Université Libre de Bruxelles

Institute for Environmental Management and Land-use Planning (IGEAT)

Faculty of Science

Master's Degree in Sciences and Environmental Management

Investigating the impact of urbanization on wild bee communities in a tropical Asian city

MSc Thesis submitted by
CLERBOIS Julien
in partial fulfilment of the requirements for the degrees of
Master in Sciences and Environmental Management
Section: Environmental Management
M-ENVIG

Academic year : 2017 – 2018

Directors : Prof. M-F. GODART (IGEAT, ULB)
Prof. N.J. VEREECKEN (Agroecology Lab, ULB)

Supervisor: Prof. J.S. ASCHER (Department of biological sciences, NUS)

Université Libre de Bruxelles

Institut de Gestion de l'Environnement et d'Aménagement du Territoire

Faculté des Sciences

Master en Sciences et Gestion de l'Environnement

Étude de l'impact de l'urbanisation sur des communautés d'abeilles sauvages en milieu tropical asiatique

Mémoire de Fin d'Études présenté par
CLERBOIS Julien
en vue de l'obtention du grade académique de
Master en Sciences et Gestion de l'Environnement
Finalité Gestion de l'Environnement
M-ENVIG

Année Académique : 2017 – 2018

Directeurs: Prof. M-F. GODART (IGEAT, ULB)
Prof. N.J. VEREECKEN (Agroecology Lab, ULB)

Superviseur: Prof. J.S. ASCHER (Département des sciences biologiques, NUS)

ACKNOWLEDGEMENTS

I hereby humbly express my gratitude to the following people without whom this Master Thesis, enriching adventure and all these new and so nice discoveries would not have been possible.

Many thanks to Associate Professor Nicolas Vereecken, who managed to convey his passion for wild bees, who thoroughly trained me with inspiring workshops, enriched my bibliography with interesting articles and provided me with wise advice.

Professor Marie-Françoise Godart, for accepting to supervise this study, for her guidance and support.

Assistant Professor John S. Ascher, for his warm welcome into the Insect Diversity Lab, for the time spent identifying the specimens collected, for his supervision, invaluable advice and his taxonomical expertise.

Research Assistants Benjamin Ho and Chui Shao Xiong, for their assistance and generosity in providing help with fieldwork, labwork and culinary expertise.

National Parks Board Manager Zestin Soh, for his kindness, for the fruitful discussions about wild bees and NParks biodiversity approach.

Finally, my parents and grandparents, for their precious financial aid and for sharing their enthusiasm and happiness about this project. My sister for her encouragement, my girlfriend for her moral support and my friends for their helpful proofreading.

ABSTRACT (English)

Wild bees are the most ecologically important and efficient pollinators worldwide. They perform crucial ecological and economic functions through floral visitation. Despite a worrying gap in knowledge on wild bee populations trends around the globe, and particularly in Asia, it is not unreasonable to expect that a large scale pollinators decline is occurring. This decline would ineluctably be linked to anthropogenic activities, as they cause a continuous loss of natural habitats, the rarefaction of food sources and the destruction of nesting sites. This is especially true in urban areas, considered as the most anthropogenically disturbed environments. However, many bee species could persist in urban areas while substantially decline in rural landscapes. Urban parks and gardens provide a steady flow of floral resource and nesting sites, have lower pesticide levels as compared to rural areas and provide an interesting habitats heterogeneity.

Despite being the third most densely populated State in the world and having lost up to 95% of its primary forests, Singapore is known as the ‘City in a Garden’ in reference to its high vegetation cover and massive investments in greenery schemes. However, as half of the total vegetation cover is under management, Singapore might not get the most out of its ecological potential. This study aimed to (I) investigate the diversity of wild bee communities across two habitats (parks vs. islands) and two management types (wild vs. manicured) in a tropical urban setting and to (II) review the management practices in these green spaces, under a wild bees conservation prism. In order to do so, six sites (three parks and three islands, either considered as wild or manicured) were surveyed over a three months long period. However, data collected over the last eight years were used in order to have a better representation of the wild bee communities occurring in these sites.

