

# Assessing the impact of *Antigonon leptopus* on Saba and St. Eustatius



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## Abstract

The spread of invasive species globally has had acknowledged impacts on species extinction, biodiversity and ecosystem services. Gauging the type and magnitude of impacts from invasive species is an important consideration in the allocation of resources towards the prevention of their spread, management and efforts towards elimination. The focus of this research was the assessment of the impacts of the invasive species Coralita (*Antigonon leptopus*) on the islands of Saba and St. Eustatius in the Dutch Caribbean. Although there was anecdotal information about its impacts available from prior studies, specific information was lacking. Whereas experimental or observational research would typically be used to assess impacts of this nature, this research attempted to identify impacts more remotely, based upon the application of a dual methodological approach. As such, whilst the main aim was to assess impacts of Coralita, the primary concern was the acquisition of information in order to make such an assessment.

Two complementary methodological frameworks were loosely applied to help guide the analytical approach. The first, the Environmental Impact Classification of Alien Taxa (EICAT), adopted by the IUCN to standardise invasive species impacts, was used to help focus the research on species and community level impacts. The analytical approaches associated with this methodology included an investigation of impacts associated with biodiversity richness, competitive exclusion and changes in species types over time and an approach to transfer the types of impacts noted for comparable species to the Coralita on the islands. The other approach was instead focussed on species characteristics (traits) and the impact that Coralita may have had on community averages, which could then be potentially linked to ecosystem function/services based on generalised relationships observed from research literature. Although these approaches were carried out separately, they were complementary, with findings from the EICAT methodology used to support those from the trait-based methodology and vice versa. Analysis included statistical testing and principal component analysis.

Overall, the impact of Coralita on individual species and communities was classed as moderate in terms of the EICAT classification level (i.e. 3 out of 5). This reflected potential impacts on biodiversity, likely impacts as a result of comparison with other invasive species and some limited evidence of competitive exclusion through analysis of co-occurrence. Trait-based evidence appears to show that Coralita has more in common with other invasive species than island species, and as such is likely to impact the structure of communities where it is found by changing average trait values. On the contrary, analysis associated with traits and levels of abundance used for this study suggest that Coralita is not having a substantial impact in the areas that it is found, at least based on the areas covered by this analysis. These somewhat conflicting findings, together with a lack of certainty in relation to these findings more generally, means that further research would be recommended to build sufficient confidence that Coralita is having a major impact. In particular, research into the implications of Coralita extent in more urban areas, where disturbance is a key driver of Coralita spread, is recommended in this regard.

Cover image Jetske Vaas, The Coralita Girls (<https://www.facebook.com/CoralitaGirls/>)

# Contents

|  |    |
|--|----|
| Abstract.....  | II |
| List of Figures and Tables .....                         | V  |
| Figures.....   | V  |
| Tables .....   | VI |
| Introduction.....  | 1  |
| The challenge of invasive species .....                  | 1  |
| The islands .....  | 5  |
| Coralita .....   | 10 |
| Research aims and design .....                           | 14 |
| Research questions .....                                 | 17 |
| Conceptual Framework.....                                | 18 |
| Theoretical Background.....                              | 18 |
| Assessing Impacts.....                                   | 18 |
| Species loss and biodiversity .....                      | 20 |
| Ecosystem services and trait values .....                | 21 |
| Methodological Framework .....                           | 26 |
| EICAT.....   | 26 |
| Species trait values.....                                | 30 |
| Methodology.....   | 32 |
| EICAT Assessment.....                                    | 33 |
| Review of comparable species impacts .....               | 33 |
| Biodiversity richness.....                               | 34 |
| Changes in species compositions .....                    | 38 |
| Trait-based analysis.....                                | 38 |
| Coralita and island species trait values.....            | 43 |
| Community weighted means.....                            | 44 |
| Coralita and other invasive species trait values .....   | 44 |
| Results.....   | 46 |
| EICAT assessment .....                                   | 46 |
| Comparable species impacts .....                         | 46 |
| Biodiversity richness.....                               | 50 |
| Species composition: change over time .....              | 51 |
| Species composition: co-occurrence.....                  | 52 |
| EICAT classification.....                                | 55 |
| Trait-based analysis.....                                | 56 |
| Coralita and island species trait values.....            | 56 |
| Community weighted means.....                            | 71 |
| Coralita and other invasive species by trait values..... | 74 |
| Discussion and conclusion .....                          | 84 |

|                       |     |
|-----------------------|-----|
| References.....       | 91  |
| Acknowledgements..... | 108 |
| TRY data.....         | 109 |
| Appendices.....       | 110 |

## List of Figures and Tables

### Figures

|   |    |
|---|----|
| <i>Figure 1:</i> Stage in species invasiveness and the barriers between each stage.....   | 3  |
| <i>Figure 2:</i> Map of the Dutch Caribbean Islands .....   | 6  |
| <i>Figure 3:</i> Historical and projected average annual temperature anomaly for the proximate region.....  | 7  |
| <i>Figure 4:</i> Historical and projected total annual precipitation for the proximate region .....   | 8  |
| <i>Figure 5:</i> Global distribution of Coralita compiled by CABI .....   | 11 |
| <i>Figure 6:</i> Distribution of Coralita on St. Eustatius, 2014.....   | 12 |
| <i>Figure 7:</i> Research design.....   | 16 |
| <i>Figure 8:</i> Ecosystem services as described by the Millennium Ecosystem Assessment .....   | 21 |
| <i>Figure 9:</i> Growth response to typical species in high and low resource environments. ....   | 22 |
| <i>Figure 10:</i> Most commonly reported plant and invertebrate traits and their association with<br>ecosystem service delivery. Thicker arrows denote a larger number of studies .....                           | 24 |
| <i>Figure 11:</i> Functional traits for which evidence has been found linking them to the drivers of change<br>and ecosystem services for vegetation. ....  | 25 |
| <i>Figure 13:</i> A decision tree showing how the EICAT classifications should be applied.....  | 29 |
| <i>Figure 14:</i> Landscape ecological map of St. Eustatius .....   | 36 |
| <i>Figure 15:</i> Landscape ecological map of Saba.....   | 37 |
| <i>Figure 16:</i> Density plots for maximum plant height for data captured via the TRY database and data<br>from other sources .....  | 42 |
| <i>Figure 17:</i> Principal component analysis projections of island individual species on the first two<br>principal components, with groupings of species that co-occur and those that do not co-occur<br>..... | 54 |
| <i>Figure 18:</i> Density distributions of trait values for species noted by de Freitas on Saba and St.<br>Eustatius.....   | 59 |
| <i>Figure 19:</i> Density distributions of trait values for species noted by de Freitas on Saba and St.<br>Eustatius.....   | 60 |
| <i>Figure 20:</i> Density distribution of leaf dry mass per leaf fresh mass for species.....  | 62 |
| <i>Figure 21:</i> Scree plot showing the percentage of explained variances explained by each of the<br>dimensions of the PCA for island species only.....   | 63 |
| <i>Figure 22:</i> Biplot showing the projections of individual species on first two principal components,<br>and the correlation of the variables to the components .....   | 66 |
| <i>Figure 23:</i> Correlations between trait variables for island species. X indicates a non-statistically<br>significant relationship .....  | 68 |

|  |    |
|--|----|
| <i>Figure 24:</i> Principal Component Analysis projections of island individual species on the first two principal components, with groupings of species by location .....   | 69 |
| <i>Figure 25:</i> Scree plot for PCA carried out for islands species traits where trait information for Coralita was not inferred from the average of climbing species across the entire dataset.....  | 70 |
| <i>Figure 26:</i> Principal Component Analysis projections of individual island species on the first two principal components, for those traits for which sources could be found for Coralita .....  | 71 |
| <i>Figure 27:</i> Scree plot for the PCA of traits for the entire dataset.....   | 76 |
| <i>Figure 28:</i> Correlations between trait variables for all dataset species. X indicates a non-statistically significant relationship .....   | 78 |
| <i>Figure 29:</i> Principal component analysis projections of species on the first two principal components, with grouping by species causing an impact on the GISD database and other species .....   | 79 |
| <i>Figure 30:</i> Principal component analysis projections of species on the first two principal components based on traits for which information was available for Coralita, with grouping by species causing an impact on the GISD database and other species..... | 80 |
| <i>Figure 31:</i> Principal component analysis projections of species on the first two principal components, with grouping by species that climb and other species .....   | 82 |
| <i>Figure 32:</i> Principal component analysis projections of species on the first two principal components based on traits for which information was available for Coralita, with grouping by species that climb and other species.....                             | 83 |

## Tables

|  |    |
|--|----|
| <i>Table 1:</i> Impact outcomes from the GISD database.....  | 19 |
| <i>Table 2:</i> Summary of methodology used in the research .....  | 32 |
| <i>Table 3:</i> Traits specifically requested from the TRY database, based on literature review .....  | 39 |
| <i>Table 4:</i> Data coverage for species requested from the TRY database and final data availability for analysis.....  | 41 |
| <i>Table 5:</i> Average trait values for Coralita, sources for values, and where sources could be found, corresponding P values for T-score tests regarding the relationship between Coralita trait values and corresponding sample trait values for climbing species .....                      | 43 |
| <i>Table 6:</i> Number of plant species listed on the IUCN GISD database as having an impact of some type by impact outcome, and the p-value results from a pair-wise comparison of species numbers having impacts for climbing species and non-climbing species, using Bernard's test..         | 47 |
| <i>Table 7:</i> Number of plant species listed on the IUCN GISD database as having at least one mechanism of impact by mechanism, and the p-value results from a pair-wise comparison of species numbers having impacts for climbing species and non-climbing species, using Bernard's test..... | 48 |
| <i>Table 8:</i> Impact outcomes and impact mechanisms for the GISD species listed as having an impact on the GISD database, with data from the CABI invasive species compendium .....  | 49 |
| <i>Table 9:</i> Number of species identified by de Freitas et al. (2012,2016) in each vegetation area on Saba and St. Eustatius.....   | 50 |

|   |    |
|---|----|
| <i>Table 10:</i> Summary of species numbers and comparison with species types listed by de Freitas (2012 and 2016), from Boldingh (1909), Stoffers (1956) and van Andel et al. (2016). .....  | 51 |
| <i>Table 11:</i> Species that do not co-occur with Coralita, but do occur with different species that do co-occur. List are the species that co-occur with the most number of species that also co-occur with Coralita. ....  | 53 |
| <i>Table 12:</i> Mean, median, standard error and relative standard error for trait values for Saba, St. Eustatius and both islands. Coralita trait values are shown for comparison, with p values associated with the T-score for Coralita for that trait by location..... | 57 |
| <i>Table 13:</i> P-values associated with Kruskal-Wallis tests on the equivalence of numeric traits for species on both islands, species only found on Saba and species only found on St. Eustatius ..  | 61 |
| <i>Table 14:</i> Eigenvalues and explained variance for the components from a PCA on island species only .....  | 64 |
| <i>Table 15:</i> Contributions of the variables to each of the principal components for the PCA of island species only .....  | 65 |
| <i>Table 16:</i> Calculated p values associated with T-tests on whether the differences in CWMs for traits with and without Coralita on the islands are significantly greater than zero .....   | 72 |
| <i>Table 17:</i> P values from T-tests of the differences between CWMs for areas where Coralita is observed, with and without Coralita .....  | 73 |
| <i>Table 18:</i> P values from T-tests of the differences between CWMs for areas where Coralita is observed, with and without Coralita, with imputed data from the PCA analysis .....   | 74 |
| <i>Table 19:</i> P-values associated with Welch T-tests on the equivalence of traits for species noted on the GISD database as having an impact and other species for which data was gathered .....   | 75 |
| <i>Table 20:</i> Principal component loadings by principal component for the trait variables for the PCA covering the entire dataset.....   | 77 |
| <i>Table 21:</i> P-values from Mann-Whitney-Wilcoxon Tests on the equivalence of traits for species that are climbing vines and other species for which data was gathered .....   | 81 |

# Introduction

## The challenge of invasive species

In 1859, English settler and enthusiastic sportsman Thomas Austin released 24 breeding European rabbits into the wild in Victoria, Australia (Williams, Parer, Coman, Burley, & Braysher, 1995). Roughly 30 years later, Eugene Schieffelin likewise released 160 starlings in New York City's Central Park (Cooke, 1928), as part of an attempt to introduce the birds mentioned by Shakespeare to America (Jernelov, 2017). Both were members of acclimatisation societies, groups that were active around the world at this time that encouraged the release of non-native species to areas recently colonised by Europeans to help with their adaptation. The implications for native wildlife and ecosystems from these (and other) releases have been dire. Rabbits are now one of the most abundant and widely distributed mammals in Australia (Williams et al., 1995) and have fundamentally altered ecosystems, with, for example, impacts on fire regimes and vegetation composition (Reddiex & Forsyth, 2006). The annual costs of rabbit control in Australia were estimated to be AUS\$60 to 70 million in 2009 (~US\$45 to US\$55 million) (Gong & Invasive Animals Cooperative Research Centre, 2009). In the USA, the economic cost of European starlings in terms of lost crops was estimated to be around US\$800 million per year (Pimentel, Lach, Zuniga, & Morrison, 2000), and although the impacts on native bird species numbers is mixed (Koenig, 2003), starlings have been identified as a possible vector for disease spread amongst wildlife and people (Linz, Homan, Gaulker, Penry, & Bleier, 2007).

As these examples illustrate, the impacts of invasive species can be both dramatic and long lasting. In a recent analysis of IUCN Red List data on species extinctions, Bellard et al. (2016) estimate that the spread of invasive species has been the second most important driver of species extinctions since 1500 (behind biological resource use), and the most important for amphibians, reptiles and mammals. In 2000, the economic costs of invasive species in the USA was estimated to be US\$120 billion per year, based on direct economic costs and costs of control only (Pimentel et al., 2000); in the EU, Kettunen et al. (2009) estimated annual costs to be at least EUR12.5 billion based on economic damages and cost of control of a sub-set of invasive species, with some species, such as *Fallopia japonica* (Japanese knotweed) and rat species together accounting for large cost estimates (EUR2.3 billion and EUR3.4 billion respectively). Conceptually, invasive species are closely linked to their impacts, with some definitions of invasive species specifically including the need for potential or actual impact for a species to be considered as such (see Box 1: Definitions). However, although their impacts are a key component that makes invasive species problematic, their ability to spread, the challenge associated with their management, and the interaction between these three elements are also fundamental aspects to consider. As the impacts of invasive species have become more recognised through improved assessments and the availability of associated datasets (Gurevitch & Padilla, 2004), the focus regarding the prevention of their spread has grown at the international level,

with the Convention on Biodiversity (CBD) and UN Sustainable Development Goals having specific targets addressing this issue. Nevertheless, the rate of introductions has grown substantially over the last 50 years as a result of population growth, trade, land use change and the movement of people (Pimentel et al., 2000). Indeed, it has been argued that species invasions can be considered an externality associated with trade (Perrings, Dehnen-Schmutz, Touza, & Williamson, 2005), with a demonstrable link between increased trade and increased invasive species spread (Westphal, Browne, MacKinnon, & Noble, 2008). Despite continued attention, with for example, a recent International Maritime Organization (IMO) agreement regarding shipping ballast water treatment to reduce species spread coming into force (IMO, 2004), recent research has shown that whilst legislation has probably been effective reducing alien species spread, the rate of change in alien species numbers shows no evidence of saturation (Seebens et al., 2017).

### Box 1: Definitions

There is a lack of consensus in relation to the terminology surrounding invasive species, with terms such as “exotic”, “alien” and “non-native” used interchangeably or defined in differing ways (Colautti & MacIsaac, 2004). This can be problematic, in that inconsistent definitions can lead to confusion, in turn resulting in to the merging of different phenomena (e.g. invasive and alien) and splitting of others, affecting the ability to generalise (Colautti & MacIsaac, 2004). In the definition of “invasive”, whether actual or potential impacts associated with the species are required is one such area where there is a lack of agreement. On the one hand, the Convention on Biodiversity (CBD) cites the need for negative impacts as part of the definition, whereas others, such as Richardson et al. (2000) suggest that the term invasive should be separate from impact and that there are other terms such as “weed” or “pest” that can fulfil this role. As noted by Blackburn et al. (2011), including the requirement for impact within the term invasive is problematic for those species that may have impact but do not become established or for species that appear to have benign impacts. Likewise, it may be that a lack of impact relates to absence of evidence rather than evidence of absence of impact (Blackburn et al., 2011). Although to a certain extent, and in line with Ricciardi et al. (2013), resolving this debate is not fundamentally important to defining and measuring impacts in this research, for clarity, the definitions for the key terms in relation to invasive species are highlighted below, following Richardson et al. (2000):

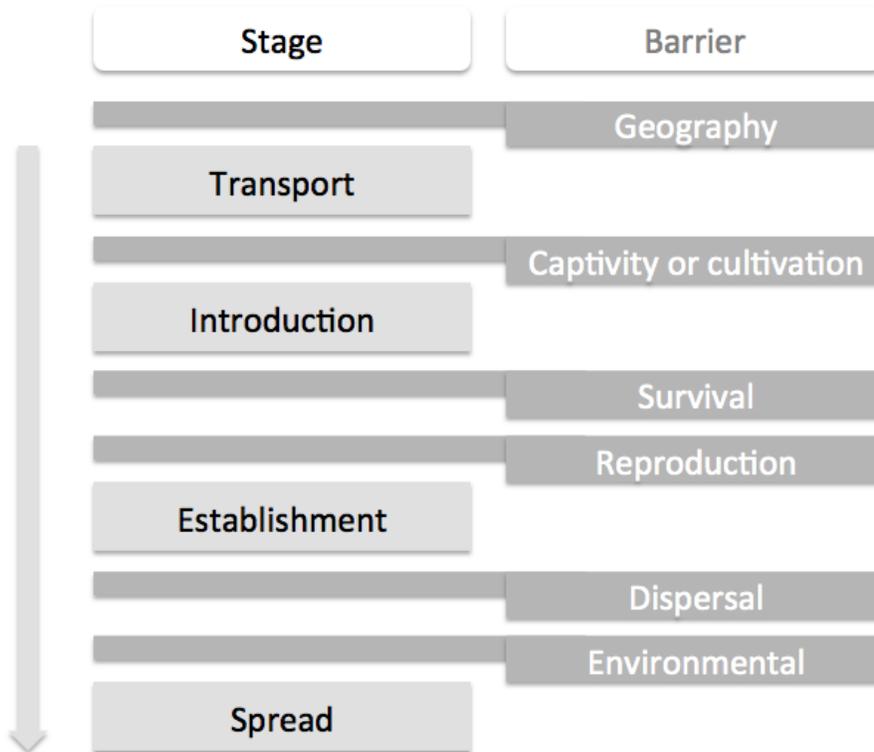
*Invasive species*, refer to species that reproduce offspring, often in large numbers, at a distance from parent populations;

*Alien species*, refer to species whose presence is due to intentional or accidental introduction by human activity (synonyms used include *non-native species*, *exotic species*);

*Pest species*, refer to species (not necessarily alien species), which have a detectable impact on ecosystems and/or socio-economic systems (synonyms used include *weeds*, *harmful species*).

There are various pathways for alien species to be introduced to an area, such as intentional release or escape (see e.g., Hulme et al. (2008)), with the importance of each pathway depending on species

taxonomic group (Saul et al., 2017). However, for a species to become invasive, several barriers must be crossed (see *Figure 1*), the ability to do so a function of various factors, including the invader characteristics (or traits), invaded community characteristics and environmental factors at the invaded location, and the interactions between these elements over time (Pyšek & Richardson, 2010; Young, Clements, & DiTommaso, 2017).



*Figure 1: Stage in species invasiveness and the barriers between each stage. Adapted from “A proposed unified framework for biological invasions” by Blackburn et al., 2011, *Trends in Ecology and Evolution*, Vol. 26, No. 7, p333. Copyright 2011 Elsevier Ltd.*

Opinions regarding the relative importance of these aspects are reflected in the variety of hypotheses proposed to explain successful species invasions (for a review of hypotheses, see e.g. Holzmüller & Jose, 2009 or Ricciardi, Hoopes, Marchetti, & Lockwood, 2013). In relation to invader fitness, the characteristics associated with successful invasive species include the efficient uptake of resources, rapid growth and reproduction, genetic variability and genetic properties, resistance to or lack of predators, and environmental modification (Holzmüller & Jose, 2009). The ability of an ecosystem to resist invasion (biotic resistance) is a reflection of the competition from resident species, biological diversity, and predation and herbivory (Levine, Adler, & Yelenik, 2004), with intrinsic

differences in ecosystem type affecting the contribution of each (Nunez-Mir et al., 2017). Abiotic factors, including climate, resource availability and episodic disturbance are also important, with, for example, altitude limiting the spread of alien species (Arévalo et al., 2005; Becker, Dietz, Billeter, Buschmann, & Edwards, 2005). In addition to these components, propagule pressure, the number of individuals released at one time and the number of occasions for release, is also widely considered an important factor (Colautti, Grigorovich, & MacIsaac, 2006; Lockwood, Cassey, & Blackburn, 2005; Simberloff, 2009), as are residence time for alien species (Richardson & Pyšek, 2006; Wilson et al., 2007), and phenotypic plasticity, the ability of a species to adjust traits to different environments (Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006; Ward, Gaskin, & Wilson, 2008). There is a close link between the ability of a species to become invasive and the magnitude of impacts (Pyšek & Richardson, 2010), with positive feedbacks between impacts and spread noted for some species, the likes of which may represent the greatest threat to ecological systems (Levine et al., 2003). These “ecosystem engineers” have the ability to modify the habitat that they invade “directly or indirectly control[ing] the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials” (Jones, Lawron, & Shachak, 1997, p1947). The growth rates of species that modify their environment in sub-optimal environments have been shown to be faster than those that do not (Cuddington & Hastings, 2004), and such modification may facilitate further exotic species invasion by virtue of amelioration of extreme conditions (Badano, Villarroel, Bustamante, Marquet, & Cavieres, 2007).

Likewise, the link between the management challenge and impacts is fairly self evident, with a larger impact suggesting a greater need for management, and the more difficult the management, the greater the potential impact over time. The challenge of control once a species becomes invasive is often substantial (Ewel et al., 1999) and whilst there are examples of successful eradication programmes (see Veitch & Clout (eds.), 2002; Wittenburg & Cock, 2001), where effective control mechanisms, long term funding and regulatory support combine to lead to species elimination (Mack et al., 2000), prevention is by far the most cost effective option (Wittenburg & Cock, 2001). In fact, for plants, there are few examples of successful eradication programmes and where such programmes have been successful, it is where populations were limited and action swift after detection (Mack & Lonsdale, 2002; Timmins & Braithwaite, 2003).

Although the challenges associated with invasive species are recognized as global, island states are often seen as particularly vulnerable to invasion due to the number of exotic species observed (Lonsdale, 1999), although evidence is mixed as to whether this is the case when invasion failure is taken into account (Diez et al., 2009). Most recent extinctions have occurred on islands (Bellard et al., 2016), particularly amongst certain taxonomic groups, although plant extinctions on islands are limited in number (Sax, Gaines, & Brown, 2002). Generally, species richness has been observed to decline as a result of invasion (Gaertner, Breeyen, Hui, & Richardson, 2009; Hejda, Pyšek, & Jarošík, 2009; Pyšek et al., 2012), although these impacts are not universal, with richness increasing following invasion in some circumstances (Pyšek et al., 2012; Sax & Gaines, 2003; Stohlgren & Rejmánek, 2014).

There is uncertainty regarding the impacts of exotic species on island plant diversity, with increases noted (Sax et al., 2002) and expected by some (Sax & Gaines, 2008), and the contrary view noted by others (Vilà et al., 2011). Based on the share of primary original vegetation, the number of endemic plants and vertebrates, and their ratio by land area, the Caribbean has been identified as one of the most important biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Understanding the impacts of invasive species in this area has therefore both local and global relevance, given the potential impacts on regulating and provisioning services locally (Cardinale et al., 2012) and loss in endemic species that may result (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011).

Whilst it is clear that the spread of invasive species and their management are also important aspects to consider, the specific focus of this study is on impacts, and in particular on those impacts associated with an invasive plant species – Coralita (*Antigonon leptopus*) - on Saba and St. Eustatius, two islands in the Caribbean. The purpose of this research is to assess which impacts, if any can be discerned in relation to this species on the islands, and in so doing, test different approaches to establishing those impacts. The following sub-sections briefly describe the islands and provide an overview of Coralita. This will then be followed by a subsection setting out the research design for this study, and the key aims and research questions that have guided the research.

## The islands

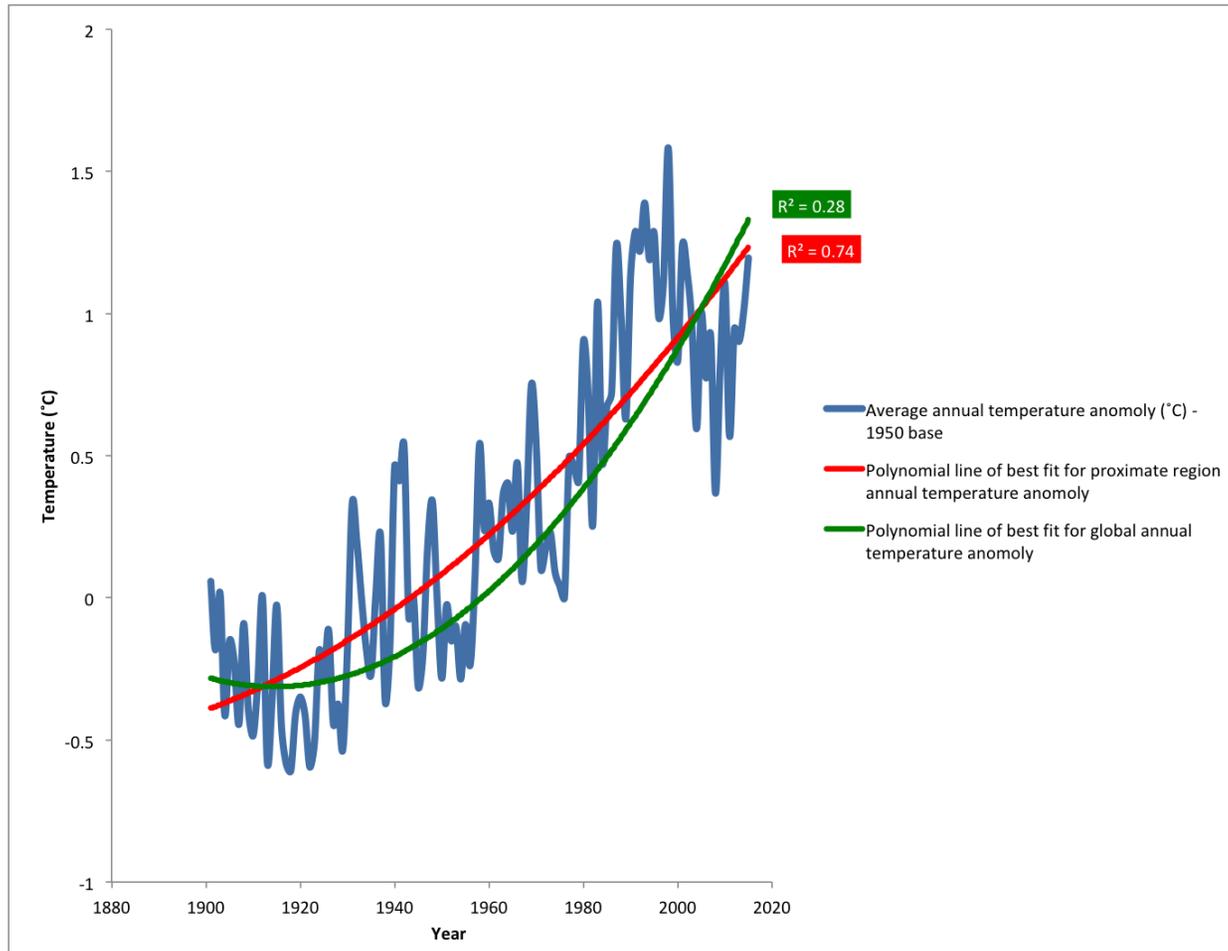
Saba and St. Eustatius are the two smaller islands (13km<sup>2</sup> and 21 km<sup>2</sup> respectively) of the Caribbean Netherlands, the third being Bonaire. Whereas Bonaire is one of the Leeward Antilles (Dutch: *Benedenwindse Eilanden*), neighbouring Saba and St. Eustatius are part of the Leeward Islands (see *Figure 2*). Prior to 2010, the islands were grouped together with Aruba (until 1986), Curaçao and St. Maarten as the Netherlands Antilles; Aruba, Curaçao and St. Maarten are now autonomous constituent countries within the Kingdom of the Netherlands, with the Caribbean Netherlands municipalities of the Netherlands (Government of the Netherlands, n.d.).

The islands are characterized by relatively warm and consistent temperatures of around 25 to 29°C, with slightly warmer average annual temperatures on Saba (CBS, 2017). Precipitation is variable by month on both islands, and although St. Eustatius was apparently wetter with total rainfall of 1600mm in 2016 compared with 624mm on Saba in the same year (CBS, 2017) this difference most likely reflects measurement locations as precipitation differences are notable at different elevations (de Freitas, Rojer, Nijhof, & Debrot, 2016) and longer term averages for the islands appear very similar (Meteorological Service of the Netherlands Antilles and Aruba, 2008).

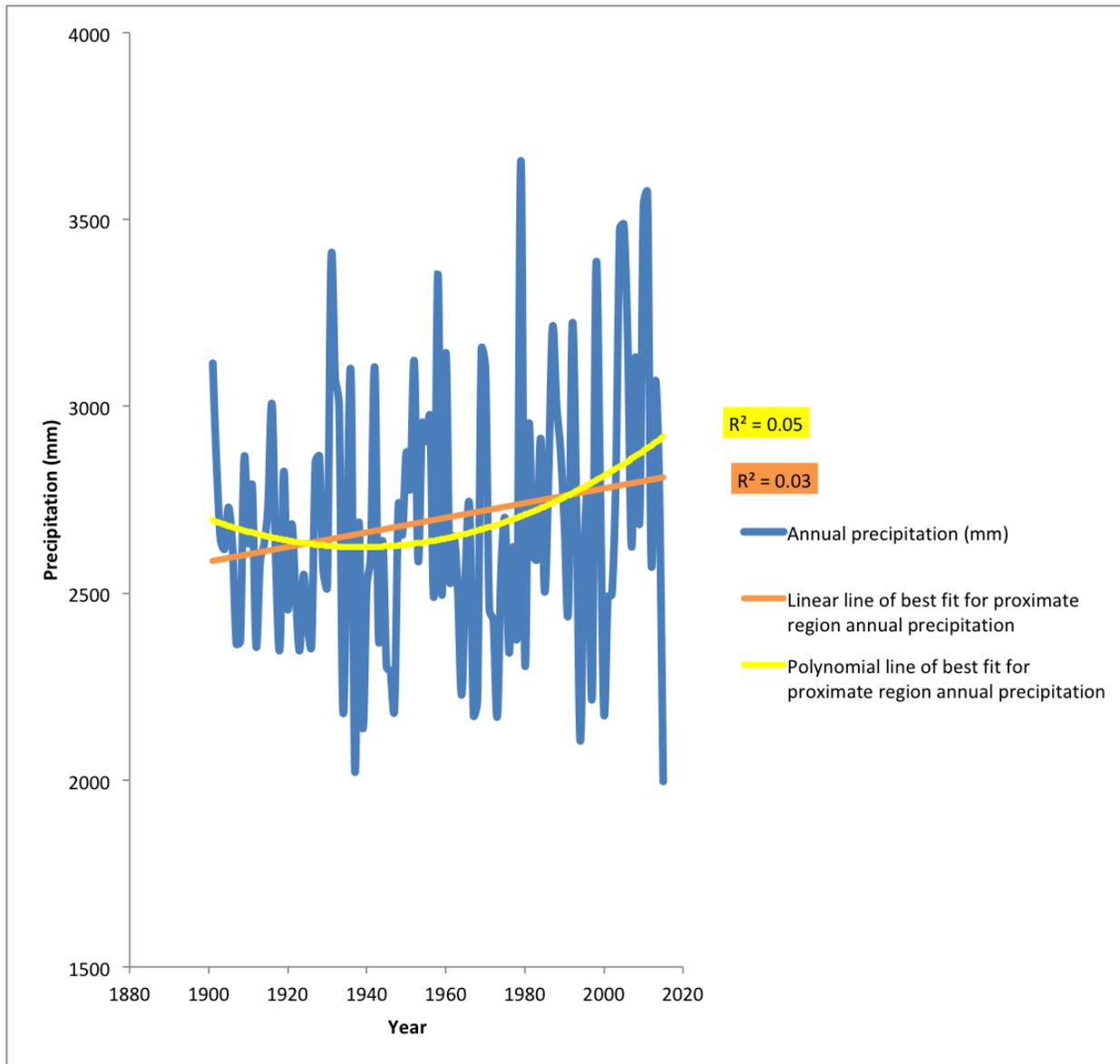


**Figure 2.** Map of the Dutch Caribbean Islands (Dutch Caribbean Nature Alliance, 2014)

Over time, average annual temperatures for the proximate region (using available data for the neighbouring British Virgin Islands and Guadeloupe from The World Bank, 2015) shows an increasing trend (see *Figure 3*). In comparison to global averages for the same period (GISTEMP Team, 2018; Hansen, Ruedy, Sato, & Lo, 2010), the polynomial line of best fit for the region has a less dramatic curvature, although the  $R^2$  is much improved (0.73 compared to a 0.29 value for the global temperature anomaly data). In contrast, data for the proximate region on annual rainfall appears to suggest a slightly increasing trend, although there is large amount of inter-annual variation (see *Figure 4*). It is important to note the changes in climate both in the past future suggest changes in species community composition, phenology and physiology (Hughes, 2000; Walther et al., 2002) and potentially an enabling climate for invasive species to spread and flourish (Hellmann, Byers, Bierwagen, & Dukes, 2008; Walther et al., 2009).



*Figure 3.* Historical and projected average annual temperature anomaly for the proximate region. Based on averaged data for Guadeloupe and the British Virgin Islands from World Bank (2015) and global data from NASA (GISTEMP Team, 2018; Hansen et al., 2010).



*Figure 4.* Historical and projected total annual precipitation for the proximate region. Based on averaged data for Guadeloupe and the British Virgin Islands from World Bank (2015).

The islands are situated in the Atlantic hurricane zone; in an average year six tropical storms in the Atlantic, Caribbean and the Gulf of Mexico mature into hurricanes within the peak hurricane season between mid-August to mid-October (Meteorological Department Curaçao, 2017). On average, hurricanes pass within 100 miles of Saba and St. Eustatius every 4-5 years, with 6 storms causing considerable damage between 1995 and 2008 (Meteorological Department Curaçao, 2017). Most recently in September of 2017, Hurricane Irma caused widespread damage on the Leeward Islands, with wind speeds such that it was the strongest hurricane ever recorded in the Atlantic Ocean (NOAA, n.d.-a). This was followed by a further category 5 hurricane, Maria, which caused severe damage on Puerto Rico and Dominica amongst other islands (NOAA, n.d.-b). Although Saba and St. Eustatius were spared the worst of these storms, the natural environment was heavily affected (de Meyer, 2017). As the disturbance caused by tropical storms provide conditions for invasive species to flourish (Bhattarai & Cronin, 2014; Goulding, Moss, & McAlpine, 2016), particularly vines and lianas (Murphy & Metcalfe, 2016), this may have implications regarding the spread of invasive species on both islands.

Due to the volcanic nature of both islands – Saba is essentially one dormant volcano rising to 877m and St. Eustatius two volcanoes are separated by lowlands formed from volcanic debris – climate varies with elevation (Boldingh, 1909; de Freitas et al., 2016). For example, precipitation in Saba is 30 percent higher at 250m compared to those calculated at 30m (de Freitas et al., 2016). As a result of these differences, vegetation varies substantially on both islands, with rainforest at high elevations and shrubland at lower elevations (de Freitas, Rojer, Nijhof, & Debrot, 2016; de Freitas, Rojer, Nijhof, & Debrot, 2012).

The populations of the islands are small, with 2,010 and 3,250 inhabitants on Saba and St. Eustatius in 2016 respectively (CBS, 2017). The public sector is the largest employer on both (CBS, 2017), and GDP per capita, although less than the mainland Netherlands in 2015 (Netherlands: US\$,44,800) (Saba: US\$24,900; St. Eustatius: US\$26,600), was broadly equivalent to that of Spain (US\$25,800) (data sources: CBS (2017), for Saba and St. Eustatius, World Bank, (2015) for the Netherlands and Spain). Tourism is a vital component of the economy of both islands, with 9,200 and 11,000 tourists arriving by air on Saba and St. Eustatius respectively in 2016 (CBS, 2017). Based on tourist surveys, around 70 percent of total tourist expenditure on both islands can be attributed to the natural environment (van Kerkhof, Schep, van Beukering, & Brander, 2014; van Kerkhof, Schep, van Beukering, Brander, & Wolfs, 2014). In the 17<sup>th</sup> century, agriculture was an important means of subsistence, and sugar cane was grown on both islands during this time and until the early 19<sup>th</sup> century (Stoffers, 1956). During this colonial period, the impact on resident vegetation from human disturbance is likely to have been substantial (de Freitas et al., 2012, 2016); as an important trade island, St. Eustatius is estimated to have had a similar population to New York City (20-25,000 people) towards the end of the 18<sup>th</sup> century (Gilmore, 2013). Although residential areas on both islands have expanded over the past few decades, agricultural lands have diminished (de Freitas et al., 2012, 2016; van Andel, van der Hoorn, Stech, Arostegui, & Miller, 2016). More recently, the

impact of free-roaming goats on the vegetation of the islands is substantial, reducing the resilience of natural vegetation and affecting natural succession (de Freitas et al., 2012, 2016).

Taken together, the changing climate and types of disturbance by anthropogenic activity on the islands serves to highlight the fact that invasion by Coralita is not occurring in isolation. It is important to take into account these changing abiotic conditions in assessing impacts. It is also important to recognise that both the current conditions and the changes occurring on the islands, in relation to climate, economic development or otherwise, are not the same as those elsewhere. Any generalisations made about invasive impacts for species taken from other locations should bear this in mind, and given that this is fundamental approach taken in this study (see further details under subsection *Research Aims and Approach*), the results need to be tempered by this fact.

## Coralita

Coralita (*sp. Antigonon leptopus*), also known as coral vine, Mexican creeper and chain-of-love amongst others (ISSG, 2015) is a perennial vine from the *Polygonaceae* (buckwheat) family (see *Box 2*).

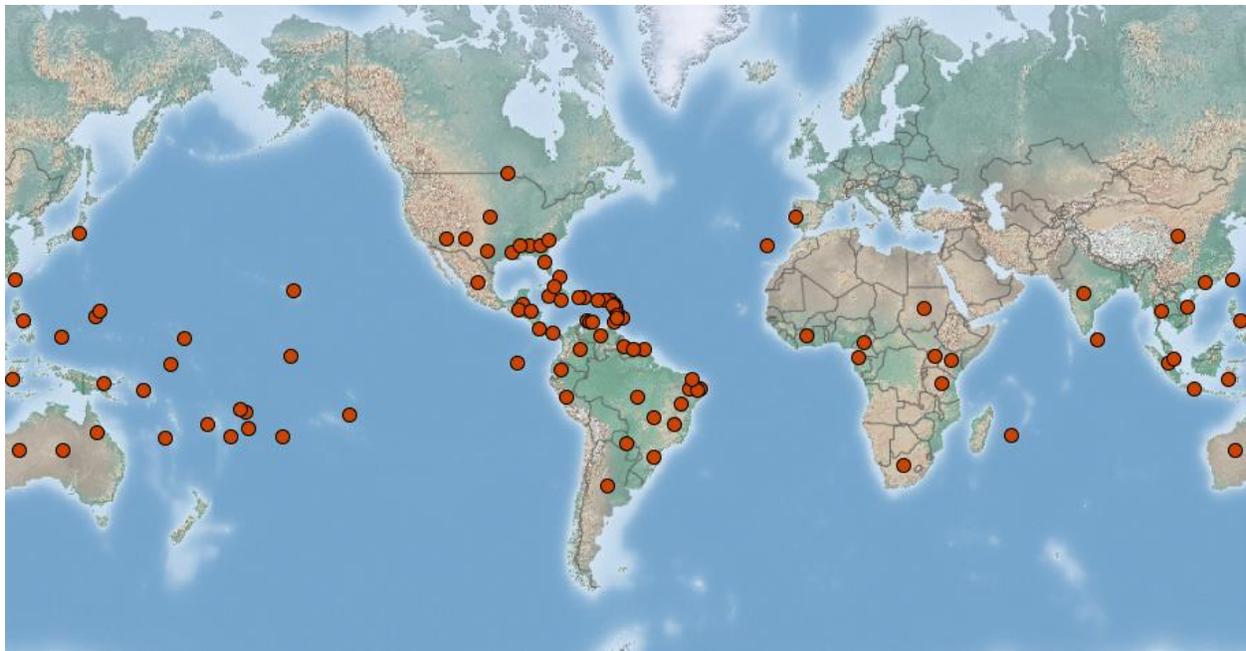
**Box 2: Taxonomic hierarchy for Coralita (sp. *Antigonon leptopus*)**

|                      |                                |
|----------------------|--------------------------------|
| <b>Kingdom</b>       | Plantae                        |
| <b>Subkingdom</b>    | Viridiplantae                  |
| <b>Infrakingdom</b>  | Embryophyta                    |
| <b>Superdivision</b> | Embryophyta                    |
| <b>Division</b>      | Tracheophyta                   |
| <b>Subdivision</b>   | Spermatophytina                |
| <b>Class</b>         | Magnoliopsida                  |
| <b>Superorder</b>    | Magnoliopsida                  |
| <b>Order</b>         | Caryophyllanae                 |
| <b>Family</b>        | Polygonaceae                   |
| <b>Genus</b>         | Antigonon                      |
| <b>Species</b>       | Antigonon leptopus Hook. & Arn |

One of three species of the *Antigonon* genus, which is a sister to the *Coccoloba* clade (Frye & Kron, 2003), Coralita is the most widespread and morphologically variable of the *Antigonon* species (Ernst & Ketner, 2007) and the only species of the three documented as invasive (Burke & DiTommaso, 2011). Originally from Mexico, Coralita has now spread across the tropics, becoming particularly problematic on tropical islands (Burke & DiTommaso, 2011) such as Guam, where it is considered one of the 20 most prevalent invasive species (Reddy, 2014). Its distribution is global however, with,

for example, evidence of naturalization in Australia, Taiwan, Pakistan and the USA amongst other countries (Ernst & Ketner, 2007) (see *Figure 5*).

Aside from use as an ornamental species, *Coralita* has also been used traditionally for medicinal purposes, with leaves and flowers used to treat a variety of ailments due to its analgesic and anti-inflammatory properties (Mamidipalli, Nimmagadda, Bobbala, & Gottumukkala, 2008). It has also been proposed as a means to shade roofs for cooling (Nayak, Srivastava, Singh, & Sodha, 1982), extracts from leaves proposed as a means to exterminate fish pathogens (Balasubramani, Deepak, Sowmiya, Ramkumar, & Perumal, 2015) and, somewhat abstractly, potentially used to synthesise gold, silver and palladium nanoparticles (Ganaie, Abbasi, & Abbasi, 2016a; Ganaie, Abbasi, & Abbasi, 2016b).

