of the Cenozoic lesser Antilles volcanic island arc (Macdonald et al. 2000; Eppinga and Pucko 2018). The island consists of two volcanic complexes, the Quill in the southeastern part and the Northern Mountains in the northwestern part of the island, which were connected by lava flows resulting from eruptions of the Quill in the early Holocene (Rojer 1997; Roobol and Smith 2004). St. Eustatius' climate is tropical, with a mean annual temperature of 25.7 °C and mean annual precipitation of 1073 mm (Rojer 1997), but climate varies with elevation (Boldingh 1909; De Freitas et al. 2012). The mountain slopes are covered by various types of forest (described in: Stoffers 1956, Rojer 1997, De Freitas et al. 2012, Van Andel et al. 2016; Eppinga and Pucko 2018). The flatter, middle part of the island connecting the volcanic complexes is called the Kultuurvlakte. This area is dominated by grasslands, and has experienced intense anthropogenic disturbance (e.g. agriculture, livestock husbandry) for hundreds of years, with a higher proportion of non-native species occurring within its lowland ecosystems (Fig. 1; De Freitas et al. 2012; Axelrod 2017; Haber et al. 2021). *Antigonon leptopus* is the most successful and aggressive invasive species on the island (Ernst and Ketner 2007; Van der Burg et al. 2012; Haber et al. 2021), and will be described in further detail in the following section.

Study species

Antigonon leptopus (Hook. & Arn., common name(s): Coral vine and Coralita) is a perennial vine that is originally from Mexico, where it can be found in a wide range of habitats (Burke and DiTomaso 2011; CABI 2017; Vandebroek et al. 2018). The species' prolific production of flowers constitutes a nectar source for honey production, and makes it a popular ornamental plant (e.g. Burke and DiTomaso 2011; Zhang et al. 2017; Vandebroek et al. 2018), which has contributed to its spread throughout the global tropics (Burke and DiTomaso 2011), including the Caribbean (Mitchell et al. 2019). *Antigonon leptopus* tends to grow a network of rhizomes, from which shoots can

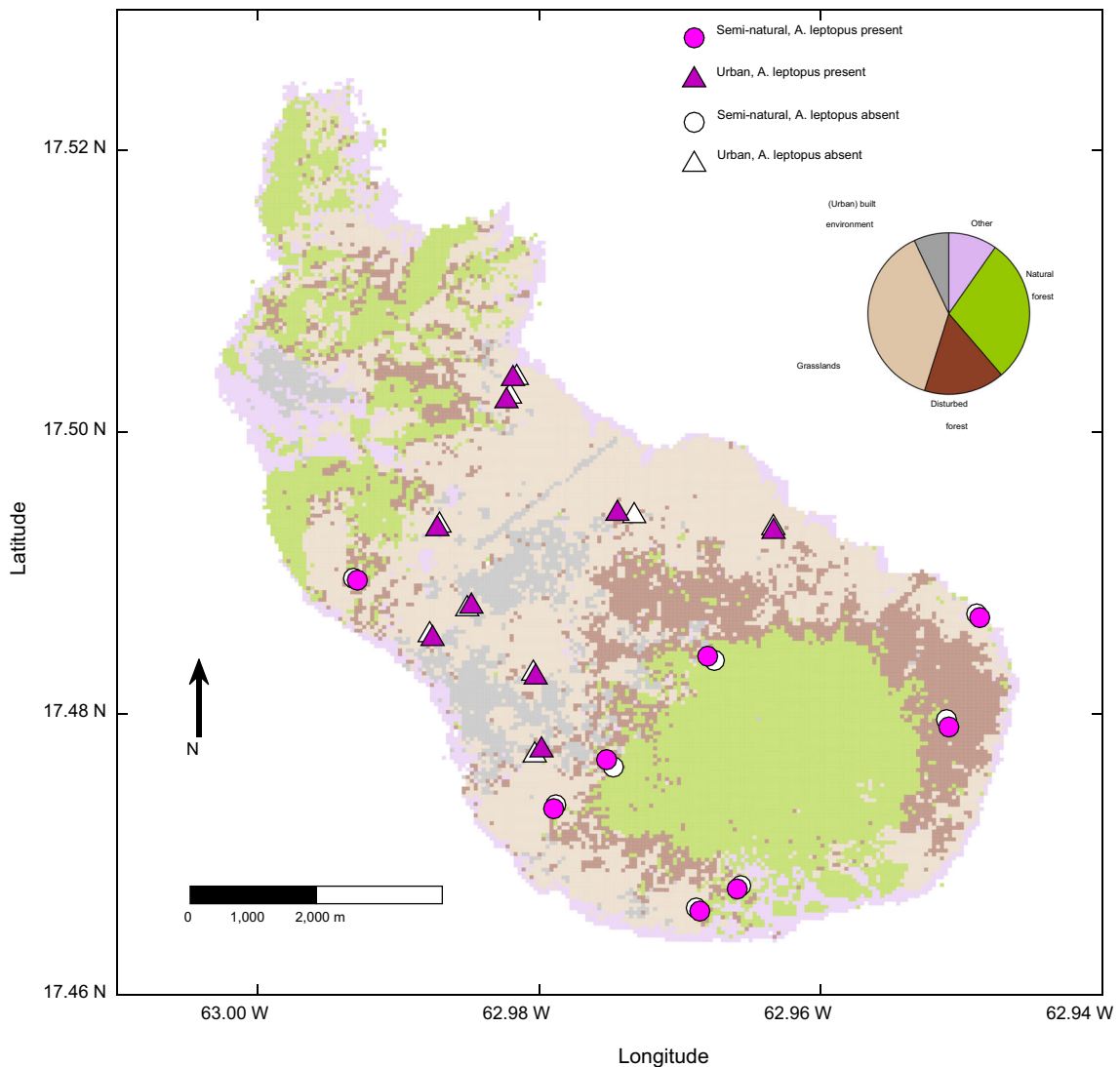


Fig. 1 Map of St. Eustatius (northern Caribbean), showing the different types of land use on the island, and the locations of the plots that were surveyed in the present study. Land use categories were identified by Helmer et al. (2008), and subsequently further aggregated into five different categories (following Haber et al. 2021). Different symbols indicate the different type of survey plots considered in the study. Magenta-