While bee communities were expected to be relatively homogenous across parks due to the generalised greenery and across islands due to their proximity to the mainland, we found that each site was composed by unique species assemblages. Nearly half of the species were replaced across sites while 16% were nested. This result suggests that each site has specific features that are particularly suited for a pool of species that possibly might not have occurred somewhere else. Nor habitat type or management type were shown to significantly influence species richness and diversity, which strongly contrast with a recent study conducted on green roofs in Singapore. Also, while the landscape context does not explain species richness and diversity, further investigations at the site level are needed. Habitat quality and specificities could better explain bee diversity and communities. At the habitat level, island networks are more specialized but also less nested, which invalidate our stated hypothesis. As well as being vulnerable habitats, islands have unique bee species assemblages that should be taken care of. In manicured sites, bee species seem to be more vulnerable when it comes to the number of flower species linked. On the contrary, flower species seem to be more vulnerable in wild sites, since they are linked to few bee species. Finally, our results suggest that unmanaged preserved parks and islands could serve as refuge for rare bee species while managed parks and islands could support pollinator species richness and abundance. This study must draw attention to the importance of preserving both wild untouched habitats and managed floral-rich urban parks in order to enhance bee diversity while maintaining ecologically stable networks.

ABSTRACT (French)

Écologiquement et économiquement parlant, les abeilles sauvages font partie des pollinisateurs les plus importants et efficaces à l'échelle mondiale. Malgré un manque inquiétant de connaissances et de données au niveau mondial, et plus particulièrement en Asie, ces incontournables pollinisateurs semblent décliner à grande échelle. Ce déclin serait inéluctablement lié aux activités anthropiques, responsables de la dégradation des habitats naturels, de la raréfaction des ressources alimentaires et la disparition de sites de nidification. Ces impacts sont particulièrement visibles en milieu urbain, considérés comme les environnements les plus perturbés par l'homme. Cependant, de nombreuses espèces d'abeilles semblent bien adaptées aux milieux urbains tout en régressant dans les campagnes. Les parcs, jardins et autres espaces verts sont source d'espaces floraux, de sites de nidification et présentent des niveaux de pesticides moins élevés qu'en milieu rural.

Bien qu'étant le troisième État le plus densément peuplé au monde, et ayant perdu plus de 95% de ses forêts primaires, Singapour est surnommée "la ville jardin" de par son importante couverture végétale et sa verdure omniprésente. Cependant, la majeure partie de ce couvert végétal étant soumis à un régime de gestion intensif, Singapour pourrait gâcher cet énorme potentiel écologique. Cette étude a pour but d'évaluer la diversité des communautés d'abeilles sauvages au sein de deux habitats différents (parcs vs. îles), eux-mêmes soumis à deux régimes de gestion distincts (naturel vs. entretenu), dans un milieu tropical fortement urbanisé. Pour ce faire, six sites ont été échantillonnés pendant trois mois. Les données collectées au cours des huit dernières années ont également été utilisées afin d'obtenir une vision plus représentative des communautés d'abeilles présentes au sein de ceux-ci.

Compte tenu du fort couvert végétal caractérisant Singapour, et compte tenu de la proximité des îles par rapport à la terre ferme, les communautés présentes au sein des différents sites était supposées homogènes. Cependant, les résultats indiquent que les sites étudiés sont composés de communautés tout à fait uniques et originales. Au sein de nos sites, les différences entre communautés s'expliquent à près de 50% par le remplacement d'espèces, et à 16% par la perte d'espèces. Ce résultat met en exergue l'importante de préserver les caractéristiques propres à chaque site, car moteur de diversité. Le type d'habitat, ainsi que le mode de gestion, ne permettent pas d'expliquer la richesse spécifique et la diversité des sites étudiés. Alors que le contexte de paysager ne semble pas être un facteur explicatif de la diversité au sein de nos sites, la qualité des habitats et leurs propriété intrinsèques méritent une plus grand attention. Parmi les deux habitats étudiés, les réseaux insulaires semblent plus spécialisés et moins emboité, se traduisant par des communautés tout à fait originales mais relativement fragiles. Dans les sites 'gérés', les espèces d'abeilles semblent être plus vulnérables car liées à moins d'espèces florale que les sites 'naturels'. *A contrario*, les espèces florales semblent être plus vulnérables dans les sites 'naturels', étant liées à relativement peu de visiteurs. Enfin, nos résultats suggèrent que les milieux préservés et non gérés ont un potentiel intéressant pour les espèces d'abeilles les moins communes tandis que les milieux gérés et peu naturels ont un potentiel intéressant au point de vue de la richesse et de l'abondance. Par le biais de cette étude, nous insistons sur l'importance à apporter aussi bien aux habitats naturels qu'aux habitats gérés afin d'entretenir et d'augmenter la diversité en abeilles sauvages tout en maintenant des réseaux écologiquement stables.