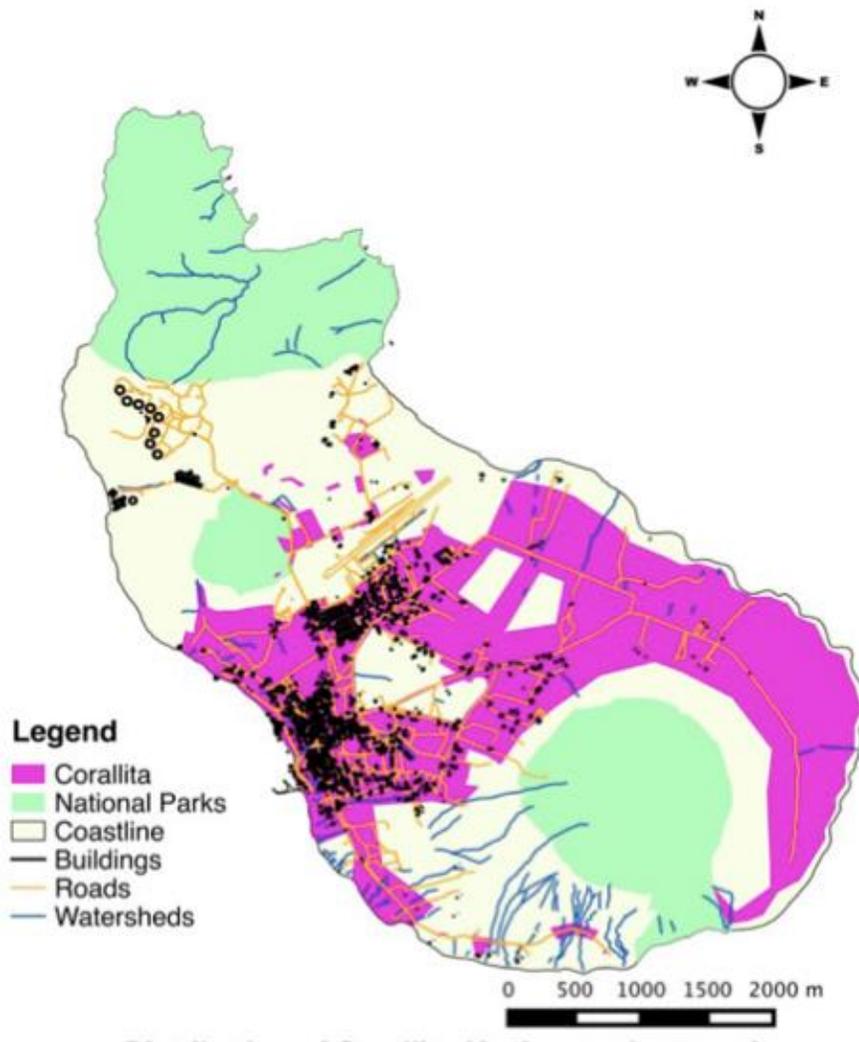


**Figure 5:** Global distribution of *Coralita* compiled by CABI. Map from *CABI Invasive Species Compendium*, 2018, *Antigonon leptopus* by CABI [original text by Rojas-Sandoval and Acevedo-Rodríguez], Wallingford, UK: CAB International. [www.cabi.org/isc](http://www.cabi.org/isc)

In 2007, Ernst and Ketner estimated that *Coralita* covered 20 percent of St. Eustatius, a figure revised to 33 percent in 2014 (Berkowitz, 2014) (see *Figure 6*). Although these figures may be overestimated (Haber et al., 2017), it is considered the most problematic invasive plant species in the Caribbean Netherlands (van der Burg et al., 2012). On St. Eustatius, although found in all areas, its distribution is apparently limited to less than 150 to 200m in elevation, due to a combination of changes in soil characteristics, the steepness of slopes and the still dense natural closed canopy of

vegetation (Ernst & Ketner, 2007). In the lowland areas of St. Eustatius, de Freitas et al. (2012) highlight a dramatic increase in the prevalence of Coralita compared to earlier vegetation mapping working carried out in the 1950's, where it is now ubiquitous and often dominant.

In common with the previously mentioned cases of rabbits and starlings, the initial spread of Coralita was intentional. However, unlike these two cases, where purposeful release was the pathway for introduction, Coralita in the Caribbean likely escaped from ornamental private gardens, with herbarium data suggesting it was introduced in the 19<sup>th</sup> century (Burke & DiTommaso, 2011). The spread of Coralita is facilitated by both rapid growth over surrounding vegetation, and through dual propagation methods of above-ground seed dispersal, and underground via roots or overground via stolons (Burke & DiTommaso, 2011).



*Figure 6: Distribution of Coralita on St. Eustatius, 2014. From The State of Antigonon Leptopus ( Corallita ) on St Eustatius in 2014, by Berkowitz, 2014, report for STENAPA, p6. Copyright 2014 The author.*

Although seeds float on water, facilitating their transport to different areas, seeds are expected to play less of a role in dispersal than the movement of tubers, stems and root cuttings, which are easily transported with soil and all of which are able to root again (Ernst & Ketner, 2007). On Curaçao, Bonaire and Aruba, Coralita is only found in areas where there is heavy disturbance, as although the fruits are an important source of food for pigeons, seeds are destroyed through digestion (van der Burg et al., 2012). Indeed, there is no evidence that there is any other means of long-distance dispersal other than that facilitated by humans (Burke & DiTommaso, 2011) and that without disturbance, Coralita has limited potential to invade (Ernst & Ketner, 2007).

Coralita climbs via tendrils, from a base that can become slightly woody with age (Burke & DiTommaso, 2011) and has been observed in St Eustatius as being 10m or greater in length (Ernst & Ketner, 2007). Although leaf blades size and shape are phenotypically plastic, leaves are generally between 10 to 16 cm in length, with leaf blades a varied shape commonly deltoid or cordate (Burke & DiTommaso, 2011). Persistent tuberous roots grow deep underground and provide an enormous food reserve for the plant even from a young age, with tubers buried up to 2m in depth and weighing up to 8kg (Ernst & Ketner, 2007). Coralita is a hardy species, able to withstand drought, different soil types (as long as well-drained) and can grow in full sunlight to light shade, although a soil of Ph. 5 – 5.5 and full sunlight is preferred (Ernst & Ketner, 2007).

Unlike the native range in Mexico, where there is a distinct flowering period, if there is sufficient water availability the plant flowers continually (Raju, Kanaka Raju, Victor, & Appala Naidu, 2001), as observed by Ernst and Ketner (2007) on St. Eustatius. Although there are three floral forms – white, pink white and pink – pink is the most common (Raju et al., 2001). Flowers are small, bisexual and grouped in numbers 23 to 25 on a compound umbellate cyme (Raju et al., 2001). Although observations by Raju et al. (2001) suggest that bees are the dominant pollinator, flower morphology is such that nectar is accessible to a variety of species. Neither cattle nor (invasive) goats have been observed to eat Coralita leaves (van der Burg et al., 2012), which, given the distribution of the plant, perhaps suggests greater pressure for herbivory on competing plants. In interviews with farmers, Ernst and Ketner (2007) found that the tubers used to be collected from ploughing fields and subsequently fed to livestock or burnt, although this practice is no longer carried out. These changes in agricultural practice, together with disturbance from increased construction, are thought by Ernst and Ketner (2007) to be the main reasons for the spread of Coralita on St. Eustatius.

There appear to be limited numbers of field studies where control approaches have been applied and tested for Coralita, with no further trials apparent aside from the work by Ernst and Ketner (2007) on St. Eustatius, Englberger's 2009 study in Micronesia (as cited in Burke & DiTommaso, 2011) and trials of short-duration goat/sheep browsing in St. Croix, in the American Virgin Islands (Muir, 2009). Both the Ernst and Ketner and Englberger studies found that chemical treatment was the most effective means of control, although substantial quantities of herbicides were required, raising questions of environmental suitability and economic costs (Burke & DiTommaso, 2011). In

St. Croix, although field trials were successful in reducing the extent of Coralita, the need for subsequent management activities due to tubers and root stock re-growth, coupled with the need for selection and pre-conditioning of lambs due to issues of leaf palatability (Muir, 2009), suggests a rather challenging practical application of control efforts by this means. Additionally, van der Burg et al. (2012) suggest that continued cutting may be effective over a number of years, although this appears to be costly and slow procedure, potentially limiting the land use for cleared areas. As previously discussed, given the difficulty associated with removal of established species, complete elimination of Coralita on the islands seems unlikely in the near term.

In terms of the impacts of Coralita on Saba and St. Eustatius, these have not been fully assessed, with reports of ecological impacts anecdotal (Burke & DiTommaso, 2011). Based on their observations in the field, Ernst and Ketner (2007) identify broad effects on the environment. These include:

- Hampering succession of native vegetation on former arable fields;
- Prevention of germination by native species;
- Smoothing crowns and hampering fruiting and flowering, eventually killing wild and ornamental trees and large shrubs;
- Affecting soil conditions through the accumulation of leaf litter;
- Posing a threat to the endangered Lesser Antillean Iguana (*Iguana delicatissima*).

## Research aims and design

At present, knowledge regarding the impacts of Coralita on Saba and St. Eustatius is scant. On the one hand, its extent has been expanding, especially on St. Eustatius de Freitas et al. (2012), which implies changes to community composition, potential species loss and changes to ecosystem function. On the other hand, Coralita may simply be replacing other species that carried out a similar function, or may have relatively benign impacts. Indeed, it is not inconceivable that tourist visitors welcome the bright pink flowers it produces, unaware of its alien origins or impacts on other sectors. The main purpose of this research therefore is to provide an assessment of the impacts of Coralita on Saba and St. Eustatius, helping to fill the gap in knowledge in relation to these impacts. This information has the potential to be of societal value in terms of understanding the need for prioritisation of resources to tackle this species. This primary aim is accompanied by a secondary aim that is more methodological in nature and concerns the ability to elucidate invasive species impacts, given a general lack of specific data available, based on different methodological approaches. The challenge of assessing impacts under these conditions is substantial and an examination of different methods with this in mind may be of value for future assessments. Clearly these two aims are

complementary, with the ability to assess impacts a function of the applicability of the methods used.

The design of the research (see *Figure 7*) is as follows. Firstly, in addressing the primary question regarding the impacts of Coralita on the islands, the theoretical background in relation to assessing invasive species impacts was investigated (see sub-section *Theoretical Background*, under section *Conceptual Framework*). Particular attention was paid to the potential for biodiversity and species loss, as well as the potential impacts on ecosystem services, “the benefits people derive from ecosystems” (Millenium Ecosystem Assessment, 2003, p3). In turn, the approaches taken to investigating species loss and impact on ecosystem services was based upon two methodological frameworks: a well-defined Environmental Impact Classification for Alien Taxa (EICAT) in terms of species loss, and a less concretely specified approach based on plant species traits. These aspects are further discussed under the sub-section *Methodological Framework* (under section *Conceptual Framework*). Importantly, these two methodological frameworks, and the subsequent analytical approach, fed back into the development of the key and sub-research questions (see below). The types of analytical approaches followed relate to the two methodological frameworks. Together with the subsequent data gathering and analysis performed, the analytical approaches are discussed together under the section *Methodology*. The findings from the research are presented in the *Results* section, which is followed by a *Discussion* section, revisiting the research questions in light of the results. This section also highlights some of the challenges faced in carrying out this research as, well as reflecting on the assumptions made and potential for further research based on the research findings.

Finally, it is important to note that the availability of data had a clear steering role in the development of the research. A lack of information on impacts was both the purpose of the research and a key challenge. As such, consideration of what information was available and how that might be utilised was vital, with a particular role in relation to the choice of methodological framework and the types of analysis performed.

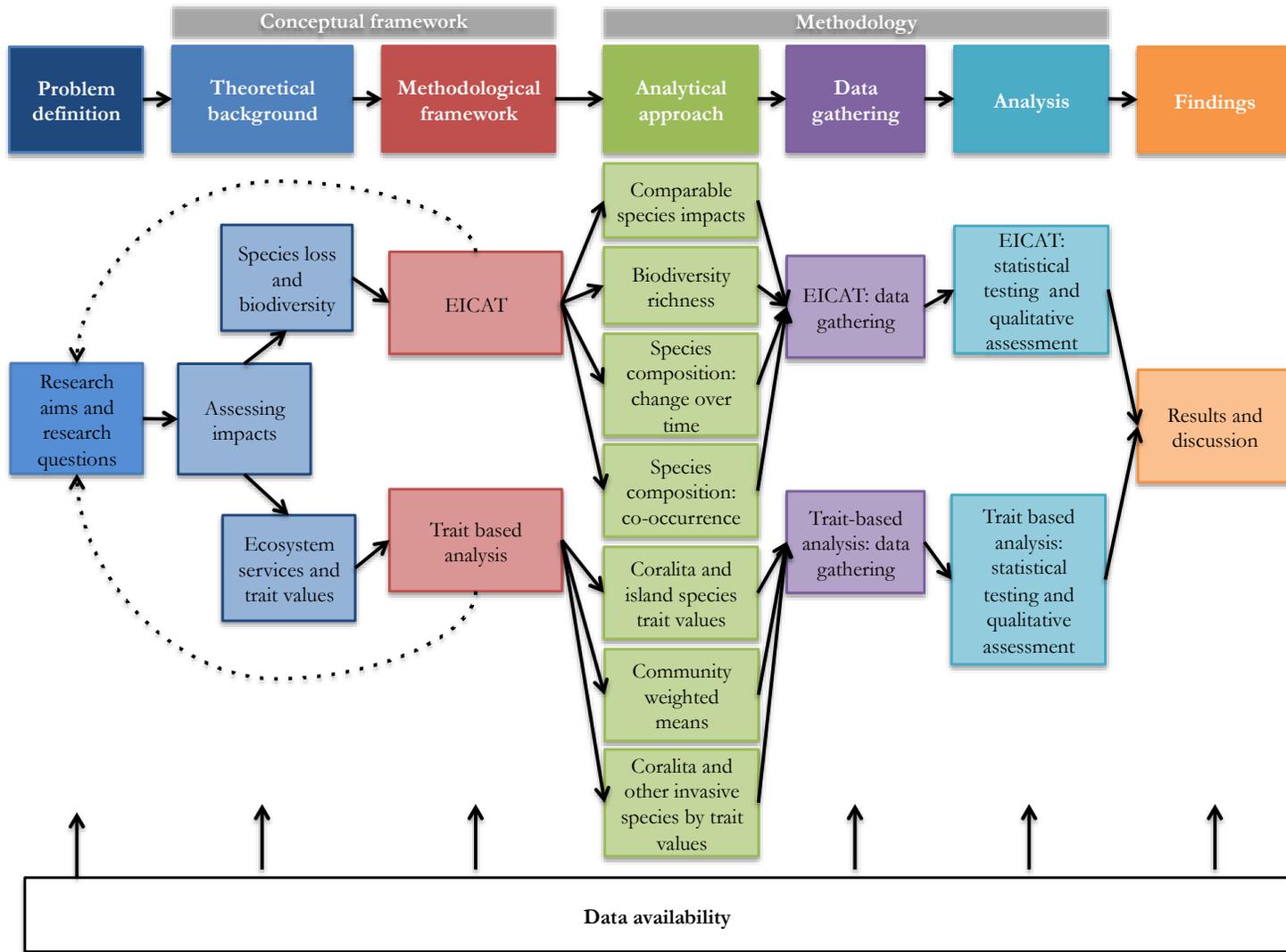


Figure 7: Research design

## Research questions

Based on the primary aim in relation to assessing Coralita's impacts on the islands and the secondary aim to investigate the ability of different methodologies to elucidate impacts, the following research questions and sub-questions have been devised. Sub-questions 1-4 primarily relate to an attempt to apply the EICAT methodology, whereas sub-questions 4-6 refer to an approach based on species traits:

- **RQ 1:** What are the impacts associated with Coralita on Saba and St. Eustatius?
  - **SQ 1:** What impacts are associated with comparable species that can be applied to Coralita on the islands?
  - **SQ 2:** How does biodiversity compare in areas where Coralita is found and areas where it is not found?
  - **SQ 3:** How has species composition on the islands changed over time and what links can be made to the spread of Coralita?
  - **SQ 4:** How do species co-occur on the islands in areas where Coralita is prevalent and what inferences can be made about species loss due to Coralita as a result?
  - **SQ 5:** How different is Coralita from other species on the islands, based on species traits?
  - **SQ 6:** Based on trait values and species abundance, how would the hypothetical removal of Coralita affect community averages and what would this imply for ecosystem services?
  - **SQ 7:** How do the traits associated with Coralita compare with other invasive species and other climbing species, and what does this imply for impacts?

**RQ 2:** Based on the application of the EICAT and trait based methodology utilised for this assessment, what strengths and weaknesses can be discerned from these approaches?

# Conceptual Framework

## Theoretical Background

### Assessing Impacts

In general, although sometimes difficult to monetise, the economic impacts from invasive species are more readily perceived and reported on than ecological changes (European Environment Agency, 2012; Vilà et al., 2010). Ecological impacts can occur at the species, community or ecosystem level, with, for example, impacts on species numbers, plant cover and soil characteristics (Pyšek et al., 2012). In a frequently cited paper, Parker et al. (1999) defined impacts from invasive species (I) as a product of their range size (R), their abundance (A) and their effect per individual (E). However, E must be defined explicitly, as the same species can have multiple effects (Ricciardi et al., 2013). There are potentially many different types of impacts that can result from invasive species: *Table 1* shows an example of the types of impact outcomes that are associated with invasive species, from a framework developed by the Invasive Species Specialist Group (ISSG) of the International Union for the Conservation of Nature (IUCN) as part of its Global Invasive Species Database (GISD) (ISSG, 2015). It is interesting to note that there is the potential for overlap between categories, with, for example, a reduction in impacted species numbers potentially affecting harvests. Whilst alien species are generally associated with negative impacts, it is important to remember that they can also provide benefits; for example, it is clear that we depend on non-native species for agricultural production, medicine and shelter (Ewel et al., 1999; Pimentel et al., 2000). Although controversial (see, for example, Nogués-Bravo, Simberloff, Rahbek, & Sanders (2016)) the introduction of exotic species to replace the ecosystem function of recently extinct species has been beneficial in some cases, such as the introduction of non-native tortoises to substitute for the role in herbivory and seed-dispersal by recently extinct species (Griffiths, Hansen, Jones, Zuël, & Harris, 2011).

There are a variety of hypotheses that have been proposed to explain the variation in impacts observed in relation to species invasion, with Ricciardi et al. (2013) identifying 19 hypotheses based around 6 main themes. Of these themes, which include hypotheses based on species traits and ecosystem traits, those based on community structure, niche-based hypotheses, hypotheses relating to a changing abiotic environment, hypotheses associated with the influx of organisms and a hypothesis related to the synergistic effects of cumulative invasions, the role of species and ecosystem traits has been proposed most extensively in relation to particularly damaging invasions (Ricciardi et al., 2013). The frequency of significant impacts associated with species and community traits and ecosystem processes was assessed by Pyšek et al. (2012) across 287 publications and 1,551 species. They found that the significance of the outcomes related to community richness and diversity and soil resources was dependent on the interaction between invasive species traits and

traits of the biome invaded, highlighting the context dependency associated with impacts (Pyšek et al., 2012). As well as this temporal and spatial dimension of invasive impacts, the potential for interaction with other non-native species can eventuate species invasion impacts (Simberloff & Von Holle, 1999). These are important points to reflect upon for this study, which in part relies on generalisations regarding recorded impacts elsewhere.

**Table 1: Impact outcomes from the GISD database**

|   |  |
|---|--|
| <b>Environmental<br/>Ecosystem<br/>(Habitat)</b>  | Modification of hydrology/water regulation, purification and quality/soil moisture<br>Modification of nutrient pools and fluxes<br>Modification of natural benthic communities<br>Modification of food web<br>Reduction in native biodiversity<br>Unspecified ecosystem modification<br>Habitat degradation<br>Habitat or refugia replacement / or loss<br>Physical disturbance<br>Modification of fire regime<br>Modification of successional patterns<br>Soil or sediment modification: erosion<br>Soil or sediment modification: bioaccumulation<br>Soil or sediment modification: modification of structure<br>Soil or sediment modification: modification of, salinity or organic substances<br>Other |
| <b>Environmental<br/>Species<br/>(Population)</b> | Population size decline<br>Species range change<br>Reduces/inhibits the growth of other species<br>Alteration of genetic resources<br>Indirect mortality<br>Plant/animal health<br>Interference with reproduction<br>Other   |
| <b>Socio-economic</b>                             | Damage to agriculture<br>Damage to forestry<br>Damage to aquaculture/mariculture/fisheries<br>Reduce/damage livestock and products<br>Human health<br>Human nuisance<br>Modification of landscapes<br>Damage to infrastructure<br>Damage to ornamentals<br>Modification of cultural, educational, aesthetic, religious and ornamental values<br>Alteration of recreational use and tourism<br>Impact on trade / international relations<br>Limited access to water, land or other<br>Other economic impact<br>Other livelihoods<br>Unknown   |

*Note.* Adapted from ISSG (2015)

## Species loss and biodiversity

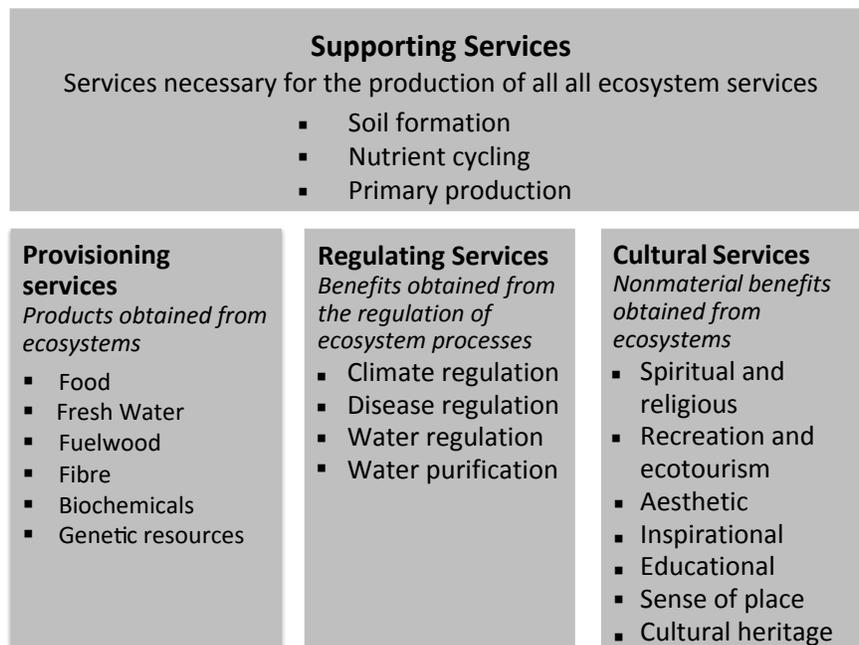
A loss of species has implications for biodiversity, both locally and at a broader scale. It is widely agreed upon that species diversity is essential for the maintenance of ecosystem functions, with individual species importance associated with their traits and the interactions with other species (Loreau et al., 2001). For example, ecosystem productivity, in terms of the efficiency of biomass production, decomposition and the recycling of nutrients (Cardinale et al., 2012), has been shown to be affected by biodiversity loss to at least the same extent as other anthropogenic drivers of productivity loss, such as changes in atmospheric CO<sub>2</sub>, water availability, herbivory and fire (Tilman, Reich, & Isbell, 2012). These impacts on productivity are also exacerbated over time, as the implications of various diversity-dependent feedbacks and complementary relationships between species are accumulated (Reich et al., 2012), with many short term experiments on biodiversity and productivity potentially underestimating the impacts of the former on the later (Cardinale et al., 2007). Biodiversity also contributes to ecosystem stability (Hautier et al., 2015; Naeem & Li, 1997; Tilman, Reich, & Knops, 2006; Yachi & Loreau, 1999), through the different responses of species to environmental fluctuation, differences in the speed of response of species to changes and to a reduction in the level of competition between species (Loreau & de Mazancourt, 2013). Biodiversity also underpins all aspects of ecosystem services (Mace, Norris, & Fitter, 2012).

The impacts of species losses are not equal across species however. The concept of keystone species, which are species “whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance” (Power et al., 1996, p609), has been used to understand the implications of the loss of different species. There are key differences in relation to the impacts of species loss by trophic level, with the loss of an apex predator equivalent to a substantial loss of plant diversity in an area (Duffy, 2003). In this sense, biological diversity in an ecosystem is important because it implies that the system is more likely to both contain key species that are vital for ecosystem function and to have sufficient complementary species on which keystone species may depend directly and indirectly (Power et al., 1996). Over the long term, the impacts of plant species loss can be dramatic, with evidence of changes in arthropod species richness noted in some instance, changing the entire trophic structure of an ecosystem (Haddad et al., 2009).

Biodiversity does not only relate to species richness however. The composition of an ecosystem in terms of the distribution of biomass amongst community species has also been shown to affect ecosystem productivity, with a reduction in “evenness” associated with decreases in productivity (Wilsey & Potvin, 2000). As such, changes in ecosystem composition as a result of invasive species can impact ecosystem function even in the case where species are not lost from an area. As previously mentioned, invasive species have had a dramatic impact on species extinction, particularly in relation to island species (Bellard et al., 2016), although the impacts from plant invasions on native species appear to be less dramatic (Sax et al., 2002). Changes in species composition however, through either a reduction in species richness or a change in the relative abundance of species in an area, may have impacts on the productivity of the ecosystem.

## Ecosystem services and trait values

Ecosystem services refer to “the benefits that people receive from ecosystems” (Millennium Ecosystem Assessment, 2003, p3), which have been broadly grouped as supporting services, provisioning services, regulating services and cultural services (see *Figure 8*).



*Figure 8* Ecosystem services as described by the Millennium Ecosystem Assessment. Adapted from *Ecosystems and Human Well-Being: A Framework for Assessment*, (p5) by the Millennium Ecosystem Assessment, 2003, Island Press, Washington, D.C. Copyright 2005 Millennium Ecosystem Assessment.

The value of an ecosystem therefore relates to these services, which in economic terms come from a combination of current direct and indirect use (e.g. food and flood control), future option values, and non-use values relating to the ability to bequest values to the future and to the value placed on knowledge of the continued existence of the habitat / species / ecosystem (see, for example, Pearce & Moran, 1994). Changes to an ecosystem, brought about by, for example, changes in land use, climate change or the introduction of invasive species, therefore have the potential to impact the services received from that ecosystem and thus the value of the ecosystem in economic terms. As previously mentioned, changes in biodiversity through species loss or community compositional changes as a result of species invasion can affect the functioning of an ecosystem, which in turn will impact ecosystem services (for examples of invasive species and their impacts on the different ecosystem services can see Charles & Dukes, 2007; Katsanevakis et al., 2014; Pejchar & Mooney,

2009; Vilà et al., 2010). The direct link between biodiversity and community composition, and ecosystem process and services has also been explored through the concept of community trait values. Although ecosystem processes and ecosystem services are distinct elements relating to ecosystems, with a number of processes collectively providing the service, (Eviner, Garbach, Baty, & Hoskinson, 2012) find that the current use of processes as proxy for ecosystem services suitably robust for current assessment.

A species can be described by its characteristics or traits. Traits in this case can be defined as “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization” (Violle et al., 2007, p884). As such, the potential number of traits for a given species is large, with the TRY plant database (Kattge et al., 2012) containing 1,830 traits. Plant traits reflect evolutionary and community assembly processes across environmental gradients (Reich et al., 2003), with trade-offs between differing plant strategies reflected in trait values (Grime, 1977). For example, so called “competitive species” have traits that maximise growth in productive and undisturbed systems, such as a dense canopy of leaves to enhance rapid growth rates (Grime, 1977). However, processes that increase plant growth rates such as high leaf turnover also leave plants less stress resistant (see Figure 9) (Chapin, Autumn, & Pugnaire, 1993).

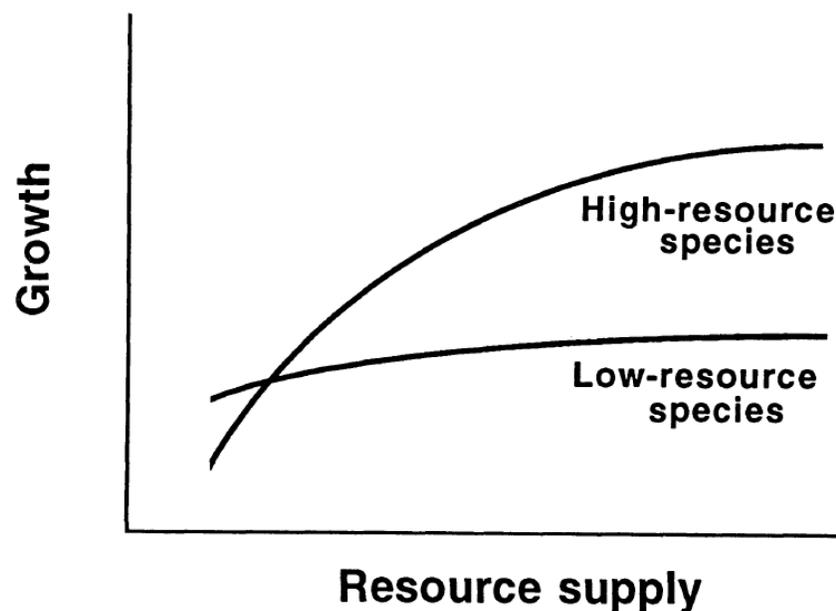
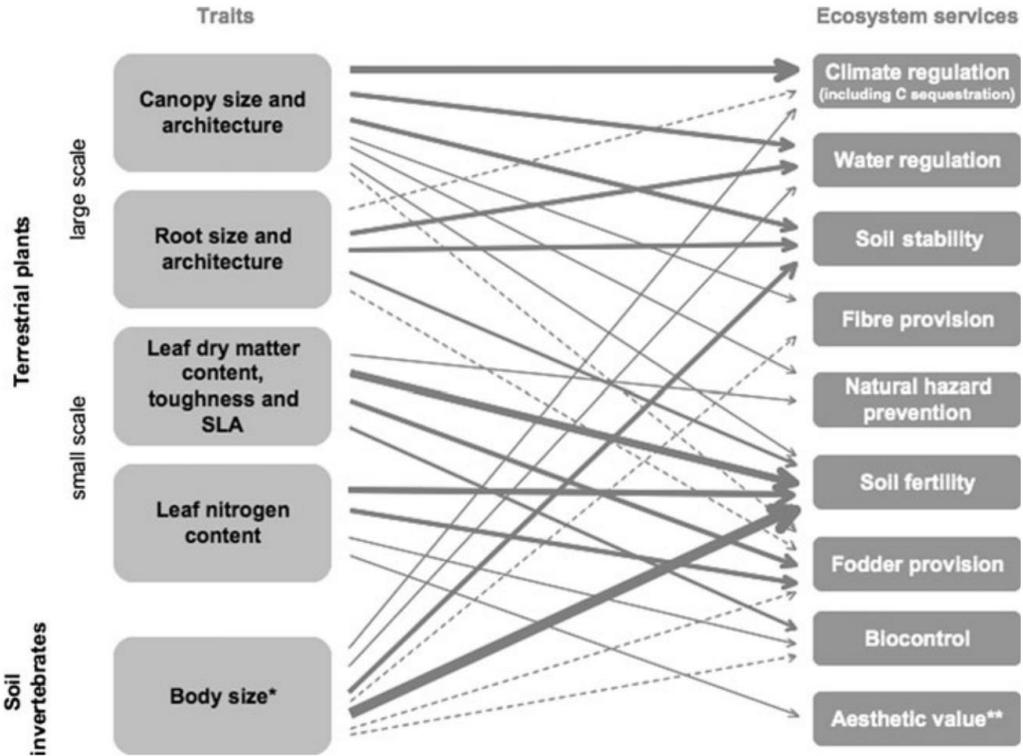


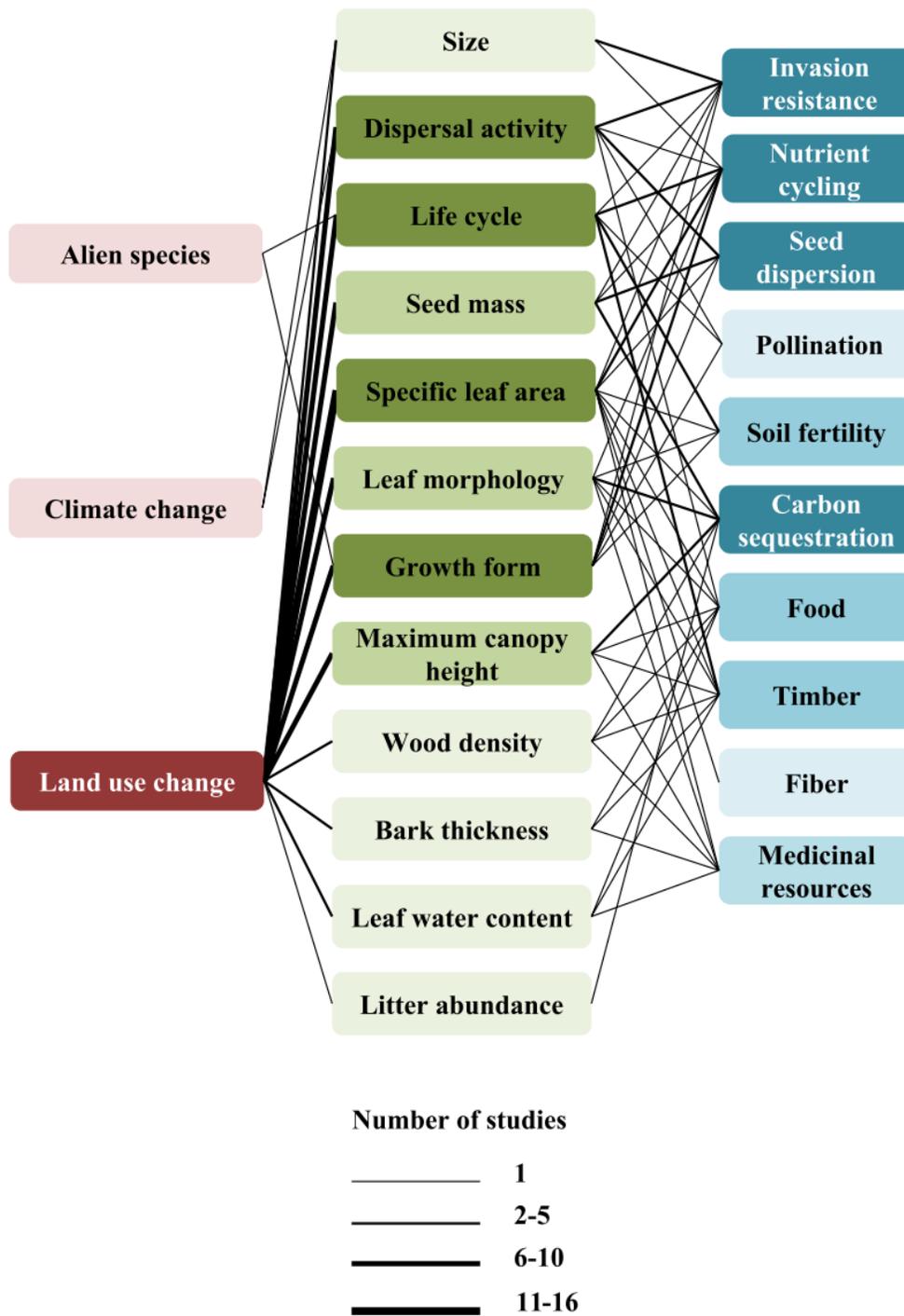
Figure 9: Growth response to typical species in high and low resource environments. From “Evolution of Suites of Traits in Response to Environmental Stress”, by Chapin et al., 1993, *The American Naturalist*, Vol. 142, Issue Supplement: Evolutionary Responses to Environmental Stress, s80. Copyright 1993 The University of Chicago Press.

Just as species is a reflection of the traits it possesses, so a community of plants in an ecosystem is a reflection of the species and their relative abundance. Changes in species compositions can have profound impacts on ecosystem processes and thus the benefits to humanity from ecosystems, with changes in community trait values directly affecting ecosystem goods and services, or indirectly affecting ecosystem processes via changes in biotic or abiotic controls (Chapin III et al., 2000). The implications for ecosystem function however depends upon the nature of the change to the community, with the type of species and community affecting functional change (Symstad, Tilman, Willson, & Knops, 1998). The “biomass ratio” hypothesis posited by Grime (2002), which states that ecosystem function in an area is determined by the trait values of the dominant plants, helps to describe the relationship between species trait values and ecosystem processes. This hypothesis is well supported empirically and theoretically (Díaz et al., 2007), with the concept of a community weighted mean (CWM), a weighting of community trait mean values by their relative abundance, used most extensively to link trait values to environmental features (Peres-Neto, Dray, & F., 2016).

The links between average community trait values and ecosystem services has been explored in a meta-analysis of studies by de Bello et al. (2010)(see *Figure 10*). More recently, a similar meta-analysis of studies linking the drivers of change to biodiversity and ecosystem services was performed by (Hevia et al., 2017). They found a number of studies that linked alien species to regulating and provisioning services, as well as studies linking functional traits to ecosystem services (see *Figure 10*). These two studies (amongst others) provide the basis for linking species traits with ecosystem services, as discussed under the sub-section *Trait-based analysis* under *Methodological Framework*.



*Figure 10:* Most commonly reported plant and invertebrate traits and their association with ecosystem service delivery. Thicker arrows denote a larger number of studies. From “Towards an assessment of multiple ecosystem processes and services via functional traits”, by De Bello et al., 2010, *Biodiversity and Conservation*, Vo. 19, Issue 10, p2881. Copyright Springer Science+Business Media B.V. 2010



*Figure 11: Functional traits for which evidence has been found linking them to the drivers of change and ecosystem services for vegetation. Adapted from “Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges” by Hevia et al., 2017, *Ecology and Evolution*, Vol. 7, Issue 3, p837. Copyright The Authors 2017.*

## Methodological Framework

There are numerous approaches that have been proposed for classifying invasive species impacts, with Nentwig et al. (2016) identifying 24 different protocols applied to different regions and taxonomic groups. For the purposes of this study, two methodological frameworks will be applied. Firstly, a recently developed framework called EICAT (Environmental Impact Classification for Alien Taxa), developed by Blackburn et al. (2014), with guidelines subsequently developed by Hawkins et al. (2015) will be used. This approach is squarely focussed on identifying impacts to native species and communities, rather than to ecosystem function or to ecosystem services, and has been adopted by the IUCN to as a means to standardise invasive species impacts. The second approach, which is less well defined, relates to the traits associated with invasive species and invaded communities. This approach follows that used by Castro-Díez et al. (2016) in assessing the impacts of invasive plants in the Balearic Islands on ecosystem properties. In place of the primary experimental measurement of ecosystem properties carried out in there study, broad linkages between trait values and ecosystem services identified by other research (e.g. (de Bello et al., 2010; Díaz et al., 2007; Funk et al., 2017; Hevia et al., 2017; Lavorel et al., 2011) will be utilised to assess ecosystem service impacts.

### EICAT

The EICAT approach builds upon another framework, the Generic Impact Scoring System (GISS), developed by Nentwig et al. (2010) and refined in Kumschick and Nentwig (2010). EICAT extends and adapts this earlier framework to include the IUCN's Global Invasive Species Database (GISD) mechanisms of impact (see *Figure 12*). Indeed, the GISS and EICAT are now almost identical: Nentwig et al. (2016) consider EICAT as one of many on-going refinements to the GISS approach. The GISS approach categorises impacts into six categories relating to environmental impact and six categories for socio-economic impacts, with a impact level for each defined ranging from 0 (no impact) to 5 (highest possible impact) (Nentwig et al., 2016). Through summation of impacts, a species can therefore be classified with a maximum impact of 60, based upon published evidence rather than expert opinion (Nentwig et al., 2016), or, as in the case for EICAT, can be classified based on the maximum score for a single category (Blackburn et al., 2014). Impact scores should relate to observed impacts in the focal range in the first instance, although impact reports for a species in previous analysis elsewhere can be considered, providing care is taken in drawing conclusions (Nentwig et al., 2016). Although the EICAT followed the GISS approach, Blackburn et al. (2014) identify five modifications: 1) impact categories are adapted to match the categories devised for the IUCN GISD; 2) impacts considered are negative only, rather than both negative and positive for the GISS; 3) a scale with five levels rather than six is used by combining the lowest two levels in the GISS; 4) impact mechanisms and 5) as previously mentioned, the score is based on the maximum impact for a category, rather than a sum of impacts across categories.

In contrast to the GISS, the IUCN GISD framework is more qualitative and does not seek to score species impact as such. Species impacts are separated into 13 mechanisms of impact (see *Figure 12*) leading to impact outcomes, which are divided into ecosystem, species and socio-economic impacts, which in turn is sub-divided into sub-outcomes (see *Table 1*).

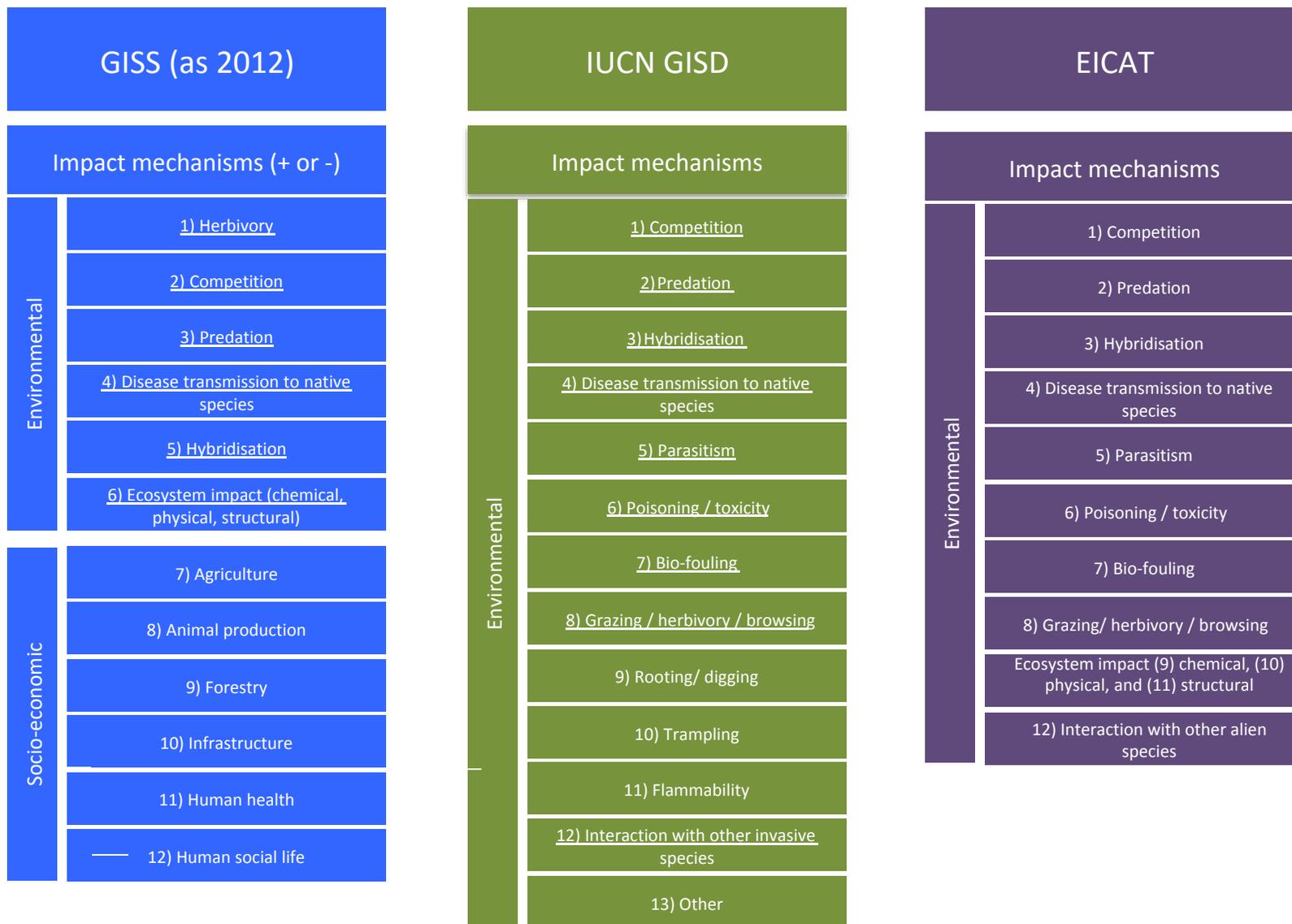
The application of category level is based on the level of biological organisation affected, from individuals to populations to communities, with the highest level of impact associated with irreversible changes at the community level (Hawkins et al., 2015). EICAT category levels include:

- 1) **Massive:** leads to local extinction and replacement of species, and irreversible changes in community composition;
- 2) **Major:** causes changes in the species composition of a community, which can be reversed if the alien species is removed;
- 3) **Moderate:** leads to reductions in population densities, but no significant changes in community composition;
- 4) **Minor:** leads to reductions in individual fitness, but no reductions in native population densities;
- 5) **Minimal:** no effect on fitness of individuals of native species

(Blackburn et al., 2014, adapted from Table 1, p.5)

A generalised decision chart developed by Hawkins et al. (2015) shows a step-wise approach to assessing impacts for each impact class (see *Figure 13*). For each species evaluated by the EICAT process there is envisaged to be a record highlighting the most severe level of impact measured, together with the level of impact measured under the current circumstances, which may vary based on natural variation or management of the species (Hawkins et al., 2015).

The EICAT approach uses the precautionary principle in assigning impact categorisation, in relation to synergistic interactions with other environmental changes where ascribing causation is unclear. In practice, this means that where changes to the native environment cannot be adequately ascribed to the invasive species or to other changes, such as climate change or land use change, the impacts will be assumed to relate to the invasive species (Blackburn et al., 2014).



**Figure 12:** Comparison between the impact mechanisms for GISS (from 2012; Kumschick et al., 2012), IUCN GISD (ISSG, 2015) and EICAT (Blackburn et al., 2014). Mechanisms underlined for GISS and IUCN GISD are directly translatable to the EICAT mechanisms.