colored symbols indicate sampling locations where the focal invasive species, *A. leptopus* was the dominant species (i.e. covering at least 50% of the plot area). Using a paired-plot design, each of these plots was compared to a nearby plot without *A. leptopus* (white symbols). Ecological impacts of *A. leptopus* were compared between areas dominated by urban (triangles) and semi-natural (circles) land cover types

grow up to 25 cm per month (Ernst and Ketner 2007). The species can also spread by seed (Burke and DiTomasso 2011). *Antigonon leptopus* can grow in challenging environments such as those with low light availability and poor soils (Vandebroek et al. 2018). The vine climbs and smothers taller vascular plants (Surendra et al. 2013), but it can also ‘creep’ by expanding laterally over bare areas or grasslands

through propagation of rhizomes, stolons or tubers (Burke and DiTomasso 2011; Vandebroek et al. 2018). The size and depth of the tubers and rhizomes of the species, as well as its hardiness and its various modes of spread make *A. leptopus* a challenging species to eradicate (Ernst and Ketner 2007; Eppinga et al. 2021). The invasion of *A. leptopus* on the Caribbean island St. Eustatius is among the most severe

infestations of this species in the world (Ernst and Ketner 2007; Burke and DiTomaso 2011; Haber et al. 2021). Hence, St. Eustatius provides a valuable case study of the impact of *A. leptopus*' invasion in plant community diversity and structure. Despite the many observations of *A. leptopus* invasions around the globe, these impacts have not yet been systematically quantified (Heger and Van Andel 2019).

Field data collection

Field data were collected in November and December of 2018. We selected 17 locations for paired plot sampling on St. Eustatius (Fig. 1). These locations covered the range on St. Eustatius in which *A. leptopus* is present in patches greater than 100 m² (Haber et al. 2021), the full plot size used in this study (see below). The median geographical (Euclidean) distance to the nearest neighboring sampling location was 526 m (range: 155–1131 m, Fig. 1). As we were interested in inferring relationships between *A. leptopus* invasion, land cover type and plant community similarity, we verified that community similarities between plots were not confounded by the geographical (Euclidean) distances between plots (Fig. 1). Indeed, we found that community similarity did not significantly correlate with the geographical (Euclidean) distance between plots (Mantel test: Spearman's $\rho = -0.03$, $p = 0.61$).

The sampling locations were stratified according to land cover type, with 9 plots occurring in urban grassland areas and 8 plots in semi-natural forest areas. These land cover classifications were based upon the land cover distribution map of St. Eustatius by Helmer et al. (2008), further aggregated into an urban and a semi-natural land cover type (Haber et al. 2021), which were also used in this study. At each location, we selected a plot invaded ($\geq 50\%$ cover) by *A. leptopus*, and a plot in close proximity that was not invaded (0–1% cover) by *A. leptopus*. The median distance between paired invaded and uninvaded plots was 36 m (range: 30–127 m, Fig. 1). This paired-plot design enabled assessment of the impact of *A. leptopus* invasion on recipient plant community diversity and structure (e.g. Vilà et al. 2006; Castro-Diéz et al. 2016). Plot size was 10 m by 10 m. Within these plots, we recorded which species were present. Photographs were taken at each plot and voucher specimens were collected and deposited at the University of Puerto Rico herbarium (code: MAPR). The status of each

species (i.e. non-native or native) was obtained from the Dutch Caribbean Species Register (Naturalis Biodiversity Center 2017) and a systematic vademecum about the vascular plants of St. Eustatius (Axelrod 2017). For a subset of locations (7 urban and 7 semi-natural plots), we also estimated the abundance (in % cover) of the species present within a 2 m by 2 m subplot that was located near the plot center. For species with a total cover of $< 10\%$ a cover estimate was made based on the number of individuals present (rounded to the nearest %), and the average size of these individuals. For species with a total cover of $> 10\%$, cover was estimated visually and rounded to the nearest 5% (i.e. 10%, 15%, ..., 100%). We used cover as a measure of abundance, as it allowed for non-destructive sampling of sites, and generally community composition as measured through cover corresponds well to estimates requiring destructive sampling (i.e. aboveground biomass, Chiarucci et al. 1999; Chen and Shiyomi 2019). The plot size of 2 m by 2 m is often used in invasive plant species' impact surveys, as it provides a compromise between sampling at the scale of plant-plant interactions, while minimizing spatial variation in other environmental variables (e.g. Vilà et al. 2006; Gallego-Fernández et al. 2019).

Data analyses

Impact on species richness and evenness, and mediation by land cover type

We tested our first hypothesis using data collected at both the full plot (10 m by 10 m) and subplot (2 m by 2 m) scale. We tested for differences in species richness using generalized linear mixed-effects models, with land cover type and degree of *A. leptopus* invasion (i.e. uninvaded or invaded) as fixed effects, and location (i.e. a pair of an invaded and an uninvaded plot) as a random effect. We used a Poisson distribution for species counts and a logarithmic link function.

Species evenness was calculated differently for the full plots and the subplots. For the full plots, the abundance of each species was calculated as the proportion of plots in which the species was present. This means that only one evenness value could be calculated for the invaded plots, and one value for the uninvaded plots, for which no statistical difference test

was employed. In contrast, for each subplot, we calculated the Shannon–Wiener index:

$$H_j = - \sum_{i=1}^n \frac{N_{i,j}}{N_{Tot,j}} \ln \frac{N_{i,j}}{N_{Tot,j}}$$

In which H is the Shannon–Wiener index for subplot j , $N_{i,j}$ is the % cover of species i in plot j , and $N_{Tot,j}$ is the total cover of subplot j (which can be higher or lower than 100%). We tested for differences in evenness using a linear mixed-effects model, with land cover type and degree of *A. leptopus* invasion as fixed effects, and location (i.e. a pair of an invaded and an uninvaded plot) as a random effect. Differences in evenness between invaded and uninvaded plots were calculated for both the urban and semi-natural land cover types. These analyses, as well as all other analyses performed in this study, were carried out in MATLAB (v. 9.6, Mathworks, 2019), making use of functions implemented in the Mapping and the Statistics and Machine Learning toolboxes.