TABLE OF CONTENT

1 INTRODUCTION 1

1.1 POLLINATING INSECTS: IMPORTANCE AND CURRENT SITUATION 1
1.1.1 POLLINATION AND BEES ASSOCIATED SERVICES 1
1.1.2 WILD BEES DECLINE AND DRIVERS 2
1.2 URBAN ECOSYSTEMS AND BIOGEOGRAPHY 3
1.3 LANDSCAPE INFLUENCE ON BEE POPULATIONS 4
1.4 SINGAPORE: THE EVER GROWING "CITY IN A GARDEN" 5
1.5 PLANT-POLLINATOR NETWORKS 8
1.6 PARKS DESIGN, MANAGEMENT AND PRACTICES 9

2 AIMS OF THE MASTER THESIS 12

3 MATERIALS AND METHODS 13

3.1 STUDY AREA 13
3.2 METHODOLOGY 16
3.2.1 DATA COLLECTION 16
3.2.1.1 Sampling protocol 16
3.2.1.2 Strengths and weaknesses of the protocol 17
3.2.1.3 Supplementary data 17
3.2.2 ENTOMOLOGICAL COLLECTION PREPARATION 18
3.2.2.1 Specimen conservation 18
3.2.2.2 Specimen pinning 18
3.2.2.3 Specimen identification 18
3.3 STATISTICAL ANALYSES 18
3.3.1 SPECIES DIVERSITY 19
3.3.1.1 Sampling effort evaluation and species richness 19
3.3.2 ALPHA (α) DIVERSITY AND ASSOCIATED INDICES 20
3.3.2.1 Simpson's indices 21
3.3.2.2 Shannon's index 21
3.3.2.3 Piélou evenness index 21
3.3.3 BETA (β) DIVERSITY AND ASSOCIATED INDICES 21
3.3.4 SPECIES DIVERSITY BETWEEN HABITATS AND MANAGEMENT TYPES 22
3.3.5 SPATIAL AUTO-CORRELATION BETWEEN SITES 23
3.4 FLOWER-BEE VISITATION NETWORKS 23
3.5 SPATIAL ANALYSIS: SITES OBSERVATIONS AND CHARACTERISATION 25
3.5.1 LOCAL FACTORS 25
3.5.2 LANDSCAPE FACTORS 25
3.5.3 LAND-USE DIGITALISATION AND MAP MAKING 25
3.5.4 LOCAL AND LANDSCAPE FACTORS' STATISTICS 26

4 RESULTS 27

4.1 Sampling effort: accumulation curves 27
4.2 Species diversity 28
4.2.1 Species richness and specimen abundance 28
4.2.2 Alpha diversity 32
4.2.3 Beta diversity 34
4.3 Hierarchical clustering and *k-means* on clustering data 35
4.4 Mantel test 36
4.5 Plant-pollinator networks 37
4.5.1 Global network 37
4.5.2 Habitats and management types networks 38
4.5.3 Sites networks 41
4.6 Sites characterisation: local and landscape factors 44
4.6.1 Local factors 44
4.6.2 Landscape factors 44