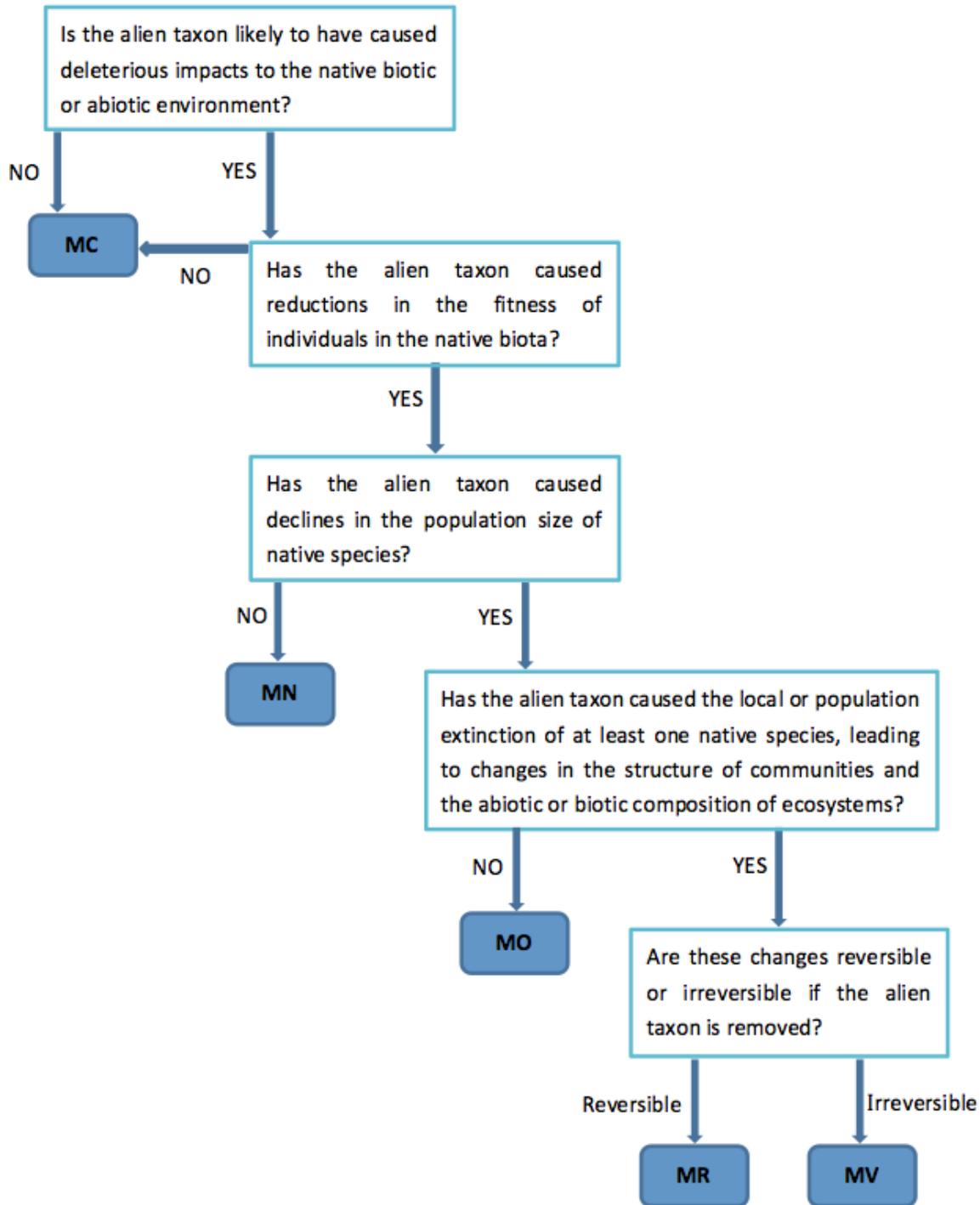


Figure 13: A decision tree showing how the EICAT classifications should be applied. From “Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT)”, Appendix S1, by Hawkins et al., 2015, *Diversity and Distributions*, Vol. 21, Issue 11, Appendix S1 p12. Copyright 2015 the authors

Finally, the framework also allows consideration of the confidence of findings, with 3 categories based on the availability and reliability of evidence (Blackburn et al., 2014):

- *High confidence*: there is direct and reliable evidence to support the assessment, which is not contradictory or controversial;
- *Medium confidence*: there is some evidence to support the assessment, but some is indirect (e.g. relating to impacts associated with other species) and / or the direction of impacts are potentially contradictory or ambiguous;
- *Low confidence*: the evidence available is limited and potentially unreliable, with no direct evidence and / or strong ambiguity

For each of the impact mechanisms the confidence of the categorisation can be assessed. In common with prior research on amphibians (Kumschick, Measey, et al., 2017) and birds (Evans, Kumschick, & Blackburn, 2016), which show the confidence relating to the impact categorisation for many species was low, given the level of information available in relation to Coralita and the secondary nature of this study, it is expected that the categorisation will likewise be low in this instance. However, to a certain extent, the ability to be able to carry out an EICAT assessment with these data limitations is itself an examination of the framework. The availability of information, particularly in remote locations, is likely to be a challenge in relation to the use of EICAT (Evans et al., 2016), so investigating the framework from this perspective can be of value.

As yet however, there appear to be few studies that have used this approach in assessing impacts (see, for example, Evans, Kumschick, & Blackburn, 2016; Kumschick et al., 2017). However, at the time of their writing, Nentwig, et al. (2016) highlighted 14 studies that have carried out a GISS impact assessment on 349 species. Although these GISS scores are not directly translatable to EICAT classifications due to differences in categories and category specifications, they are broadly equivalent (Kumschick, Vimercati, et al., 2017).

## Species trait values

The documented relationships between trait values, ecosystem process and ecosystem services for plant species allows an alternative approach to assessing invasive species. Although not formally defined, the approach is based upon the idea that invasive species alter the ecological community, which in turn impact the ecosystem process in that system (as per Castro-Díez et al., 2016). This approach is clearly very different to the EICAT framework, which is rather concerned with the impacts on species and communities, as opposed to ecosystem processes and services, and is based more indirectly on the characteristics of species, rather than the direct evidence of impact. It is important to note that there are synergies between the two approaches, which are discussed within the *Methodology* section.

The ability of a species to influence the average community trait values depends on three aspects. Firstly, the species trait values would need to be somewhat different to the community average. If this was not the case, then clearly the community average values would not expect to change radically and thus the impacts on ecosystem services would be minimal (based upon this framework). This is intuitively logical and might imply that the invasive species replaces a similar native species with minimal impact. This idea of the importance of differences between invasive species traits and communities has been demonstrated by recent research on nitrogen cycling and leaf and litter traits, which shows that it is dissimilarity with native communities rather than absolute values for traits that better predict impacts on nitrogen cycling (Lee et al., 2017). Secondly, the abundance of the invasive species within an area needs to be sufficient to alter the average trait values. Again, this is intuitively logical, in that an invasive species in an area that is relatively rare would be expected to have a commensurately smaller impact than an abundant species. This is closely linked to Grime's aforementioned biomass ratio hypothesis (Grime, 2002). Finally, the impact of an invasive species will depend upon the specific species impacted. Clearly if a keystone species is badly affected, the implications for ecosystem processes will be larger than might otherwise be the case. This implies the need for temporal data regarding species change, which, as discussed within the methodology and later during the results sections, is a challenge for this study.

This approach clearly relies on both the availability and quality of data, and the ability to generalise regarding traits and ecosystem services. On this later point, de Bello et al. (2010) highlight that several of the relationships between trait value and ecosystem services observed in their meta-analysis are not consistent, with different studies finding, for example, a positive and a negative relationship between root depth and erosion prevention. This implies that the relationships between plant traits and ecosystem services are more complex than a simple one to one correlation, with potentially interactions between traits and abiotic factors just some of the elements that could govern these relationships. As such, care needs to be taken in interpreting any findings in relation to traits and ecosystem services, with qualification regarding the ability to generalise these relationships.

# Methodology

The two methodological frameworks that were followed for this research – EICAT and species trait values – guide the analytical approach, data gathering and analytical tasks that form the methodology (see summary in *Table 2*). As discussed earlier, the availability of data acted as a constraint in relation to the types of analytical approaches associated with each framework, and to the form of analysis. The ultimate aim of the methodology was to gather sufficient information to assess Coralita’s impacts on the islands, with the limitations implied by the limited available information in mind.

**Table 2: Summary of methodology used in the research**

| Methodological framework    | Analytical approach                                 | Analysis  | Key data source (s)  |
|-----------------------------|---|---|--|
| <b>EICAT assessment</b>     | Review of comparable species impacts                | Assess relevant literature on Coralita impacts (discussed within the introduction)                          | Various including Burke & DiTommaso, 2011; Ernst & Ketner, 2007; Raju et al., 2001; van der Burg et al., 2012  |
|                             |   | Review broad impacts and mechanisms of impact from invasive plant species                                   | GISD Database - ISSG, 2015   |
|                             |   | Climbing species impacts  | CABI   |
|                             | Biodiversity assessment                             | Richness in areas with Coralita and areas without Coralita  | de Freitas et al., 2012, 2016  |
|                             | Species composition: change over time               | Assess changes to species composition by location over time   | Boldingh, 1909; de Freitas et al., 2012, 2016; Stoffers, 1956; van Aniel, van der Hoorn, Stech, Arostegui, & Miller, 2016                                |
|                             | Species composition: co-occurrence                  | Assess possible changes to species composition by location through co-occurrence analysis                   | de Freitas et al., 2012, 2016  |
| <b>Species trait values</b> | Coralita and island species trait values            | Compare Coralita with other species on the islands  | Plant species and abundance on the islands - de Freitas et al., 2012, 2016   |
|                             | Community weighted means                            | Assess the hypothetical implications for community weighted mean values of traits with and without Coralita | Relevant traits for analysis - various including de Bello et al., 2010; Sandra Díaz et al., 2007; Hevia et al., 2017; Kattge et al., 2011; Lavorel, 2013 |
|                             | Coralita and other invasive species by trait values | Assess the difference between Coralita and other invasive species   | Plant traits - TRY database - Kattge et al., 2011  |

Where necessary, data analysis was performed in R (R Core Team, 2018), with various packages employed depending upon requirements. The analysis types, together with the relevant packages are listed in the Appendices (see *Table A1*). Data entry was carried out primarily in Microsoft Excel.

## EICAT Assessment

Based on the EICAT mechanisms framework (see *Figure 12*), only the mechanisms (1) Competition; (3) Hybridization); (4) Transmission of diseases to native species; (6) Poisoning/toxicity; (9), (10) & (11) Chemical, physical, or structural impact on ecosystems; (12) Interaction with other alien species were relevant for this assessment. Guidance associated with attributing scores to mechanisms from Hawkins et al. (2015) is shown in the Appendices (see *Table A2*), with the associated approach to assigning confidence levels for categorisation shown in the Appendices (see *Table A3*). The different analytical approaches taken in relation to the EICAT assessment either aim to identify impacts that can be generalised and applied to the Coralita on the islands, or to identify impacts on specific species on the islands directly.

### Review of comparable species impacts

As discussed within the introduction, there is limited information regarding the impacts of Coralita available, beyond somewhat anecdotal information. Whilst this information is still valuable, in line with EICAT guidelines, the impacts associated with comparable species and comparable environmental circumstances may be of use in assessing the impacts associated with Coralita. What constitutes a comparable set of species and / or environmental circumstances is left somewhat ambiguous in the guidelines however. For the purposes of this study, a broad understanding of impacts related to plant species will be investigated, with gradually increasing levels of specification to tease out relevant impacts.

In the first instance, the Global Invasive Species Database (GISD), maintained by the Invasive Species Specialist Group of IUCN (2015) was mined to assess the types of impacts associated with invasive plant species. The GISD contains information for the worst invasive species, based on consultation with experts and through analysis of available data. Of the 868 species listed, more than half (468) are plant species, and of these, 252 are listed as having defined impacts, based on the impact outcomes listed in *Table 1*. The vast majority of these plant species were terrestrial (95 percent). Of the terrestrial species, there were 2,418 global locations where impacts were noted, though these were heavily skewed by location, with more than half of the locations in the USA. Finally, 28 of these species were established to be climbing species, by cross referencing these species with those listed on the TRY database (Kattge et al., 2012) and a listing maintained online by the University of Georgia's (USA) Center for Invasive Species and Ecosystem Health (Invasive.org, 2018). In order to assess whether the listed impacts for climbing species differed from those listed for non-climbing species, Barnard's exact tests were applied for each of the impact outcome types listed. Barnard's test is a means to compare categorical variables presented in a 2x2 contingency matrix (i.e. Group A: Y/N count; Group B: Y/N count) and is considered a more powerful test than the more widely used Fisher's tests (Andrés & García, 1999).

Although impact information on the GISD is collated from each of the species profiles, it is not altogether clear why some species are listed as having an impact of a certain type and not of others. As discussed below, the Centre for Agriculture and Biosciences International (CABI) invasive species compendium (CABI, 2018) appears to ascribe many more impact types to the same set of climbing species, with Coralita not listed as one of the species as having a defined impact on GISD but listed as having defined impacts on CABI. As such, it is assumed that the impacts listed for the GISD are more certain, whereas those for CABI, given the availability of knowledge regarding Coralita's impacts and the listing of impacts there, may be more speculative.

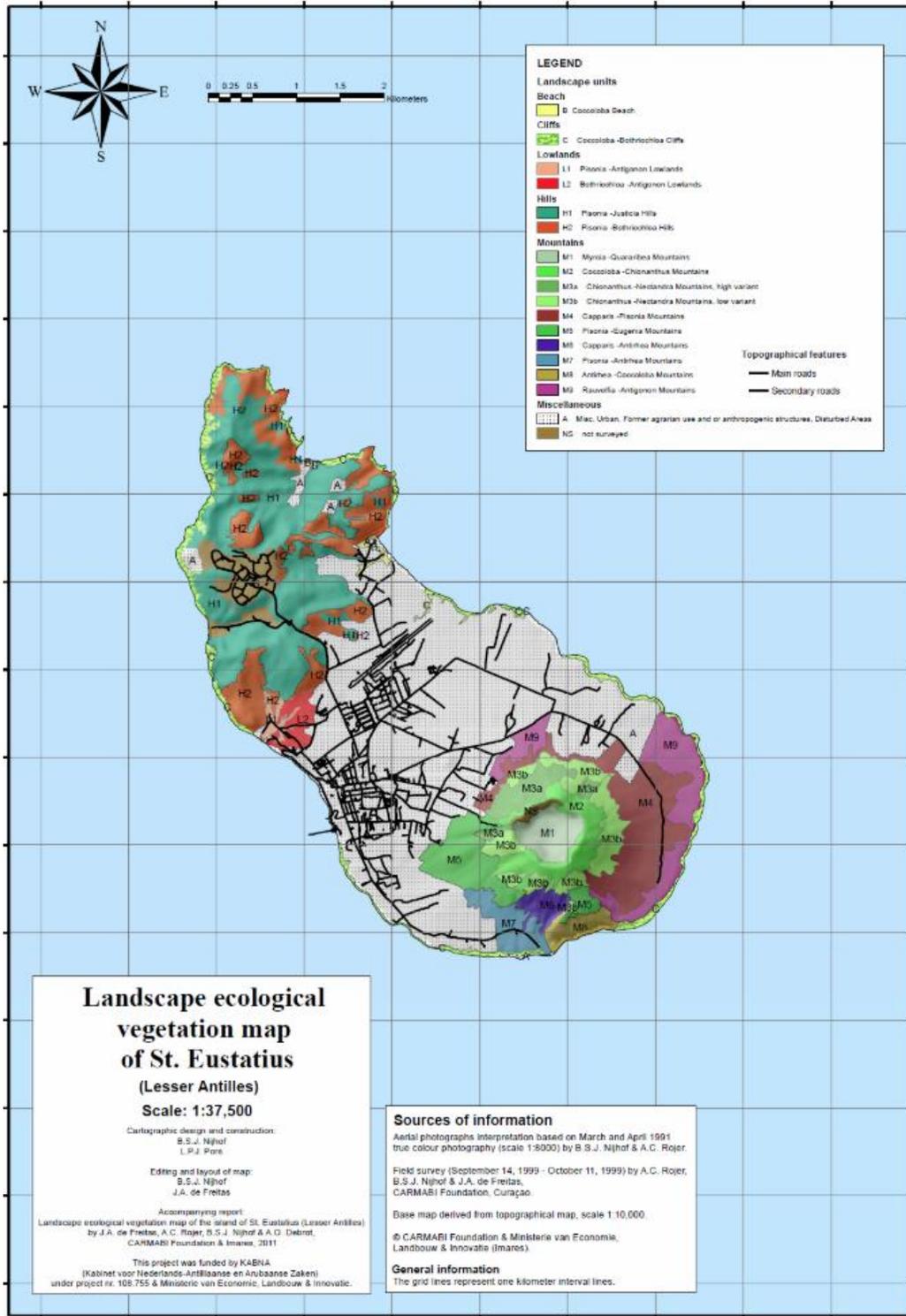
Secondly, the impacts associated with climbing species on the CABI invasive species compendium were investigated further, together with further information regarding the species characteristics and geographical extent. By narrowing the search for comparable species to those with identified impacts on the GISD database, this ensures that the comparable species has a defined impact and that there is likely to be sufficient and reliable information in relation to this species. It is worth bearing in mind that this approach potentially biases the inferred impact in relation to Coralita by this method, as the most damaging species are likely to be those for which there is the most information, and hence have impacts on the GISD database listed.

## Biodiversity richness

The reports by de Freitas et al. (2012 and 2016) (hereafter “de Freitas reports”) were used to build a picture of the species composition in different sites on the islands. Based on a number of vegetation sample plots across the islands, these studies mapped the main landscape types based on vegetation types, geology and geomorphology within each area, leading to 16 sub-landscape types in St. Eustatius and 9 different sub-landscape types on Saba (de Freitas et al., 2012, 2016) (see *Figure 14* and *Figure 15*). These sub-landscape types were associated with 12 vegetation types and 9 types respectively on the islands, based on the presence or absence of a combination of species. For each vegetation type, the species encountered within the sample plots were noted in the reports, with the frequency of occurrence of that species per plot and the average vegetation cover of that species per plot noted. Note that the average vegetation cover per plot exceeded 100 percent, as cover was based on a three dimensional space. Coralita was identified in one vegetation type in Saba and in four vegetation types on St. Eustatius, and was the dominant species for one of these vegetation types on St. Eustatius. Together, the frequency of occurrence and cover were combined to give a broad approximation of species cover by vegetation type, with vegetation cover weighted by species occurrence. As presence and cover data gathered in the reports were based on ranges, with presence noted on a scale of I to V, and cover on a scale of 1 to 10, weighted cover was simplified to be the mid-point of each range. For example, *Chorizanthe purpureus* was noted on Saba in vegetation type 1 to have a presence of V, meaning that it was found in between 81 and 100 percent of sample plots, and to have a cover of 2, meaning a vegetation cover of between 16 and 25 percent. The midpoint

weighted vegetation cover was then calculated as  $90.5\% * 20.5\% = 22.625\%$ . Overall, there were 458 species in the reports, of which 271 were listed in St. Eustatius and 317 on Saba. It is important to note that the field surveys of vegetation cover that were utilised by both reports occurred some time ago, in 1999. Although substantial changes in the vegetation composition may have occurred since this time, these sources are the only available describing species occurrence and abundance within distinct areas on both islands. It is also important to note that species compositions in more urban areas on the islands were outside the scope of the original de Freitas reports. Given Coralita is most associated with disturbed areas, this is a fundamental constraint in assessing impacts based on species abundance in the study.

Species richness a simple measure of biodiversity, can readily be calculated from these de Freitas reports based on the number of species found in vegetation groups on the islands. A comparison of species richness for locations where Coralita is found and other areas was performed with a Welch T-test to test the equivalence of species richness between the two area types.



**Landscape ecological  
vegetation map  
of St. Eustatius  
(Lesser Antilles)**

**Scale: 1:37,500**

Cartographic design and construction:  
B.S.J. Nijhof  
L.P.J. Pore

Editing and layout of map:  
B.S.J. Nijhof  
J.A. de Freitas

Accompanying report:  
Landscape ecological vegetation map of the island of St. Eustatius (Lesser Antilles)  
by J.A. de Freitas, A.C. Rojer, B.S.J. Nijhof & A.C. Dibinet,  
CARMABI Foundation & Imanet, 2011

This project was funded by KABNA  
(Kabinet voor Nederlands-Antilleanse en Arubaanse Zaken)  
under project nr. 108.755 & Ministerie van Economie, Landbouw & Innovatie.

**Sources of information**

Aerial photographs interpretation based on March and April 1991  
true colour photography (scale 1:8000) by B.S.J. Nijhof & A.C. Rojer

Field survey (September 14, 1999 - October 11, 1999) by A.C. Rojer,  
B.S.J. Nijhof & J.A. de Freitas,  
CARMABI Foundation, Curacao

Base map derived from topographical map, scale 1:10,000.

© CARMABI Foundation & Ministerie van Economie,  
Landbouw & Innovatie (Imanet).

**General information**

The grid lines represent one kilometer interval lines.

**Figure 14:** Landscape ecological map of St. Eustatius. From “A Landscape ecological vegetation map of Sint Eustatius (Lesser Antilles)” by de Freitas et al., 2012, IMARES Wageningen UR (University & Research centre), IMARES report C053/12. p34. Copyright 2012 IMARES Wageningen UR



Figure 15: Landscape ecological map of Saba. From “A Landscape ecological vegetation map of Saba (Lesser Antilles)” by de Freitas et al., 2016, IMARES Wageningen UR (University & Research centre), IMARES report C195/15. p26. Copyright 2016 IMARES Wageningen UR

## Changes in species compositions

Beyond the studies in St. Eustatius and Saba by de Freitas et al. (2012 and 2016), which form an important part of the subsequent research on traits (see below), there have been other studies over time that have catalogued species encountered on the islands. These include studies by Boldingh (1909), Stoffers (1956) and more recently on St. Eustatius only, van Andel et al. (2016). Although the information contained within these different studies is presented in slightly different ways, it is relevant to consider whether this information could be used to assess the change in species composition over time on the islands as a whole and in relation to particular areas. As such, species information was gathered from the sources, standardised to accepted species names as far as possible (according to The Plant List (2013)) and analysed for changes over time.

Species composition can also be assessed in terms of patterns of co-occurrence of species. Based on the information of species occurrence by location contained within de Freitas et al. (2012 and 2016), by comparing the species that co-occur with Coralita with those that do not co-occur with Coralita, we can assess whether there are any noticeable differences in trait values (see below) between the two. Should there be any major differences, then this may imply that Coralita is atypical and thus impacting the type of species found within an area. Additionally, by assessing the co-occurrence patterns of species that co-occur and do not co-occur with Coralita, the species that are most likely to have been excluded from an area due to Coralita could be identified.

## Trait-based analysis

The analytical approaches associated with the trait-based analysis methodological framework were based on the need to gather information on species occurrence on the islands and the plant trait information for those species.

As with the assessment of biodiversity, the second step in this approach involved assessing which plant traits would be most relevant to assessing impacts, in terms of constructing a picture of the plant community and linking this to prior work on ecosystem services. A brief literature review of studies that utilised trait information to make inferences about community composition was completed (see Appendices: *Table A4*) and compared with the availability of data on the TRY database, resulting in a set of primary traits to be requested (see and *Box 3*: The TRY database). Although the initial objective was to analyse both categorical data (e.g. leaf phenology type, plant nitrogen fixing capacity) and real-value data (e.g. plant maximum height), in order to simplify subsequent analysis, only real-value data was used (see *Table 3*).

**Table 3: Traits specifically requested from the TRY database, based on literature review**

| <b>Trait</b>   | <b>Referenced by</b>  |
|--|---|
| <b>Leaf area</b>   | Ackerly & Cornwell (2007); Baruah et al. (2017); de Bello et al. (2010); Díaz et al. (2004); Osunkoya et al. (2010)   |
| <b>Leaf carbon content per leaf dry mass</b>                       | Osunkoya et al. (2010)  |
| <b>Leaf dry mass per leaf fresh mass</b>                           | de Bello et al. (2010); Díaz et al. (2007); Hevia et al. (2017); Lavorel et al. (2011); Pfestorf et al. (2013); Tabassum & Leishman (2016); Weiher et al. (1999)  |
| <b>Leaf lifespan</b>   | Kattge et al. (2011)  |
| <b>Leaf nitrogen content per leaf area</b>                         | Leishman (1999)   |
| <b>Leaf nitrogen content per leaf dry mass</b>                     | de Bello et al. (2010); Díaz et al. (2007); Kattge et al. (2011); Lavorel et al. (2011); Leishman (1999); Osunkoya et al. (2010)  |
| <b>Leaf phosphorous content per leaf dry mass</b>                  | Kattge et al., (2011); Lavorel et al. (2011); Leishman (1999)   |
| <b>Leaf thickness</b>  | de Bello et al. (2010); Díaz et al. (2004)  |
| <b>Plant height</b>  | Ackerly & Cornwell (2007); Akasaka, Takada, Kitagawa, & Igarashi (2012); Baruah, Molau, Bai, & Alatalo (2017); de Bello et al. (2010); Díaz et al. (2004, 2007); Hevia et al. (2017); Kattge et al. (2011); Kunstler et al. (2016); Lavorel et al. (2011); Leishman (1999); Lohbeck, Winowiecki, Aynekulu, Okia, & Vågen (2018); Pfestorf et al. (2013); Shipley et al. (2006); Weiher et al. (1999)                                |
| <b>Seed dry mass</b>   | Ackerly & Cornwell (2007); Díaz et al. (2004); Hevia et al. (2017); Kattge et al. (2011); Leishman (1999); Pfestorf et al. (2013); Vile et al. (2006); Weiher et al. (1999)   |
| <b>Specific leaf area (SLA)</b>                                    | Ackerly & Cornwell (2007); Cortois, Schröder-Georgi, Weigelt, van der Putten, & De Deyn (2016); de Bello et al. (2010); Díaz et al. (2004, 2007); Hevia et al. (2017); Kattge et al. (2011); Kunstler et al. (2016); Leishman (1999); Osunkoya, Bayliss, Panetta, & Vivian-Smith (2010); Pfestorf et al. (2013); Shipley, Vile, & Garnier (2006); Tabassum & Leishman (2016); Vile, Shipley, & Garnier (2006); Weiher et al. (1999) |
| <b>Stem dry mass per stem fresh volume (stem specific density)</b> | Ackerly & Cornwell (2007); Hevia et al. (2017); Kunstler et al. (2016); Lohbeck et al. (2018); Shipley et al. (2006); Weiher et al. (1999)  |

In addition to these traits, information for species for a further set of traits were requested from the TRY database, based on the number of species for which there was information; all traits for which there were more than 3,000 species were requested. This was primarily to limit the need for further requests for information in future, given the time required for data release approval. Information was requested from the TRY database for the 252 species taken from the GISD database for which there was impact information, and for the species mentioned in the de Freitas reports, once species names had been standardised as per The Plant List (2013). Although there were a number of dataset holders that did not respond to the initial request or a subsequent email sent requesting data access, generally most information was made available as requested.

**Box 3: The TRY database (TRY, 2018)**

The TRY database is a collection of more than 350 datasets on plant traits, with trait information for almost 140,000 species. There are around 1,800 traits relating to 2.6 million individual plants, with information available on request following registration. Some information is available directly, whereas other datasets are only made available upon request from the dataset owner via the online data request tool. The TRY network is headed by the Max Planck Institute for Biodiversity, and Future Earth.

The three main objectives of TRY are:

- 1) to gather, harmonise and distribute published and unpublished data on a web-archived database;
- 2) to promote approaches aimed at understanding biodiversity and ecosystem function that use traits as a basis;
- 3) to serve as a benchmark for the calibration and validation of future global dynamic ecosystem models.

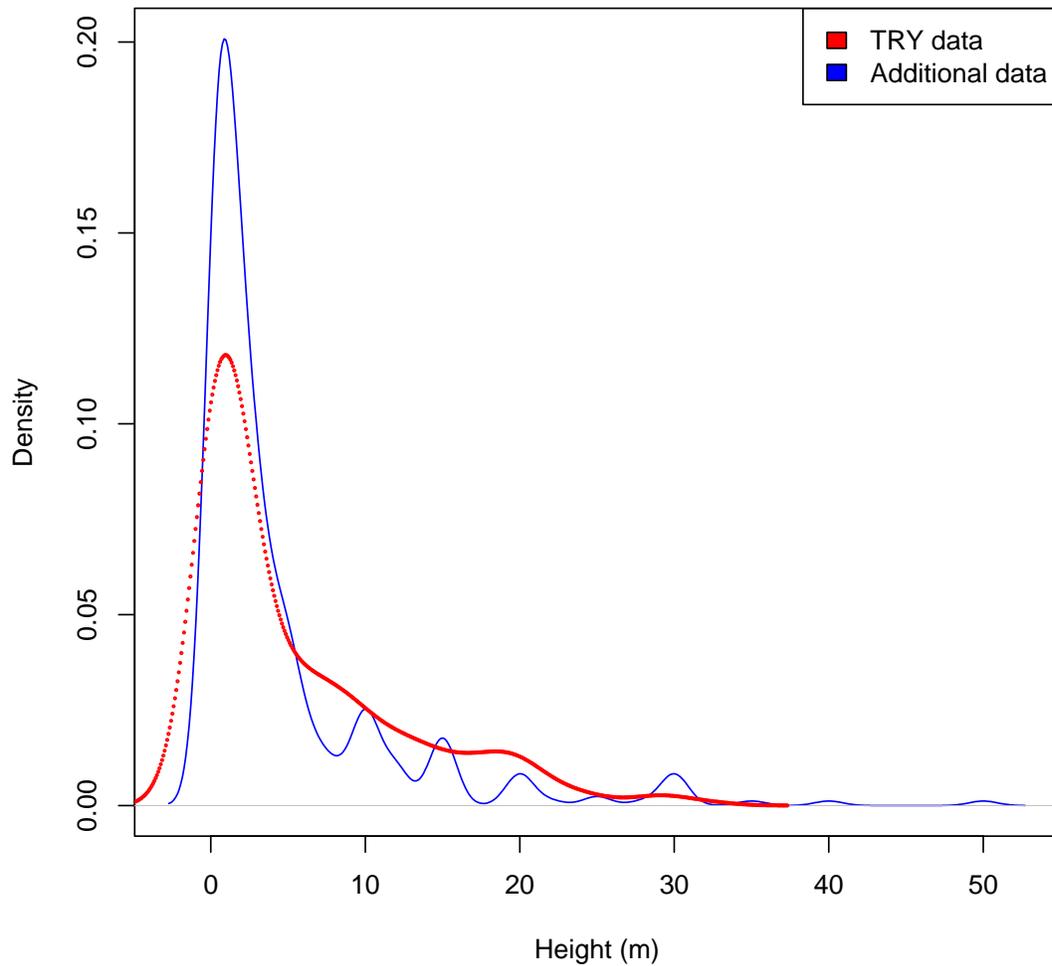
This returned a dataset contained more than 381,000 rows, which when reduced to contain only trait specific information, still contained more than 114,000 rows. For the specific traits identified, data was cleaned and standardised where necessary, and some trait values combined into a single metric (e.g. specific leaf area (SLA) is a composite of different traits on the TRY database). For the majority of the traits, standardisation had already been completed, although it is important to note that some of the data related to specific measurements, some to average measurements, some to minimums and some to maximums. As such, although the data was taken at face value, it is worth remembering that the average trait values per species are less precise than may appear. It is also important to note that there are likely duplicates in the data, which may affect the average values used for each trait for each species. For example, at least one dataset references the TRY database itself and rather less obviously it is likely that some of the datasets expand on other dataset information already contained within the database.

Overall, for the 663 species and 12 real-data traits for which information was requested, 73 percent of data was missing from the database, with up to 50 percent data coverage for seed mass and only 5 percent for leaf lifespan (see *Table 4*).

**Table 4: Data coverage for species requested from the TRY database and final data availability for analysis**

| Trait                                      | TRY percentage data availability | Final data availability for analysis | Final data availability for Saba and St. Eustatius |
|--|----------------------------------|--------------------------------------|--|
| Leaf area                                  | 36%                              | 36%                                  | 31%  |
| Leaf carbon content per leaf dry mass      | 19%                              | 19%                                  | 13%  |
| Leaf dry mass per leaf fresh mass          | 18%                              | 18%                                  | 10%  |
| Leaf longevity                             | 5%                               | 5%                                   | 4%   |
| Leaf nitrogen content per leaf area        | 20%                              | 21%                                  | 16%  |
| Leaf nitrogen content per leaf dry mass    | 32%                              | 32%                                  | 24%  |
| Leaf phosphorous content per leaf dry mass | 24%                              | 24%                                  | 21%  |
| Leaf thickness                             | 18%                              | 18%                                  | 15%  |
| Plant maximum height                       | 42%                              | 99%                                  | 98%  |
| Seed dry mass                              | 50%                              | 50%                                  | 41%  |
| Specific leaf area (SLA)                   | 34%                              | 34%                                  | 25%  |
| Stem specific density (SSD)                | 21%                              | 21%                                  | 19%  |
| All traits average                         | 27%                              | 31%                                  | 26%  |

In order to test the implications of missing data, and to improve data coverage, missing maximum plant height information was sought from various online sources, including the CABI invasive species compendium, the Tropicos database maintained by the Missouri Botanical Garden (Missouri Botanical Garden, 2018) and others (see Appendices: *Table A5*). A Mann-Whitney test was carried out to assess the equivalence of the maximum plant height data for data captured via TRY and data on height found elsewhere. The  $p$  value returned, 0.22, means that we fail to reject the hypothesis of statistical equality between the TRY and other height data groups, which is somewhat self-evident from the density plots for both sets of data (see *Figure 16*). This finding is reassuring in relation to the remainder of the dataset, as it implies that there is no clear bias in terms of data being available in the TRY database towards, for example, taller species. However, it is important to note that this does not mean that there could be no bias in relation to missing data for other traits, but it is encouraging nonetheless.



**Figure 16:** Density plots for maximum plant height for data captured via the TRY database and data from other sources

For Coralita, there was only information available on the TRY database for seed dry mass. As such, a variety of other sources were sought to complete the data (see *Table 5*). Where no external source could be found for the data, and as no trait values aside from maximum height correlated with significance with seed mass (see *Results*), the mean value for climbing species was used. This is clearly a challenging assumption to make, especially as the trait values for Coralita for which sources could be found appear to show significant differences to other climbing species, based on p-values for T-score tests. However, there were limited further options in this regard in relation to missing information for Coralita.

**Table 5: Average trait values for Coralita, sources for values, and where sources could be found, corresponding P values for T-score tests regarding the relationship between Coralita trait values and corresponding sample trait values for climbing species**

| Trait  | Value | Source                      | T-score p-values for Coralita and climbing species |
|--|-------|-----------------------------|--|
| Leaf area (mm <sup>2</sup> )                                     | 1,220 | Zahriyani & Yuwono (2014)   | 0.00*  |
| Leaf carbon content per leaf dry mass (mg g <sup>-1</sup> )      | 1.26  | Average of climbing species |  |
| Leaf dry mass per leaf fresh mass (g g <sup>-1</sup> )           | 0.36  | Priya et al. (2014)         | 0.00*  |
| Leaf longevity (month)   | 30    | Average of climbing species |  |
| Leaf nitrogen content per leaf area (g m <sup>-2</sup> )         | 1.26  | Average of climbing species |  |
| Leaf nitrogen content per leaf dry mass (mg g <sup>-1</sup> )    | 26.98 | Average of climbing species |  |
| Leaf phosphorous content per leaf dry mass (mg g <sup>-1</sup> ) | 1.68  | Average of climbing species |  |
| Leaf thickness (mm)  | 0.22  | Average of climbing species |  |
| Plant maximum height (m)   | 12    | Burke & DiTommaso (2011)    | 0.00*  |
| Seed dry mass (mg)   | 70.5  | TRY                         | 0.56   |
| Specific leaf area (SLA) (mm <sup>2</sup> mg <sup>-1</sup> )     | 24.55 | Average of climbing species |  |
| Stem specific density (SSD) (mg mm <sup>-3</sup> )               | 0.44  | Average of climbing species |  |

\* Reject the null hypothesis that Coralita is not different to other climbing species for this trait with 95% confidence

## Coralita and island species trait values

In order to assess the difference between Coralita and other islands species, mean and median trait values were calculated, with T-score tests used to assess whether Coralita trait values were significantly different from those mean values across the islands, and for Saba and St. Eustatius separately. Note that T-score tests, rather than Z-score tests, were more appropriate in this instance, given the limited data availability for some traits on each island.

In addition, in order to compare Coralita with other species more holistically, a principal component analysis (PCA) was performed on the trait values for species. PCA is a technique used to evaluate large and multidimensional datasets, extracting the most important information by creating new variables, or components, that capture the majority of variation in the dataset. These components are linear combinations of the variables in the dataset, with the first component capturing the most variation in the dataset, the second, which must be orthogonal to the first, capturing the second most and so on (for a fuller description of PCA, see Abdi and Williams (2010)). As PCA requires a complete dataset to carry out analysis, the recommended approach suggested by Dray and Josse (2015) to impute missing values through a regularised iterative PCA method was performed using the R package “missMDA” (for a summary of R packages used in this research and their authorship,

see Appendices, *Table A1*). This completed dataset was then used as input into another R package “FactomineR”, to perform the PCA, with the resulting PCA depicted in plots generated by the R packages “factoextra” and “corrplot”. In order to simplify the interpretation of the trait variables within components, a varimax rotated PCA was also performed, with the R package “psych” used for this purpose. Varimax is an orthogonal rotation method, principally developed for factor analysis but also employed in PCA, whereby the principal components are rotated to generate new components such that each new component contains a smaller number of variables describing a larger proportion of the variation (for a fuller description of varimax and other rotation methods in PCA, see Abdi (2003) or Abdi & Williams (2010)).

## Community weighted means

Community weighted mean (CWM) values for each of the traits for species on the islands were calculated in R using the package “FD”, based on the trait values sourced from the TRY database and the species abundances estimated from the de Freitas reports. In order to assess the implications of Coralita to the areas where it was observed, the CWM for trait values was also calculated for those areas, but with Coralita removed. In this way, the relative abundance of the co-occurring species with Coralita was assumed to remain constant. T-tests were then performed for each of the differences in CWM traits between the with-Coralita and without-Coralita cases, by area where Coralita was found (i.e. five areas and five differences, per trait), in order to test whether the differences were significant.

## Coralita and other invasive species trait values

In addition to the assessment of trait differences between island species and Coralita, a broader assessment of trait differences covering the entire dataset of traits (i.e. island species and GISD species) has been performed, to tease out differences between species types. This approach is more akin to the review of comparable species impacts performed as part of the EICAT assessment, and seeks to understand whether there are clear differences in trait values between GISD species and island species, between climbing species and non-climbing species, and as previously discussed above, between species that co-occur with Coralita and those that do not. As well as a PCA in relation to traits for the entire dataset (see above), various statistical tests were performed to adjudicate whether differences between groups were significant. Where sufficient data was available to assume a normal distribution, Welch T-tests were performed to test for the equivalence of two groups (Welch T-tests, as opposed to normal T-tests do not assume equal variances between groups, see (Delacre, Lakens, & Leys, 2017)). Otherwise, Mann-Whitney tests were performed to compare two

groups, with Kruskal-Wallis tests performed where more than one group was compared to first identify whether significant differences in variances could be found with the groups.

# Results

## EICAT assessment

The results of the EICAT assessment depend on the information gathered under the related species impact assessment and the assessment of changes to species composition. The following sub-sections describe the findings from this analysis, with the implications for the EICAT assessment addressed in a later sub-section.

### Comparable species impacts

The impact outcomes on the IUCN GISD database related to plant species covered a wide range of the impact outcomes listed in *Table 1*. There was an uneven spread of impact types however (see *Table 6*). Those impact categories most frequently listed, a reduction in native biodiversity and habitat degradation are both broad, with some other categories conceivably classified as sub-categories of these impact outcomes. Indeed, when species that were said to have caused a reduction in native diversity and/ or habitat degradation were excluded, there were only 54 species with at least one other type of impact.

There were no significant differences found between the number of species with impacts associated with climbing species and the number of those species that do not climb ( $p$ -values  $> 0.05$ ; fail to reject the null hypothesis that they climbing species and non-climbing species cause the same impacts). It is, however, important to remember that the absence of impact category (or mechanism of impact) associated with these species does not mean that there is no impact of that type. Rather it implies that either the species does not cause that particular type of impact or the impact has not been sufficiently categorised at this stage.

**Table 6:** Number of plant species listed on the IUCN GISD database as having an impact of some type by impact outcome, and the p-value results from a pair-wise comparison of species numbers having impacts for climbing species and non-climbing species, using Bernard's test

| Outcome type                       | Impact outcome category   | Number of species with impact | Share of total number of species with impact | P values from Barnard's tests for climbing species and non-climbing species |
|------------------------------------|---|-------------------------------|--|---|
| Environmental Ecosystem - Habitat  | Reduction in native biodiversity  | 173                           | 72%  | 0.38  |
|                                    | Habitat degradation   | 95                            | 40%  | 0.46  |
|                                    | Modification of hydrology/water regulation, purification and quality /soil moisture | 43                            | 18%  | 0.32  |
|                                    | Modification of successional patterns   | 41                            | 17%  | 0.42  |
|                                    | Modification of nutrient pool and fluxes  | 32                            | 13%  | 0.84  |
|                                    | Modification of fire regime   | 29                            | 12%  | 0.15  |
|                                    | Soil or sediment modification   | 16                            | 7%   | 0.61  |
|                                    | Habitat or refugia replacement/loss   | 12                            | 5%   | 0.23  |
|                                    | Unspecified ecosystem modification  | 11                            | 5%   | 0.61  |
|                                    | Modification of food web  | 10                            | 4%   | 0.49  |
|                                    | Modification of natural benthic communities   | 3                             | 1%   | 0.69  |
|                                    | Primary production alteration   | 2                             | 1%   | 0.84  |
|                                    | Physical disturbance  | 1                             | 0%   | 0.95  |
|                                    | Other   | 1                             | 0%   | 0.95  |
| Environmental Species - Population | Reduces/inhibits the growth of other species  | 52                            | 22%  | 0.06  |
|                                    | Plant/animal health   | 14                            | 6%   | 0.95  |
|                                    | Alteration of genetic resources   | 9                             | 4%   | 0.32  |
|                                    | Interference with reproduction  | 5                             | 2%   | 0.55  |
|                                    | Indirect mortality  | 1                             | 0%   | 0.95  |
|                                    | Population size decline   | 1                             | 0%   | 0.95  |
|                                    | Other   | 1                             | 0%   | 0.95  |
| Socio-Economic                     | Damage to agriculture   | 71                            | 30%  | 0.95  |
|                                    | Alteration of recreational use and tourism  | 26                            | 11%  | 0.69  |
|                                    | Limited access to water, land and other   | 24                            | 10%  | 0.75  |
|                                    | Damage to infrastructures   | 19                            | 8%   | 0.11  |
|                                    | Human health  | 19                            | 8%   | 0.11  |
|                                    | Reduce/damage livestock and products  | 19                            | 8%   | 0.97  |
|                                    | Human nuisance  | 16                            | 7%   | 0.97  |
|                                    | Damage to forestry  | 10                            | 4%   | 0.49  |
|                                    | Modification of landscape   | 7                             | 3%   | 0.17  |
|                                    | Other economic impact   | 6                             | 3%   | 0.88  |
|                                    | Damage to aquaculture/mariculture/ fishery  | 5                             | 2%   | 0.55  |
|                                    | Other livelihoods   | 4                             | 2%   | 0.61  |

For the mechanisms of impact listed on the GISD database for plant species, by far the most likely mechanism was competition (see *Table 7*). As with impact outcomes, we fail to reject the null hypothesis that the climbing species and non-climbing species are as likely to have the same mechanisms of impact ( $p$ -values  $> 0.05$ ).

**Table 7:** Number of plant species listed on the IUCN GISD database as having at least one mechanism of impact by mechanism, and the p-value results from a pair-wise comparison of species numbers having impacts for climbing species and non-climbing species, using Bernard's test

| Impact mechanism category               | Number of species with mechanism | Share of total number of species with mechanism | Pair-wise comparison P values from Barnard's tests for climbing species and non-climbing species |
|---|----------------------------------|---|--|
| Competition                             | 205                              | 97%   | 0.84   |
| Interaction with other invasive species | 28                               | 13%   | 0.15   |
| Flammability                            | 25                               | 12%   | 0.21   |
| Poisoning/Toxicity                      | 17                               | 8%  | 0.12   |
| Disease transmission                    | 16                               | 8%  | 0.60   |
| Hybridisation                           | 9                                | 4%  | 0.32   |
| Other                                   | 8                                | 4%  | 1.00   |
| Parasitism                              | 5                                | 2%  | 0.06   |
| Rooting/Digging                         | 5                                | 2%  | 0.50   |
| Predation                               | 3                                | 1%  | 0.68   |
| Bio-fouling                             | 1                                | 0%  | 0.92   |
| Grazing/Herbivory/Browsing              | 1                                | 0%  | 0.92   |

The further information on impacts accessed from the CABI species compendium for the 26 climbing species identified highlights a much wider variety of impacts, and impact mechanisms than shown on the GISD database (see *Table 8* and complete table by species in Appendices: *Table A6*). For example, for *Abrus precatorius*, the GISD database includes a single habitat impact outcome: modification of nutrient pools and fluxes. In contrast, CABI lists seven different impact outcomes, including altered trophic levels, damaged ecosystem services, ecosystem change/ habitat alteration, negatively impacts human health, negatively impacts animal health, reduces native biodiversity and threat to / loss of native species. As might be expected based on the growth form of climbing vines, for nearly all species the potential to smother native vegetation and form impenetrable thickets forms a key part of the invasive species impact. In several cases (e.g. *Abrus precatorius*, *Cardiospermum grandiflorum*) either the seeds or other parts of the plants are toxic to humans or animal species, which does not appear to be the case in relation to Coralita. Where mentioned, the majority of species appear to favour disturbed ground rather than closed canopy, and like Coralita many species appear to be able to spread both vegetatively and by seed.