Subsequently, we analyzed the impacts of *A. leptopus* invasion on the structure of recipient plant communities. We used the abundance of *A. leptopus* in 2 m by 2 m subplots as an indicator of invasion stage, and assessed whether invasion stage correlated with species richness in both the subplots and full plots. Following Bradley et al. (2019), we tested whether the recipient plant community richness was better described by a linear per capita effect of *A. leptopus* or a non-linear per capita effect. A non-linear per capita effect would suggest density-dependent impacts, which may depend on the invasive species exceeding a critical abundance threshold, for example (Thiele et al. 2010; Bradley et al. 2019; Michaels et al. 2020). Specifically, we fitted both linear and a non-linear regression models and tested significance of (non-)linear model terms using the confidence intervals of the regression coefficients.

Community similarity between invaded and uninvaded plots

To test our second hypothesis, we assessed similarities between plant communities using the presence-absence data of the species observed in both the full plots and the subplots. The high dimensionality of these data was reduced through non-metric Multi-Dimensional Scaling (nMDS). The nMDS procedure extracts

a limited number of axes that explain variation between observations without making distributional assumptions, and is widely used in analyses of plant community similarity (e.g. Hedman et al. 2000; McCune and Grace 2002; Pucko et al. 2011). We compared the community similarity between invaded and uninvaded plots, and examined how this comparison depended on land cover type. We limited the analyses to two nMDS axes, because this provided reliable fits with stress values < 0.2 (Clarke 1993; Pucko et al. 2011; Barfknecht et al. 2020). Stress values are used to assess the goodness-of-fit of the ordination, quantifying the degree of mismatch between the (rank-ordered) multi-variate distance between plots and their relative distance in the two-dimensional ordination space (Pucko et al. 2011). For each group of plots, we calculated the convex hull, i.e. the polygon formed by all observations of the group in community composition space, as a measure describing the variation of community composition within that group and its overlap with other plot groups (Villéger et al. 2008).

Assessing change in the structure of recipient plant communities

To test our third hypothesis, we examined whether *A. leptopus* invasion was associated with the disassembly of species in recipient plant communities by analyzing how species co-occurrence patterns differed between invaded and uninvaded plots (Sanders et al. 2003; Santoro et al. 2012; de Miguel et al. 2016). For this analysis, we used observations at the full plot scale. Specifically, we quantified for each species pair the degree of co-occurrence through the standardized C-score (Stone and Roberts 1990; Gotelli and Ulrich 2010):

$$C_{pq} = \frac{(k_p - K)(k_q - K)}{k_p k_q}$$

In which C_{pq} indicates the standardized C-score for the pair formed by species p and species q , and K is the number of plots in which these two species co-occur. The parameters k_p and k_q indicate the number of occurrences of species p and species q , respectively. The standardized C-score varies between 0 and 1, where 0 indicates that one species' occurrence completely overlaps with the other species' occurrence (k_p

and/or k_q equals K) and 1 indicates no overlap in occurrence (K equals zero). The C-score of a community is then given by the average C-score of the $n(n-1)/2$ species pairs in the n species community. Subsequently, a randomization test can be used to derive the probability of observing a particular C-score under the null hypothesis of random community assembly (Gotelli 2000; Gotelli and Ulrich 2010). Specifically, after calculating C-scores for multiple randomizations of the co-occurrence matrix, it is possible to calculate a Standardized Effect Size (SES, e.g. Gotelli and Rohde 2002; Sanders et al. 2003; Ulrich and Gotelli 2010):

$$SES_{pq} = \frac{C_{pq,obs} - \bar{C}_{pq,sim}}{\sigma_{pq,sim}}$$

In which SES_{pq} is the standardized effect size for the standardized C-score of the pair formed by species p and species q , $C_{pq,obs}$ is the standardized C-score as described above, $\bar{C}_{pq,sim}$ is the average corresponding C-score of the replicate (randomized) simulations, and $\sigma_{pq,sim}$ is the standard deviation of these replicate C-scores. Principles of a single sample t-test can then be used to test the null hypothesis that the SES does not differ from 0 (e.g. Gotelli and Rohde 2002; Sanders et al. 2003). Specifically, SESs larger than 2 indicate significant segregation of plant species, and SESs smaller than -2 indicate significant aggregation of plant species. Values in between -2 and 2 then indicate a species co-occurrence pattern that does not differ from randomly assembled communities (Sanders et al. 2003; Ulrich and Gotelli 2010). For this analysis, we selected the subset of species (besides *A. leptopus*) that occurred at least 5 times in the dataset ($n = 46$ species, $n_{\text{native}} = 37$, $n_{\text{non-native}} = 6$, $n_{\text{undetermined}} = 3$). Although the dominance of *A. leptopus* was used to distinguish invaded plots from uninvaded plots, the species itself was not used in the C-score analysis quantifying community structure in these plots (following Sanders et al. 2003).

The species co-occurrence matrix was randomized through sequentially swapping the elements of two-by-two submatrices of the form $\begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$, yielding a matrix of the form $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$, or vice versa (Gotelli and Entsminger 2001; Gotelli and Rohde 2002; Ulrich 2004; Gotelli and Ulrich 2010). The row and column

indices of the first submatrix element and either the row or the column index of the second and third submatrix elements were randomly selected. Through this procedure, the species co-occurrence matrix is randomized, while keeping constant the number of species in each plot, and the total number of occurrences of each species in the dataset. First, 30,000 submatrices were selected and its elements swapped (Lehsten and Harmand 2006), after which each randomized matrix used in the analysis was created by a fixed number of additional swaps (following Gotelli and Ulrich 2010). In this study, we used 3,000 additional swaps for each randomized matrix, generating 2,000 randomized co-occurrence matrices in total for each of the analyses described above.

Native and non-native species responses to *A. leptopus* invasion

To test our fourth hypothesis, we used the species presence data from all full plots (including the occurrence data of *A. leptopus*), and calculated C-scores and SESs as described above. Subsequently, we compared the SESs of *A. leptopus*—native species pairs and *A. leptopus*—non-native species pairs. Because the SESs of native and non-native species pairs and *A. leptopus* were sufficiently normally distributed (verified with Jarque–Bera tests: native species: $JB = 1.28$, $p = 0.37$; non-native species: $JB = 0.70$, $p = 0.33$), and variances in SES were similar for both groups (verified with a Bartlett test: $X_1^2 = 0.009$, $p = 0.93$), we compared the difference between the native and non-native species groups using a two-sample t-test. Similar to the community-level C-score analysis, we selected the subset of species that occurred at least 5 times in the full plots for the pairwise analysis. In this analysis, negative SESs reflect a tendency to co-occur with *A. leptopus*, while positive SESs reflect a tendency to occur separately from *A. leptopus*.