5 DISCUSSION 47

5.1 Sampling effort 47
5.2 Abundance across sites, between habitats and management types 48
5.3 Sites diversity assessment 48
5.4 Local and landscape factor assessment 50
5.5 Habitats diversity assessment: parks vs. islands 51
5.6 Management types diversity assessment: wild vs. manicured 51

6 CONCLUSIONS, LIMITATIONS AND PROSPECTS 52

7 BIBLIOGRAPHY 53

8 APPENDIXES I

FIGURES AND TABLES

Figures

Figure 1: Geographic location of Singapore. Adapted from Mapsland (2018). 5
Figure 2 : Land use changes in Singapore, 1819-1990 (excluding offshore islands and reclaimed lands). PRIMARY = primary forest, CULTIVATED = cultivated land and tree crops; SECONDARY = secondary grass land and scrub land forest; URBAN = urban areas, parks and gardens (Chua, 2015)6
Figure 3: Distribution of vegetation types across Singapore. Retrieved from (Yee et al., 2011)........... 7
Figure 4: Example of a typical weighted two-level interaction network. The upper level represents the hosts whereas the lower one represents the visitors (flowers and bees from Singapore in this example). The boxes' width varies in proportion to the species abundance whereas the links' width varies in proportion to the number of interactions observed. Bee pictures courtesy of the Insect Diversity Lab (Department of Biological Sciences, National University of Singapore). 8
Figure 5: Park Connector Network (PCN) projections for 2030. This network aims to connect the parks, nature reserves and other green spaces thanks to vegetated pedestrian and cycle lanes (Ministry of National Development, 2013) 10
Figure 6: Connector Networks examples showing two radically different designs. The Punggol Park Connector (A) appears to be very neat and intensively managed whereas the Bukit Timah Rail Corridor (B) is basically a dirt path surrounded by spontaneous vegetation. Pictures copyrights Julien Clerbois. 10
Figure 7 : Singapore map representing locality of sampled sites (red dots). (A) Dairy Farm, (B) Hort Park, (C) St. John's Island, (D) Coney Island, (E) Pulau Ubin, (F) Pasir Ris. Singapore basemap and layers retrieved from the Urban Redevelopment Authority (2016). Forests and Nature reserves are represented in dark green, parks in light green. 15
Figure 8 : NParks authorized research pass 16
Figure 9 : Graphical illustration of turnover and nestedness involving four island communities (A–D) and three sites in each island (Baselga, 2010).. 22
Figure 10: Stages of land-use digitalisation in ArcGIS : Pasir Ris.. 26
Figure 11: Species accumulation curve for the whole database. One sampling unit equals one sampling session at a given sampling date in a given sampling site.. 27
Figure 12: Species accumulation curves for each habitat and management type. One sampling unit equals one sampling session at a given sampling date in a given sampling site............................... 28
Figure 13: Number of specimens collected per species (ordered by family). 29
Figure 14: Number of specimens collected in each sampling site.. 29
Figure 15: Number of species per sampling site. 29
Figure 16: Heatmap giving the species density in each site. 30
Figure 17: Species abundance rank, in descending order, for each habitat and management type.... 31
Figure 18: Venn diagrams showing the number of shared and unshared species between habitats and management types.. 31
Figure 19: Number of species per habitat and management type.. 32
Figure 20: Simpson and Piélou's indices for each site.. 33
Figure 21: Alpha diversity across habitats and management types characterized by the Shannon's diversity index. 34
Figure 22: Hierarchical clustering of sites based on bootstrapping of a Hellinger distance matrix of bee species abundances. The dendrogram is clustered using the Ward's (minimum variance) method and based on Euclidean distances. AU (approximately unbiased) and BP (bootstrap probability) values (%) are highlighted in red and green respectively.. 35
Figure 23: K-means cascade plot showing the group attributed to each site for each partition........... 36
Figure 24: Graphical representation of the Mantel test assessing if neighbouring sites are more likely to harbour more similar communities of wild bees... 36
Figure 25: Presence / absence visitation web for all sites.. 37
Figure 26: Graphical representation of the cumulative degree distributions of both trophic levels. This graph is generated thanks to the 'degreedistr' function of the 'bipartite' package in R (Dormann et al., 2017) : "The function first calculates degrees for each species, then constructs a cumulative