**Table 8: Impact outcomes and impact mechanisms for the GISD species listed as having an impact on the GISD database, with data from the CABI invasive species compendium**

| Impact outcome  |                   | Impact mechanism  |                   |
|---|-------------------|---|-------------------|
| Type  | Number of species | Type  | Number of species |
| Reduced native biodiversity   | 21                | Competition - monopolising resources                                | 18                |
| Ecosystem change /habitat alteration                                | 17                | Competition - shading   | 14                |
| Threat to / loss of species   | 16                | Competition - smothering  | 14                |
| Damaged ecosystem services  | 13                | Rapid growth  | 13                |
| Monoculture formation   | 12                | Competition - strangling  | 8                 |
| Modification of successional patterns                               | 11                | Rooting   | 5                 |
| Negatively impacts agriculture                                      | 10                | Causes allergic responses   | 4                 |
| Reduced amenity values  | 9                 | Poisoning   | 4                 |
| Threat to/ loss of endangered species                               | 9                 | Produces spines, thorns or burrs                                    | 3                 |
| Negatively impacts animal health                                    | 8                 | Hybridisation   | 2                 |
| Negatively impacts forestry   | 8                 | Interaction with other species                                      | 2                 |
| Negatively impacts human health                                     | 7                 | Allelopathic  | 1                 |
| Modification of nutrient regime                                     | 6                 | Herbivory / grazing/ browsing                                       | 1                 |
| Modification of fire regime   | 5                 | Pest and disease transmission                                       | 1                 |
| Negatively impacts tourism  | 5                 |   |                   |
| Host damage   | 4                 |   |                   |
| Negatively impacts livelihoods                                      | 4                 |   |                   |
| Altered trophic level   | 3                 |   |                   |
| Infrastructure damage   | 3                 |   |                   |
| Modification of hydrology   | 2                 |   |                   |
| Damages animal/plant products                                       | 1                 |   |                   |
| Negatively impacts aquaculture/fisheries                            | 1                 |   |                   |
| Negatively impacts cultural/traditional practices                   | 1                 |   |                   |
| <b>Total number of species for which data was available on CABI</b> | <b>20</b>         | <b>Total number of species for which data was available on CABI</b> | <b>20</b>         |

It is clear that extrapolating all of these broad impacts to Coralita would suggest a serious issue for the islands, although it is important to note that there is overlap between impact outcomes evident: e.g. reduction in native biodiversity and negatively impacts native species. Like Coralita, the majority of these species have the potential to invade disturbed areas and the edges of non-disturbed areas, potentially forming mono-culture-type thickets as native vegetation is overtopped and smothered. The impacts highlighted on the GISD database and in further research summarised by CABI also highlight the worst-case scenario for species invasion impacts. The choice of species to represent Coralita impacts in this instance, based on the different abiotic and biotic conditions faced by the invading species seems somewhat challenging. None of these 20 species for which there was information on CABI are from the same *Polygonaceae* family, and even if this was the case it would be

hard to justify the use of this species as an analogue, given the differences with the family, which comprises herbs, shrubs, woody vines and trees (Frye & Kron, 2003). In addition, the distribution of the climbing species is broadly similar, with most species invasive in tropical areas where soil is well drained. Rather, in this instance, a broad understanding of the capacity for invasive impacts in relation to species competition, and impacts on biodiversity and habitat change seems to exist for Coralita as it does for these invasive climbing vines and other invasive species.

## Biodiversity richness

The number of species found by vegetation type in the de Freitas reports is shown in *Table 9*: clearly some vegetation areas have greater species richness than others.

**Table 9:** Number of species identified by de Freitas et al. (2012, 2016) in each vegetation area on Saba and St. Eustatius. Bold relates to areas where Coralita was identified

| Saba            |                   |   | St. Eustatius           |                   |   |
|-----------------|-------------------|---|-------------------------|-------------------|---|
| Vegetation area | Number of species | Maximum share of vegetation by the dominant species | Vegetation area         | Number of species | Maximum share of vegetation by the dominant species |
| Saba 1          | 79                | 4%  | St. Eustatius 1         | 36                | 7%  |
| Saba 2          | 91                | 7%  | <b>St. Eustatius 2</b>  | <b>70</b>         | 4%  |
| Saba 3          | 118               | 6%  | St. Eustatius 3         | 94                | 5%  |
| Saba 4          | 90                | 4%  | St. Eustatius 4         | 86                | 7%  |
| Saba 5          | 87                | 7%  | St. Eustatius 5         | 103               | 4%  |
| Saba 6          | 72                | 9%  | St. Eustatius 6         | 43                | 8%  |
| <b>Saba 7</b>   | <b>62</b>         | 6%  | St. Eustatius 7         | 41                | 10%   |
| Saba 8          | 40                | 28%   | <b>St. Eustatius 8</b>  | <b>87</b>         | 5%  |
| Saba 9          | 48                | 11%   | <b>St. Eustatius 9</b>  | <b>50</b>         | 11%   |
|                 |                   |   | <b>St. Eustatius 10</b> | <b>30</b>         | 28%   |
|                 |                   |   | St. Eustatius 11        | 32                | 29%   |
|                 |                   |   | St. Eustatius 12        | 45                | 13%   |
|                 |                   |   | St. Eustatius 13        | 26                | 37%   |

At first glance it would seem that areas where Coralita is found have a lower number of species, especially for vegetation types 9 and 10 on St. Eustatius. However a Welch T-test to assess whether the number of species differs significantly between the Coralita and non-Coralita sites generates a p-value of 0.59, which means that we can not reject the null hypothesis that the mean species numbers

in areas where Coralita is found and areas where it is not found are the same. A similar Welch T-test comparison between species richness on Saba and St. Eustatius, also generates a non-significant p-value (0.10). Despite this, it is worth noting that areas in vegetation type 10 on St. Eustatius have Coralita as the dominant species type, with other vegetation types having a least an order of magnitude difference in the relative share of Coralita compared to other species. The correlation between the maximum share of the dominant species is strong (-0.71) and highly significant (p-value 0.0002), which shows that the larger the share of the dominant species, Coralita or otherwise, the lower the species richness expected.

## Species composition: change over time

After construction of a database highlighting the observed species types that could be readily found in per area and converted to species names from the TRY database Boldingh (1909), Stoffers (1956), de Freitas et al. (2012 and 2016) and van Andel et al. (2016), it is clear to see that the scope of the species assessment varied (see *Table 10*). Whereas Boldingh (1909) and de Freitas et al. (2012 and 2016), and Stoffers (1956) gathered information on all species identified in particular areas / plots, van Andel et al. (2016) limited the detailed description of species observed to tree species on St. Eustatius. Note that for several species, no equivalent species could be found on the TRY database: in some instances the species name was not recognized on the list of plant names as an accepted or synonym according to The Plant List (2013) (e.g. *Mapourea eustatiana*) or more likely, the species was not as yet listed on TRY (e.g. *Tolumnia velutina*). In some cases species were not defined beyond their genus by authors, and whilst these may have been listed on the TRY database, there would be some incongruity with species listed by others when the full species name was used.

**Table 10:** Summary of species numbers and comparison with species types listed by de Freitas (2012 and 2016), from Boldingh (1909), Stoffers (1956) and van Andel et al. (2016). Note that species numbers refer to species that could be identified and matched with those listed on the TRY database

|                      |   | Boldingh | Stoffers | de Freitas | van Andel |
|----------------------|---|----------|----------|------------|-----------|
| <b>Saba</b>          | Species numbers   | 365      | 311      | 312        | NA        |
|                      | Species not found by de Freitas et al. (2016)   | 79       | 64       | NA         | NA        |
|                      | Species found by de Freitas et al. (2016), but not noted by this source – Saba          | 60       | 59       | NA         | NA        |
| <b>St. Eustatius</b> | Species numbers   | 319      | 291      | 264        | 68        |
|                      | Species not found by de Freitas et al. (2012) – St. Eustatius                           | 79       | 59       | NA         | 16        |
|                      | Species found by de Freitas et al. (2012), but not noted by this source – St. Eustatius | 94       | 125      | NA         | NA        |
| <b>Both</b>          | Species numbers   | 215      | 174      | 139        | NA        |

What is striking from this analysis is the number of species that have either been identified by de Freitas et al. (2012 and 2016) and not by the other sources, and the number of species that vice versa were identified by other sources but not by de Freitas et al. (2012 and 2016). In part this is a reflection of the different areas sampled: species data for Bolding (1909) and Stoffers (1956) covered the entirety of the islands (as far as possible), whereas de Freitas et al. (2012 and 2016) did not gather information for species in urban areas. This is particularly important on St. Eustatius, where a substantial proportion of the surface area was excluded (see *Figure 14*).

For the areas of St. Eustatius where de Freitas et al., (2012) identified Coralita as dominant (L1 and L2 in *Figure 14*), van Andel et al. (2016) noted that the same types of species were found during their assessment. Although difficult to judge given the information available, a similar area was said to be dominated by *Croton* species (e.g. *Croton Flavens*) by Stoffers (1956). Although *Croton flavens* was said to occur in other areas, de Freitas did not note it as a species (or indeed any other species of *Croton*) in these areas. Assuming at least some overlap, this suggests that the community composition of this area may have changed. Whether this is a result of invasion by Coralita or another mechanism, such as human disturbance, is unclear.

Thus, having spent substantial effort in compiling a database with species information from the various reports, unfortunately it would appear that the differences in species compositions appear to be too different to assess potential changes over time. There is no clear trajectory in the data over time, and it is clear that the differences between compositions are as likely due to the different locations surveyed as actual changes in compositions. Although a disappointing result, this again highlights the issue of data availability and comparability when attempting to assess invasive species impacts over time.

## Species composition: co-occurrence

Based on the information on species types and location contained within the de Freitas reports, it is possible to inspect the relative co-occurrence of species on the islands and make inferences about competitive exclusion as a result of Coralita extent.

A matrix depicting the co-occurrence of species across the islands was developed, enabling the identification of species that did not co-occur with Coralita, but did co-occur with species that Coralita co-occurred with. As might be expected, given the overlap between species within sites, there were a large number of species that fit the criterion of not co-occurring with Coralita but co-occurring with at least one species that did: 252, which is more than half of the total number species analysed. *Table 11* shows the species that co-occur with the most number of species that co-occur with Coralita, but do not co-occur themselves; also shown is the number of times that these the species co-occurs with species that co-occur with Coralita (i.e. includes co-occurring with the same species in different areas).

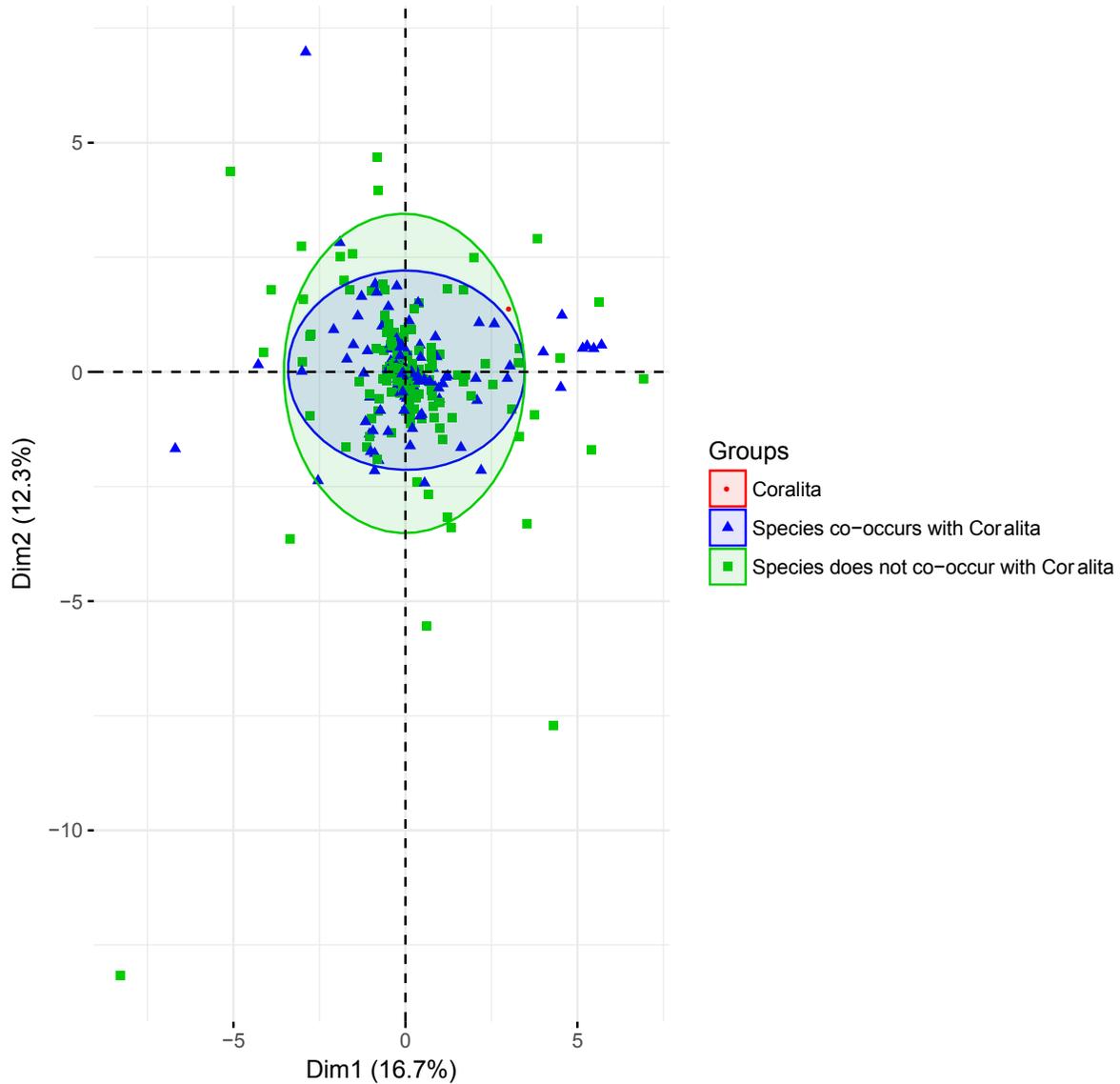
**Table 11:** Species that do not co-occur with Coralita, but do occur with different species that do co-occur. Listed are the species that co-occur with the most number of species that also co-occur with Coralita.

|                                   | Different species        |      | Different occurrences        |      |
|-----------------------------------|--------------------------|------|------------------------------|------|
|                                   | No. of different species | Rank | No. of different occurrences | Rank |
| <i>Tragia volubilis</i>           | 138                      | 1    | 357                          | 1    |
| <i>Capparis baducca</i>           | 119                      | 2    | 197                          | 8    |
| <i>Ipomoea tiliacea</i>           | 118                      | 3    | 319                          | 2    |
| <i>Cheilanthes microphylla</i>    | 118                      | 4    | 155                          | 22   |
| <i>Guettarda odorata</i>          | 118                      | 5    | 190                          | 11   |
| <i>Phoradendron trinervium</i>    | 116                      | 6    | 246                          | 3    |
| <i>Annona muricata</i>            | 112                      | 7    | 239                          | 4    |
| <i>Celtis iguanaea</i>            | 112                      | 8    | 166                          | 21   |
| <i>Schaefferia frutescens</i>     | 112                      | 9    | 137                          | 32   |
| <i>Physalis angulata</i>          | 109                      | 10   | 144                          | 25   |
| <i>Melicoccus bijugatus</i>       | 103                      | 11   | 191                          | 10   |
| <i>Euphorbia tithymaloides</i>    | 103                      | 12   | 172                          | 19   |
| <i>Microgramma heterophylla</i>   | 102                      | 13   | 235                          | 5    |
| <i>Pavonia spinifex</i>           | 99                       | 14   | 169                          | 20   |
| <i>Pithecellobium unguis-cati</i> | 96                       | 15   | 173                          | 18   |

The sheer number of species highlighted by this approach limits the ability to suggest that Coralita has had a deleterious impact on these species. However, for the 29 species that co-occur in the area identified by de Freitas et al. (2012) as having the largest relative abundance of Coralita (Area 10 on St. Eustatius), each of the species listed in *Table 11* co-occurs with a minimum of 9 species (*Microgramma heterophylla*), up to a maximum of 24 species (*Euphorbia tithymaloides*). None of the species are identified as climbing vines, suggesting that if Coralita had a role in either displacing or preventing the growth of these species, it was not via simple replacement of like-for-like species. Although for these species competitive exclusion could be a reason that they are not found in the areas where Coralita is found, it could also reflect different other factors, such as the abiotic conditions not being suitable for that species.

Borrowing from the principal component analysis below for species traits on the islands (see subsection *Trait based analysis* for a fuller description), it is possible to interpret the implications for co-occurrence with Coralita on species via the plant traits at a group rather than species level (see *Figure 17*, and Appendices: *Figure A1*, *Figure A2*, *Figure A3* and *Figure A4* for similar plots for other principal components). As the 95 percent confidence ellipse for co-occurring species is enclosed with the ellipse for species that do not co-occur, this suggests that co-occurring species are not

substantially different to other species on the islands. In this sense, Coralita does not appear to have an impact on types of species in the areas that it is found. However, one could also argue that the variation in species in the areas where Coralita is found is less than for other species on the islands, which might imply some impact on the variability of traits as a result of Coralita. Of course, this is may also simply reflect the variation in environmental and ecological conditions on the islands, as previously discussed, which could be more variable in places where Coralita is not found.



**Figure 17:** Principal component analysis projections of island individual species on the first two principal components, with groupings of species by species that co-occur and those that do not co-occur with Coralita

## EICAT classification

As permitted under the EICAT framework, in the absence of suitable impact information for the specific species in the specific location considered, comparable species impacts can be inferred. For the purposes of this assessment, climbing species that have a defined impact on the GISD database have been used for this purpose. Although information from the GISD database is somewhat sparse and gives no real indication of differences between climbing species and non-climbing species, the data from the CABI invasive species compendium provide a range of impacts that are associated with invasive climbing species, many of which would be relevant to Coralita. Whilst climbing species can have very different characteristics, the types of impact are likely to be fairly similar given the growth life form. As shown in *Table 8*, climbing species often outcompete other species by monopolising resources and by shading and smothering. This then has the impact of reducing native biodiversity habitats and individual species.

Direct impacts on biodiversity from the observation of Coralita in an area in terms of species richness are not generally observable in the dataset. However, the data appears to demonstrate the fact that the existence of a very dominant species reduces the overall number of species in an area. For one of the vegetation types, Coralita is the dominant species, and as a consequence the number of species in those areas was comparatively low. However it is not possible given the quantity and quality of data to assess whether the dominance of Coralita is especially deleterious to biodiversity in comparison to the dominance of other species, although it is important to note that Coralita can become dominant and thus negatively influence biodiversity.

Although the ability to make inferences about the impact of Coralita on species and vegetation composition over time is limited by the comparability of datasets, it is possible to investigate the potential impacts on species by inspecting co-occurrence patterns. Some species have been identified that could potentially have been excluded from plots where Coralita was found, based on the number of species that they co-occur with that also co-occur with Coralita. However, the validity of this finding is reduced through the examination of species traits through principal component analysis, which finds no clear relationship between a species co-occurring and a difference in trait values.

Based on the EICAT framework, and assuming these climbing species constitute comparable species and based on knowledge about Coralita, the impact mechanisms of (1) Competition and (9), (10) & (11) Chemical, physical, or structural impact on ecosystems are the most relevant for Coralita. Basing the level of impact on the CABI data would suggest that a massive impact is likely, although this is rather imprecise, as it would imply that the impact for all invasive vines would likewise be deleterious in all locations. Likewise, the assessment of biodiversity impacts suggests that Coralita has the potential to become a dominant species and this impact biodiversity levels in terms of species richness to a significant extent. The investigation of specific information regarding the

impact on species via examination of co-occurrence is somewhat inconclusive, as although there are species that would appear to be competitively excluded, the differences in species by whether they co-occur or not does not seem substantial. Based on these considerations, the classification of the impact level would therefore be set at moderate (leads to reductions in population densities, but no significant changes in community composition), given comparable species impacts, (potential) biodiversity impacts and species co-occurrence information. Clearly the categorisation of confidence in these findings would be low at best, and arguably could be such that the EICAT could not be performed due to lack of information (classified as DD, data deficient).

## Trait-based analysis

### Coralita and island species trait values

*Table 12* shows the mean, median and standard error for trait values for both of the islands, and Saba and St. Eustatius separately. As the standard error depends on the mean of the data, the relative standard error (SE/mean) has also been calculated to give an indication as to how variable the data is for a given trait compared to other traits. It is clear from cursory examination of the mean and median values that the distribution of trait values is heavily skewed in some instances (e.g. leaf area, plant maximum height). For some traits there is also large data spread, influenced by outlying values (e.g. seed dry mass, leaf longevity). The skew and spread of data can more clearly be seen in *Figure 18* and *Figure 19*, which also shows the relative position of Coralita within the distributions. In some instances, Coralita appears to reflect the median value of the data (e.g. leaf area, leaf nitrogen content per leaf dry mass, leaf thickness), whereas in other cases, Coralita is less typical of the dataset (e.g. height, leaf lifespan). The p values associated with T-scores to show the relative location of Coralita within the data for each trait seem to imply that for most traits, Coralita would be far enough removed from the mean value such that it could be considered different from the distribution. The non-normal distribution for most traits however means such a finding is perhaps less reliable than visual inspection of the trait distributions (N.B. log transformation of the data and subsequent testing, does not change these findings).

Between islands, the differences in summary statistics appear relatively minor. This in part reflects the fact that a large number of species observed by de Freitas et al. (2012, 2016) on both islands: 139 species are found on both islands, which represents 45 percent of species on Saba and 53 percent of species on St. Eustatius. There are some differences however, with leaf area noticeably greater both in mean and median terms on Saba, and a substantially greater variation in seed mass on Saba, influenced to a large part by the observation of mango (*Mangifera indica* – dry seed mass 16.5g) on Saba but not on St. Eustatius in the areas surveyed by de Freitas et al. (2012, 2016).

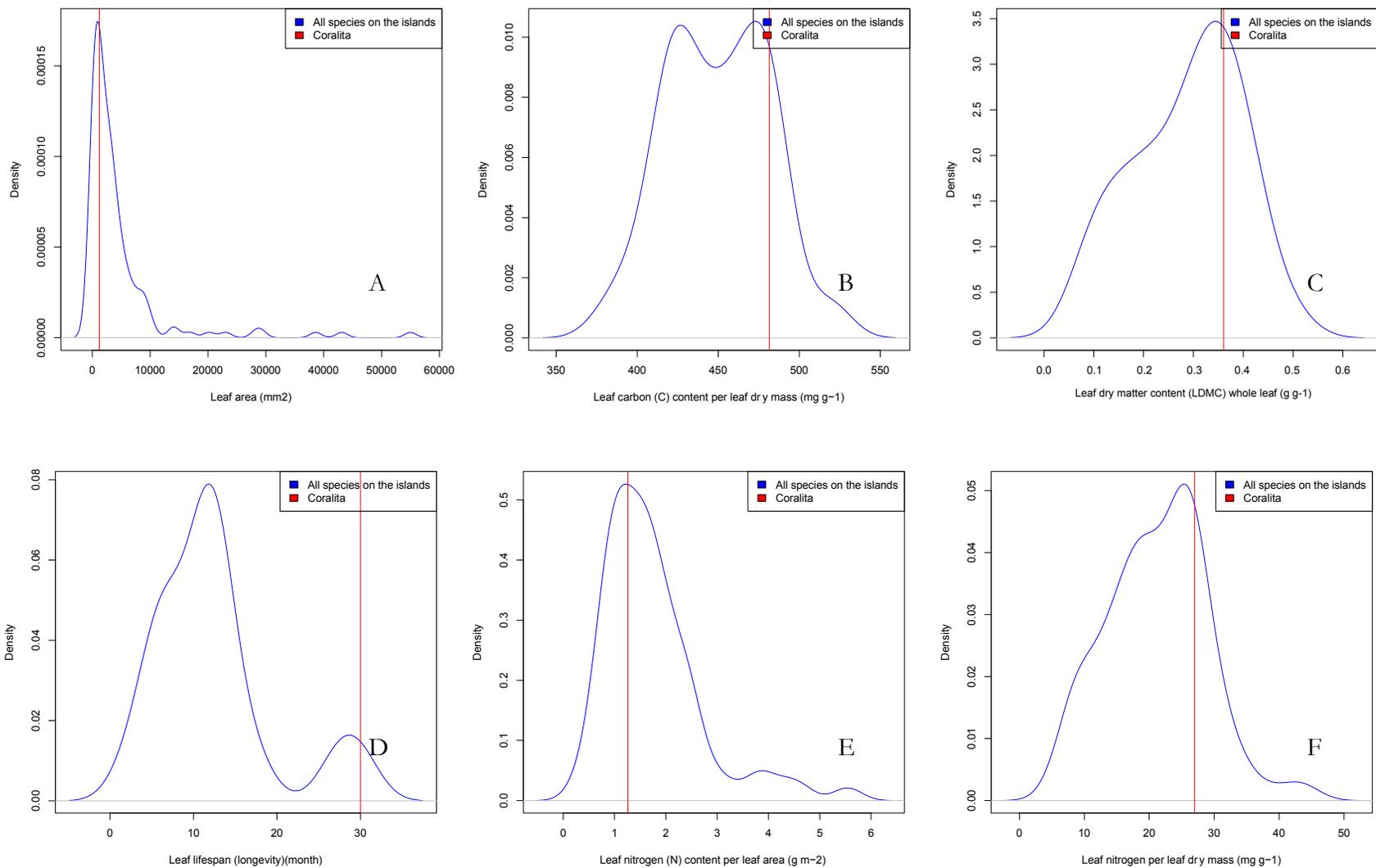
**Table 12:** Mean, median, standard error and relative standard error for trait values for Saba, St. Eustatius and both islands. Coralita trait values are shown for comparison, with p values associated with the T-score for Coralita for that trait by location

| Location            | Trait   | Mean trait values | Median trait values | Standard error trait value | Relative standard error | Coralita trait value | T-score p value |
|---------------------|---|-------------------|---------------------|----------------------------|-------------------------|----------------------|-----------------|
| <b>Both islands</b> | Leaf area (mm <sup>2</sup> )                                    | 4611.08           | 2340.03             | 686.57                     | 14.89%                  | 1220.00              | 0.00*           |
|                     | Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | 449.53            | 449.59              | 4.23                       | 0.94%                   | 481.51               | 0.00*           |
|                     | Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )   | 0.29              | 0.31                | 0.02                       | 5.74%                   | 0.36                 | 0.00*           |
|                     | Leaf longevity (month)  | 12.24             | 12.00               | 1.74                       | 14.25%                  | 30.00                | 0.00*           |
|                     | Leaf nitrogen (N) content per leaf area (g m <sup>-2</sup> )    | 1.74              | 1.58                | 0.12                       | 6.76%                   | 1.26                 | 0.00*           |
|                     | Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | 21.24             | 21.64               | 0.75                       | 3.54%                   | 26.98                | 0.00*           |
|                     | Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> ) | 1.56              | 1.35                | 0.10                       | 6.47%                   | 1.67                 | 0.26            |
|                     | Leaf thickness (mm)   | 0.26              | 0.22                | 0.03                       | 12.66%                  | 0.22                 | 0.19            |
|                     | Plant maximum height (m)  | 4.75              | 2.00                | 0.30                       | 6.38%                   | 12.00                | 0.00*           |
|                     | Seed dry mass (mg)  | 199.58            | 4.90                | 95.21                      | 47.71%                  | 70.50                | 0.18            |
|                     | SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | 18.55             | 17.11               | 0.93                       | 5.03%                   | 24.55                | 0.00*           |
|                     | Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.63              | 0.62                | 0.02                       | 2.99%                   | 0.44                 | 0.00*           |
| <b>Saba</b>         | Leaf area (mm <sup>2</sup> )                                    | 4741.85           | 2340.03             | 849.78                     | 17.92%                  | 1220.00              | 0.00*           |
|                     | Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | 449.12            | 448.90              | 4.30                       | 0.96%                   | 481.51               | 0.00*           |
|                     | Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )   | 0.27              | 0.28                | 0.02                       | 8.50%                   | 0.36                 | 0.00*           |
|                     | Leaf longevity (month)  | 11.70             | 12.00               | 2.61                       | 22.32%                  | 30.00                | 0.00*           |
|                     | Leaf nitrogen (N) content per leaf area (g m <sup>-2</sup> )    | 1.63              | 1.50                | 0.13                       | 7.76%                   | 1.26                 | 0.01*           |
|                     | Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | 20.94             | 21.48               | 0.82                       | 3.92%                   | 26.98                | 0.00*           |
|                     | Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> ) | 1.55              | 1.36                | 0.12                       | 8.02%                   | 1.67                 | 0.32            |
|                     | Leaf thickness (mm)   | 0.27              | 0.21                | 0.04                       | 16.15%                  | 0.22                 | 0.21            |
|                     | Plant maximum height (m)  | 4.75              | 2.00                | 0.36                       | 7.51%                   | 12.00                | 0.00*           |
|                     | Seed dry mass (mg)  | 226.52            | 5.14                | 140.02                     | 61.81%                  | 70.50                | 0.27            |
|                     | SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | 20.00             | 17.65               | 1.18                       | 5.91%                   | 24.55                | 0.00*           |
|                     | Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.60              | 0.61                | 0.02                       | 3.32%                   | 0.44                 | 0.00*           |

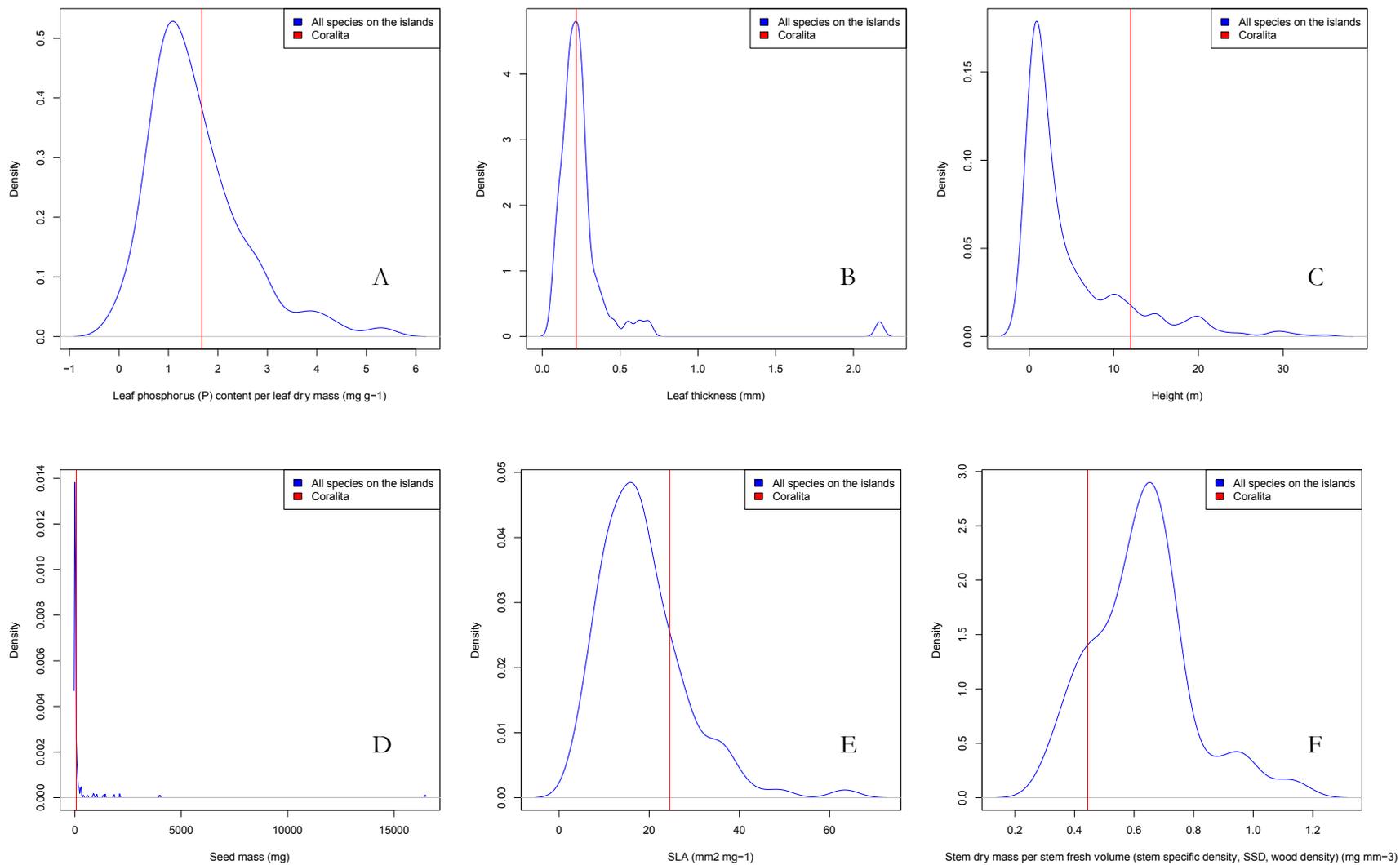
**Table 12. (cont.)**

| Location      | Trait   | Mean trait values | Median trait values | Standard error trait value | Relative standard error | Coralita trait value | T-score p value |
|---------------|---|-------------------|---------------------|----------------------------|-------------------------|----------------------|-----------------|
| St. Eustatius | Leaf area (mm <sup>2</sup> )                                    | 3510.63           | 1880.79             | 506.14                     | 14.42%                  | 1220.00              | 0.00*           |
|               | Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | 447.54            | 446.64              | 5.48                       | 1.22%                   | 481.51               | 0.00*           |
|               | Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )   | 0.32              | 0.34                | 0.02                       | 6.04%                   | 0.36                 | 0.03*           |
|               | Leaf longevity (month)  | 13.26             | 12.00               | 2.10                       | 15.81%                  | 30.00                | 0.00*           |
|               | Leaf nitrogen (N) content per leaf area (g m <sup>-2</sup> )    | 1.92              | 1.63                | 0.17                       | 8.63%                   | 1.26                 | 0.00*           |
|               | Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | 21.77             | 22.28               | 1.04                       | 4.78%                   | 26.98                | 0.00*           |
|               | Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> ) | 1.63              | 1.35                | 0.12                       | 7.59%                   | 1.67                 | 0.70            |
|               | Leaf thickness (mm)   | 0.21              | 0.20                | 0.02                       | 7.89%                   | 0.22                 | 0.84            |
|               | Plant maximum height (m)  | 4.92              | 2.00                | 0.38                       | 7.64%                   | 12.00                | 0.00*           |
|               | Seed dry mass (mg)  | 105.48            | 5.77                | 29.02                      | 27.52%                  | 70.50                | 0.23            |
|               | SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | 17.69             | 16.51               | 1.24                       | 7.02%                   | 24.55                | 0.00*           |
|               | Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.64              | 0.65                | 0.02                       | 3.54%                   | 0.44                 | 0.00*           |

\* Reject the hypothesis that Coralita is a member of the same population for this trait, with 95% confidence



**Figure 18:** Density distributions of trait values for species noted by de Freitas on Saba and St. Eustatius. (A) Leaf area; (B) Leaf carbon per leaf dry mass (C) Leaf dry mass per leaf fresh mass; (D) Leaf longevity; (E) Leaf nitrogen content per leaf area; and (F) Leaf nitrogen content per leaf dry mass



**Figure 19:** Density distributions of trait values for species noted by de Freitas on Saba and St. Eustatius. (A) Leaf phosphorous content per leaf dry mass; (B) Leaf thickness; (C) Plant maximum height; (D) Seed mass; (E) Stem dry mass per stem fresh volume (SLA); and (F) Stem specific density

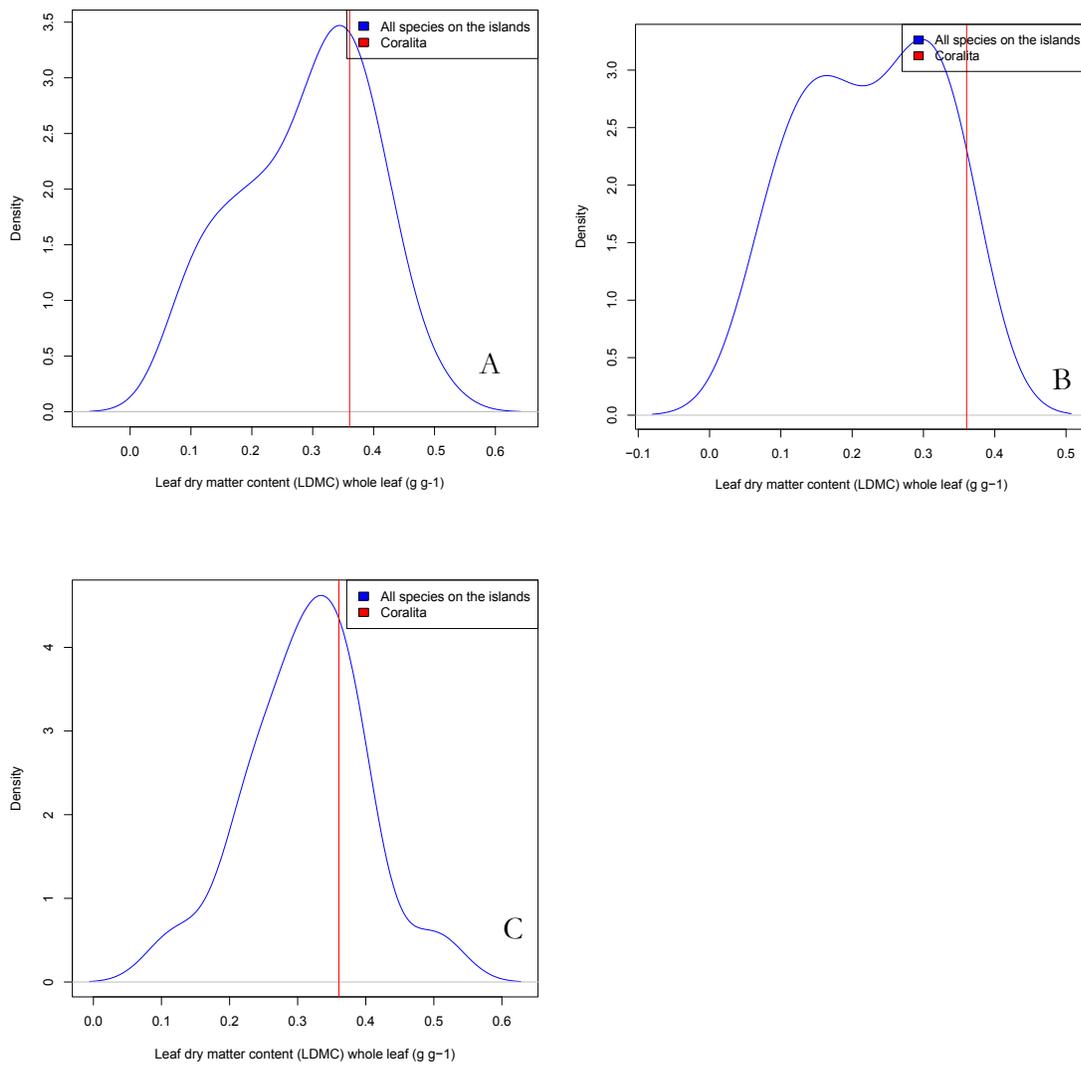
The differences between the trait values for species that occur only on Saba, those that appear only on St. Eustatius and those species that occur on both islands were explored statistically via an initial Kruskal-Wallis test (see *Table 13*).

**Table 13:** P-values associated with Kruskal-Wallis tests on the equivalence of numeric traits for species on both islands, species only found on Saba and species only found on St. Eustatius

| Traits  | P value |
|---|---------|
| Leaf area (mm <sup>2</sup> )  | 0.35    |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> )     | 0.62    |
| Leaf dry matter content (LMDC) whole leaf (g g <sup>-1</sup> )      | 0.02*   |
| Leaf longevity (month)  | 0.93    |
| Leaf nitrogen (N) content per leaf area (g mg <sup>-2</sup> )       | 0.15    |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )               | 0.74    |
| Leaf phosphorus (P) content per leaf dry mass (mg g <sup>-1</sup> ) | 0.70    |
| Leaf thickness (mm)   | 0.22    |
| Plant maximum height (m)  | 0.20    |
| Seed mass (mg)  | 0.12    |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                             | 0.08    |
| Stem dry mass per stem fresh volume (SSD) (mg mm <sup>-3</sup> )    | 0.19    |

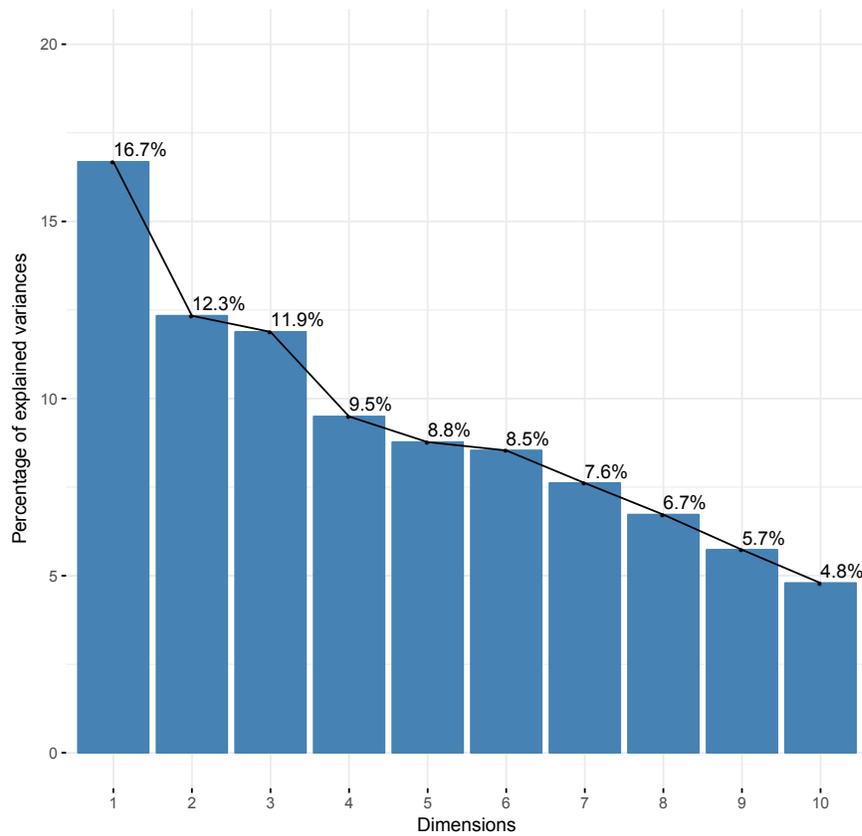
\* Reject the hypothesis that the species from Saba- only, St. Eustatius-only and both islands are statistically the same, with 95 percent confidence

There was only one plant trait for which the hypothesis of equality between the samples covering Saba only, St. Eustatius only and both island species could be rejected: leaf dry matter content. Subsequent Mann-Whitney-Wilcoxon tests between the different samples resulted in statistically significant differences between the species only on Saba and species on both islands (p value 0.02) and between Saba and St. Eustatius samples (p value 0.02). Species in samples from St. Eustatius only and both islands were not found to be statistically different (p value 0.36). Examining the density distributions more closely shows that the kurtosis for these trait values is noticeable less for Saba than for the species on both islands or on St. Eustatius only, and that the median value is also lower on Saba, where *Coralita* appears less usual compared to other species on the islands. Although this is an interesting finding, it is important to note that there are only 14 data points for Saba-only species, 17 for St. Eustatius-only and 13 for both island species for this trait, which limits the strength of this finding.



**Figure 20:** Density distribution of leaf dry mass per leaf fresh mass for species: A) occurring on both islands; B) only occurring on Saba; and C) only occurring on St. Eustatius

As well as investigating the traits individually, a principal component analysis (PCA) has been performed to understand the variation within the database more generally and attempt to reduce that variation to the most important components. However, as shown in *Figure 21*, the breakdown of shares of variation attributed to the principal components appears to limit the ability to reduce the dataset to a smaller selection of components, without losing information.



**Figure 2f:** Scree plot showing the percentage of explained variances explained by each of the dimensions of the PCA for island species only

There are a number of approaches that have been suggested to decide how many dimensions to retain. Kaiser’s rule (Kaiser, 1960) suggests that all components that explain a greater share of variation than a single variable should be retained (i.e. the eigenvalue is greater than one): in this instance, this suggests retaining the first six components (see *Table 14*).