Results

Impact on species richness and evenness

In the field survey, 181 different plant species were encountered, of which 106 species were native species, and 27 species were (likely) non-native

species. Of the remaining species observations, many comprised observations of small seedlings; 18 of these species were identified at the genus level, nine at the sub-family level, and 13 at the family level. For the remaining eight species, only a more general description could be established. For these species, the native/non-native status remained undetermined. Species richness was 39% lower in plots invaded by *A. leptopus* (Fig. 2a; generalized linear mixed-effects model: $N_{\text{Uninvaded}} = 25.9$ species, $N_{\text{Invaded}} = 15.8$ species, $t_{30} = -4.69$, $p = 5.5 \cdot 10^{-5}$). The impact of *A. leptopus* on species richness was similar in areas with semi-natural and urban land cover (Fig. 2a; urban =

39% lower, semi-natural = 39% lower, $t_{30} = 0.57$, $p = 0.57$). A similar trend was found for the smaller subplots, where species richness was 51% lower in plots invaded by *A. leptopus* (Fig. 2b; generalized linear mixed-effects model: $N_{\text{Uninvaded}} = 10.3$ species, $N_{\text{Invaded}} = 5.1$ species, $t_{24} = -4.69$, $p = 9.1 \cdot 10^{-5}$). This impact of *A. leptopus* on species richness in subplots was higher in areas with urban land cover than in areas with semi-natural land cover (Fig. 2b; generalized linear mixed-effects model: urban = 66% lower, semi-natural = 34% lower, $t_{24} = 2.22$, $p = 0.036$). In line with this observation, plots invaded by *A. leptopus* had lower species evenness than

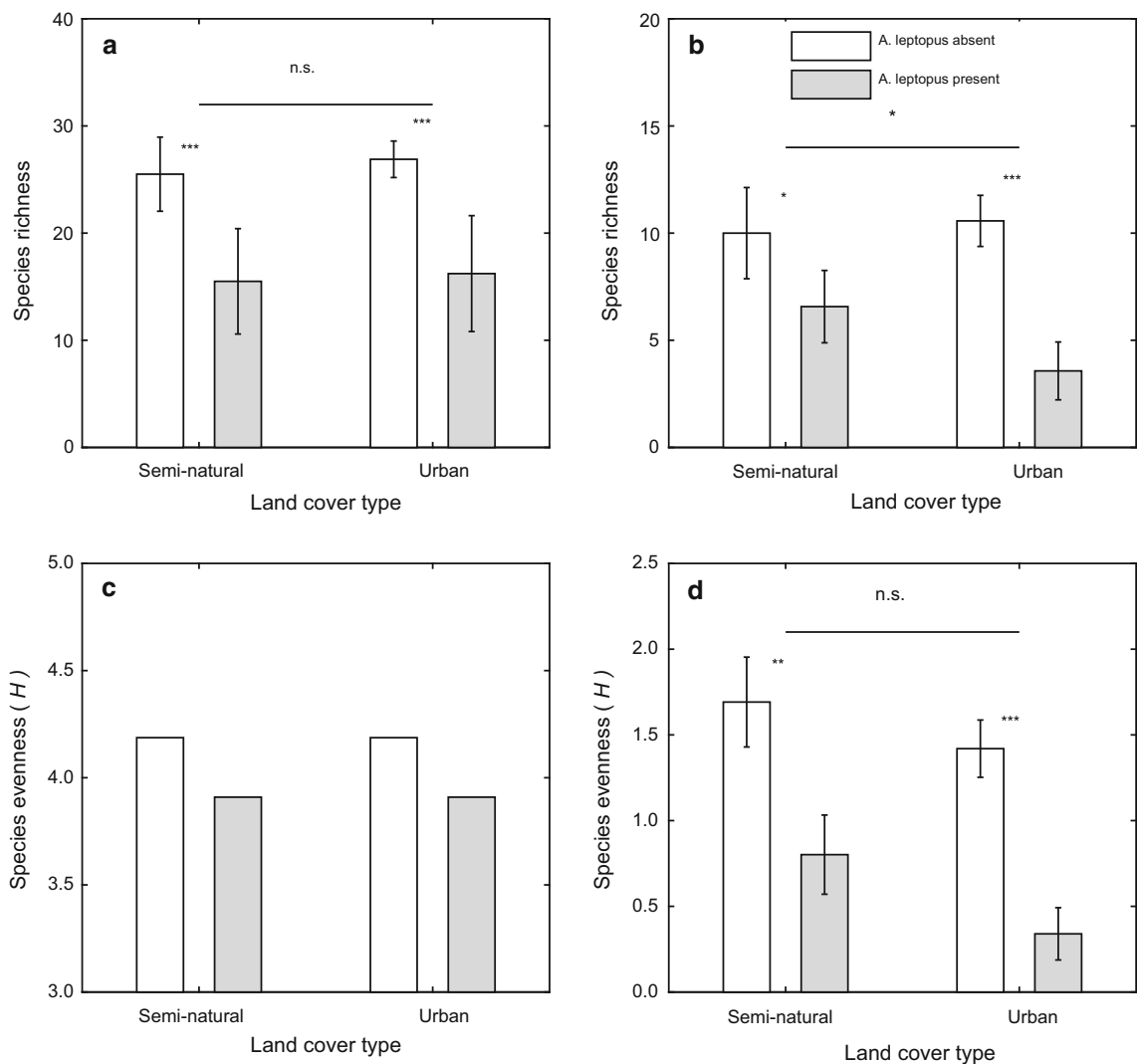


Fig. 2 The impact of invasion by *A. leptopus* on species richness and evenness in 10 m by 10 m plots (left) and in 2 m by 2 m subplots (right). Asterisks indicate significant differences: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; n.s.: not significant

uninvaded plots (Fig. 2c, Fig. 2d; linear mixed-effects model for subplots: $H_{\text{Uninvaded}} = 1.56$, $H_{\text{Invaded}} = 0.57$, $t_{24} = -3.95$, $p = 0.0006$). Species evenness was similar in subplots with semi-natural and urban landcover (Fig. 2d; linear mixed-effects model $t_{24} = -1.00$, $p = 0.33$), and also the impact of *A. leptopus* invasion on species evenness was similar in subplots of both land cover types (Fig. 2d; linear mixed-effects model for subplots: Land cover type * Invasion interaction effect: $t_{24} = -0.60$, $p = 0.56$).

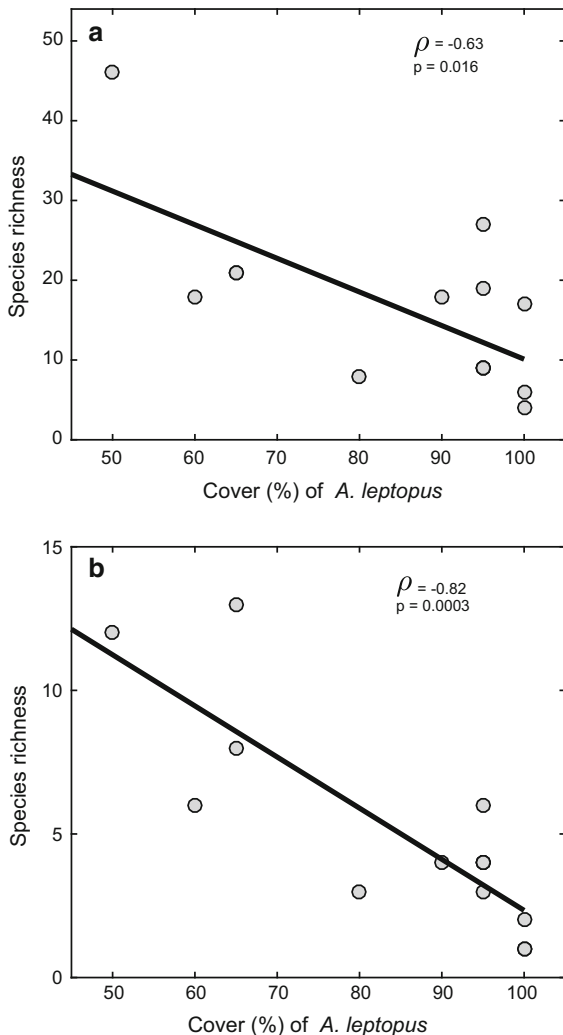


Fig. 3 Species richness decline with increasing abundance of *A. leptopus* (in % cover) in 10 m by 10 m plots (top) and in 2 m by 2 m subplots (bottom). Results of Spearman rank correlation tests are shown in the upper right corner of each plot. Trend lines indicate linear least squares fits

Using the cover of *A. leptopus* in the subplot as an indicator for invasion stage, we found that species richness of the full plots (Fig. 3a) and subplots (Fig. 3b) declined with increasing dominance of *A. leptopus* (Spearman rank correlations: full plots: $\rho_{12} = -0.63$, $p = 0.016$; subplots: $\rho_{12} = -0.82$, $p = 0.0003$). The trends in the data suggested that the impacts on species richness increased linearly with *A. leptopus* cover, as non-linear effects were not significant for either the full plot or subplot species richness data (least square model fitting: full plots: partial $R^2 = 0.12$, $p = 0.10$; subplots: partial $R^2 < 0.01$, $p = 0.98$).

Community similarity between invaded and uninvaded plots

Variation in species composition between invaded plots was much smaller than the variation between uninvaded plots (Fig. 4a). As a result, invaded plots covered a much smaller proportion of the community composition space spanned by the two nMDS axes (Fig. 4a). For the 10 m by 10 m semi-natural plots, the area of the convex hull spanned by invaded plots was only 8% of the area spanned by uninvaded plots (Fig. 4a). For the 10 m by 10 m urban plots, the area of the convex hull spanned by invaded plots equaled 19% of the area spanned by uninvaded plots (Fig. 4a). The same pattern was observed for the 2 m by 2 m subplots, in that invaded subplots only spanned a small proportion of the community composition space as compared to the uninvaded subplots (Fig. 4b). In contrast to the full plots, the largest relative difference between invaded and uninvaded plots occurred in the urban plots. More specifically, the area of the convex hull spanned by invaded urban subplots was only 2% of the area spanned by uninvaded urban subplots (Fig. 4b). The area of the convex hull spanned by invaded semi-natural subplots was 16% of the area spanned by uninvaded semi-natural plots (Fig. 4b). Rather than occupying a different part of the community composition space, the convex hulls of invaded urban plots and subplots was fully captured within the convex hull of uninvaded semi-natural plots and subplots (Fig. 4), with the exception of one invaded urban plot and one invaded semi-natural plot, which contained relatively high numbers of species ($n = 27$ and $n = 45$, respectively).

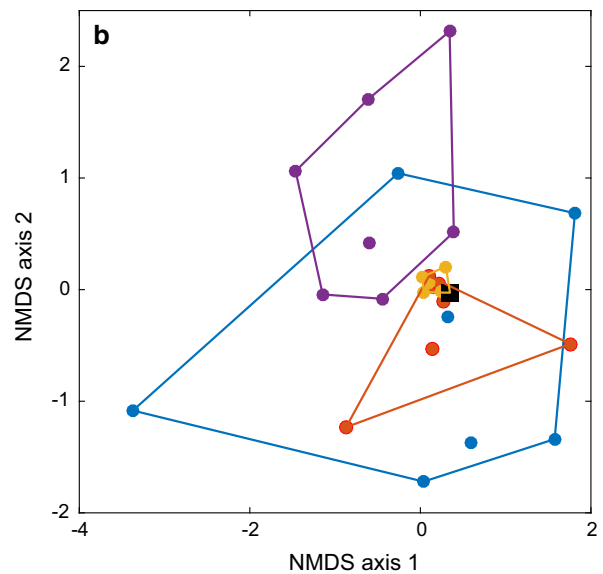
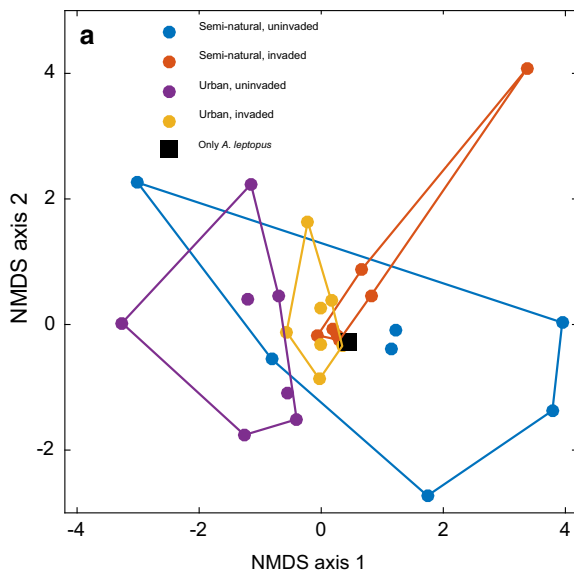