**Table 14: Eigenvalues and explained variance for the components from a PCA on island species only**

|                     | Eigenvalue | Percentage of variance explained | Cumulative percentage of variance explained |
|---------------------|------------|----------------------------------|---|
| <b>Component 1</b>  | 2.00       | 16.68                            | 16.68                                       |
| <b>Component 2</b>  | 1.49       | 12.34                            | 29.02                                       |
| <b>Component 3</b>  | 1.43       | 11.88                            | 40.90                                       |
| <b>Component 4</b>  | 1.14       | 9.50                             | 50.39                                       |
| <b>Component 5</b>  | 1.05       | 8.77                             | 59.16                                       |
| <b>Component 6</b>  | 1.03       | 8.54                             | 67.70                                       |
| <b>Component 7</b>  | 0.91       | 7.61                             | 75.31                                       |
| <b>Component 8</b>  | 0.81       | 6.72                             | 82.04                                       |
| <b>Component 9</b>  | 0.69       | 5.73                             | 87.77                                       |
| <b>Component 10</b> | 0.58       | 4.79                             | 92.56                                       |
| <b>Component 11</b> | 0.49       | 4.09                             | 96.64                                       |
| <b>Component 12</b> | 0.40       | 3.36                             | 100   |

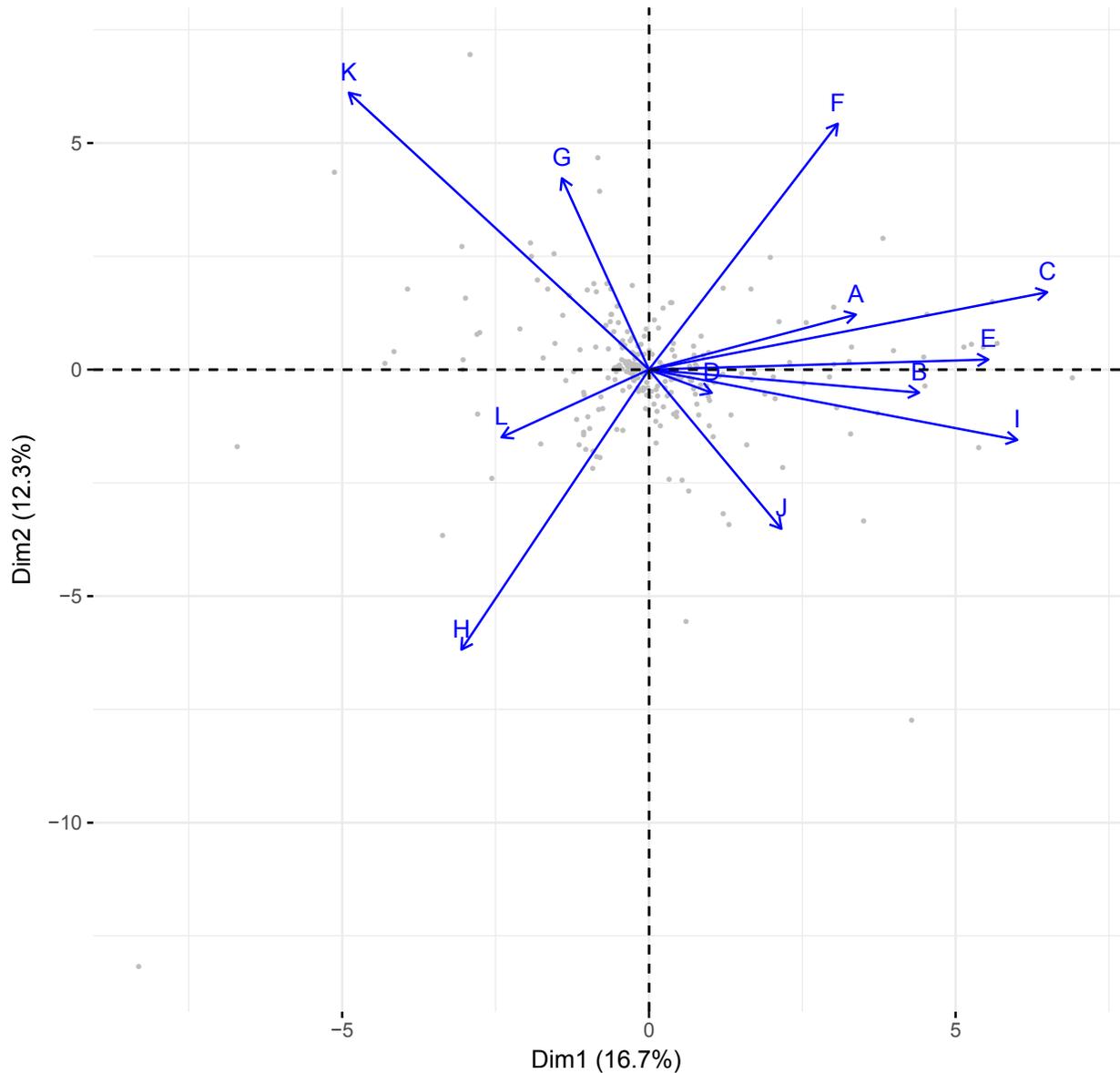
An alternative approach proposed by (Cattell, 1966) involves investigating the scree plot and seeing where a clear change occurs in the relative gradient of the scree plot. Based on *Figure 21* however, no clear change can be discerned, although arguably the gradient change between dimensions four and five might suggest that four components should be retained. A third approach involves the arbitrary selection of share of total variation explained and discarding subsequent components, with 70 percent of variation a commonly utilised cut-off (Jolliffe & Cadima, 2016). In this case, seven components should be retained. Based on these multiple considerations, six components have been retained for analysis. Given the relatively small distinction between components in terms of the variance explained, and the reduction in the variance that would be attributable to components following rotation, varimax rotation has not been performed: *Table A7* in the Appendices shows the percentage of variance explained and the variable loadings for such a rotation.

The contribution of the variables to first six principal components is shown in *Table 15*. For the first two principal components, specific leaf area (SLA) explains the largest amount of variance. However, given the relative spread of variance explained by the components, the importance of this is less than had the two components explained a larger proportion of the variance in the dataset on their own.

**Table 15:** Contributions of the variables to each of the principal components for the PCA of island species only

|   | PC1   | PC2   | PC3   | PC4   | PC5   | PC6   |
|---|-------|-------|-------|-------|-------|-------|
| Leaf area                                 | 5.81  | 1.02  | 31.62 | 0.10  | 10.93 | 0.73  |
| Leaf carbon (C) content per leaf dry mass | 9.91  | 0.18  | 0.47  | 30.50 | 4.87  | 1.90  |
| Leaf dry mass per leaf fresh mass (LDMC)  | 21.53 | 2.02  | 0.57  | 7.82  | 3.18  | 1.32  |
| Leaf longevity                            | 0.54  | 0.18  | 1.62  | 39.99 | 21.25 | 9.45  |
| Leaf nitrogen (N) content per leaf area   | 15.62 | 0.03  | 17.81 | 0.39  | 11.14 | 0.06  |
| Leaf nitrogen per leaf dry mass           | 4.83  | 20.35 | 6.79  | 2.88  | 2.90  | 8.54  |
| Leaf phosphorus content per leaf dry mass | 1.03  | 12.32 | 5.20  | 0.00  | 12.40 | 32.43 |
| Leaf thickness                            | 4.77  | 26.38 | 1.45  | 6.45  | 15.23 | 3.97  |
| Plant maximum height                      | 18.41 | 1.67  | 11.95 | 0.98  | 0.40  | 0.08  |
| Seed dry mass                             | 2.38  | 8.54  | 4.15  | 8.66  | 5.02  | 15.30 |
| SLA                                       | 12.22 | 25.77 | 5.39  | 1.86  | 1.22  | 0.18  |
| Stem specific density (SSD)               | 2.95  | 1.54  | 13.00 | 0.35  | 11.46 | 26.04 |

*Figure 22* shows a biplot of the PCA for island species on the first two principal components. Although difficult to specify, the first principal component is most correlated with a) specific leaf area, leaf N content per leaf dry mass, leaf P content per leaf dry mass and b) leaf thickness, seed dry mass. These attributes are generally most closely associated either with (a) plants with a strategy of rapid growth for relatively low leaf investment (Poorter & Bongers, 2006) or contrastingly, to (b) plants that invest in leaf construction rather than rapid growth (Mediavilla, Garcia-Ciudad, Garcia-Criado, & Escudero, 2008). This trade-off between leaf potential rate of return and duration of return has been noted in ecological literature (see, for example, Grime (1977); Westoby et al. (2002)), and can be seen by the negative correlation between a) and b) traits.



**Figure 22:** Biplot showing the projections of individual species on first two principal components, and the correlation of the variables to the components

**A)** Leaf area; **B)** Leaf C per leaf dry mass; **C)** Leaf dry mass per leaf fresh mass (LDMC); **D)** Leaf longevity; **E)** Leaf N content per leaf area; **F)** Leaf N content per leaf dry mass; **G)** Leaf P content per leaf dry mass; **H)** Leaf thickness; **I)** Plant maximum height; **J)** Seed dry mass; **K)** Specific leaf area (SLA); and **L)** Stem specific density

It is important to note that, in itself, leaf longevity (G on biplot) is not highly correlated with this component. However, this may simply be an artefact of the lack of data in the original dataset for this trait. The interpretation for seed dry mass on this component is difficult to assess. As with leaf traits, there is a generally assumed trade-off in plants between seed size and seed number as

strategies, with seed number a predictor of establishment opportunities and seed size closely associated with establishment success (Westoby et al., 2002). As seed number is not a variable considered in the database it is not possible to assess whether this would be correlated with this principal component. Broadly speaking however, this principal component could be said to represent an axis of plant strategy between short-term rapid growth, and longer-term growth. The second principal component is more difficult to interpret, with the combination of traits not obviously connected. This component is most positively correlated with leaf dry mass per leaf fresh mass (LDMC), plant maximum height, leaf nitrogen content per leaf area and leaf carbon per leaf dry mass, and most negatively correlated with SLA and leaf thickness.

Interestingly, the positive correlation between traits (represented as the angle between vectors) is more pronounced for those traits correlated with the second component, with, for example, leaf area and leaf dry mass per leaf fresh mass highly correlated based on the coefficients of the variables for these two components. These relationships can more readily be seen in *Figure 23*, which depicts the correlations between traits for islands species, and the significance of those correlations.

Coralita, which is the point closest to the letter A on *Figure 22*, appears most associated with the second undefined principal component, and also slightly more associated with rapid growth than reproduction or resilience (as per principal component one). This appears to be in line with knowledge about Coralita on the islands (and invasive vines in general), which grows rapidly and is more likely to spread vegetatively through disturbed areas rather than via seed dispersal. It is also important to note the close association with Coralita and LDMC (variable C in the biplot); this is in line with the noted difference between the islands and the relative similarity of Coralita to the mean value for Saba.

The relationship of Coralita to the other island species is shown in *Figure 24*. Based on these two principal components, Coralita appears to be towards the edge of the 95 percent confidence interval for species. This implies that the traits associated with Coralita are atypical for the islands, and perhaps suggest that these elements have enabled Coralita to spread readily. It is important to reiterate that the total variance of the dataset described by the first two principal components is around 30 percent, with the third, fourth, fifth and sixth components together explaining almost 40 percent of the data. However, for the most part, the location of Coralita outside of the 95 confidence intervals for the other island species is maintained for these other components (see Appendices: *Figure A5*, *Figure A6*, *Figure A7* and *Figure A8*).

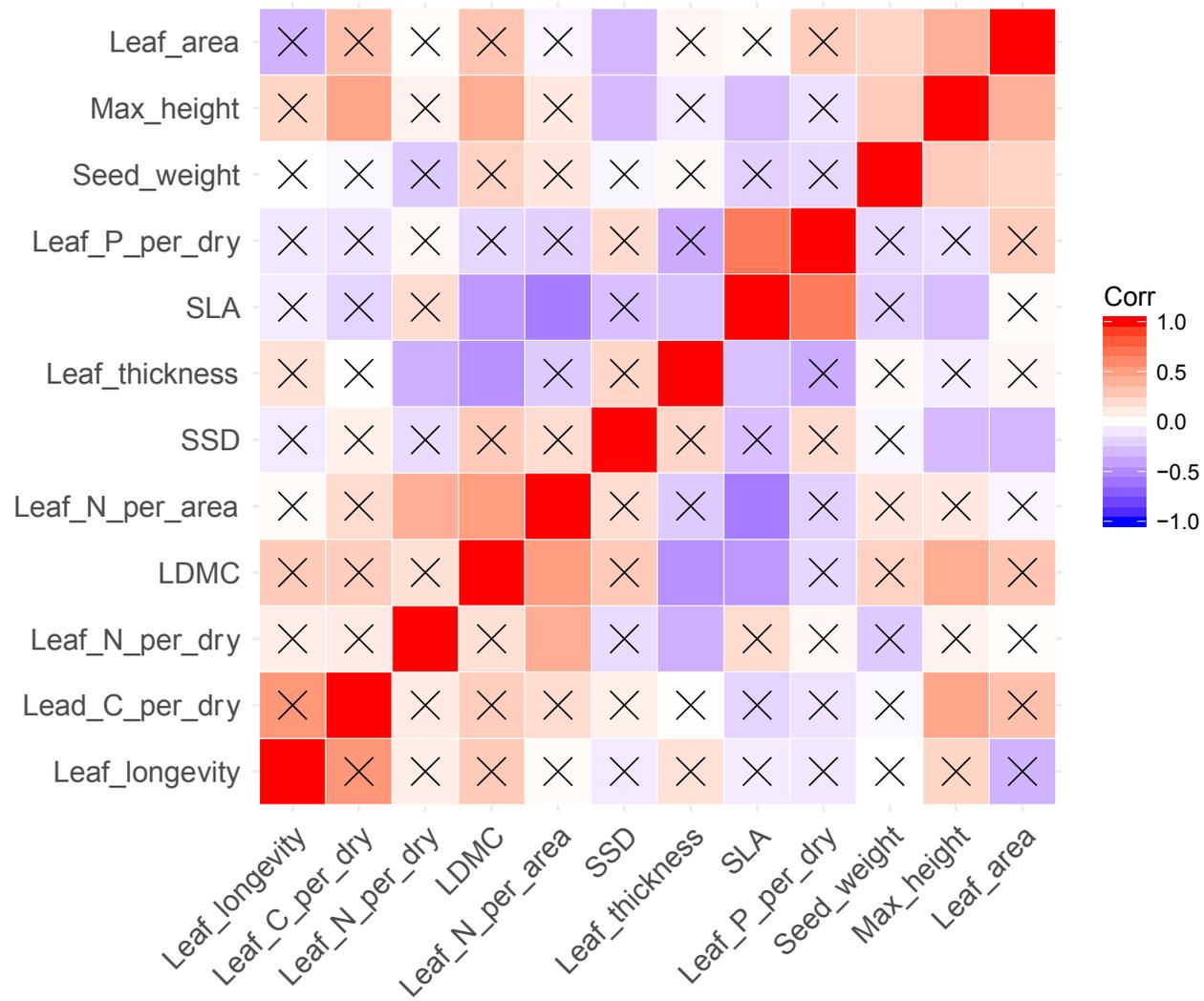
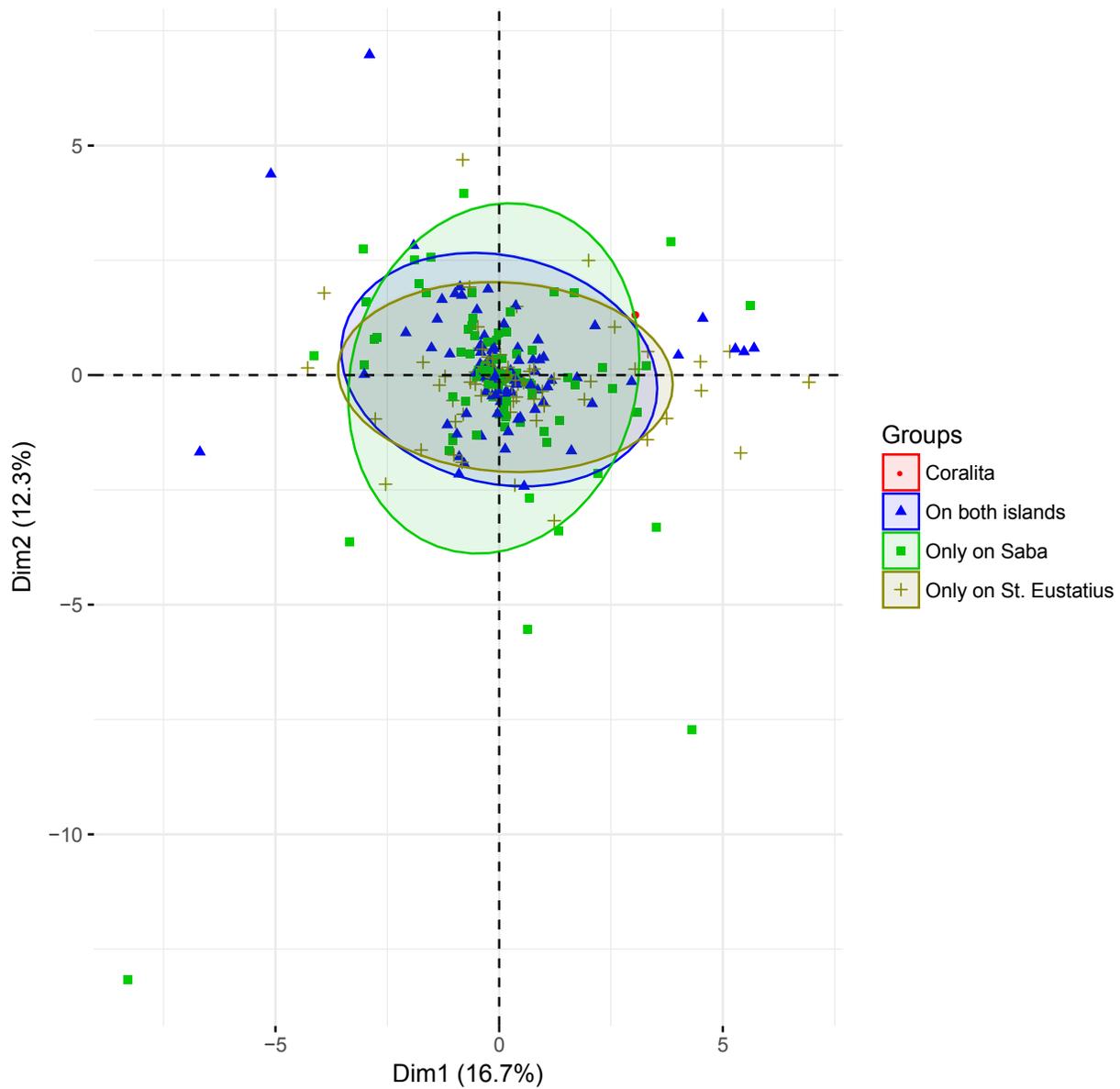


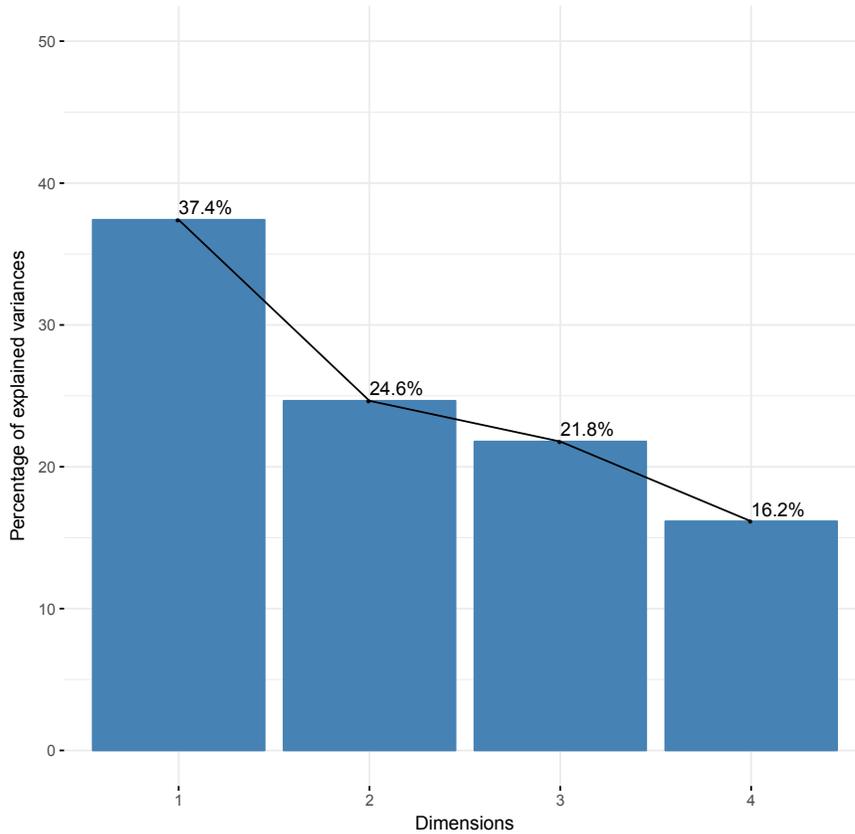
Figure 23: Correlations between trait variables for island species. Crosses indicate a non-statistically significant relationship



**Figure 24:** Principal Component Analysis projections of island individual species on the first two principal components, with groupings of species by location

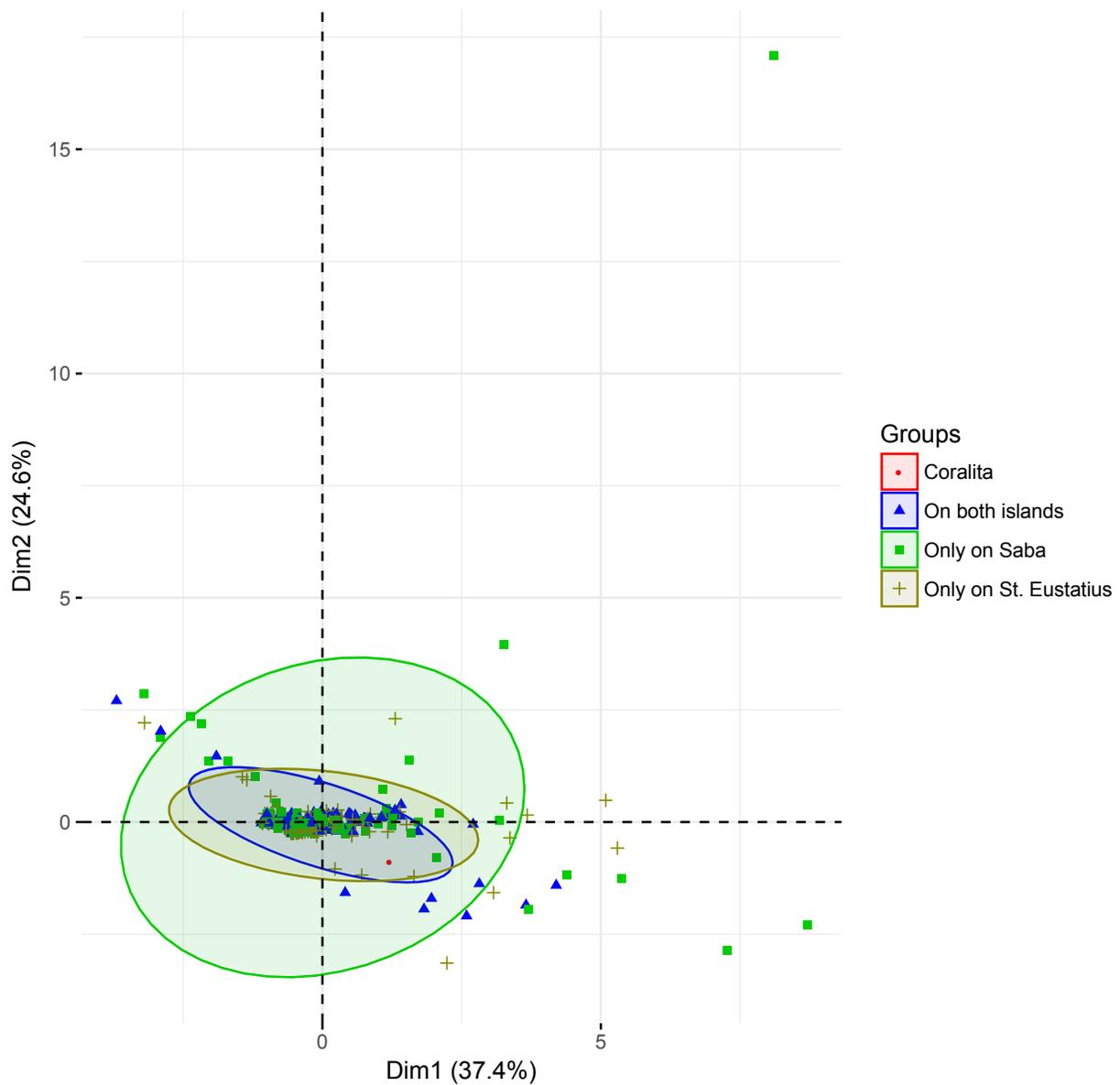
A further consideration in relation to these results is the source of data for Coralita. For the majority of traits the average value of climbing species was used as a proxy for the value for Coralita, as no sources of data could be found. In order to test the validity of the results for Coralita for all traits, further PCA was performed for a subset of traits including only those traits for which information was available for Coralita: leaf area, LDMC, maximum plant height and seed dry mass. In this case, the variation described by the first principal components was much greater (see *Figure 25*), although

given the reduced dataset, this is expected. Indeed, only the first principal component has an eigenvalue greater than one.



**Figure 25:** Scree plot for PCA carried out for islands species traits where trait information for Coralita was not inferred from the average of climbing species across the entire dataset

In contrast to the PCA for all traits considered, the relationship between Coralita and other species on the islands was more typical (see *Figure 26*). This implies one of two things: either 1) the imputed values for Coralita using the other climbing species data in the entire dataset are such that they overestimate the difference between Coralita and other island species or 2) those values are broadly accurate and these components are more different to other island species. There is also a methodological point to consider, in that removing a large number of traits reduces the total variation in the dataset more generally. Each principal component thus reflects the variation in fewer variables, meaning that Coralita would have to vary by a greater amount for each variable in order to be placed outside of the ellipses. Additionally, the impact of outliers for a single trait (see the point to the top right of *Figure 26*) is amplified in relation to the extent of the 95 percent confidence ellipses, although in this case this would only affect the ellipse for Saba.



**Figure 26.** Principal Component Analysis projections of individual island species on the first two principal components, for those traits for which sources could be found for Coralita

### Community weighted means

Although the information in relation to traits for island species is instructive, the prior analysis does not take into account the abundance of the species on the islands. In order to assess the implications of Coralita to the areas where it is found, the community weighted mean (CWM) for each trait was calculated for each area. Coralita was then artificially removed from these same areas, and the CWM recalculated. The difference between the two CWM's per area was then calculated, with these

differences per area examined together statistically via T-tests to assess whether the differences were significantly different from zero. This approach makes the assumption that the presence of Coralita did not change the relative abundance of other species to each other (i.e. the removal of Coralita mean that the other species simply expanded their abundance by the same proportion). Clearly this is a challenging assumption, given the prior analysis regarding the potential implications of Coralita to specific species, but is unfortunately necessary in the absence of comparable temporal datasets. The results of the analysis on CWM are shown in *Table 16*, with p-values calculated in relation to those vegetation areas where Coralita was found, and p-values for all vegetation types on the islands to assess the overall impact of Coralita on the islands.

**Table 16:** Calculated p values associated with T-tests on whether the differences in CWMs for traits with and without Coralita on the islands are significantly greater than zero

| Traits   | P value for differences between CWM with and without Coralita: only in areas where observed | P value for differences between CWM with and without Coralita: all areas |
|--|---|--|
| Leaf area (mm <sup>2</sup> )                                     | 0.18  | 0.17   |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> )  | 0.29  | 0.25   |
| Leaf dry mass per leaf fresh mass (LDMC (g g <sup>-1</sup> ))    | 0.31  | 0.27   |
| Leaf longevity(month)  | 0.04*   | 0.07   |
| Leaf nitrogen (N) content per leaf area (g mg <sup>-2</sup> )    | 0.24  | 0.21   |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )            | 0.93  | 0.92   |
| Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> )  | 0.36  | 0.31   |
| Leaf thickness (mm)  | 0.55  | 0.50   |
| Plant maximum height (m)   | 0.34  | 0.30   |
| Seed mass (mg)   | 0.37  | 0.32   |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                          | 0.31  | 0.27   |
| Stem dry mass per stem fresh volume (SSD) (mg mm <sup>-3</sup> ) | 0.32  | 0.28   |

\* Reject the hypothesis that there is no difference between CWM trait values with and without zero, with 95 percent confidence

There is only one instance where the CWM trait values are significantly different when Coralita is excluded, in relation to leaf longevity for areas where Coralita is found on the islands. Note that this finding does not hold when all locations noted by de Freitas are included (i.e. when assessing whether Coralita impacts the island more generally, rather than where it is found). Unfortunately, leaf longevity is one of the least well represented traits from the TRY database for the species requested, with only 4 percent of data available for island species (see *Table 4*). In addition, the value for Coralita was based on the trait value of a single climbing species for which there was information, which itself was much greater than the average by some margin. Together, these

aspects preclude the interpretation of this finding with any confidence, as it most likely an artefact of missing data.

Overall, this then implies that Coralita has no major impacts on ecosystem services in these areas, assessed via differences in trait values.

In order to assess what the abundance of Coralita would have to be in order for there to be statistically different differences in the CWM for trait values for areas with Coralita and where Coralita was hypothetically removed from those areas, the abundance of Coralita was artificially increased. If the relative share of Coralita was increased for the vegetation types where it was identified such that it constituted the same proportion of the total vegetation as the maximum share observed (28 percent) (i.e. Coralita abundance in the five areas observed increased to 28 percent in each), then the differences in CWM for many of the variables became significant based on T-tests of differences from zero (*Table 17*). In this instance it is more relevant to note the variables for which no statistically significant result could be found: LDMC, leaf nitrogen per leaf dry mass, leaf phosphorous per leaf dry mass, leaf thickness and seed dry mass. For these traits, even if the abundance of Coralita in areas that it was observed was increased to the maximum share observed, the CWM would not change (i.e. fail to reject the hypothesis that the CWM values were the same).

**Table 17: P values from T-tests of the differences between CWMs for areas where Coralita is observed, with and without Coralita**

| Trait   | P value |
|---|---------|
| Leaf area (mm <sup>2</sup> )                                    | 0.048*  |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | 0.001*  |
| Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )   | 0.109   |
| Leaf longevity (month)  | 0.001*  |
| Leaf nitrogen (N) content per leaf area (g m <sup>-2</sup> )    | 0.002*  |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | 0.089   |
| Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> ) | 0.283   |
| Leaf thickness (mm)   | 0.196   |
| Plant maximum height (m)  | 0.001*  |
| Seed dry mass (mg)  | 0.907   |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | 0.000*  |
| Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.003*  |

\* Reject the hypothesis that there is no difference between CWM trait values with and without Coralita, with 95 percent confidence

Finally, as an approach to assess the implications for a complete dataset on CWM differences, the imputed trait values utilised for the PCA were used, together with the complete information on

abundance. Whilst the imputed values are in essence derived from the observed values in the dataset, the abundance information for those species for which there was no trait information could be utilised. As before, the comparison between CWM values for areas containing Coralita and the CWM values for those same areas in the absence of Coralita are not significantly different (see *Table 18*).

**Table 18.** P values from T-tests of the differences between CWMs for areas where Coralita is observed, with and without Coralita, with imputed data from the PCA analysis

| Trait   | P values |
|---|----------|
| Leaf area (mm <sup>2</sup> )                                    | 0.33     |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | 0.34     |
| Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )   | 0.34     |
| Leaf longevity (month)  | 0.34     |
| Leaf nitrogen (N) content per leaf area (g m <sup>-2</sup> )    | 0.34     |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | 0.32     |
| Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> ) | 0.40     |
| Leaf thickness (mm)   | 0.35     |
| Plant maximum height (m)  | 0.34     |
| Seed dry mass (mg)  | 0.32     |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | 0.34     |
| Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.34     |

## Coralita and other invasive species by trait values

The database of traits developed includes information for the species listed as having an impact on the GISD database. It is also instructive to investigate the entire dataset to understand how atypical Coralita is in comparison to these species, as well as those on the islands. In this way, it is possible to link the impacts from the GISD database with the trait analysis, merging part of the EICAT assessment approach with the second trait based approach.

Firstly, a comparison of trait values for species listed as having impacts on the GISD database and the remaining species (i.e. island species, excluding two species listed on the GISD database that were also observed on the islands) on the trait dataset has been performed (see *Table 19*, and Appendices: *Table A8* for mean, median standard error and relative standard error information). Based on Welch T-tests to test the equivalence of the mean values for each population, two traits have p-values such that the hypothesis of equivalence is rejected: leaf nitrogen per leaf dry mass and

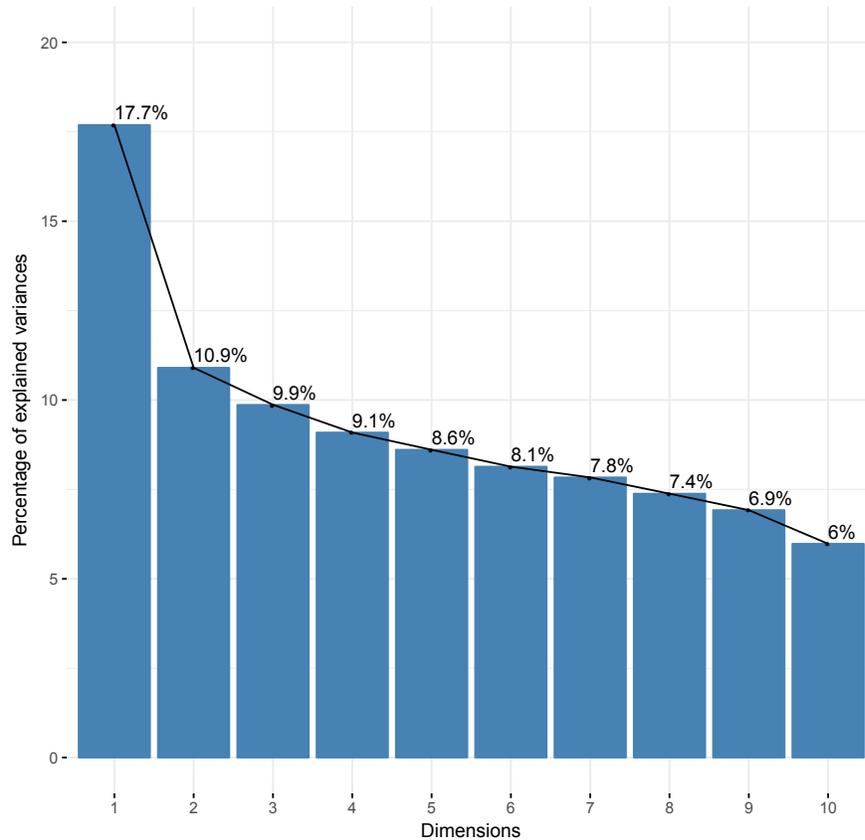
SLA. As previously discussed, leaf traits including SLA and leaf nitrogen are associated with faster growing species, which may suggest that invasive species grow more rapidly than the islands species.

**Table 19:** P-values associated with Welch T-tests on the equivalence of traits for species noted on the GISD database as having an impact and other species for which data was gathered

| Trait   | P value for differences between GISD species and other species |
|---|--|
| Leaf area (mm <sup>2</sup> )  | 0.14   |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> )     | 0.24   |
| Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )       | 0.21   |
| Leaf lifespan (longevity)(month)                                    | 0.56   |
| Leaf nitrogen (N) content per leaf area (g mg <sup>-2</sup> )       | 0.88   |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )               | 0.01*  |
| Leaf phosphorus (P) content per leaf dry mass (mg g <sup>-1</sup> ) | 0.65   |
| Leaf thickness (mm)   | 0.36   |
| Plant maximum height (m)  | 0.11   |
| Seed mass (mg)  | 0.19   |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                             | 0.03*  |
| Stem dry mass per stem fresh volume (SSD) (mg mm <sup>-3</sup> )    | 0.00*  |

\* Reject the hypothesis that the mean trait values for the samples for traits are the same, with 95 percent confidence

In order to investigate the relationship between traits more holistically, a further PCA was performed on the entire dataset. As before, the share of variance explained by the first principal components was low, with a gradual decline in explanatory power evident for all principal components beyond the first component (see *Figure 27*). Only the first five principal components have eigenvalues greater than one, and the cumulative share of variance explained by the dataset only reaches 70 percent between the sixth and seventh component. Again, this reduces the explanatory power of two-dimensional plots and the ability to reduce the dataset with confidence. Given the relatively low proportion of variance explained by each principal component, varimax rotation has again not been performed on the data.



**Figure 27:** Scree plot for the PCA of traits for the entire dataset

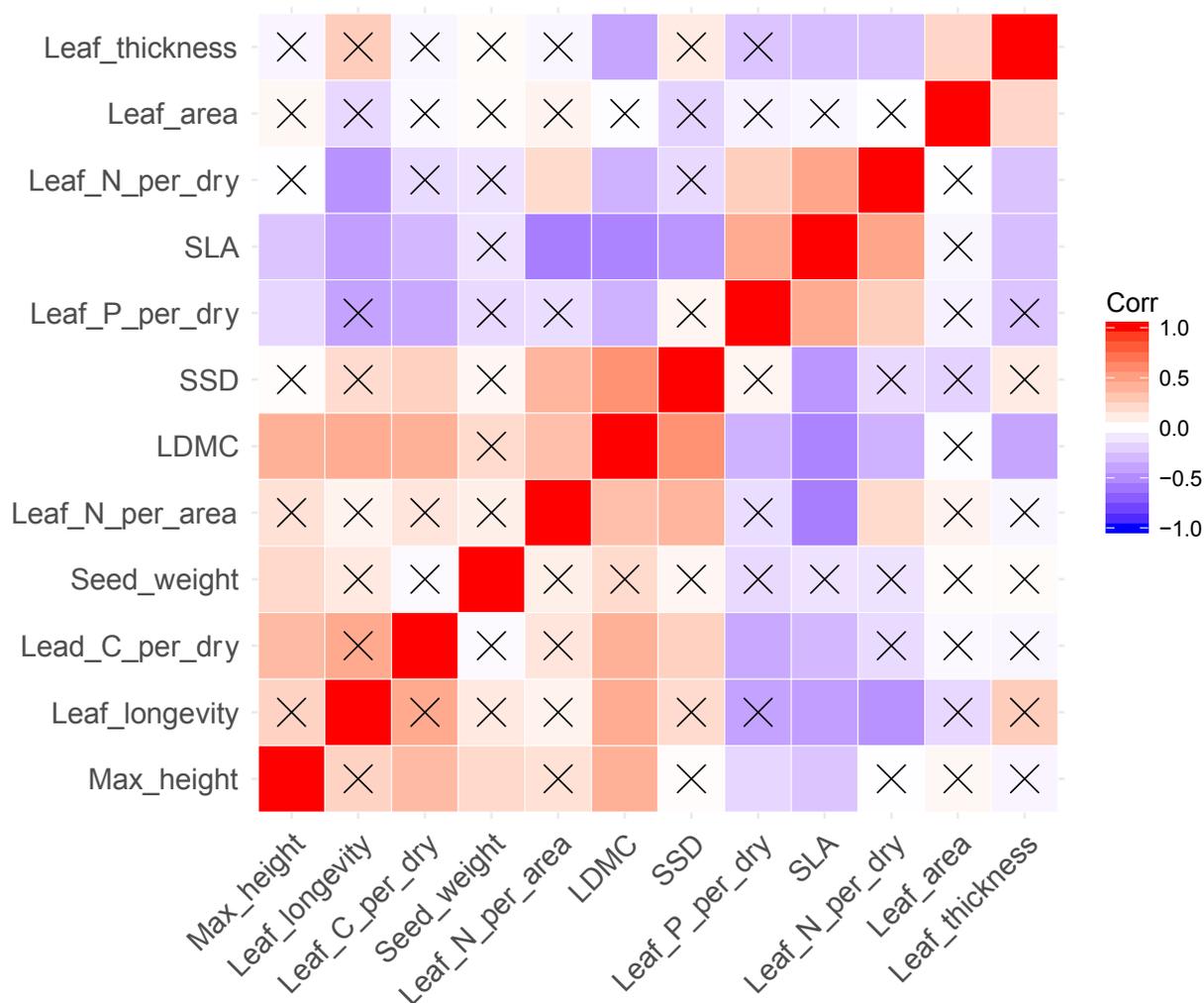
The loadings for the variables by each principal component are shown in *Table 20*, with the first six principal components shown.

The first principal component is most strongly correlated with SLA, LDMC, leaf carbon per leaf dry mass, leaf nitrogen per leaf dry mass and plant maximum height. Evidence from literature suggests that generally SLA and LDMC are strongly negatively correlated (Vile et al., 2005; P. J. Wilson, Thompson, & Hodgson, 1999), which can be observed both in relation to principal component one here, and more generally across the entire dataset (see *Figure 28*). Greater LDMC is associated with reduced soil fertility and lower growth rates, in contrast to SLA (Hodgson et al., 2011) and has been used as a predictor of plant strategy along an axis of resource capture, usage and availability (P. J. Wilson et al., 1999). This component may therefore represent this axis, with plant maximum height and leaf carbon content also elements generally associated with a longer term growth strategy with high construction and maintenance costs (Osunkoya et al., 2010; Westoby & Wright, 2006). The remaining principal components are more closely associated one or two variables. For example, principal component two is most associated with leaf thickness and leaf nitrogen per leaf area: more

robust, thicker and longer lasting leaves are associated with less nitrogen per unit mass (Loomis, 1997).

*Table 20: Principal component loadings by principal component for the trait variables for the PCA covering the entire dataset Correlations > 0.4 are in bold*

| Trait   | PC1          | PC2          | PC3         | PC4         | PC5          | PC6          |
|---|--------------|--------------|-------------|-------------|--------------|--------------|
| Leaf area (mm <sup>2</sup> )                                    | 0.02         | -0.03        | -0.02       | 0.49        | <b>-0.52</b> | -0.29        |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | <b>0.56</b>  | 0.17         | -0.07       | -0.14       | -0.15        | 0.01         |
| Leaf dry mass per leaf fresh mass (LDMC (g g <sup>-1</sup> ))   | <b>0.67</b>  | 0.33         | -0.34       | -0.15       | 0.02         | -0.18        |
| Leaf longevity (month)  | 0.27         | -0.20        | -0.05       | -0.19       | 0.01         | <b>0.71</b>  |
| Leaf nitrogen (N) content per leaf area (g m <sup>-2</sup> )    | 0.32         | 0.32         | <b>0.70</b> | 0.01        | -0.16        | -0.06        |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | <b>-0.47</b> | <b>0.58</b>  | 0.27        | 0.14        | -0.20        | 0.21         |
| Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> ) | -0.29        | 0.17         | 0.05        | -0.26       | <b>0.43</b>  | <b>-0.44</b> |
| Leaf thickness (mm)   | 0.01         | <b>-0.74</b> | 0.29        | 0.16        | -0.12        | -0.08        |
| Plant maximum height (m)  | <b>0.44</b>  | 0.28         | 0.01        | <b>0.46</b> | 0.14         | 0.22         |
| Seed dry mass (mg)  | 0.19         | -0.04        | 0.12        | <b>0.57</b> | <b>0.66</b>  | 0.02         |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | <b>-0.79</b> | 0.17         | -0.07       | 0.05        | 0.07         | 0.24         |
| Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.19         | -0.07        | <b>0.62</b> | -0.34       | 0.14         | 0.00         |

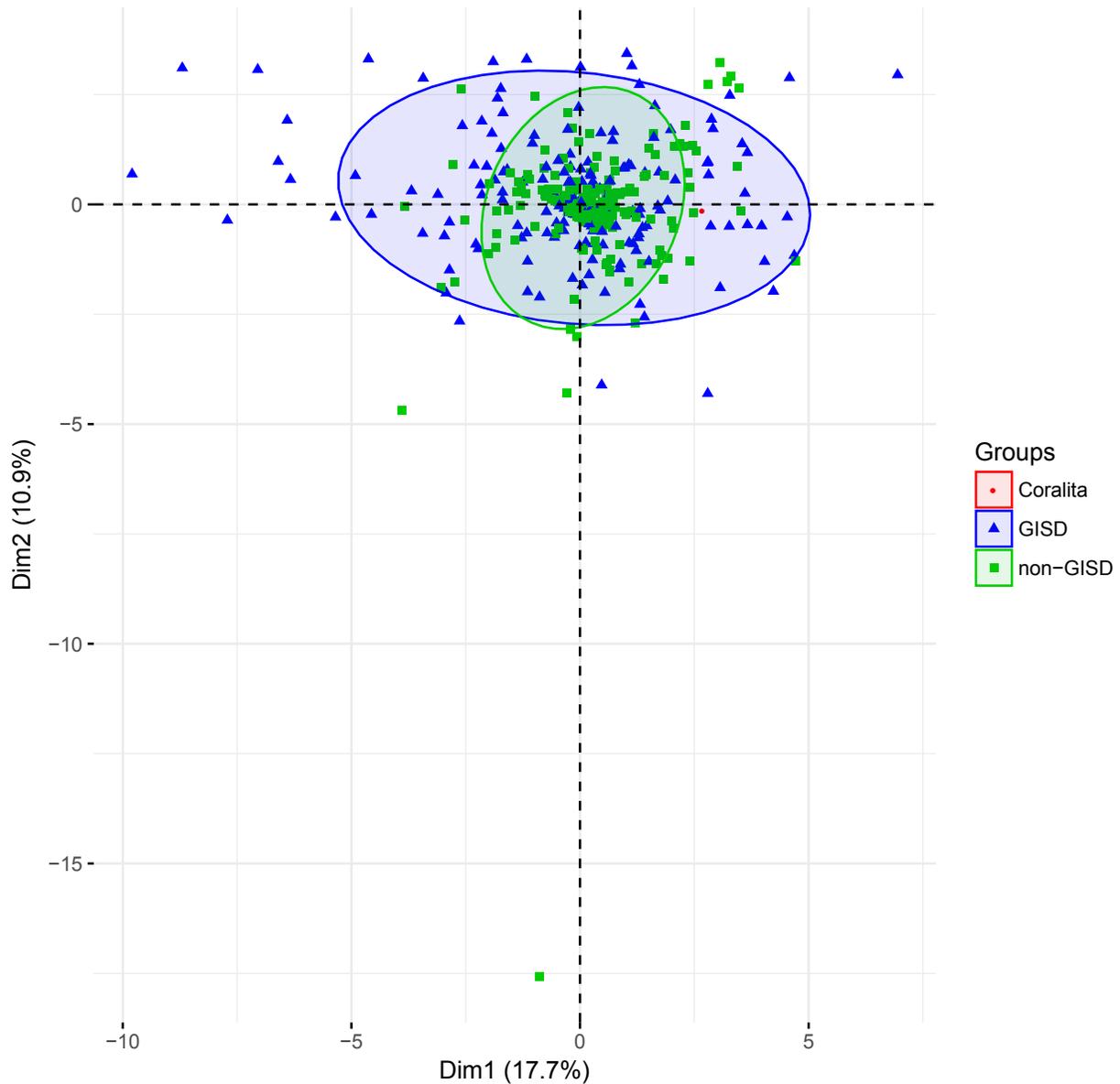


**Figure 28:** Correlations between trait variables for all dataset species. X indicates a non-statistically significant relationship

Returning to the differences between species listed on the GISD database as having impacts and those other species on the database, there is clear difference in terms of the variability of species traits for the GISD species as compared to the non-GISD species, over the first two components (see *Figure 29*). Coralita sits just outside the 95 percent ellipse for non-GISD species, suggesting it is atypical for the islands. This finding is replicated by almost all of the subsequent plots for individuals on the other components, with the exception of the plot for components four and five (see Appendices: *Figure A9*, *Figure A10*, *Figure A11* and *Figure A12*).