Fig. 4 Ordination of plant community composition in 10 m by 10 m plots (left) and 2 m by 2 m subplots (right), which were either uninvaded or invaded by *A. leptopus*, and within urban or

semi-natural land cover types. In both panels, a monoculture of *A. leptopus* is indicated with a black square

Assessing change in the structure of recipient plant communities

Species co-occurrence patterns suggested that uninvaded communities were characterized by species segregation, as species tended to co-occur less frequently than what would be expected from random co-occurrence of plant species (Standardized Effect Size (SES) > 2; Fig. 5). In contrast, species co-occurrence patterns in invaded plots were within the range that would be expected based on random co-occurrence of plant species ($\text{abs}(\text{SES}) < 2$; Fig. 5). Hence, these invaded plant communities exhibited random co-occurrence patterns, meaning that there were no patterns consistent with either species aggregation or segregation.

Native and non-native species responses to *A. leptopus* invasion

There were 37 native species and six non-native species (besides *A. leptopus*) that appeared in five or more of the full plots studied. Three species, belonging to the genera *Cyperus*, *Desmanthus* and *Galactica*, also appeared in more than five plots, but could not be determined at the species level, meaning that their status (i.e. native or non-native) could not be

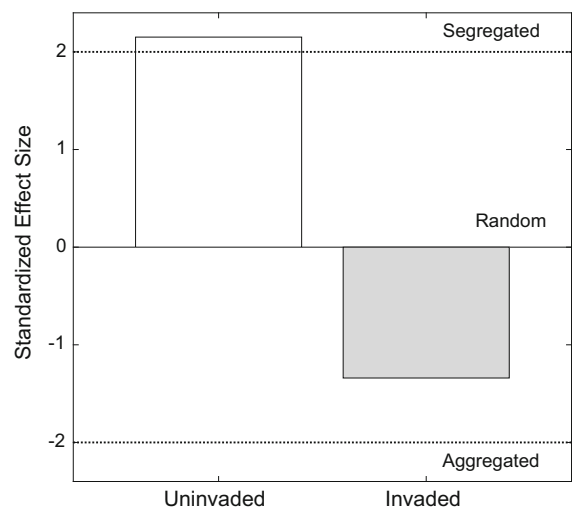


Fig. 5 Standardized effect sizes of plant community structure in plots invaded by *A. leptopus* and in uninvaded plots, as compared to randomly structured communities. The dotted lines indicate the + 2 and -2 standard deviations levels separating random co-occurrence patterns from segregated and aggregated patterns, respectively.

determined either (Table 1). Considering the former two groups of plant species, there was no difference between native and non-native species regarding their tendency to co-occur with *A. leptopus* (two-sample t-test, $\text{SES}_{\text{native}} = 2.11$, $\text{SES}_{\text{non-native}} = 1.29$,

Table 1 Frequency of occurrence of plant species in plots uninvaded and invaded by *A*

Species name	Status (native or non-native)	Occurrence in uninvaded plots (n = 17)	Occurrence in invaded plots (n = 17)	SES
<i>Cuscuta americana</i>	Native	7	0	4.3025
<i>Desmodium triflorum</i>	Native	9	2	4.1286
<i>Vachellia macracantha</i>	Native	12	5	4.0901
<i>Rauvolfia viridis</i>	Native	14	7	4.0567
<i>Pisonia subcordata</i>	Native	6	0	3.8395
<i>Stylosanthes hamata</i>	Native	9	3	3.4905
<i>Senna bicapsularis</i>	Native	8	2	3.451
<i>Quadrella cynophallophora</i>	Native	5	0	3.4423
<i>Physalis pubescens</i>	Native	5	0	3.325
<i>Desmodium cf. tortuosum</i>	Native	8	3	3.0645
<i>Sida glomerata</i>	Native	10	5	2.884
<i>Phyllanthus amarus</i>	Native	5	1	2.6219
<i>Opuntia triacanthos</i>	Native	5	1	2.6154
<i>Ruellia tuberosa</i>	Native	5	1	2.5916
<i>Catharanthus rosea</i>	Non-native	6	2	2.5081
<i>Dactyloctenium aegyptium</i>	Non-native	8	4	2.4049
<i>Melochia tomentosa</i>	Native	4	1	2.2061
<i>Antheaphora hermaphroditica</i>	Native	4	1	2.1587
<i>Vachellia tortuosa</i>	Native	4	1	2.1134
<i>Citharexylum spinosum</i>	Native	4	1	2.0972
<i>Pentalinon luteum</i>	Native	4	1	2.0797
<i>Azadirachta indica</i>	Non-native	5	2	2.079
<i>Solanum bahamense</i>	Native	11	8	2.0503
<i>Justicia sessilis</i>	Native	5	2	2.0014
<i>Randia aculeata</i>	Native	7	4	1.9807
<i>Lantana involucrata</i>	Native	6	3	1.9774
<i>Spermacoce remota</i>	Native	11	9	1.6201
<i>Leucaena leucocephala</i>	Non-native	8	6	1.5646
<i>Volkameria aculeata</i>	Native	4	2	1.5589
<i>Heteropterys purpurea</i>	Native	5	3	1.5261
<i>Corchorus aestuans</i>	Native	4	2	1.4791
<i>Stigmaphyllon emarginatum</i>	Native	4	2	1.4675
<i>Sida cordifolia</i>	Native	9	8	1.1158
<i>Commelina erecta</i>	Native	5	4	1.0684
<i>Galactica</i> sp.	Undetermined	4	3	1.0371
<i>Waltheria indica</i>	Native	6	5	1.0014
<i>Heliotropium angiospermum</i>	Native	4	3	0.9919
<i>Melochia pyramidata</i>	Native	4	3	0.9673
<i>Cyperus</i> sp.	Undetermined	9	11	-0.016