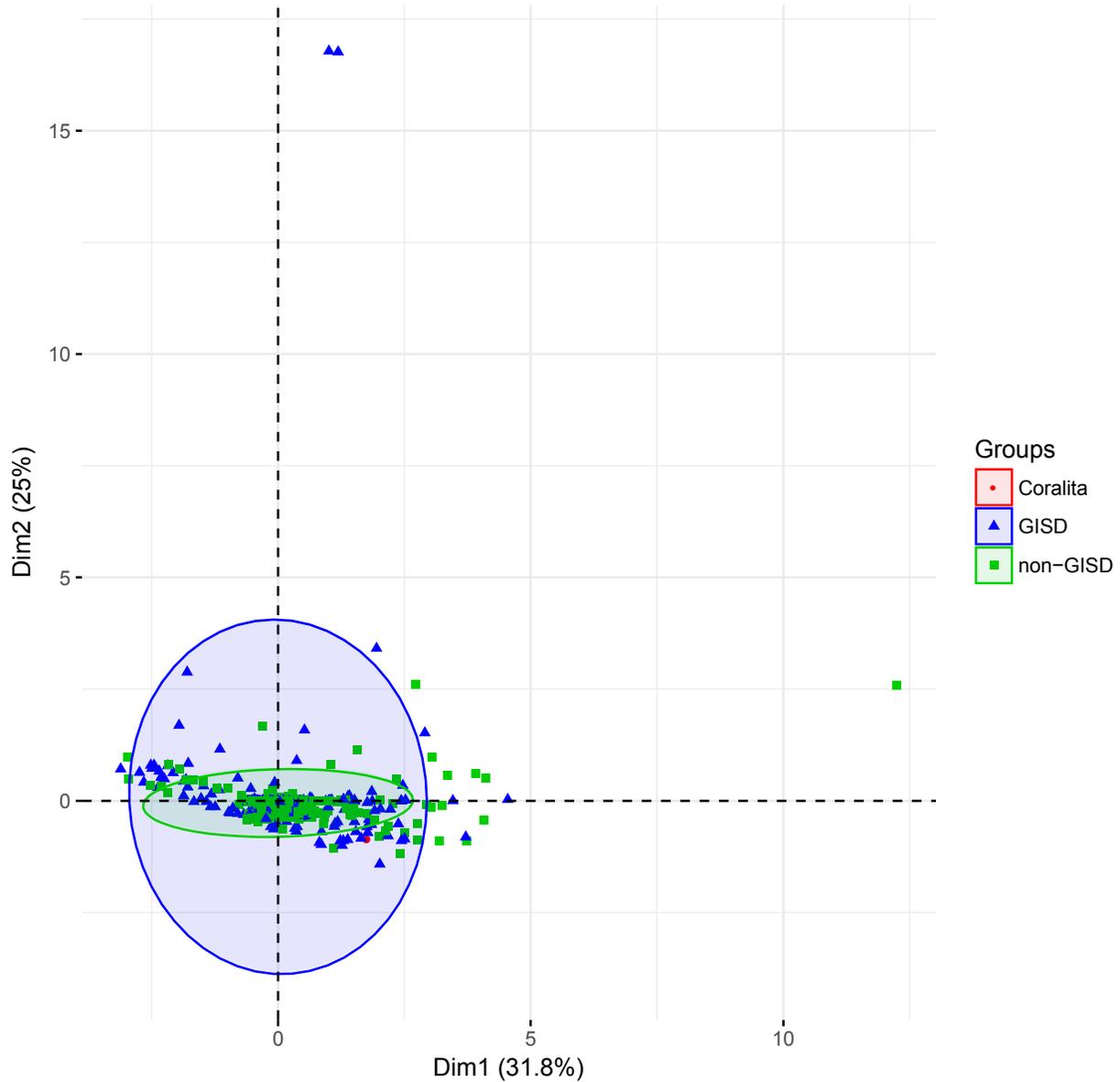
To a certain extent the finding that the invasive species are more variable than the other plants on the database is not unusual, in that the invasive plants cover a broader spectrum of locations, which

would suggest a range of plant strategies associated with biotic and abiotic conditions. However, it is interesting that the non-GISD ellipse is almost completely contained within the non-GISD ellipse, which suggests that the trait values for invasive species are more extreme than for the species on the islands. It is also relevant to note that the shape of the ellipses is slightly different, with the non-GISD ellipse showing variation for the species that is greater towards the second principal component, and the GISD ellipse on the contrary more skewed towards variation in the first principal component.



**Figure 29:** Principal component analysis projections of species on the first two principal components, with grouping by species causing an impact on the GISD database and other species

These findings are reproduced when a PCA is performed for the variables for which information was available for Coralita (see *Figure 30*). It is important to note that the interpretation of the principal components is quite different for this reduced dataset compared to the dataset including all traits.



**Figure 30.** Principal component analysis projections of species on the first two principal components based on traits for which information was available for Coralita, with grouping by species causing an impact on the GISD database and other species

In addition to an assessment of the differences between GISD and non-GISD species, given the growth form of Coralita it is also instructive to assess the differences between climbing species and non-climbing species. Here, due to the relatively limited numbers of climbing vine species for which

there is trait information, Mann-Whitney-Wilcoxon Tests were performed to assess the statistical equivalence for plants traits between climbing vines and other species. The p-values from those tests are shown in *Table 21*, with statistics showing mean, median, standard error and relative standard error shown in Appendices *Table A9*.

**Table 21: P-values from Mann-Whitney-Wilcoxon Tests on the equivalence of traits for species that are climbing vines and other species for which data was gathered**

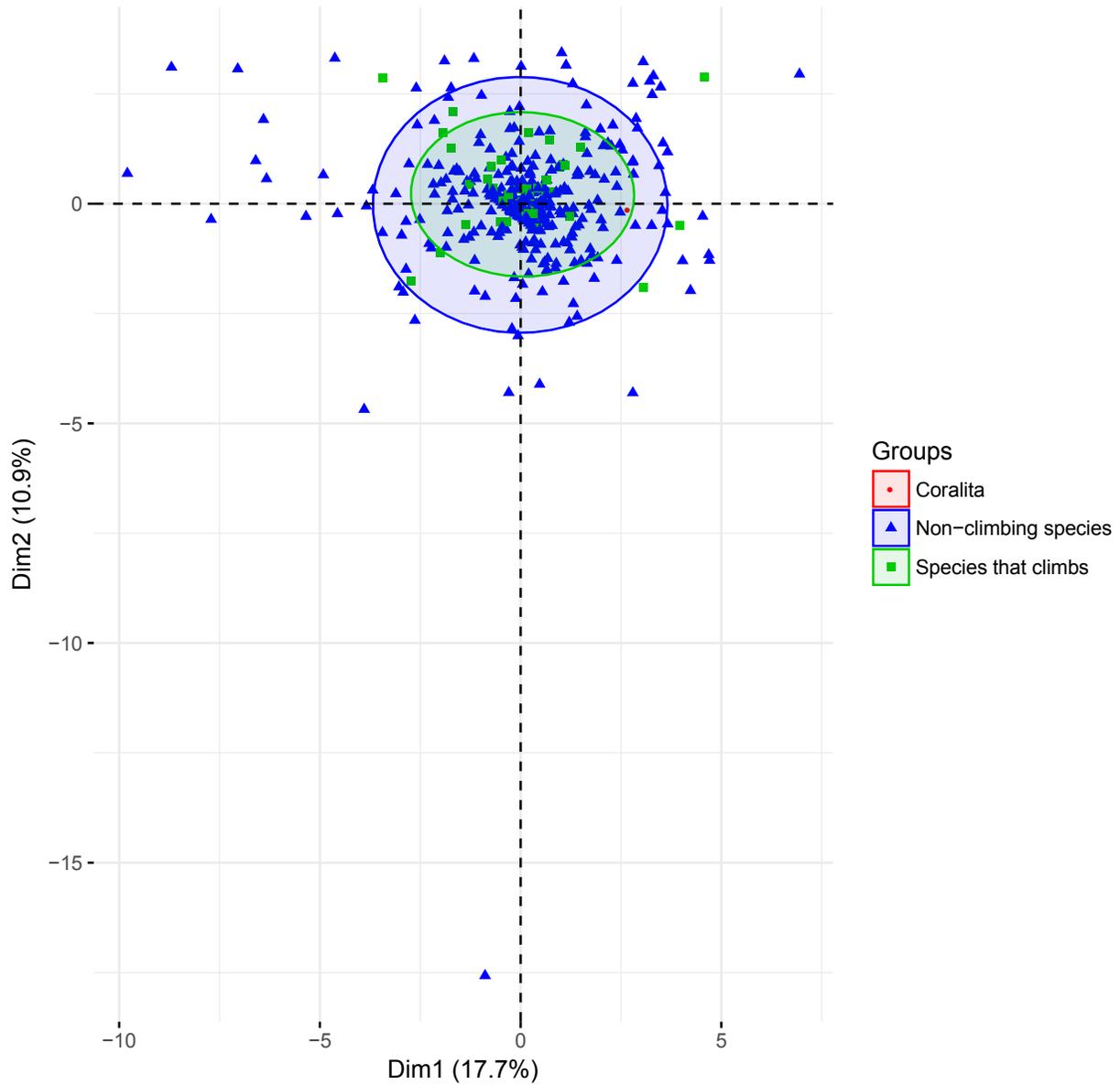
| Trait   | P value |
|---|---------|
| Leaf area (mm <sup>2</sup> )                                    | 0.02*   |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | 0.16    |
| Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )   | 0.01*   |
| Leaf longevity (month)  | 0.00*   |
| Leaf nitrogen (N) content per leaf area (g mg <sup>-2</sup> )   | 0.02*   |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | 0.64    |
| Leaf phosphorus per leaf dry mass (mg g <sup>-1</sup> )         | 0.21    |
| Leaf thickness (mm)   | 0.82    |
| Plant maximum height (m)  | 0.00*   |
| Seed mass (mg)  | 0.00*   |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | 0.49    |
| Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.73    |

\* Reject the hypothesis of statistical equivalence between the two populations, with 95% confidence

Here there are a number of clear differences in trait values for climbing species and non-climbing species. In particular it appears that the traits most associated with longer duration growth, which requires substantial investment in construction and maintenance are most different. Note that plant maximum height is a somewhat difficult trait to consider in relation to climbing vines (and epiphytes). Clearly their maximum height depends upon the organic and non-organic structures that can support them, with the maximum length of vine taken as the maximum height. When vines become the dominant species, smothering other vegetation and forming mats or small bushes of vegetation, the average height in the area would be expected to fall, as the vines themselves have insufficient woodiness to grow beyond a relatively low height.

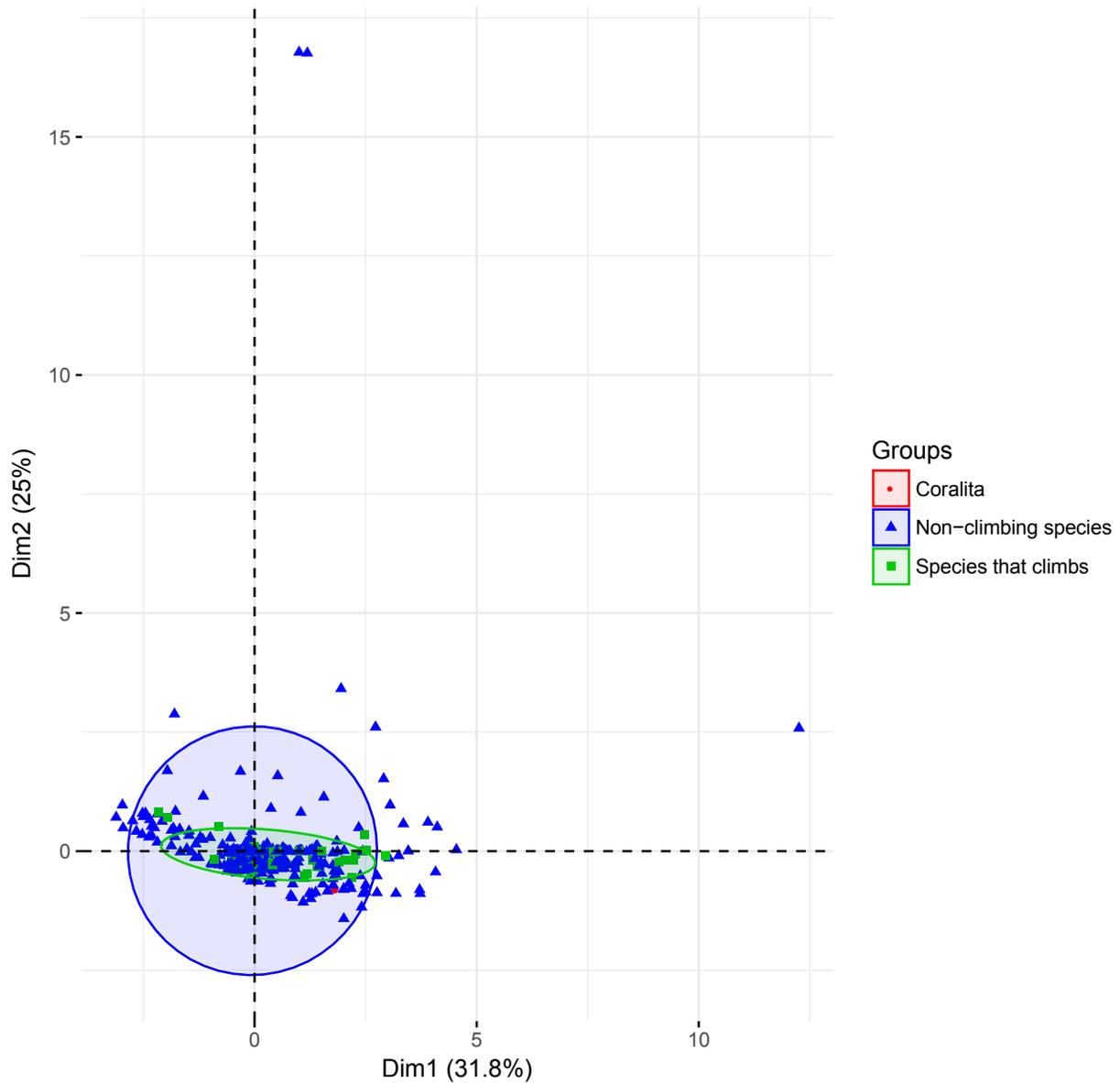
As with the differences between GISD and non-GISD species, the grouping of individuals from the PCA for the entire dataset into climbing species and other species shows one group entirely encircling the other (see *Figure 31*). In this case, the non-climbing species 95 percent confidence ellipse completely surrounds the climbing species ellipse. This suggests that climbing species are more similar than are other species, which again is intuitively coherent given the variation in plant life forms in the non-climbing species group. Interestingly, *Coralita* is situated towards the edge of the climbing species ellipse. Again, these relationships are broadly found for two-dimensional plots

for the different principal components, with the exception of the plot for components 5 and 6, which is influenced by the limited data on plant longevity for climbing species (see Appendices: *Figure A13*, *Figure A14*, *Figure A15* and *Figure A16*).



**Figure 31:** Principal component analysis projections of species on the first two principal components, with grouping by species that climb and other species

As before, these findings are replicated somewhat when considering only the traits for which there was information on Coralita (see *Figure 32*).



**Figure 32:** Principal component analysis projections of species on the first two principal components based on traits for which information was available for Coralita, with grouping by species that climb and other species

It is, however, important to note that Coralita falls outside of the 95 percent confidence ellipse for climbing species based on this reduced dataset. As the missing values for Coralita were imputed from the average of climbing species, this PCA result may have more relevance. This implies that Coralita’s traits are outside of the normal range for climbing species. Note that climbing species include both invasive species (30 species) and non-invasive species (50 species).

# Discussion and conclusion

Assessing the impacts of an invasive species within an area is a challenging task, and ideally first-hand information based on experimental or high quality observational data should be used to do so. In this instance, neither types of information were available, necessitating the use of various techniques to either derive impacts from other research or from more abstract considerations of community change based on species characteristics. The key objective of this research has been to gather sufficient and reliable information to assess the key research question on the impacts of Coralita on Saba and St. Eustatius. In order to do so, two methodological frameworks were used to loosely structure different analytical approaches, the EICAT and a trait-based framework. These analytical approaches were used to develop the research questions, which form the basis of the subsequent discussion below.

***SQ 1: What impacts are associated with comparable species that can be applied to Coralita on the islands?***

At a high level, the evidence from research literature on the impacts of invasive species suggests that these impacts can be both substantial and diverse (Gaertner et al., 2009; Hejda et al., 2009; Nentwig, 2007; Pyšek et al., 2012). From a review of IUCN's GISD database (ISSG, 2015), it is clear that whilst there are a range of impacts associated with plant species, a reduction in biodiversity and, to a lesser extent, habitat degradation are almost ubiquitous impact types for invasive plant species. These broad findings are replicated when investigating the impacts associated with climbing species from the same database and from further investigation of impacts using the CABI invasive species compendium for those same climbing species (CABI, 2018). Although this evidence suggests that liana species can have a range of characteristics and impacts, with, for example, some species being highly poisonous, some having thorns or barbs and some impacting fire regimes, the mechanisms of impact for these species are generally the same and closely related to their functional type. Invasion is carried out via competition with other species, through resource capture, shading, smothering and strangling supportive tree structures, potentially leading to a monoculture of dense mats of shrub like growth. Arguably, the broad impacts then associated with lianas could be transferred to Coralita, with the extent of the species mediating the magnitude of the impact.

It is, however, important to note that the impact information entered on these databases for plant species represent the worst-case scenarios observed for these invasive plant species, which occurred under specific biotic and abiotic conditions. As highlighted by Pyšek et al. (2012), due to the context dependency of impacts, the ability to transfer these findings to a particular species in a certain location is thus questionable, with the potential to grossly overstate both the magnitude and type of impacts. Indeed, the inability to identify a comparable species to Coralita beyond climbing species in general is a reflection of the same challenge, with circumstances changing the appropriateness of

comparison. Without this ability to be more focussed in identifying a comparable species in a comparable location, this information can only be used to express the potential extent of impacts associated with Coralita on the islands, and is thus of limited value in defining specific impacts.

However, one way to address this restriction is through an assessment of the similarities between invasive and climbing species, and Coralita and other island species, as per sub-question seven.

*SQ 7: How do the traits associated with Coralita compare with other invasive species and other climbing species, and what does this imply for impacts?*

Information on plant species traits was requested from the TRY database (Kattge et al., 2011) for species observed as occurring on the islands from two reports on vegetation by de Freitas et al. (2012, 2016) and for those species listed on the GISD database as having a defined impact. For certain plant traits (leaf nitrogen per leaf dry mass, specific leaf area (SLA) and stem specific density), the differences between GISD species and the other species on the database were significant, which was partially reflected in the results from a principal component analysis (PCA) on all species traits, with individual species grouped likewise into GISD and non-GISD species. In this PCA, GISD species were less tightly spread than non-GISD species when projecting species trait values on the principal components, with the 95 percent confidence ellipse for non-GISD species completely enveloped by the 95 percent ellipse for GISD species. This suggests that GISD species had a greater range of trait values, which in some ways is unsurprising given the range of locations where these invasive species are found in comparison to the specific location of the other species on the islands. However it also adds some credence to the view that invasive species and native species traits are different, a conclusion that has been contested in recent time in research literature (see Hulme & Bernard-Verdier (2018) for a fuller discussion). The location of Coralita within these ellipses was instructive, with Coralita occurring outside of the 95 percent confidence ellipse for non-GISD species but within the GISD ellipse. This suggests that Coralita has more in common with the GISD species than with island species, and potentially has implications for the discussion above in relation to the transferral of impacts from GISD species to Coralita on the islands. This strengthens the case for the ability to transfer some of these impacts identified for invasive species in general. These findings are replicated when performing a PCA on a reduced dataset, excluding traits for which the values for Coralita were imputed from the averaged trait values of climbing species.

A similar analysis has been performed in relation to climbing species and non-climbing species. Again, this approach allows consideration of the similarities between Coralita and other climbing species. As before with the GISD and non-GISD grouping, there were a number of traits for which there was a significant difference between climbing species and non-climbing species detected (e.g. leaf area, leaf dry mass per fresh mass). However, in contrast to the comparison between invasive species and other island species, the PCA projecting the principal components on the species and grouped by climbing and non-climbing species shows that climbing species can be considered a

subset of other species, with the 95 percent confidence ellipse for climbing species enveloped by the same ellipse for non-climbing species. In this sense, the variation in trait values for climbing species is less, which is intuitively coherent given that climbing species represent a single functional type, compared to the multiple functional types for the other species. As with the differences discussed above for climbing species and other species in relation to impacts, the differences between climbing species based on traits and other species appears relatively minor however. For Coralita, considering the entire range of species means that it falls within the 95 percent confidence ellipse for climbing species (which include invasive and non-invasive species). However, for the PCA on the reduced number of traits for which specific information for Coralita was available, Coralita falls outside of this ellipse. As the missing traits for Coralita were imputed from the average of climbing species, this PCA may be of more relevance and implies that compared to the other climbing species in the database, Coralita was atypical. This implies that a transfer of impacts associated with invasive species in general is as relevant to Coralita as a specific consideration of climbing species impacts. However, as discussed, given the minor high-level differences between invasive climbing species and other invasive species impacts, such a specification would be of little value anyway.

Clearly this trait-based approach is very dependent on the data from de Freitas and on the data from the TRY database. For the de Freitas et al. data, performing such an analysis is based on the assumption that de Freitas et al. were able to accurately define vegetation on the islands. Additionally, the approach taken to calculate abundance, which was more relevant to the analytical approaches described below, was based on the midpoint of estimated regarding vegetation cover and species presence. This generated a point estimate for species abundance in an area, when in reality a range should be applied and results tested on this basis, although it should be noted that this form of analysis would be a significant challenge (i.e. varying each species abundance level compared to each other species and performing the analysis as many times as this would entail). For the TRY database, as previously discussed, there were a range of types of values for traits, such as single observations, means, maximums and minimums, which implies that the accuracy of the information taken at face value would be less than otherwise would be the case based on a single type of metric for traits. In addition, as there were many missing values for species trait values, it was effectively assumed that there was no bias in this missing values, which, despite the analysis performed on height data, would need to be established with further data testing.

*SQ 2: How does biodiversity compare in areas where Coralita is found and areas where it is not found?*

Although species richness is a somewhat crude measure for defining biodiversity (source), it is a useful indicator of biodiversity insurance (Naeem & Li, 1997), and has the benefit of being simple to understand and relatively trivial to calculate. Based on the data on species abundances from the two reports by de Freitas et al. (2012, 2016) the level of species richness in areas where Coralita was found was not significantly different to the other areas. The data showed a clear negative correlation between richness and the maximum share of the dominant species. For invasive species, this

suggests that successful spread to an area leading to dominance by that species would lead to a reduction in species richness. In this sense the impact of a species is closely tied to its abundance in an area, which while seemingly obvious may help to explain the contrasting findings in relation to invasive species impacts on biodiversity (see for example, Gaertner, Breeyen, Hui, & Richardson, (2009) compared to Sax & Gaines (2003)). For Coralita, there is only one vegetation type and associated areas where it is the dominant species on the islands, which can help to explain the lack of significant impact on species richness observed. Although in this sense Coralita is no different from the other species that are dominant in each area in terms of impacting species richness, the fact that it can reach a position of dominance shows that it has the potential to impact biodiversity.

*SQ 3: How has species composition on the islands changed over time and what links can be made to the spread of Coralita?*

Unfortunately, having gathered and inspected the species observations from different sources at time periods more thoroughly, the ability to assess species change over time with the detail required has not been possible. Although there may be some evidence that Coralita has displaced what was the dominant species in an area, the confidence in this finding is low, given the different sampling locations and data reporting methods.

*SQ 4: How do species co-occur on the islands in areas where Coralita is prevalent and what inferences can be made about species loss due to Coralita as a result?*

An assessment of competitive exclusion was carried out based on co-occurrence information of Coralita with other species and those species with each other. There were many species that did not co-occur with Coralita but did co-occur with species that did. Given this high number of species, it is difficult to say with any certainty about the impact that Coralita may have had, although for those species that co-occurred with a substantial number species which co-occurred with Coralita, it is probable that Coralita played some part in their absence from the area. Of course, there are many other factors that contribute to the absence of a species from an area, and the fact that none of the species with the largest number of co-occurring species with Coralita were climbing species suggests that Coralita has not directly replaced a species from an area. Evidence from the PCA on plant traits for island species, whereby co-occurring species were a sub-set of non co-occurring species also suggests that Coralita does not have a dramatic role in displacing species, although it is worth reiterating the earlier point above regarding the abundance of Coralita and the potential impact that was observed in relation to biodiversity.

*SQ 5: How different is Coralita from other species on the islands, based on species traits?*

Trait values for all island species were compared with those for Coralita statistically, with the majority of trait values judged to be significantly different from the mean trait value. Due to the skew in data, these findings should be viewed with caution however. In addition, in order to investigate variation within the database for island species a principal component analysis was performed on trait values. As with the PCA for all species on the constructed database, this PCA for island species only also showed Coralita to be somewhat atypical for island species, although unlike the whole dataset PCA, a further PCA on data excluding information inferred for Coralita from average values of climbing species shows that for those traits it was fairly typical. This implies either that the imputed trait values for Coralita were unreasonably different from normal trait values for the islands, or that these imputed traits accurately represent Coralita trait values and were thus the most important in terms of identifying the differences between groups. This has implications for the assessment of impacts, as if the differences observed across the dataset between Coralita and island species is a function of imputed values over-playing the differences, then the potential effects that Coralita has and could have on communities by altering community averages would be likewise over-estimated.

*SQ 6: Based on trait values and species abundance, how would the hypothetical removal of Coralita affect community averages and what would this imply for ecosystem services?*

Evidence based on community weight mean (CWM) values for traits suggests that the removal of Coralita would not affect average trait values substantially, assuming that the relative share of abundances between species would not change dramatically. This was even the case when the imputed values from the PCA for island species were used to complete trait values for species that were missing, but for which there was information on abundances. To test the implication of the further spread of Coralita, the abundances for Coralita were artificially adjusted for all areas where it was found in the reports by de Freitas et al., to the maximum abundance share. In this instance the majority of CWM trait values were sufficiently different when Coralita was removed from these areas, again highlighting that Coralita is somewhat atypical for the species on the islands. However at present, across the areas where Coralita is found, there does not appear to be a clear difference in CWM values as a result of Coralita, and hence the no link to impacts at an ecosystem functioning or ecosystem services level.

Clearly these findings together paint a rather inconclusive picture about the impacts that Coralita is having on the islands.

*RQ 2: Based on the application of the EICAT and trait based methodology utilised for this assessment, what strengths and weaknesses can be discerned from these approaches?*

Ultimately the main aim of the EICAT approach is the standardisation of invasive species impacts into comparable classification levels. Such a classification is based on clear and reliable information as far as possible. As such, the approach is less concerned with the means of gathering information to make that assessment, which has been the underlying focus of this study. Rather the approach has been used as a way to frame the idea of species and community impacts and to consider the types of impacts that might result from an invasive species. The usefulness of this methodology in attempting to gather the information to make an assessment has therefore been limited to the final classification and to the initial stages of developing analytical approaches to tease out information to judge impacts. The ability to use impacts from other species and other locations and apply them to other species, with the clear caveat that this would imply a very low confidence assessment, has in some way been vital for this assessment. Of course, this is not to say that the justification for classification in this way can be missing completely, but the approach is more positive and encourages initial assessment and subsequent improvement, rather than simply suggesting that if there is no direct evidence there can be no assessment at all.

In contrast, the trait-based methodology has been very useful as a means to assess impacts, providing an elegant approach to theoretically assess the impact of a species via its difference in trait values compared to the invaded community. This approach does rest on some rather important assumptions however, discussed above in relation to missing data and the accuracy of information and subsequent estimation from the data on vegetation cover on the islands.

Overall, this research has highlighted the difficulty of making such an assessment of impacts without executing primary research. A body of evidence has been produced through application of various techniques, that suggest:

- 1) Based on the impacts of other invasive species, and the evidence suggesting that Coralita is more like these species than island species, it is likely that Coralita is also having an impact on species and communities;
- 2) Biodiversity appears to be affected in the area where Coralita is the most prevalent species;
- 3) There are a number of species that may have been excluded from areas due to competition from Coralita;
- 4) Coralita's traits appear to suggest that it is sufficiently different from other island species, which in turn has implications for community trait values.

None of these aspects are particularly certain however, in the sense of definitively proving that Coralita has an impact on species, communities or ecosystems on the islands. Indeed some evidence, such as the analysis performed on CWMs, suggests that Coralita is not sufficiently widespread or sufficiently different from other species, to be having much of an impact at present, at least in the

areas analysed. Further research would be needed, mostly in relation to urban areas where Coralita is most prevalent, to build sufficient confidence that Coralita is having a major impact.

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# Appendices

*Table A1: R packages and associated functions used in this research*

| <b>R Package(s)</b> | <b>Specific function (s)</b> | <b>Purpose</b>  | <b>Author</b>                         |
|---------------------|------------------------------|---|---------------------------------------|
| <b>corrplot</b>     | corrplot(...)                | Visualisation of correlations between variables                     | Wei & Simko (2017)                    |
| <b>exact</b>        | exact.test(...)              | Application of Bernard's test                                       | Calhoun (2016)                        |
| <b>factoextra</b>   | fviz_eig(...)                | PCA scree plot  | Kassambara & Mundt (2017)             |
|                     | fviz_PCA_ind(...)            | PCA plot showing individuals  |                                       |
|                     | fviz_PCA_var(...)            | PCA plot showing variables  |                                       |
|                     | fviz_PCA_var(...)            | PCA biplot showing individuals and variables                        |                                       |
| <b>FactoMineR</b>   | PCA(...)                     | Carry out a PCA   | Lê et al. (2008)                      |
| <b>FD</b>           | Functcomp(...)               | Calculate community weighted mean trait values                      | Laliberté, Legendre, & Shipley (2014) |
| <b>missMDA</b>      | estim_ncpPCA (...)           | Estimate the number of dimensions for a PCA                         | Josse & Husson (2016)                 |
|                     | imputePCA(...)               | Impute missing values in order to carry out subsequent PCA analysis |                                       |
| <b>psych</b>        | principal(...)               | Carry out a Varimax rotated PCA                                     | Revelle (2018)                        |

**Table A2: EICAT criteria for assigning impact category by relevant mechanism**

|   | <b>Massive (MV)</b>  | <b>Major (MR)</b>   | <b>Moderate (MO)</b>  | <b>Minor (MN)</b>   | <b>Minimal Concern (MC)</b>  |
|---|--|---|---|---|--|
| (1) Competition   | Competition resulting in replacement or local extinction of one or several native species; changes in community composition are irreversible   | Competition resulting in local or population extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien taxon is removed   | Competition resulting in a decline of population size of at least one native species, but no changes in community composition   | Competition affects fitness (e.g., growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations  | Negligible level of competition with native species; reduction of fitness of native individuals is not detectable  |
| (4) Transmission of diseases to native species                          | Transmission of diseases to native species resulting in replacement or local extinction of native species (i.e., species vanish from communities at sites where they occurred before the alien arrived); changes in community composition are irreversible   | Transmission of diseases to native species resulting in local or population extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien taxon is removed  | Transmission of diseases to native species resulting in a decline of population size of at least one native species, but no changes in community composition  | Transmission of diseases to native species affects fitness (e.g., growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations   | The alien taxon is not a host of diseases transmissible to native species or very low level of transmission of diseases to native species; reduction of fitness of native individuals is not detectable  |
| (6) Poisoning / toxicity  | The alien taxon is toxic/allergenic by ingestion, inhalation, or contact to wildlife or allelopathic to plants, resulting in replacement or local extinction of native species; changes in community composition are irreversible  | The alien taxon is toxic/allergenic by ingestion, inhalation, or contact to wildlife or allelopathic to plants, resulting in local or population extinction of at least one native species (i.e., species vanish from communities at sites where they occurred before the alien arrived), leading to changes in community composition, but changes are reversible when the alien taxon is removed | The alien taxon is toxic/allergenic by ingestion, inhalation, or contact to wildlife or allelopathic to plants, resulting in a decline of population size of at least one native species, but no changes in community composition (native species richness)                           | The alien taxon is toxic/allergenic by ingestion, inhalation, or contact to wildlife or allelopathic to plants, affects fitness (e.g., growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations  | The alien taxon is not toxic/allergenic/ allelopathic, or if it is, the level is very low, reduction of fitness of native individuals is not detectable  |
| (9), (10) & (11) Chemical, physical, or structural impact on ecosystems | Many changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient and water cycling; or disturbance regimes; or changes in natural succession, resulting in replacement or local extinction of native species (i.e., species vanish from communities at sites where they occurred before the alien arrived); changes (abiotic and biotic) are irreversible | Changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient cycling; or disturbance regimes; or changes in natural succession, resulting in local extinction of at least one native species, leading to changes in community composition, but changes are reversible when the alien taxon is removed   | Changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient cycling; or disturbance regimes; or changes in natural succession, resulting in a decline of population size of at least one native species, but no changes in community composition | Changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient cycling; or disturbance regimes; or changes in natural succession detectable, affecting fitness (e.g., growth, reproduction, defence, immunocompetence) of native individuals without decline of their populations | No changes in chemical, physical, and/or structural biotope characteristics; or changes in nutrient cycling; or disturbance regimes; or changes in natural succession detectable, or changes are small with no reduction of fitness of native individuals detectable |

**Table A2: (cont.)**

|   |   |  |   |  |  |
|---|---|--|---|--|--|
| (12) Interaction with other alien species | Interaction of an alien taxon with other aliens (e.g., pollination, seed dispersal, habitat modification) facilitates replacement or local extinction of one or several native species (i.e., species vanish from communities at sites where they occurred before the alien arrived), and produces irreversible changes in community composition that would not have occurred in the absence of the species. These interactions may be included under other impact categories (e.g., predation, apparent competition) but would not have resulted in the particular level of impact without an interaction with other alien taxa. | Interaction of an alien taxon with other aliens (e.g., pollination, seed dispersal, habitat modification) facilitates local or population extinction of at least one native species, and produces changes in community composition that are reversible but would not have occurred in the absence of the species. These interactions may be included under other impact categories (e.g., predation, apparent competition) but would not have resulted in the particular level of impact without an interaction with other alien taxa. | Interaction of an alien taxon with other aliens (e.g., pollination, seed dispersal, habitat modification) facilitates a decline of population size of at least one native species, but no changes in community composition; changes would not have occurred in the absence of the species. These interactions may be included under other impact categories (e.g., predation, apparent competition) but would not have resulted in the particular level of impact without an interaction with other alien taxa. | Interaction of an alien taxon with other aliens (e.g., pollination, seed dispersal) affects fitness (e.g., growth, reproduction, defence, immunocompetence) of native species' individuals without decline of their populations; changes would not have occurred in the absence of the species. These interactions may be included under other impact categories (e.g., predation, apparent competition) but would not have resulted in the particular level of impact without an interaction with other alien taxa. | Interaction of an alien taxon with other aliens (e.g., pollination, seed dispersal) but with minimal effects on native species; reduction of fitness of native individuals is not detectable |
|---|---|--|---|--|--|

**Note.** From “Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT)”, Appendix S1, by Hawkins et al., 2015, *Diversity and Distributions*, Vol. 21, Issue 11, Appendix S1 p22, Copyright 2015 the authors

**Table A3: Guidance in relation to the confidence rating of the EICAT assessment**

| Confidence level  | Examples  |
|---|---|
| <b>High</b> (approx. 90% chance of assessment being correct)      | There is direct relevant observational evidence to support the assessment;<br><i>and</i><br>Impacts are recorded at the typical spatial scale over which original native communities can be characterized;<br><i>and</i><br>There are reliable/good quality data sources on impacts of the taxa;<br><i>and</i><br>The interpretation of data/information is straightforward;<br><i>and</i><br>Data/information are not controversial or contradictory.  |
| <b>Medium</b> (approx. 65-75% chance of assessment being correct) | There is some direct observational evidence to support the assessment, but some information is inferred;<br><i>and/or</i><br>Impacts are recorded at a spatial scale which may not be relevant to the scale over which original native communities can be characterized, but extrapolation or downscaling of the data to relevant scales is considered reliable, or to embrace little uncertainty;<br><i>and/or</i><br>The interpretation of the data is to some extent ambiguous or contradictory.   |
| <b>Low</b><br>(approx. 35% chance of assessment being correct)    | There is no direct observational evidence to support the assessment, e.g. only inferred data have been used as supporting evidence;<br><i>and/or</i><br>Impacts are recorded at a spatial scale which is unlikely to be relevant to the scale over which original native communities can be characterized, and extrapolation or downscaling of the data to relevant scales is considered unreliable or to embrace significant uncertainties.<br><i>and/or</i><br>Evidence is poor and difficult to interpret, e.g. because it is strongly ambiguous.<br><i>and/or</i><br>The information sources are considered to be of low quality or contain information that is unreliable. |

*Note.* From “Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT)”, Appendix S1, by Hawkins et al., 2015, *Diversity and Distributions*, Vol. 21, Issue 11, Appendix S1 p29, Copyright 2015 the authors

**Table A4: Review of plants traits used in various relevant**

| <b>Author (s)</b>                    | <b>Title</b>   | <b>Traits used</b>  |
|--------------------------------------|--|---|
| <b>Ackerly &amp; Cornwell (2007)</b> | A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components                     | Wood density, specific leaf area (SLA), maximum height  |
| <b>Akasaka, et al. (2012)</b>        | Invasive non-native species attributes and invasion extent: Examining the importance of grain size   | Height, seed size, human use, clonality, longevity, life form   |
| <b>Bardgett et al. (2014)</b>        | Going underground: root traits as drivers of ecosystem processes   | Root depth, root length density, root branching, root diameter, specific root length (SRL), root tissue density, root dry matter content, nutrient uptake kinetics, root respiration, release of root exudates, interactions between roots and soil biota such as associations with mycorrhizal fungi and rhizobia (in legumes), but also interactions with pathogens   |
| <b>Baruah et al. (2017)</b>          | Community and species-specific responses of plant traits to 23 years of experimental warming across subarctic tundra plant communities             | Leaf length, leaf width, plant height   |
| <b>Cortois et al. (2016)</b>         | Plant–soil feedbacks: role of plant functional group and plant traits  | Relative growth rate, SLA, SRL, percent arbuscular mycorrhizal fungi colonization   |
| <b>de Bello et al. (2010)</b>        | Towards an assessment of multiple ecosystem processes and services via functional traits   | Life form, root depth, photosynthetic capacity, nitrogen (N) fixing capacity, leaf dry matter content (LDMC), lignin, leaf N content, SLA, leaf toughness, labile carbon (C), litter diversity, litter amount, association with arbuscular mycorrhizal fungi, root organic acids, root length, root biomass, size, terpene content, time of flowering, tissue chemistry, canopy density and size, leaf area, phenology, stomatal conductance, decompostability, canopy architecture, seed output, flower traits, flammability |
| <b>Díaz et al. (2004)</b>            | The plant traits that drive ecosystems: Evidence from three continents   | Leaf size, SLA, leaf strength, inrolling of lamina, leaf thickness, canopy height, woodiness, mean distance between ramets, life span, shoot phenology, seed mass, seed shape   |
| <b>Díaz et al. (2007)</b>            | Incorporating plant functional diversity effects in ecosystem service assessments  | Root biomass, root length, SRL, root N content, vegetative height, SLA, LDMC, leaf N content, leaf N to phosphorous (P) ratio, leaf tensile strength, flowering phenology   |
| <b>Fontana et al. (2014)</b>         | What plant traits tell us: Consequences of land-use change of a traditional agro-forest system on biodiversity and ecosystem service provision     | Growth form, edible or healing effect, pollination agent, life strategy, dominance in situ, mowing tolerance, flower colour, Red List species   |
| <b>Hevia et al. (2017)</b>           | Trait-based approaches to analyse links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges | Size, dispersal activity, seed mass, SLA, leaf morphology, growth form, maximum canopy height, wood density, leaf water content, bark thickness, litter abundance   |
| <b>Kattge et al. (2011)</b>          | TRY - a global database of plant traits  | Many, including seed mass, plant height, leaf longevity, SLA, leaf N, leaf P, photosynthesis per dry mass, photosynthesis per N content, photosynthesis per leaf area   |
| <b>Kunstler et al. (2016)</b>        | Plant functional traits have globally consistent effects on competition  | Wood density, SLA, maximum height   |

**Table A4: (cont.)**

| <b>Author (s)</b>                     | <b>Title</b>  | <b>Traits used</b>   |
|---------------------------------------|---|--|
| <b>Lavorel et al. (2011)</b>          | Using plant functional traits to understand the landscape distribution of multiple ecosystem services   | Vegetative height, LDMC, leaf N concentration, leaf P concentration, flowering onset   |
| <b>Leishman (1999)</b>                | Leaf trait relationships of native and invasive plants: Community- and global-scale comparisons   | N mass, SLA, leaf nitrogen concentration, P mass, leaf P concentration, photosynthetic capability, dark respiration, leaf area per unit area plant mass, growth form, seed mass, relative growth rate, height, DNA content   |
| <b>Lohbeck et al. (2018)</b>          | Trait-based approaches for guiding the restoration of degraded agricultural landscapes in East Africa   | Wood density, adult height, N fixing, deciduous, invasive, exotic  |
| <b>Osunkoya et al. (2010)</b>         | Leaf trait co-ordination in relation to construction cost, carbon gain and resource-use efficiency in exotic invasive and native woody vine species | Total biomass, leaf area, SLA, relative growth rate, total N and C per leaf dry mass, ash content per dry mass, heat of combustion, leaf carbon, photosynthetic nitrogen-use efficiency, Photosynthetic energy-use efficiency, instantaneous water use efficiency, leaf 13C: 12C ratio   |
| <b>Pfester et al. (2013)</b>          | Community mean traits as additional indicators to monitor effects of land-use intensity on grassland plant diversity                                | SLA, LDMC, vegetative plant height, reproductive plant height, vegetative spread, clonality, leaf distribution, seed mass, seed number per ramet, terminal velocity, seedbank longevity index, life history  |
| <b>Shipley et al. (2006)</b>          | From plant traits to plant communities: A statistical mechanistic approach to biodiversity  | Proportion perennial, seed number, seed maturation date, SLA, aboveground vegetation mass, stem mass, leaf mass, height  |
| <b>Tabassum &amp; Leishman (2016)</b> | Trait values and not invasive status determine competitive outcomes between native and invasive species under varying soil nutrient availability    | SLA, Amass, LDMC, relative growth rate, stem length  |
| <b>Vile et al. (2006)</b>             | A structural equation model to integrate changes in functional strategies during old-field succession   | Annual vs. perennial, vegetation mass, stem mass at first seed dispersal, leaf mass at first seed dispersal, SLA, maximum reproductive height, reproductive mass at first seed dispersal, no. of seeds per individual per annum, mean seed mass, flowering date, date of seed maturation |
| <b>Weiher et al. (1999)</b>           | Challenging Theophrastus: A common core list of plant traits for functional ecology   | Seed mass, dispersal type, above-ground biomass, onset of flowering, seed shape, clonality, SLA, height, life history, resprouting ability, stem density, leaf water content   |