Table 1 continued

Species name	Status (native or non-native)	Occurrence in uninvaded plots (n = 17)	Occurrence in invaded plots (n = 17)	SES
<i>Desmanthus</i> sp.	Undetermined	2	3	−0.0478
<i>Annona muricata</i>	Native	2	3	−0.0599
<i>Lippia alba</i>	Native	2	3	−0.0948
<i>Centrosema virginianum</i>	Native	6	8	−0.1021
<i>Abrus precatorius</i>	Non-native	2	4	−0.4915
<i>Bothriochloa pertusa</i>	Non-native	13	16	−0.836
<i>Jatropha gossypifolia</i>	Native	14	17	−1.2713

leptopus on St. Eustatius, northern Caribbean. From the co-occurrence patterns of each species with *A. leptopus*, pairwise Standardized Effects Scores (SES) are calculated. SES scores below −2 indicate that co-occurrence with *A. leptopus* is more likely than expected from random occurrence. SES scores above 2 indicate that co-occurrence is less likely than expected from random co-occurrence. The table lists the subset of 43 species (besides *A. leptopus*) that occurred at least five times in the surveyed plots. Bold values indicate species that showed significant segregation from *A. leptopus*

$t_{41} = 1.38$, $p = 0.17$). Of the species that occurred at least five times in the dataset, 52% had a significantly positive C-score, reflecting a reduced occurrence in *A. leptopus*-invaded plots. This group consisted of 21 native species and three non-native species (Table 1). In contrast, none of the species had a significantly negative C-score, which would reflect an increased occurrence in invaded plots. The group of eight species that did have a negative (yet not significant) C-score consisted of four native species (*Jatropha gossypifolia*, *Centrosema virginianum*, *Lippia alba* and *Annona muricata*, Table 1), two non-native species (*Bothriochloa pertusa* and *Abrus precatorius*, Table 1), as well as the *Cyperus* and *Desmanthus* spp. mentioned above (Table 1).

Discussion

There is an urgent need to increase our understanding of the impacts of non-native plant invasions on the relatively high and unique biodiversity of (sub-)tropical islands, as these systems are particularly susceptible to plant invasions (Kueffer et al. 2010; Essl et al. 2019). In these systems, invasive vines form a particular risk given their potential to modify environmental conditions and exert strong effects on recipient plant communities (Gordon 1998; Harris et al. 2007; Bray et al. 2017; Gordon et al. 2017). Although *A. leptopus* is a prominent example of a vine

that has successfully invaded (sub-)tropical islands around the globe, its impacts on recipient plant communities have not yet been systematically quantified. In this study, we systematically assessed the impact of *A. leptopus* on species richness, community homogenization, community disassembly and species-specific responses to invasion.

Corroborating our first hypothesis, there was a linear decline in species richness with increasing cover of *A. leptopus*, yielding levels of species richness that were 40%-50% lower than observed in uninvaded paired plots. This potential impact of *A. leptopus* on species richness is similar to the impacts observed for the most successful non-native wetland invaders in central Europe (Hejda et al. 2009), and is considerably higher than the average impact on species richness of primary producers in terrestrial habitats (16%) as obtained from meta-analysis (Mollot et al. 2017). Indeed, many non-native plant species seem to have smaller impacts on recipient plant communities, as observations of non-native and native species richness also include weakly negative or even positive relationships (Seabloom et al. 2013; Martin-Forés et al. 2016, 2017), even at the relatively small plot scales considered in this study (Peng et al. 2019). Furthermore, at the smaller subplot scale, impacts were more negative and stronger in areas with urban land cover than in areas with semi-natural land cover. Although these latter findings corroborated with previous findings of invasive species impacts in semi-natural and

urban landscapes (González-Moreno et al. 2017; Gutiérrez-Cánovas et al. 2020), it should be noted that in these previous studies the semi-natural and urban habitats comprised a disturbance gradient within the same type of (coastal) ecosystem. In our current study, two levels of disturbance were considered, with the difference corresponding to a change from forest communities in semi-natural landscapes to grasslands in urban landscapes. Hence, we could not disentangle the effects of differential biotic resistance of grassland-dominated and forest-dominated landscapes, and the degree of disturbance, for example. Future studies could also sample disturbance gradients within each type of land cover, in order to assess the interaction between *A. leptopus* invasion and disturbance in further detail (González-Moreno et al. 2017; Gutiérrez-Cánovas et al. 2020).

The results also corroborated our second hypothesis, suggesting that *A. leptopus* invasion homogenizes recipient plant communities. Observing biotic homogenization at the relatively small spatial scales examined suggests that the focal invasive species is a strong competitor that reduces community diversity and complexity (Lambdon et al. 2008). We did not find evidence for *A. leptopus* driving a turnover in plant community composition, as the composition of invaded plots occupied a subset of the community space spanned by uninvaded plots. Community turnover could be the result of an ‘invasional meltdown’ process, where the successful invasion of one species triggers subsequent invasions (Simberloff and Von Holle 1999; Simberloff 2006). The lack of turnover is again consistent with *A. leptopus* being a strong competitor, which may also limit the establishment of other non-native plant species and thereby reduce the potential for invasional meltdown (Rauschert and Shea 2017).