**Table A5: Additional resources utilised beyond the TRY database to capture information regarding plant maximum height**

| Resource name  | Citation  |
|--|---|
| <i>Article</i> - Abrus Precatorius Linnaeus and its biological activities - a review   | Ghosh, Mitra, Jha, & Mitra (2017)                               |
| <i>Research paper</i> - Evaluation of antiulcer activity of roots of Acacia catechu Willd.(Mimosoideae)  | Alambayan, Vats, Sardana, & Sehwat (2015)                       |
| <i>Web database</i> - www.http://powo.science.kew.org  | Royal Botanical Gardens Kew (2018)                              |
| <i>Book</i> - A guide to plants in the Blue Mountains of Jamaica   | Iremonger (2002)  |
| <i>Web database</i> – www.efloras.org  | eFloras (2018)  |
| <i>Web database</i> – Cabi Invasive Species Compendium   | CABI (2018)   |
| <i>Web database</i> – Global Invasive Species Database   | ISSG (2015)   |
| <i>Report</i> - Monitoreo de la población de la guacamaya verde en la Reserva de la Biosfera Tehuacán-Cuicatlán  | Bonilla-Ruz, Aguilar, García, Reyes, & Salinas (2005)           |
| <i>Web database</i> – World Flora Online (http://sweetgum.nybg.org/science/world-flora/)   | World Flora Online (2018)                                       |
| <i>Web database</i> – Pacific Island Ecosystems at Risk (http://www.hear.org/pier/species/bidens_cynapiifolia.htm)   | US Forest Service (2013)  |
| <i>Report</i> - Invasive plant risk assessment: Green shrimp plant   | State of Queensland (2016)                                      |
| <i>Web database</i> – African Plant Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an)  | Conservatoire et Jardin botaniques de la Ville de Genève (2018) |
| <i>Web-host</i> – Biodiversity Heritage Library – compendium of various sources (https://www.biodiversitylibrary.org/)   |   |
| <i>Book</i> - The Flora of Barro Colorado Island   | Croat (1978)  |
| <i>Web database</i> – www.prota4u.org  | Plant Resources of Tropical Africa (2018)                       |
| <i>Book</i> - RHS encyclopedia of plants and flowers   | Brickell (2010)   |
| <i>Article</i> - An inside review of Cissampelos pareira Linn: a potential medicinal plant of India  | Arora, Sharma, Devi, Bainsal, & Siddiqui (2012)                 |
| <i>Web database</i> - www.tramil.net/  | TRAMIL (2018)   |
| <i>Web database</i> - Flora Virtual El Verde (http://floraelverde.catec.upr.edu/)  | Estación Biológica El Verde (2013)                              |
| <i>Book</i> - Common trees of Puerto Rico and the Virgin Islands   | Little & Wadsworth (1964)                                       |
| <i>Web database</i> – Ecocrop (www.ecocrop.fao.org)  | FAO (2007)  |
| <i>Web database</i> – PlantZA (http://pza.sanbi.org)   | SANBI (2018)  |
| <i>Web database</i> - https://www.fnps.org/plants/   | Florida Native Plant Society (2018)                             |
| <i>Web database</i> – <b>Herbario Virtual Austral Americano</b> (https://herbariovaa.org)  | ASU (2018)  |
| <i>Web database</i> – Flora of the Guianas Online (http://portal.cybertaxonomy.org/flora-guianas/)   | Flora of the Guianas Programme (2018)                           |
| <i>Web database</i> – Australian Tropical Rainforest Plants (http://keys.trin.org.au/key-server/data/0e0f0504-0103-430d-8004-060d07080d04/media/Html/acknow.htm) | Hyland, Whiffin, & Zich (2010)                                  |
| <i>Web database</i> – DCNA (http://www.dcnanature.org/nature/species/)   | Dutch Caribbean Nature Alliance (2014)                          |
| <i>Book</i> - <b>Tropical Trees of Florida and the Virgin Islands: A guide to identification, characteristics and uses.</b>                                      | Kirk (2009)   |

|   |   |
|---|---|
| <i>Book</i> – Wildflowers of Texas  | Eason (2018)  |
| <i>Article</i> - <b>Revision of Hillia (Rubiaceae)</b>  | Taylor (1994)   |
| <i>Article</i> - <b>On the Identity of Jacquinia armillaris (Theophrastaceae) and Related Species</b>   | Stähl (1992)  |
| <i>Article</i> - <b>Flora of Panama: Part VI. Family 88. Zygophyllacea</b>  | Woodson, Schery, & Porter (1969)                        |
| <i>Web database</i> – Tree Fact Sheets<br>( <a href="http://hort.ufl.edu/database/trees/trees_scientific.shtml">http://hort.ufl.edu/database/trees/trees_scientific.shtml</a> ) | Environmental Horticulture University of Florida (2018) |
| <i>Web database</i> - Flora of Zimbabwe: Species information  | Hyde, Wursten, Ballings, & Palgrave (2018)              |
| <i>Web database</i> - Atlas of Florida vascular plants  | Wunderlin & Hansen (2018)                               |
| <i>Article</i> - Saurocory in Melocactus violaceus  | Figueira, Vasconcellos-Neto, Garcia, & de Souza (1994)  |
| <i>Book</i> - Vines and Climbing Plants of Puerto Rico and the Virgin Islands   | Acevedo-Rodríguez (2005)                                |

**Table A6:** Information from the CABI species compendium for climbing species listed on the GISD database as having an impact outcome

| Species                           | Impact outcomes  | Impact mechanisms  | Key characteristics   | Distribution  |
|-----------------------------------|--|--|---|---|
| <b>Abrus precatorius</b>          | Altered trophic level<br>Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Negatively impacts human health<br>Negatively impacts animal health<br>Reduced native biodiversity<br>Threat to/ loss of native species   | Causes allergic responses<br>Herbivory/grazing/browsing<br>Poisoning<br>Rooting  | Twining or trailing agricultural weed, highly toxic seeds, reach 3m in length, spread by seed which are produced in large quantities an remain viable for up to a year                                    | Native to Africa, Asia, Malaysia, Australia and the Pacific Region but has since been introduced to the neotropics                                  |
| <b>Akebia quinata</b>             | Altered trophic level<br>Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Modification of hydrology<br>Modification of nutrient regime<br>Modification of successional patterns<br>Negatively impacts forestry<br>Reduced native biodiversity<br>Threat to/ loss of endangered species<br>Threat to/ loss of native species | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Competition - strangling<br>Rapid growth            | Woody, deciduous vine, used as ornamental plant, drought and shade tolerant, reproduces clonally  | Native to Eastern Asia, East and Central China, Japan and Korea. Now introduced to Canada, Europe, Oceania and the USA                              |
| <b>Anredera cordifolia</b>        | Modification of successional patterns<br>Monoculture formation<br>Negatively impacts forestry<br>Negatively impacts tourism<br>Reduced amenity values<br>Reduced native biodiversity<br>Threat to/ loss of endangered species<br>Threat to/ loss of native species   | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Competition<br>Rapid growth                         | Grows from rhizomes, has aerial tubers, stems 3 to 6 m in length, rarely reproduce sexually   | Native to South America, global spread adapted to Europe  |
| <b>Caesalpinia decapetala</b>     | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Negatively impacts agriculture<br>Reduced native biodiversity  | Competition - monopolizing resources<br>Produces spines, thorns or burrs   | Sprawling shrub or climber, 5 to 10m tall   | Native range Himalayas, Sri Lanka, China, Korea and Japan, now naturalised tropical and sub tropical regions and Islands                            |
| <b>Cardiospermum grandiflorum</b> | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Modification of successional patterns<br>Monoculture formation<br>Reduced native biodiversity<br>Threat to/ loss of native species   | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Competition - strangling<br>Rapid growth<br>Rooting | Climbs via tendrils, reaches 5-8m in height, sexual reproduction, but also vegetative spread via suckering and root fragments, fruits float and aid transport   | Confusion native range but assumed only native Americas, invasive in South Africa, Australia, Pacific Islands and Southern EU Islands (e.g. Sicily) |
| <b>Clematis vitalba</b>           | Negatively impacts agriculture<br>Negatively impacts human health<br>Negatively impacts animal health<br>Negatively impacts tourism<br>Reduced amenity values<br>Reduced native biodiversity   | Competition - monopolizing resources<br>Pest and disease transmission  | Seeds wind dispersed, colonises disturbed areas, climbs tall trees and reduces forests to low growing infestations, stems can grow 10m in length, twines, dumping garden waste also contributes to spread | Native to Europe, naturalised North of its native EU range, naturalises USA, Australia and NZ   |

Table A6: (cont.)

| Species                              | Impact outcomes  | Impact mechanisms  | Key characteristics  | Distribution   |
|--------------------------------------|--|--|--|--|
| <b>Coccinia grandis</b>              | No information   | No information   | Grows aggressively and smothers, grows between 9 and 28m long, tuberous root system and tendrils, spread by seeds carried by birds, rodents and maybe pigs, also spread by tubers and stems        | Native to East Africa, introduced to Aus, Caribbean, Southern USA and Pacific  |
| <b>Colubrina asiatica</b>            | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Modification of nutrient regime<br>Modification of successional patterns<br>Monoculture formation<br>Reduced native biodiversity<br>Threat to/ loss of endangered species<br>Threat to/ loss of native species   | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Rapid growth<br>Rooting | Outcompetes for space and light, seeds spread by currents and birds, vigorous rerouting from stems, adventitious sprouting, roots where stem returns from ground, vigorous sprouting after cutting | Native to west Africa, China South-eastern Asia, Australia and several islands in Pacific. Introduced to West Indies, Mexico and Florida |
| <b>Cryptostegia grandiflora</b>      | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Negatively impacts agriculture<br>Negatively impacts human health<br>Negatively impacts animal health<br>Negatively impacts tourism<br>Reduced amenity values<br>Reduced native biodiversity   | Competition - monopolizing resources   | Highly invasive in semi-arid ecosystems, lag before becomes invasive, can grow as sub-shrub but woody climber , stems twine , can grow to 20-30m, roots can penetrate 12m, spread by seed          | Broad, native to south-west Madagascar   |
| <b>Cryptostegia madagascariensis</b> | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Host damage<br>Infrastructure damage<br>Monoculture formation<br>Negatively impacts agriculture<br>Negatively impacts cultural/traditional practices<br>Negatively impacts forestry<br>Negatively impacts human health<br>Negatively impacts animal health<br>Negatively impacts livelihoods<br>Negatively impacts aquaculture/fisheries<br>Negatively impacts tourism<br>Reduced native biodiversity<br>Threat to/ loss of endangered species<br>Threat to/ loss of native species<br>Damages animal/plant products | Causes allergic responses<br>Hybridization<br>Interaction with other invasive species<br>Rapid growth                | Fast growing woody vine, many seeds dispersed by wind, floodwater, or stuck to animal fur, twines, 6-8 m in length,  | Native to Madagascar, closely related to gradiflora, widely distributed to India, Kenya, Brazil, Hawaii, Australia                       |

Table A6: (cont.)

| Species                       | Impact outcomes  | Impact mechanisms  | Key characteristics   | Distribution   |
|-------------------------------|--|--|---|--|
| <b>Cynanchum rossicum</b>     | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Negatively impacts agriculture<br>Negatively impacts animal health<br>Negatively impacts tourism<br>Reduced amenity values<br>Reduced native biodiversity  | Competition - monopolizing resources<br>Pest and disease transmission  | Climbing and twining vine, fibrous root system, stems grow 1 to 3m high, self-pollination, spread by seeds  | Native to Ukraine and south-west Russia, introduced to USA   |
| <b>Euonymus fortunei</b>      | Ecosystem change/ habitat alteration<br>Reduced native biodiversity<br>Threat to/ loss of endangered species<br>Threat to/ loss of native species  | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Rapid growth  | Grows 12-22m tall with support of aerial roots or can form dense shrub 1m high, propagated via cuttings but can be grown from seed, can reproduce vegetatively forming roots where branches connect to the ground, seeds dispersed by birds | Native to Asia, from Japan to the Philippines. Introduced globally but most reports on naturalisation from USA |
| <b>Hedera helix</b>           | Negatively impacts human health<br>Negatively impacts animal health<br>Reduced native biodiversity<br>Threat to/ loss of endangered species<br>Threat to/ loss of native species   | Competition - monopolizing resources   | Can grow to 30m long, creeps along forest floor then climbs forest canopy to fruit and seed, seeds dispersed by birds, combination sexual reproduction and vegetative propagation, tolerant of environmental conditions, shallow roots      | Native to Europe, spread to temperate areas and beyond   |
| <b>Lygodium microphyllum</b>  | Modification of fire regime<br>Modification of successional patterns<br>Monoculture formation<br>Reduced amenity values<br>Reduced native biodiversity<br>Threat to/ loss of native species  | Allelopathic<br>Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Rapid growth                        | Climbing fern, aggressively invaded forest wetlands, spores produced and dispersed by wind, tolerant to fire  | V broad range: native to tropical and subtropical Africa, Asia and Oceania, introduced to USA                  |
| <b>Macfadyena unguis-cati</b> | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Host damage<br>Infrastructure damage<br>Modification of nutrient regime<br>Modification of successional patterns<br>Monoculture formation<br>Reduced native biodiversity<br>Threat to/ loss of native species<br>Transportation disruption | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Competition - strangling<br>Rapid growth<br>Rooting | Climbs up to 15m; widely used as ornamental; spreads by seeds and vegetatively via tubers and stem pieces   | Native to tropical America from Mexico to Argentina and the West Indies. Naturalised globally                  |
| <b>Merremia peltata</b>       | No information   | No information   | Stems grow from large tuber, climbs up to 30m, stems milky juice,   | Ranges from East Africa through Indian Ocean, South and South-East Asia and to many Pacific Islands            |

Table A6: (cont.)

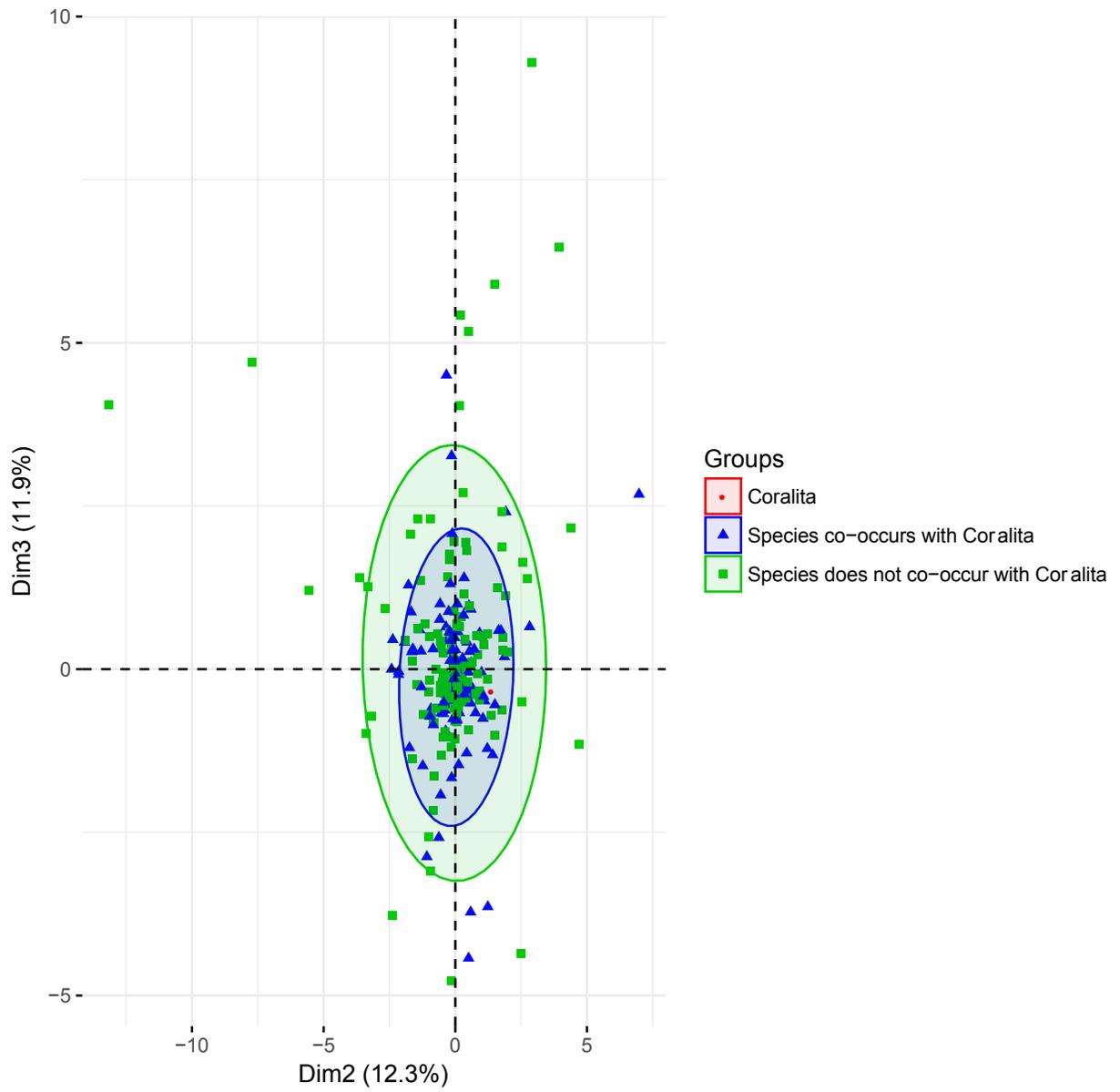
| Species                   | Impact outcomes   | Impact mechanisms  | Key characteristics   | Distribution  |
|---------------------------|---|--|---|---|
| <b>Merremia tuberosa</b>  | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Host damage<br>Modification of successional patterns<br>Monoculture formation<br>Reduced native biodiversity<br>Threat to/ loss of native species   | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Competition - strangling<br>Rapid growth<br>Rooting           | Reproduces sexually by seeds and vegetatively from cuttings, twines, 10-15m in length, milky latex,   | Native to Mexico and Central America, naturalized and cultivated Africa, South Am, Caribbean, China, Pacific, Australia                                   |
| <b>Mikania micrantha</b>  | Ecosystem change/ habitat alteration<br>Negatively impacts agriculture<br>Reduced native biodiversity<br>Threat to/ loss of endangered species  | Competition - monopolizing resources<br>Competition - smothering<br>Competition - strangling<br>Rapid growth   | Produces many seeds, can shoot from runners and suckers and regenerate from stems,  | Native to central and southern America, now widespread except Africa, not problematic everywhere (e.g. Aus) due to climate                                |
| <b>Mimosa diplotricha</b> | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Host damage<br>Modification of fire regime<br>Modification of nutrient regime<br>Modification of successional patterns<br>Monoculture formation<br>Negatively impacts agriculture<br>Negatively impacts forestry<br>Negatively impacts human health<br>Negatively impacts animal health<br>Negatively impacts livelihoods<br>Reduced amenity values<br>Reduced native biodiversity<br>Threat to/ loss of native species | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Poisoning<br>Rapid growth<br>Produces spines, thorns or burrs | Scrambling strongly branched shrub that grows to 1/2m, climbs other via spiny stems, taproot 1-2m depth, reproduces only by seed, prolific no. of seeds, introduced via contaminated crop seeds, seeds very hardy with long dormancy period | Native to neotropics including much of South and Central America, as well as Caribbean, now widespread in wet tropics and subtropics (Aus, Vanuatu etc.), |
| <b>Paederia foetida</b>   | Ecosystem change/ habitat alteration<br>Increases vulnerability to invasions<br>Modification of fire regime<br>Modification of successional patterns<br>Monoculture formation<br>Negatively impacts agriculture<br>Negatively impacts forestry<br>Negatively impacts livelihoods<br>Reduced amenity values<br>Reduced native biodiversity<br>Threat to/ loss of native species  | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Rapid growth<br>Rooting                                       | Twining vines, trail across ground, characterised by extreme polymorphism, up to 10m long stems, likes disturbance, produces sexually by seed, seed dispersal by wind and birds   | South East and East Asian origin, introduced New Guinea, Sri Lanka, Hawaii, Florida   |

Table A6: (cont.)

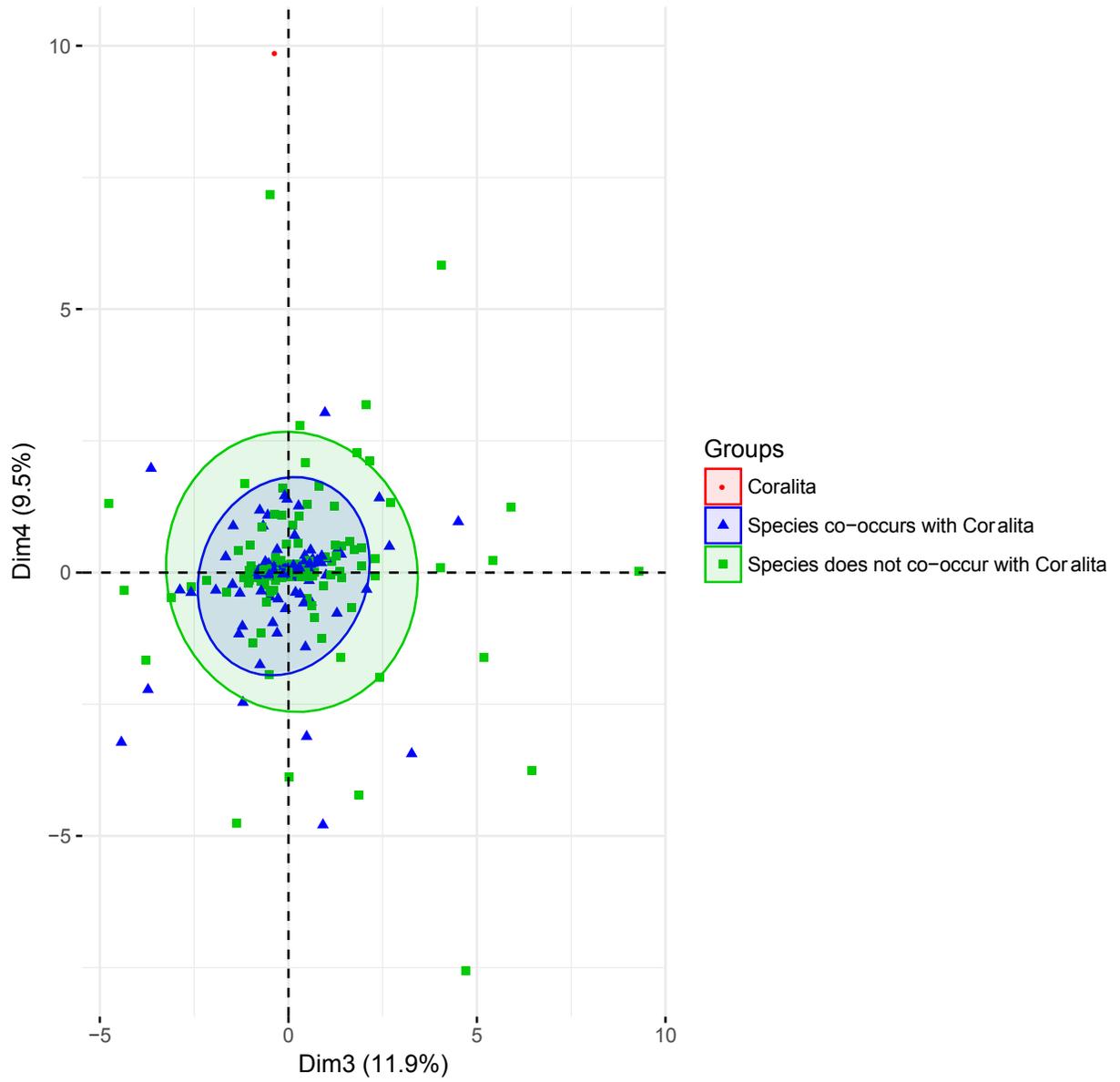
| Species                             | Impact outcomes  | Impact mechanisms   | Key characteristics   | Distribution  |
|-------------------------------------|--|---|---|---|
| <b>Pueraria montana var. lobata</b> | Damaged ecosystem services<br>Ecosystem change/ habitat alteration<br>Infrastructure damage<br>Modification of fire regime<br>Modification of hydrology<br>Modification of nutrient regime<br>Modification of successional patterns<br>Monoculture formation<br>Negatively impacts agriculture<br>Negatively impacts forestry<br>Negatively impacts livelihoods<br>Reduced amenity values<br>Reduced native biodiversity<br>Threat to/ loss of endangered species<br>Threat to/ loss of native species | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Competition - strangling<br>Competition<br>Rapid growth                            | Produces large tubers up to 2m long that can weigh as much as 180kg, stems up to 30m in length and strong, v fast growing, new roots where nodes come into contact with ground, twines, prefers open areas or edges of canopy, mostly veg growth as seed production is poor, like many legumes symbiotic relationship with N fixing bacteria, | Native to East Asia, broad range but apparently only a problem in South Eastern USA   |
| <b>Rosa bracteata</b>               | No information   | No information  | No information  |   |
| <b>Rosa multiflora</b>              | Damaged ecosystem services<br>Increases vulnerability to invasions<br>Modification of fire regime<br>Negatively impacts forestry<br>Reduced amenity values<br>Reduced native biodiversity  | Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Competition - strangling<br>Produces spines, thorns or burrs                       | Deciduous liana, stems climb to 6m, inter-twinning, invades where open canopy (disturbed)   | Native to East Asia, introduced to Pakistan, South Africa, North America, Australia and New Zealand   |
| <b>Solanum tampicense</b>           | No information   | No information  | No information  |   |
| <b>Syngonium podophyllum</b>        | Altered trophic level<br>Ecosystem change/ habitat alteration<br>Host damage<br>Monoculture formation<br>Negatively impacts agriculture<br>Reduced native biodiversity<br>Threat to/ loss of endangered species<br>Threat to/ loss of native species   | Causes allergic responses<br>Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Competition - strangling<br>Poisoning<br>Rapid growth | 10m in length, milky latex when wounded, climbing by means of adventitious roots produced at the nodes, copious fruit, spreads by seeds and vegetatively by stem segments,  | Native to Mexico, Central America and parts of South America. widely introduced as an ornamental in tropical and subtropical regions and currently it can be found in the United States (Florida and Hawaii), South Africa, Australia, Singapore, Malaysia, China, the West Indies, and on several islands in the Pacific , ornamental vine |
| <b>Vinca major</b>                  | No information   | No information  | No information  |   |
| <b>Wisteria floribunda</b>          | No information   | No information  | No information  |   |

*Table A6: (cont.)*

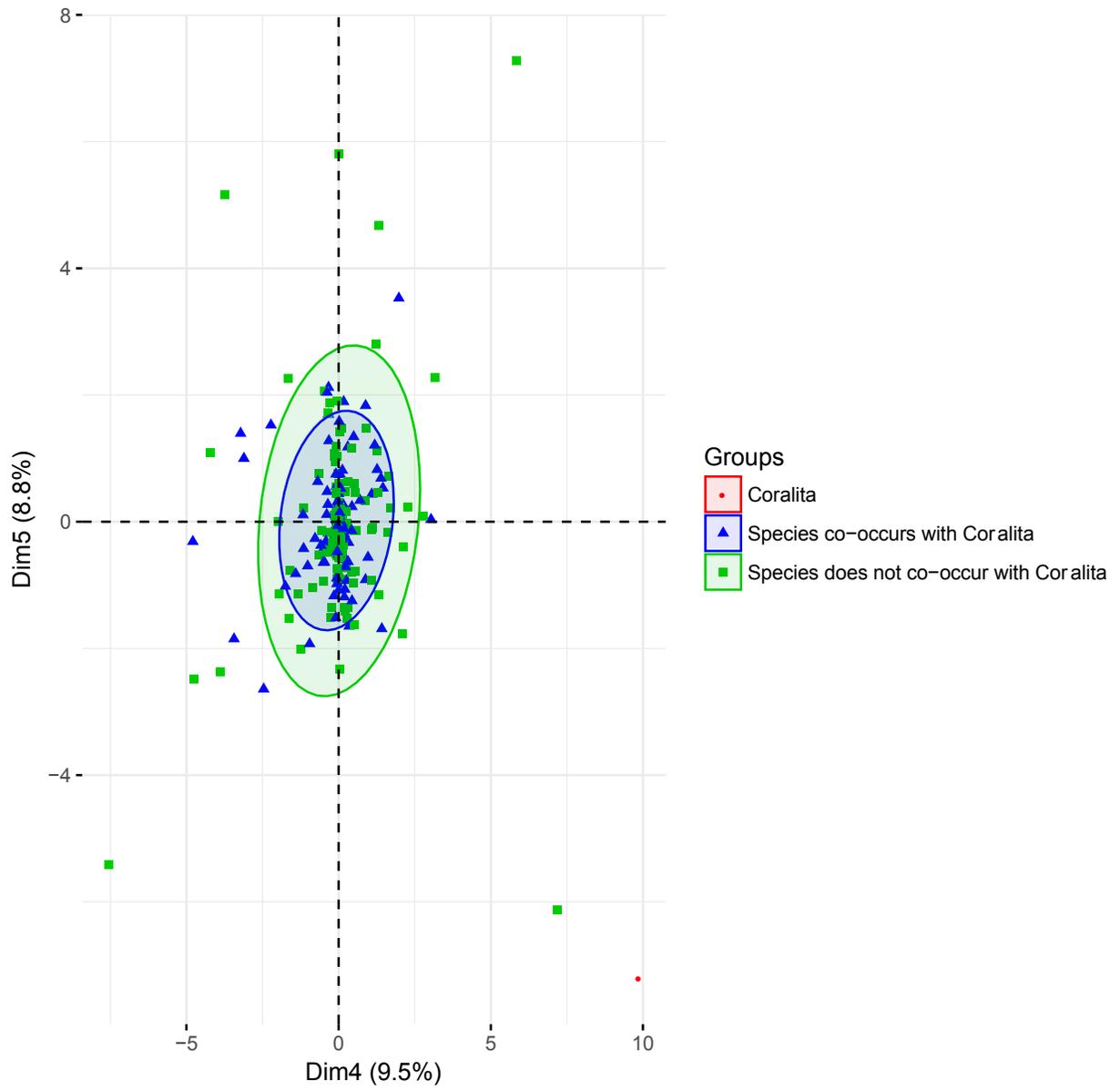
| Species                  | Impact outcomes  | Impact mechanisms   | Key characteristics  | Distribution                  |
|--------------------------|--|---|--|-------------------------------|
| <b>Wisteria sinensis</b> | Ecosystem change/ habitat alteration<br>Host damage<br>Increases vulnerability to invasions<br>Modification of nutrient regime<br>Modification of successional patterns<br>Monoculture formation<br>Negatively impacts forestry<br>Negatively impacts human health<br>Negatively impacts animal health<br>Reduced native biodiversity<br>Threat to/ loss of native species | Causes allergic responses<br>Competition - monopolizing resources<br>Competition - shading<br>Competition - smothering<br>Hybridization<br>Interaction with other invasive species<br>Poisoning<br>Rapid growth | Woody, deciduous vine that can climb to 20 m; twines; vines spread across the ground; insect pollinated and can produce vegetatively via cut stems | Native to China, global range |



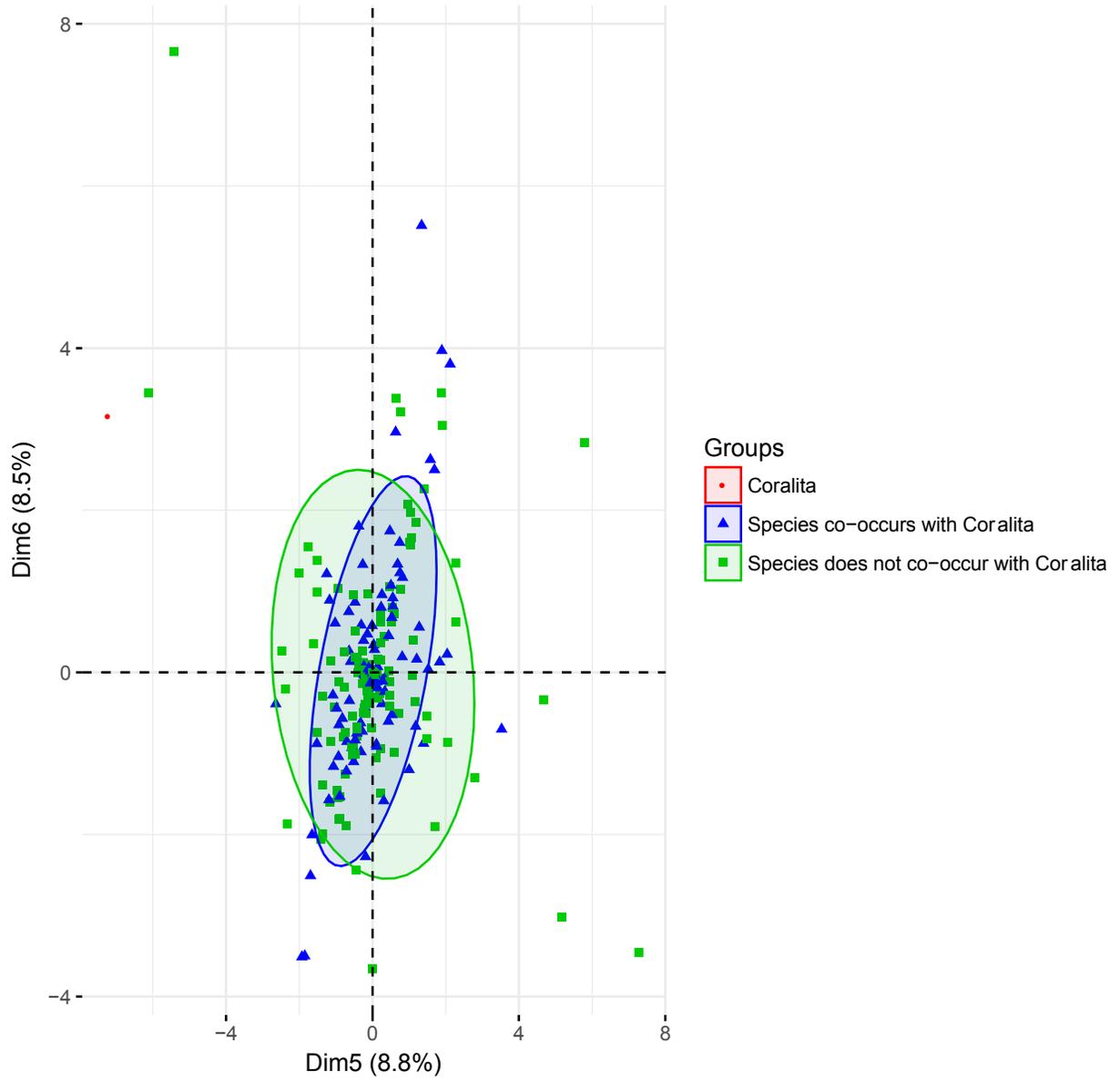
*Figure A1:* Principal component analysis projections of island individual species on the second and third principal components, with groupings of species that co-occur and those that do not co-occur



*Figure A2:* Principal component analysis projections of island individual species on the third and fourth principal components, with groupings of species that co-occur and those that do not co-occur



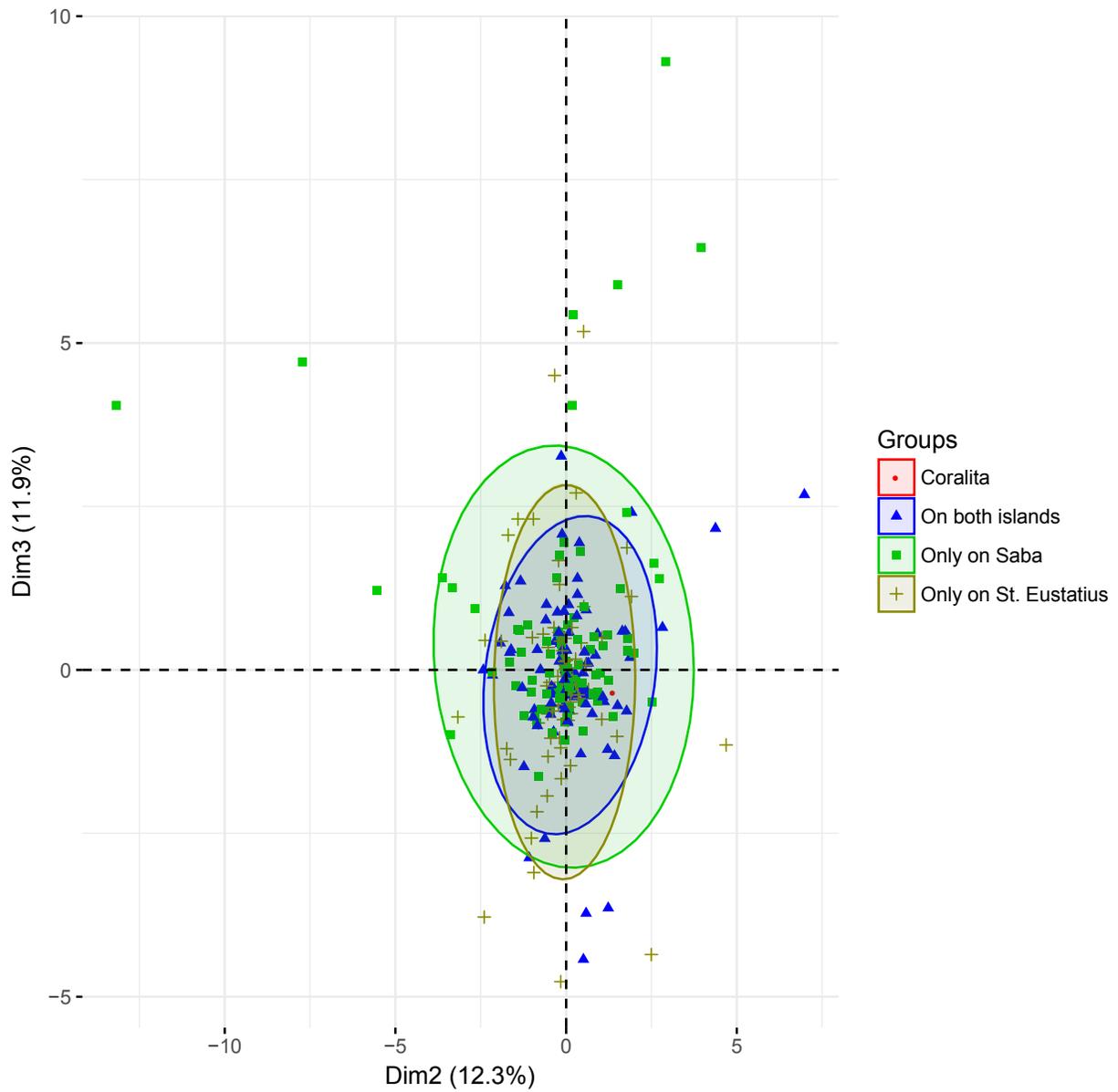
*Figure A3:* Principal component analysis projections of island individual species on the fourth and fifth principal components, with groupings of species that co-occur and those that do not co-occur



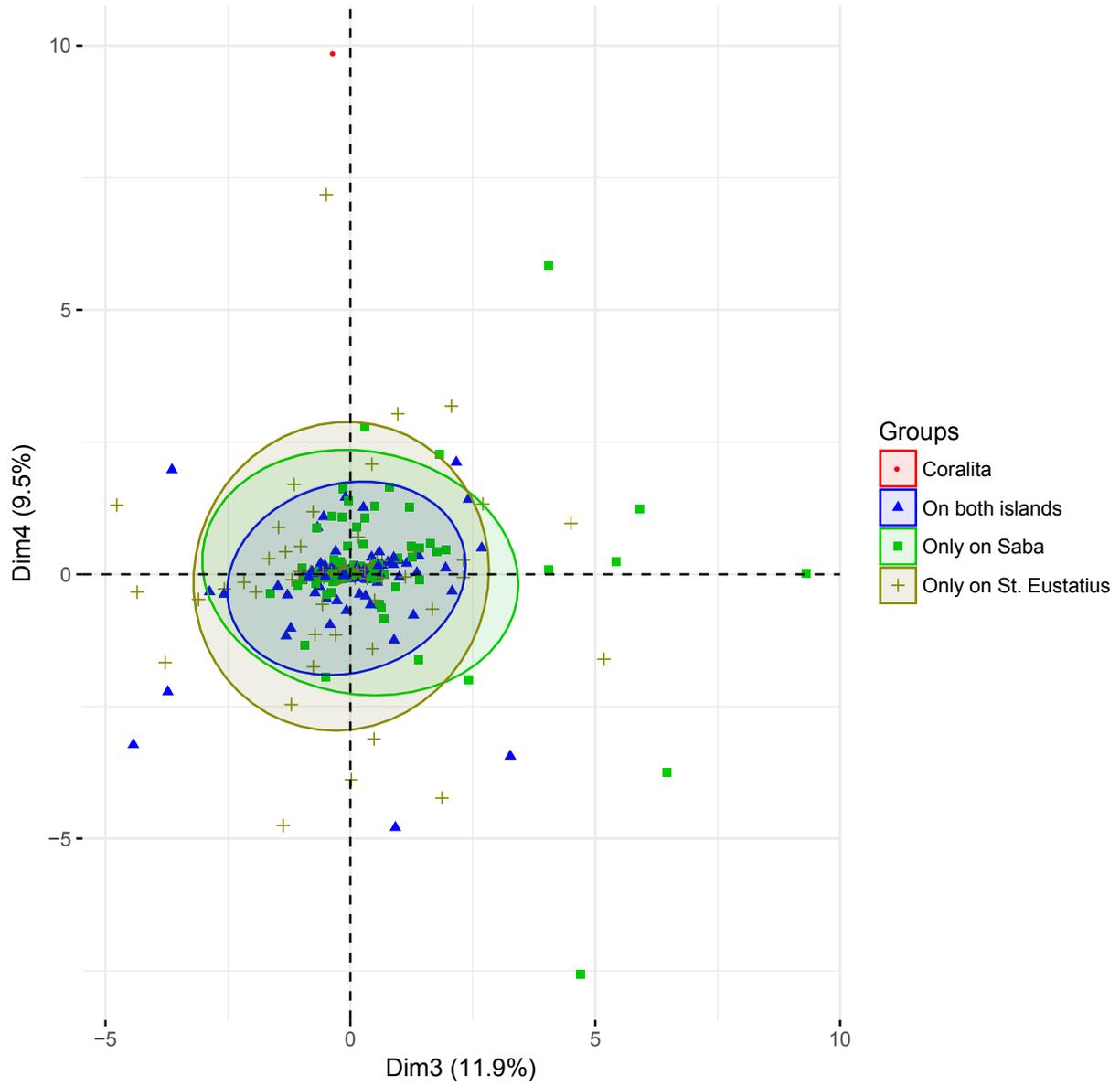
*Figure A4:* Principal component analysis projections of island individual species on the fifth and sixth principal components, with groupings of species that co-occur and those that do not co-occur

*Table A7: Loadings and percentage variance explained for a varimax rotated PCA for island species plant traits*

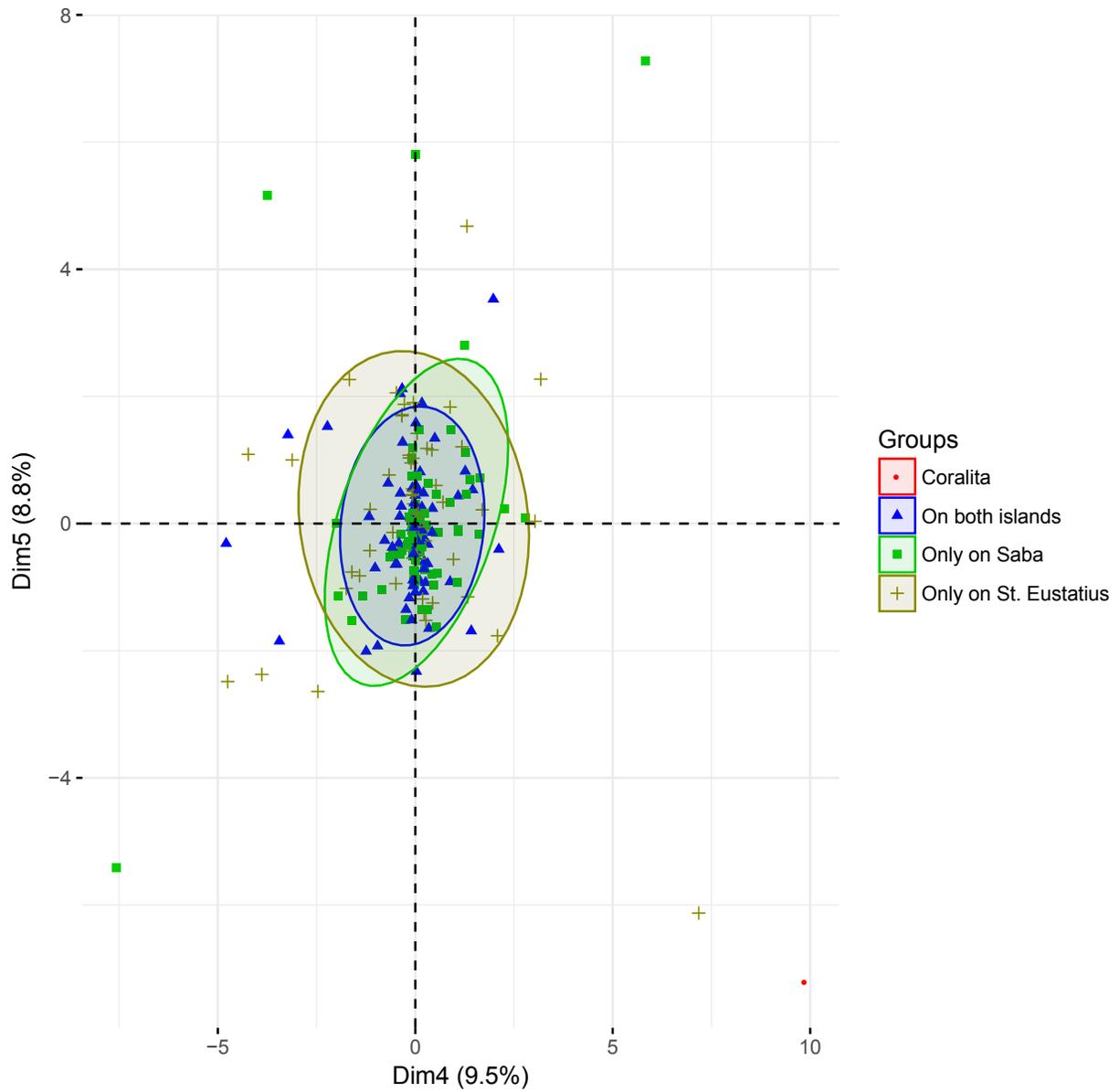
| Traits  | RC1   | RC2   | RC3   | RC4   | RC5   | RC6   | RC7   | RC8   | RC9   | RC10  |
|---|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Leaf area (mm <sup>2</sup> )                                    | -0.01 | 0.02  | 0     | 0.07  | 0.15  | 0.02  | 0.07  | -0.1  | 0.98  | -0.07 |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | 0.05  | 0.02  | 0.04  | 0.98  | 0.11  | -0.02 | -0.01 | 0     | 0.07  | 0.08  |
| Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )   | 0.43  | 0.75  | -0.07 | 0.07  | 0.16  | -0.11 | 0.05  | -0.11 | 0.09  | -0.02 |
| Leaf longevity (month)  | 0.01  | 0.01  | 0.01  | 0.08  | 0.03  | 0     | 0     | -0.02 | -0.07 | 0.99  |
| Leaf nitrogen (N) content per leaf area (g m <sup>-2</sup> )    | 0.62  | 0.12  | 0.59  | 0.15  | -0.15 | 0.14  | 0.07  | 0.07  | 0     | -0.02 |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | -0.08 | 0.09  | 0.91  | 0     | 0.09  | -0.13 | -0.02 | -0.06 | 0     | 0.02  |
| Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> ) | -0.12 | 0.01  | 0     | -0.01 | -0.03 | 0     | 0.98  | 0.03  | 0.07  | 0     |
| Leaf thickness (mm)   | 0.24  | -0.87 | -0.21 | 0.02  | 0.03  | -0.09 | 0.01  | -0.03 | 0.03  | -0.02 |
| Plant maximum height (m)  | 0.11  | 0.07  | 0.05  | 0.12  | 0.94  | 0.12  | -0.03 | -0.06 | 0.15  | 0.03  |
| Seed dry mass (mg)  | 0.07  | 0.01  | -0.08 | -0.02 | 0.11  | 0.97  | 0     | -0.03 | 0.02  | 0     |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | -0.87 | 0.05  | 0.09  | -0.01 | -0.15 | -0.05 | 0.17  | -0.03 | 0.02  | -0.02 |
| Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.03  | -0.03 | -0.04 | 0     | -0.06 | -0.03 | 0.03  | 0.99  | -0.09 | -0.02 |
|   |       |       |       |       |       |       |       |       |       |       |
| Percentage of variance explained                                | 13%   | 12%   | 11%   | 9%    | 9%    | 9%    | 9%    | 9%    | 9%    | 9%    |



*Figure A5: Principal Component Analysis projections of island individual species on the second and third principal components, with groupings of species by location*



**Figure A6:** Principal Component Analysis projections of island individual species on the third and fourth principal components, with groupings of species by location



*Figure A7: Principal Component Analysis projections of island individual species on the fourth and fifth principal components, with groupings of species by location*

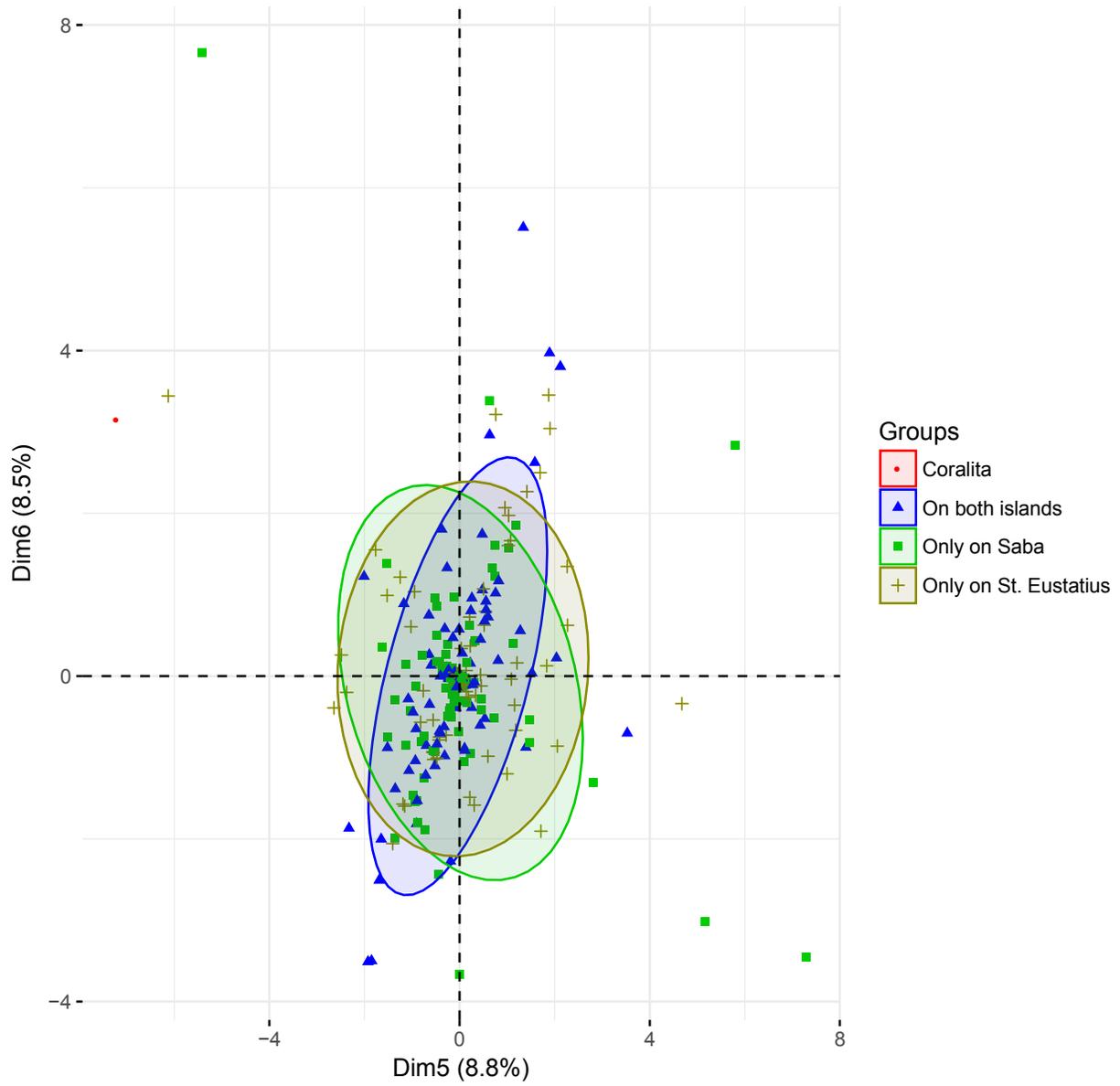
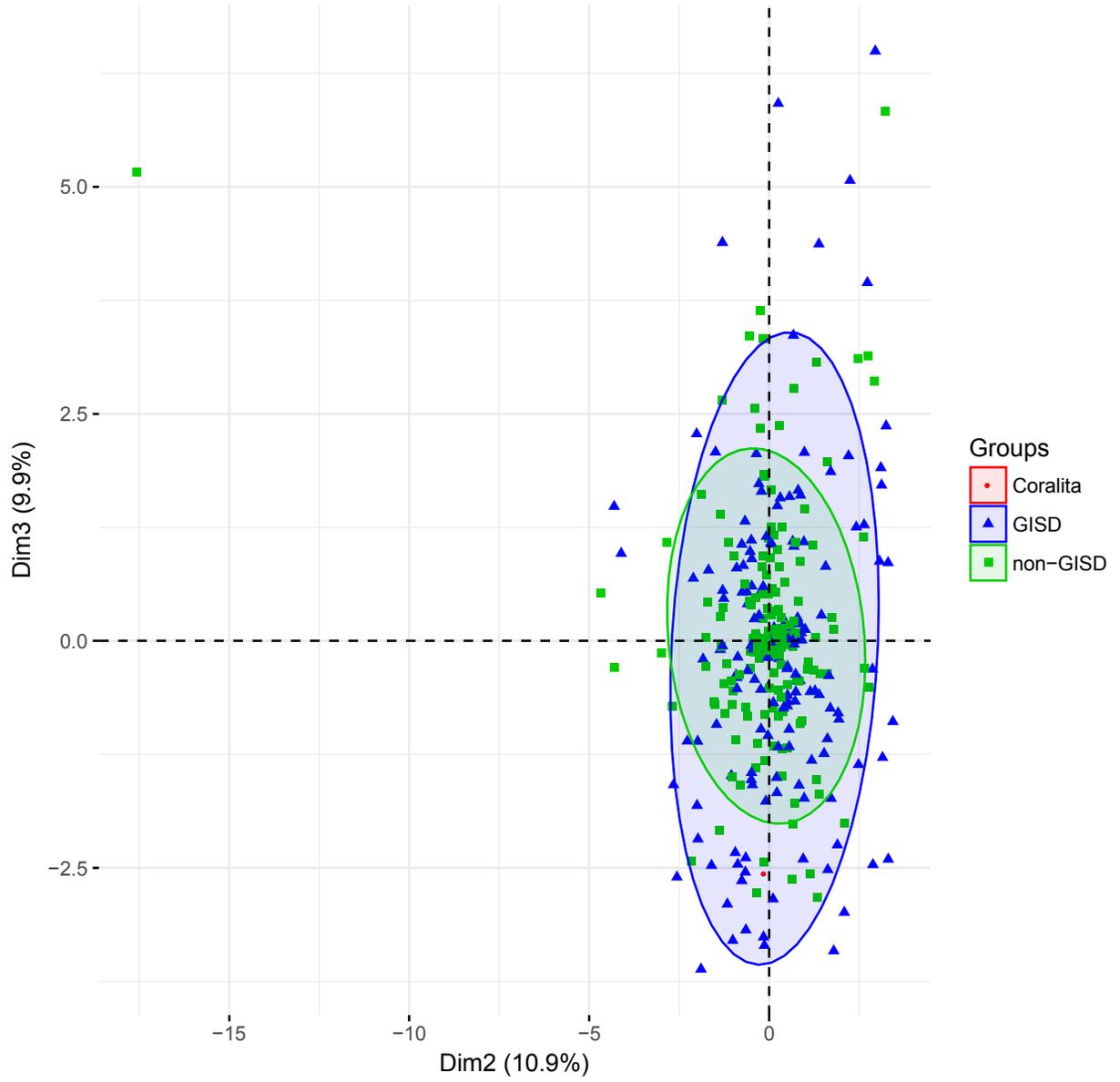


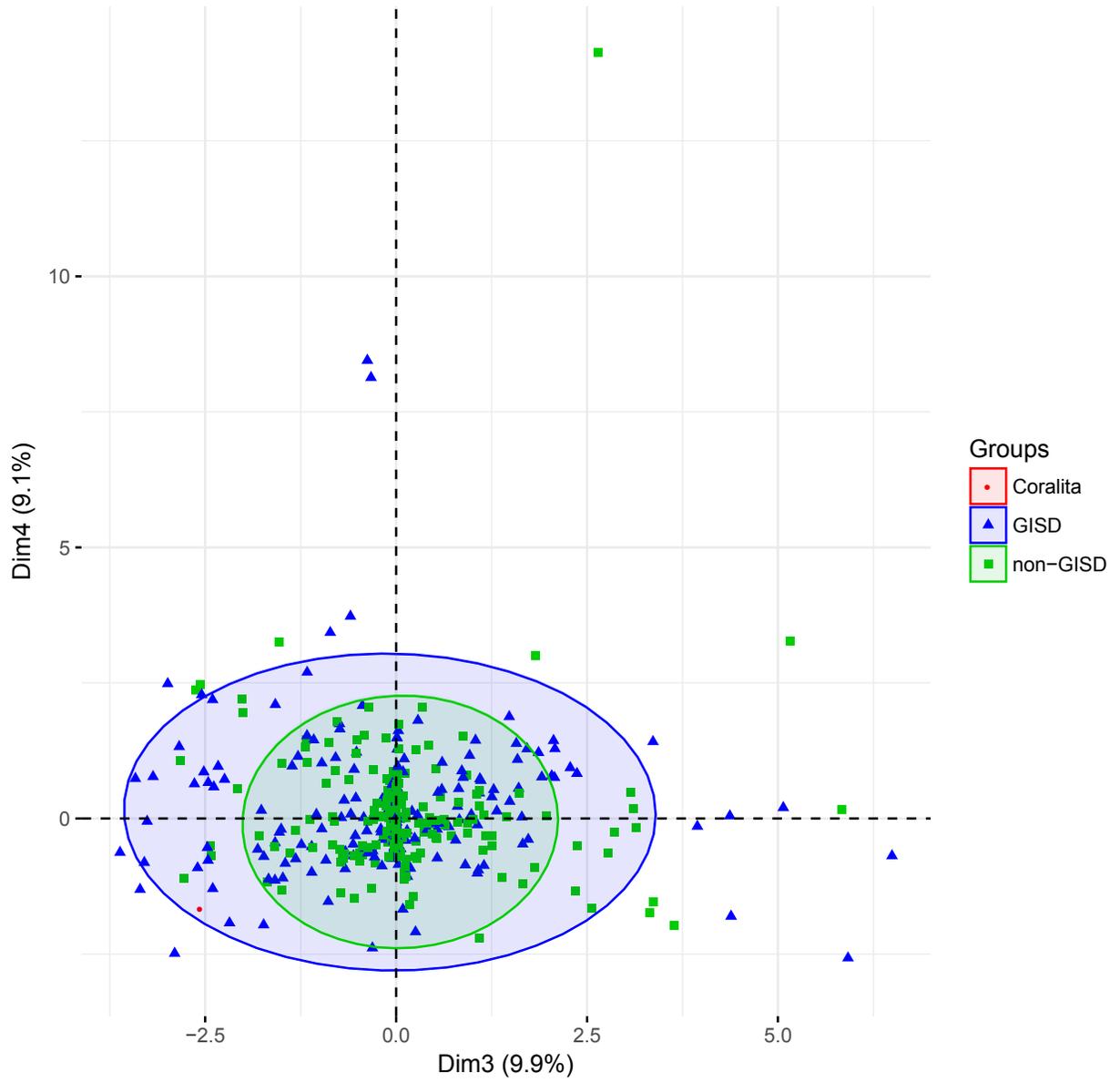
Figure A8: Principal Component Analysis projections of island individual species on the fifth and sixth principal components, with groupings of species by location

*Table A8:* Mean, median, standard errors and relative standard errors for plant traits, separated by the those species from the GISD database and other species

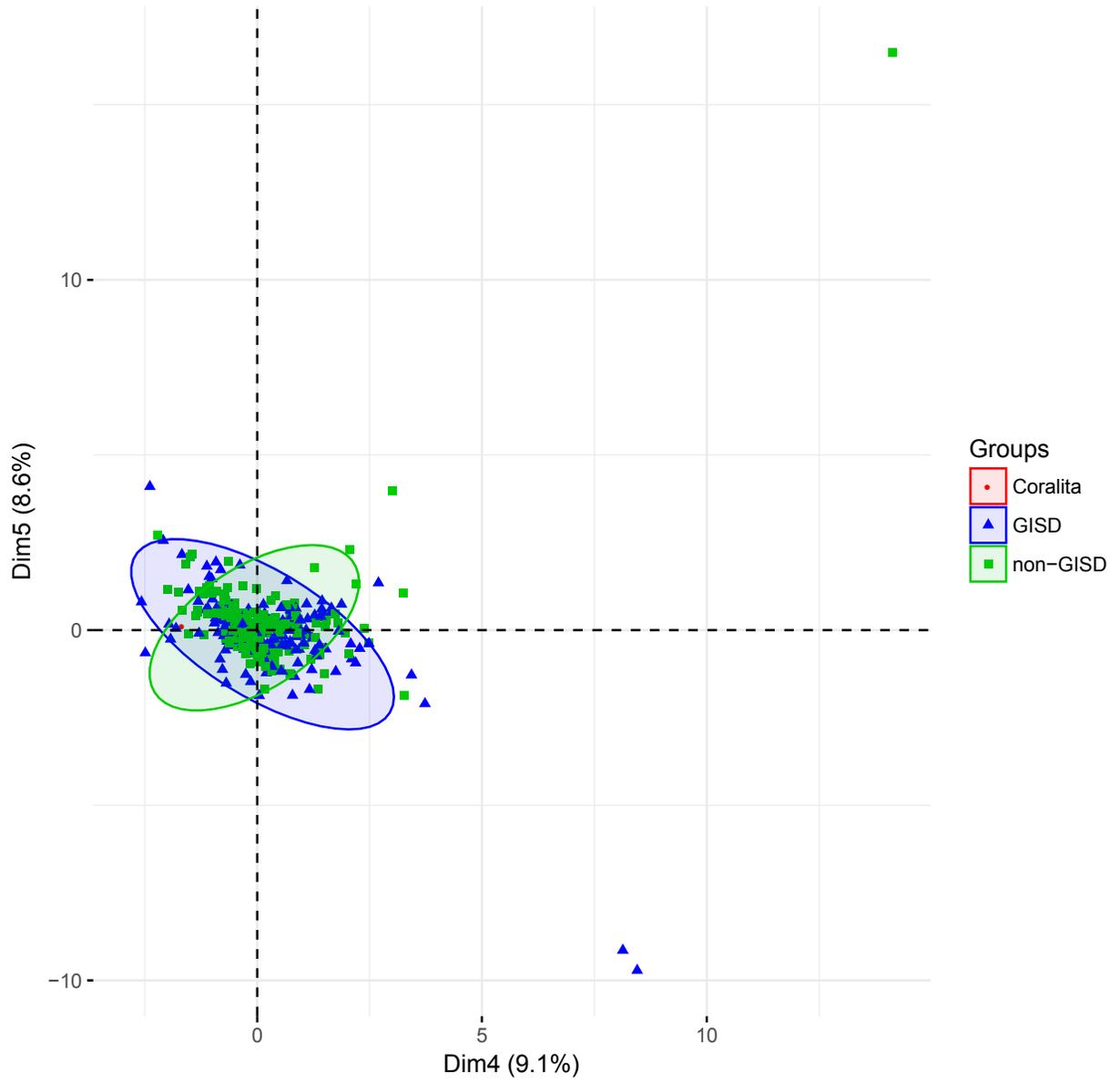
|  | Mean         |                  | Median       |                  | Standard error |                  | Relative standard error |                  |
|--|--------------|------------------|--------------|------------------|----------------|------------------|-------------------------|------------------|
|  | GISD species | Non-GISD species | GISD species | Non-GISD species | GISD species   | Non-GISD species | GISD species            | Non-GISD species |
| <b>Leaf area (mm<sup>2</sup>)</b>                                    | 10,498.24    | 4,477.95         | 2,219.94     | 2,430.96         | 3,960.28       | 665.24           | 0.38                    | 0.15             |
| <b>Leaf carbon (C) content per leaf dry mass (mg g<sup>-1</sup>)</b> | 456.96       | 448.30           | 451.13       | 449.53           | 5.63           | 4.64             | 0.01                    | 0.01             |
| <b>Leaf dry mass per leaf fresh mass (LDMC (g g<sup>-1</sup>))</b>   | 0.26         | 0.29             | 0.26         | 0.31             | 0.01           | 0.02             | 0.05                    | 0.06             |
| <b>Leaf longevity (month)</b>  | 10.53        | 12.19            | 6.68         | 12.00            | 2.18           | 1.86             | 0.21                    | 0.15             |
| <b>Leaf nitrogen (N) content per leaf area (g m<sup>-2</sup>)</b>    | 1.77         | 1.74             | 1.43         | 1.59             | 0.13           | 0.12             | 0.07                    | 0.07             |
| <b>Leaf nitrogen per leaf dry mass (mg g<sup>-1</sup>)</b>           | 24.13        | 21.09            | 22.45        | 21.20            | 0.93           | 0.78             | 0.04                    | 0.04             |
| <b>Leaf phosphorus content per leaf dry mass (mg g<sup>-1</sup>)</b> | 1.58         | 1.51             | 1.32         | 1.32             | 0.11           | 0.10             | 0.07                    | 0.06             |
| <b>Leaf thickness (mm)</b>   | 0.23         | 0.27             | 0.19         | 0.22             | 0.02           | 0.04             | 0.07                    | 0.13             |
| <b>Plant maximum height (m)</b>                                      | 5.64         | 4.71             | 2.00         | 2.00             | 0.50           | 0.31             | 0.09                    | 0.07             |
| <b>Seed dry mass (mg)</b>  | 67.91        | 204.98           | 4.96         | 4.44             | 15.50          | 102.27           | 0.23                    | 0.50             |
| <b>SLA (mm<sup>2</sup> mg<sup>-1</sup>)</b>                          | 22.47        | 18.32            | 17.61        | 17.05            | 1.60           | 0.94             | 0.07                    | 0.05             |
| <b>Stem specific density (SSD) (mg mm<sup>-3</sup>)</b>              | 0.51         | 0.63             | 0.49         | 0.62             | 0.03           | 0.02             | 0.05                    | 0.03             |



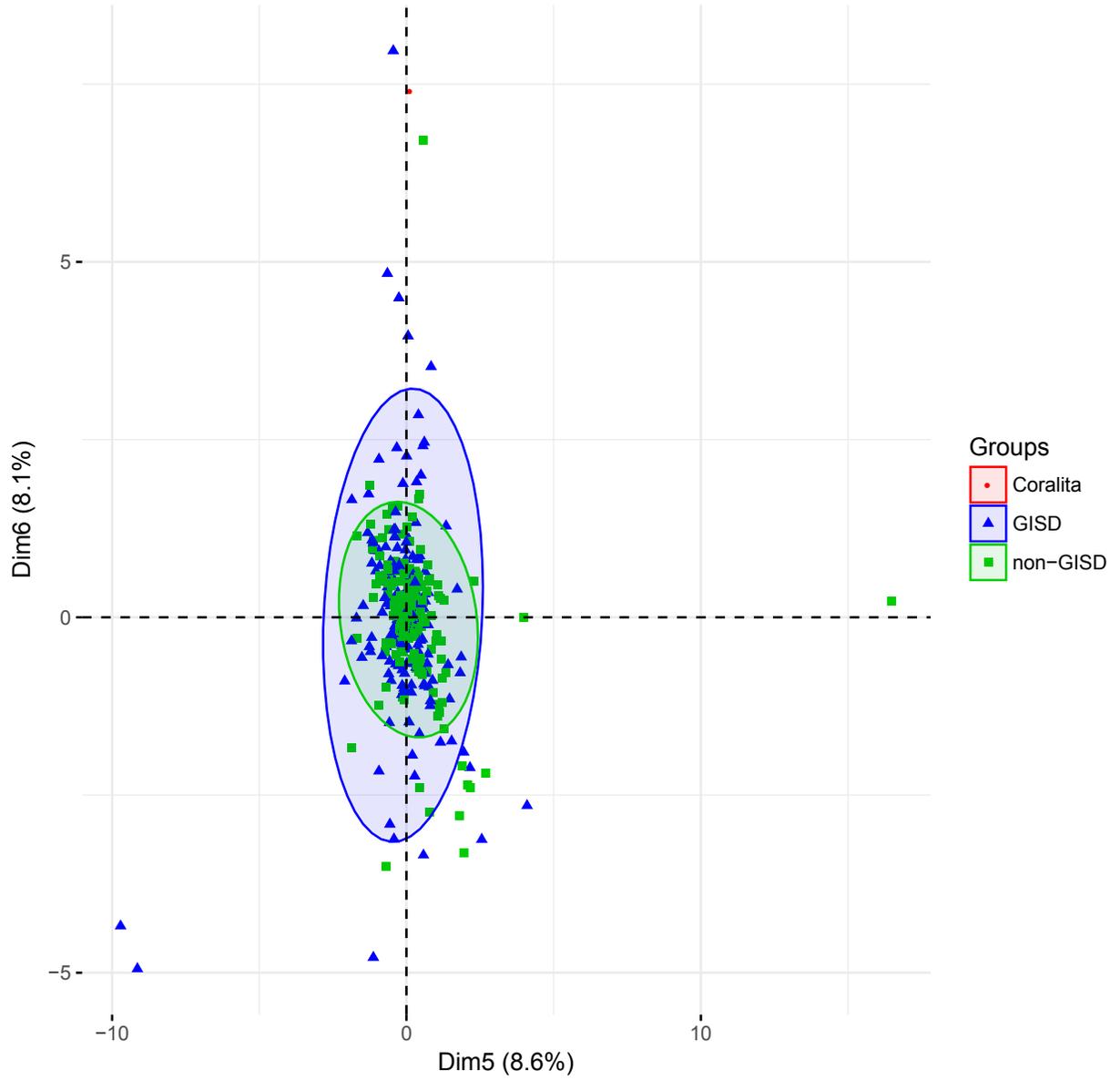
*Figure A9:* Principal component analysis projections of species on the second and third principal components, with grouping by species causing an impact on the GISD database and other species



*Figure A10:* Principal component analysis projections of species on the third and fourth principal components, with grouping by species causing an impact on the GISD database and other species



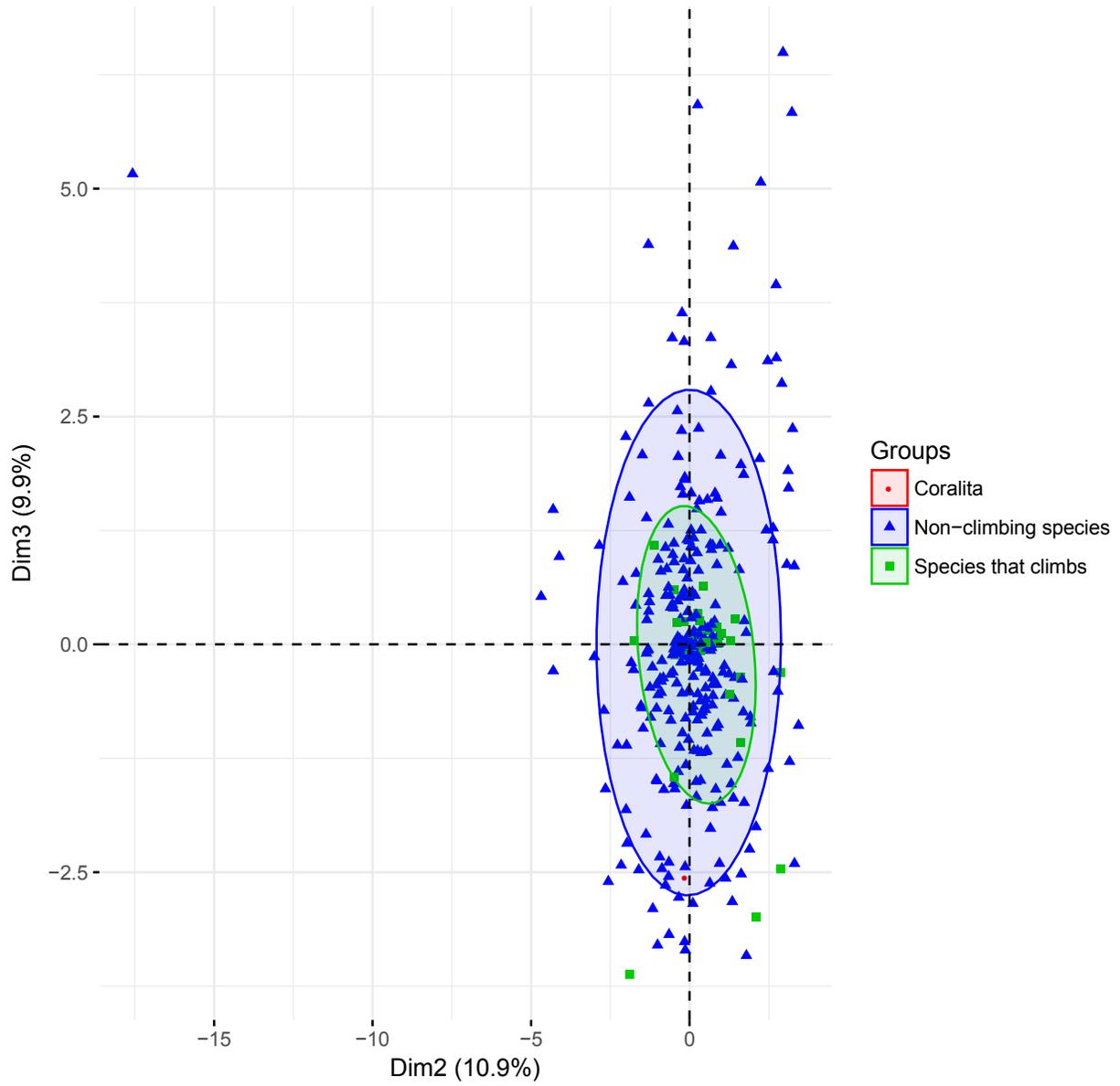
*Figure A11:* Principal component analysis projections of species on the fourth and fifth principal components, with grouping by species causing an impact on the GISD database and other species



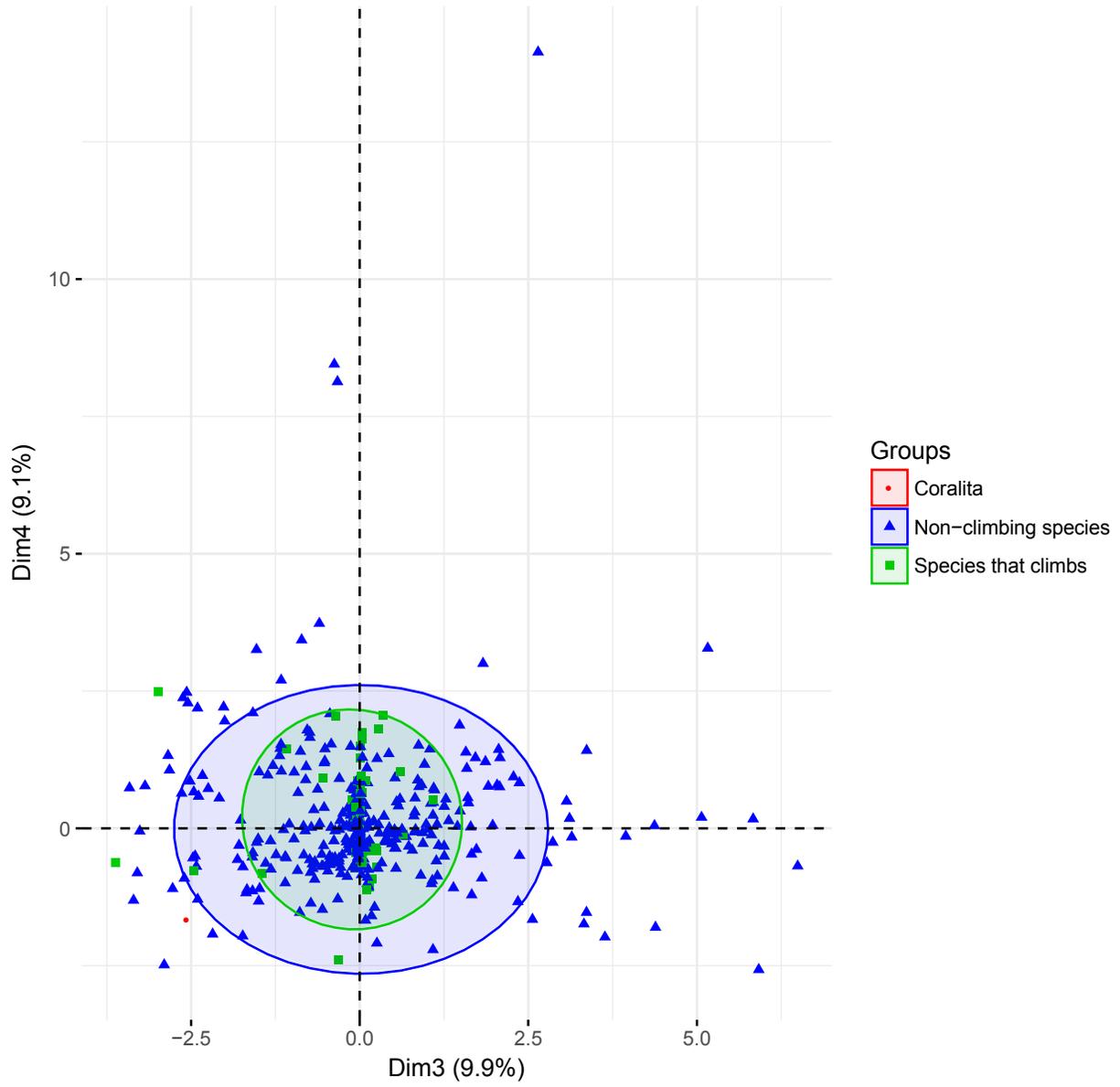
*Figure A12:* Principal component analysis projections of species on the fifth and sixth principal components, with grouping by species causing an impact on the GISD database and other species

*Table A9:* Mean, median, standard errors and relative standard errors for plant traits, separated by climbing species and species that do not climb

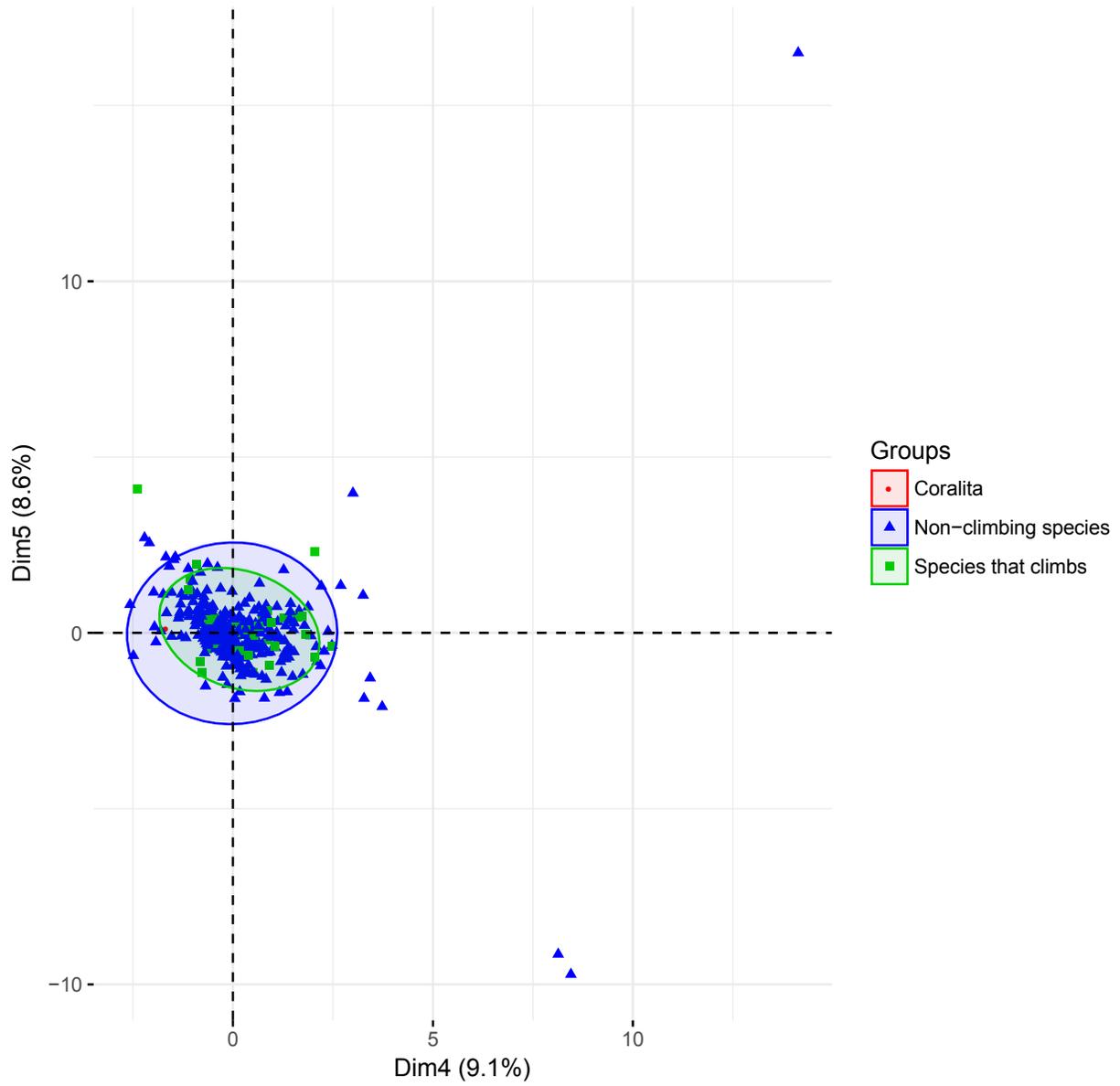
|   | Mean             |                      | Median           |                      | Standard error   |                      | Relative standard error |                      |
|---|------------------|----------------------|------------------|----------------------|------------------|----------------------|-------------------------|----------------------|
|   | Climbing species | Non-climbing species | Climbing species | Non-climbing species | Climbing species | Non-climbing species | Climbing species        | Non-climbing species |
| Leaf area (mm <sup>2</sup> )                                    | 3,264.40         | 7,919.47             | 2,590.76         | 2,191.94             | 543.38           | 2,189.23             | 0.17                    | 0.28                 |
| Leaf carbon (C) content per leaf dry mass (mg g <sup>-1</sup> ) | 481.51           | 451.03               | 461.72           | 449.65               | 25.25            | 3.53                 | 0.05                    | 0.01                 |
| Leaf dry mass per leaf fresh mass (LDMC) (g g <sup>-1</sup> )   | 0.26             | 0.27                 | 0.28             | 0.28                 | 0.03             | 0.01                 | 0.10                    | 0.04                 |
| Leaf longevity (month)  | 30.00            | 10.14                | 30.00            | 8.25                 | -                | 1.25                 | -                       | 0.12                 |
| Leaf nitrogen (N) content per leaf area (g m <sup>-2</sup> )    | 1.26             | 1.81                 | 1.20             | 1.54                 | 0.14             | 0.10                 | 0.11                    | 0.05                 |
| Leaf nitrogen per leaf dry mass (mg g <sup>-1</sup> )           | 26.98            | 22.45                | 27.01            | 21.66                | 1.80             | 0.66                 | 0.07                    | 0.03                 |
| Leaf phosphorus content per leaf dry mass (mg g <sup>-1</sup> ) | 1.67             | 1.52                 | 1.16             | 1.35                 | 0.23             | 0.08                 | 0.14                    | 0.05                 |
| Leaf thickness (mm)   | 0.22             | 0.25                 | 0.22             | 0.22                 | 0.02             | 0.02                 | 0.09                    | 0.08                 |
| Plant maximum height (m)  | 8.94             | 4.56                 | 5.50             | 1.62                 | 0.96             | 0.27                 | 0.11                    | 0.06                 |
| Seed dry mass (mg)  | 102.18           | 141.57               | 12.91            | 2.72                 | 56.15            | 58.68                | 0.55                    | 0.41                 |
| SLA (mm <sup>2</sup> mg <sup>-1</sup> )                         | 24.55            | 20.25                | 22.97            | 16.68                | 2.49             | 1.06                 | 0.10                    | 0.05                 |
| Stem specific density (SSD) (mg mm <sup>-3</sup> )              | 0.44             | 0.58                 | 0.44             | 0.61                 | 0.08             | 0.02                 | 0.18                    | 0.03                 |



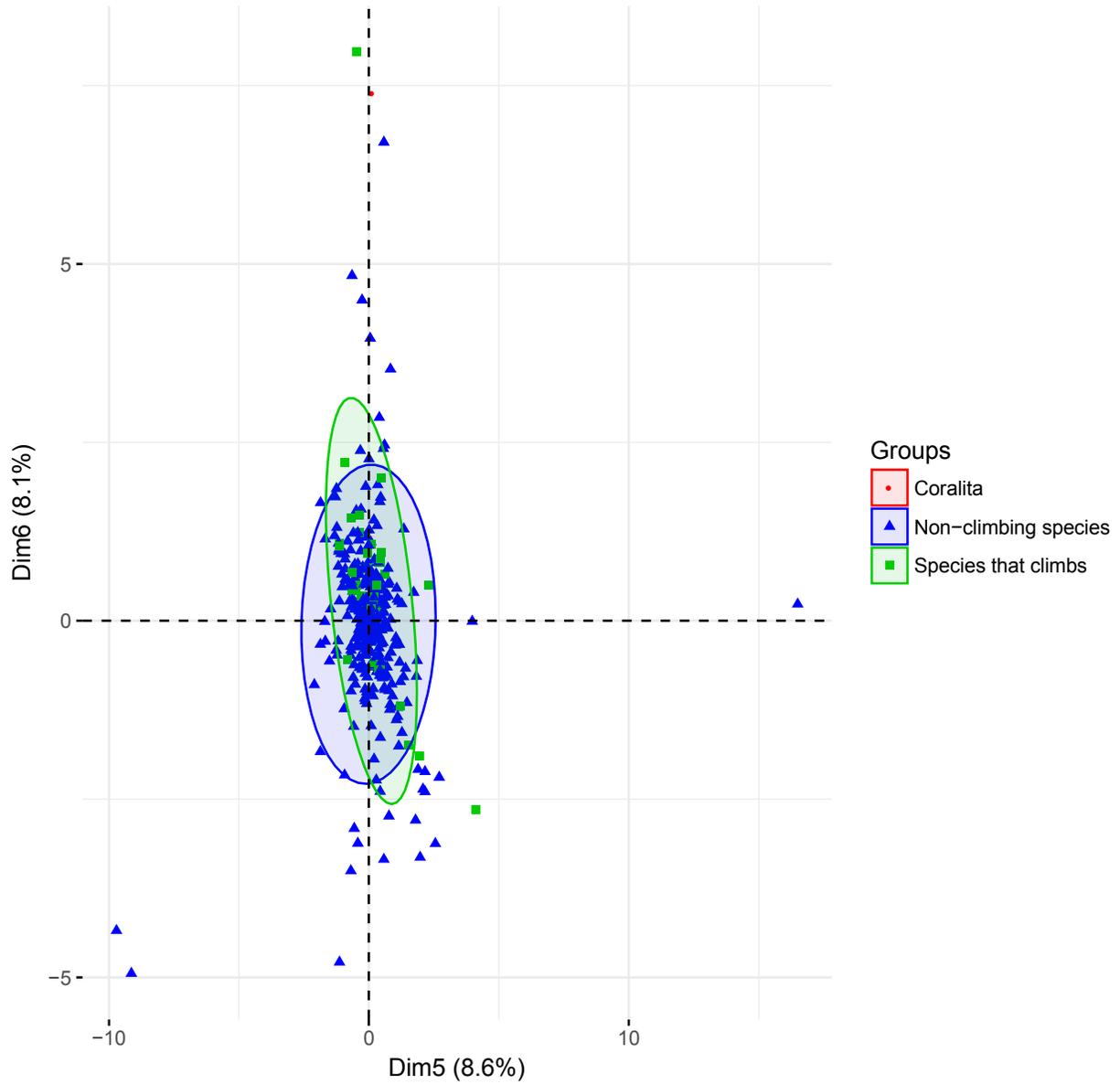
*Figure A13:* Principal component analysis projections of species on the second and third principal components, with grouping by species that climb and other species



*Figure A14:* Principal component analysis projections of species on the third and fourth principal components, with grouping by species that climb and other species



*Figure A15:* Principal component analysis projections of species on the fourth and fifth principal components, with grouping by species that climb and other species



**Figure A16:** Principal component analysis projections of species on the fifth and sixth principal components, with grouping by species that climb and other species