Consistent with our third hypothesis, we found evidence for species segregation in uninvaded plots, pointing to the competitive interactions expected in benign environments (Maestre et al. 2009; Santoro et al. 2012; de Miguel et al. 2016). In contrast, co-occurrence patterns in invaded plots were not significantly different from expectations based on random co-occurrence. This change toward less segregation may be explained by species’ persistence being limited to the invasion stages where *A. leptopus* is not yet fully dominant. The resulting co-occurrence patterns in invaded plots suggest that *A. leptopus*

invasion is associated with the disassembly of recipient plant communities. Our results suggest that the order of species loss due to invasion may be driven by stochastic processes, as most species exhibited reduced occurrence in plots invaded by *A. leptopus*, while none exhibited significant increases in occurrence. This latter observation is inconsistent with our fourth hypothesis, which stated that other non-native species may be better able to coexist with *A. leptopus* (Stotz et al. 2020). It should be noted, however, that the relatively small number of non-native species included in our test of this hypothesis offered limited power, and hence hampered generalization of our findings into broader conclusions about native and non-native species responses to *A. leptopus* invasion. This type of community disassembly can emerge as a result of altered interactions between species (Sanders et al. 2003), or as a result of these interactions becoming a less important driver of community dynamics when superseded by the impacts of the successful invasive species (e.g. Chen et al. 2020). Together with the other lines of results presented above, our findings point to the latter mechanism in the case of *A. leptopus*’ invasion on St. Eustatius. More specifically, our results suggest that *A. leptopus* invasion leads to local exclusion of plant species. Furthermore, our results are consistent with *A. leptopus* being a superior competitor, exerting similarly negative effects on all species within recipient plant communities, and potentially leaving few opportunities for other (non-native) species to establish. While we did not study the specific mechanisms driving the competition between *A. leptopus* and other plant species, previous research suggests that both below-ground competition (for water and soil nutrients, Dillenburg et al. 1993; Meunier et al. 2021) and aboveground competition (for light, Paul and Yavitt 2011; Meunier et al. 2021) may be important to consider when studying these competitive interactions between vines and recipient plant communities.

The fieldwork for this study was carried out at one period in time, providing a snapshot of recipient plant community diversity and structure. Although the paired-plot design aims to maximize the comparability of uninvaded and invaded plots (e.g. Vilà et al. 2006; Castro-Díez et al. 2016), the retrospective nature of the analysis makes it impossible to fully attribute differences within plot pairs to the invasion of the focal species of interest (e.g. Sanders et al. 2003). Although

inferred levels of species richness in invaded plots with relatively low *A. leptopus* cover were similar to those observed in uninvaded plots (Figs. 2, 3), previous studies have also suggested that *A. leptopus* may need some form of disturbance to gain a foothold in recipient plant communities (Ernst and Ketner 2007). However, once established, *A. leptopus* may drive additional plant community processes that exacerbate the initial disturbance, in line with the idea of invasive species acting as “back-seat drivers” of ecosystem change (Bauer 2012). The uninvaded plots described in this study contribute to other recent observations describing pre-invasion conditions on St. Eustatius (e.g. Van Andel et al. 2016; Madden et al. 2019), which may provide valuable reference data in the future that allow for a more direct assessment of the consequences of invasion using a longitudinal design.

In this study, we took a taxonomic perspective on quantifying plant community diversity and structure. Recent research has proposed various ways to use plant functional traits to link taxonomic diversity to ecosystem structure and functioning (Mayfield et al. 2005; Villéger et al. 2008; Laliberté and Legendre 2010; Van Kleunen et al. 2010; Drenovsky et al. 2012; Laliberté and Tylianakis 2012; Molinari and D’Antonio 2014; Castro-Díez et al. 2016). Plant functional trait diversity is not necessarily related to taxonomic diversity, as plant communities may vary in the degree of functional redundancy (Mayfield et al. 2005; Funk et al. 2017; Gutiérrez-Cánovas et al. 2020). Analyses of changes in plant functional diversity could highlight which specific ecosystem functions may be affected by *A. leptopus* invasion (cf. Molinari and D’Antonio 2014). Such consequences of plant invasions on ecosystem functioning and the provisioning of ecosystem services are an important concern (Tordoni et al. 2019; Milanović et al. 2020). Although recent research has attempted to assess the functional implications of *A. leptopus* invasion in the Caribbean using a trait-based approach, current gaps in species trait data availability need to be filled in order to answer this question confidently (Sweeney 2018). Given the unique evolutionary history of the Caribbean, a phylogenetic approach would provide another valuable and complementary perspective (Veron et al. 2017). More specifically, such a perspective could provide a link between reductions in recipient plant community richness, and the extent to which this reduction leads to a loss in both phylogenetic diversity

and evolutionary distinctiveness within invaded areas (Jucker et al. 2013; Veron et al. 2017). The latter component of biodiversity is particularly relevant for setting conservation priorities (Lehtomäki et al. 2019).

Projected environmental changes in the Caribbean region, such as the increased frequency of strong hurricanes (Knutson et al. 2015; Eppinga and Pucko 2018), may fundamentally alter disturbance regimes of Caribbean ecosystems. Alterations of disturbance regimes may affect the frequency of non-native species introductions, and alter competitive interactions between native and non-native species already present (White et al. 2006). In general, invasive species are often capable of exploiting ecosystem disturbances as a means to gain competitive advantage over native species (Moles et al. 2008; Van Kleunen et al. 2010; Jauni et al. 2015). Similar behavior has been attributed to *A. leptopus* (Ernst and Ketner 2007; Vandebroek et al. 2018; Heger and Van Andel 2019; Eppinga et al. 2021; Haber et al. 2021). Here we showed how *A. leptopus* invasion is associated with substantial changes in recipient plant community diversity and structure. Combining multiple lines of observation, we conclude that the impacts of *A. leptopus* are consistent with those of a strong competitor that exerts strong negative effects on most species of the recipient plant community. Locally, these negative effects may induce a stochastic exclusion process that leads to more homogenized subsets of pre-invasion communities, which is reflected in random co-occurrence patterns. These results highlight the need to develop monitoring programs to study the relationship between initial disturbances, invasion by *A. leptopus* and subsequent impacts of the invasion on ecosystem functioning. Such monitoring programs may aid in articulating the need to develop management strategies that prevent or limit the expansion and impacts of invasive species and maintain the unique biodiversity within Caribbean ecosystems (Mauder et al. 2008; Banda et al. 2016; Debrot et al. 2018; Rojas-Sandoval and Ackerman 2020).

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Availability of data and material Source data underlying this manuscript can be accessed from the Yoda Data Repository of Utrecht University at <https://doi.org/10.24416/UU01-S9NW62>

Code availability Matlab code written to perform the described analyses are available from the corresponding author upon reasonable request.

Declarations

Conflicts of interest The authors have no relevant financial or non-financial interests to disclose.

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