distribution with them, and finally fits three different functions to these distributions: exponential, power law and truncated power law”. 38
Figure 27: Parks, islands, wild sites and manicured sites’ visitation networks indices. 39
Figure 28: Betalink interactions network between islands and parks. Each dot represents a bee (at the base of the arrow) or a flower (at the tip of the arrow) species. The arrow represents the interaction between the two species. Closer dots are more likely to share the same links. Blue dots represent species that are only found in islands, green dots represent species that are only found in parks and grey dots represent species that are common to both habitats. 40
Figure 29: Betalink interactions network between manicured sites and wild sites. Each dot represents a bee (at the base of the arrow) or a flower (at the tip of the arrow) species. The arrow represents the interaction between the two species. Closer dots are more likely to share the same links. Blue dots represent species that are only found in manicured sites, green dots represent species that are only found in wild sites and grey dots represent species that are common to both management types. 40
Figure 30: Sites’ flower-bee visitation networks associated indices. 41
Figure 31: Flower-bee visitation network and associated indices - St John's Island. 42
Figure 32: Flower-bee visitation network and associated indices - Dairy Farm 43
Figure 34: Land-use digitalisation - St John's Island... 45
Figure 35: Land-use digitalisation - Dairy Farm.. 46

Tables

Table 1: Site details. From left to right: full site name, code for in-text reference, site coordinates, study site area in hectares, site type (defines site habitat type, either park or island), and site management (“wild” defines sites covered in spontaneous vegetation, while “manicured” defines sites under heavy maintenance and management). 15
Table 2: Summary of the variables used in both aggregations. 25
Table 3: Number of species per site when we rarefy the community to 100 specimens per site......... 29
Table 4: Summary of alpha diversity indices per site, habitat and management type. Highlighted values represent the highest results per index inside each category. 33
Table 5: Results of the Levene's test, Shapiro-Wilk's test and One-way ANOVA on habitats and management types’ alpha diversity indices. 34
Table 6: Differentiation of beta diversity index among habitats, management types and sites........... 34
Table 7: Linear regression results on the local variables. 44
Table 8: Linear regression results on the first aggregation. 44
Table 9: Linear regression results on the second aggregation.. 44

Appendixes

Appendix 1: Photographs of Dairy Farm’s habitats and distinctive features. I
Appendix 2: Photographs of Hort Park’s habitats and distinctive features.. I
Appendix 3: Photographs of St John’s Island’s habitats and distinctive features................................. II
Appendix 4: Photographs of Coney Island’s habitats and distinctive features. II
Appendix 5: Photographs of Pulau Ubin’s habitats and distinctive features. III
Appendix 6: Photographs of Pasir Ris’ habitats and distinctive features. III
Appendix 7: Observed and extrapolated species richness (SR) in each habitat (yellow), management type (blue) and site (green). Chao, Jackknife1, Jackknife2 and Bootstrap are non-parametric species richness estimators. Site names: CI = Coney Island, SJ = St John's Island, PU = Pulau Ubin, HP = Hort Park, PR = Pasir Ris, DF = Dairy Farm. IV
Appendix 8: Habitats and management types' extrapolated species richness with non-parametric estimators (Chao, Jackknife1, Jackknife2 and Bootstrap). IV
Appendix 9: Global flower-bee visitation network. The upper level represents the flower species (red), the lower level represents the bee species (blue). Boxes’ width varies in proportion to the species abundance whereas the links’ width varies in proportion to the number of interactions observed......... V

Appendix 10: Potential apparent competition (PAC) imposed and experienced by bees at the global network level. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees.......................................VI
Appendix 11: Standardized specialization index (d') of bees at the global network level.....................VI
Appendix 12: Potential apparent competition (PAC) imposed and experienced by plants at the global network level. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees......................................VII
Appendix 13: Standardized specialization index (d') of plants at the global network level.................VII
Appendix 14: Flower-bee visitation network and associated indices - Parks....................................VIII
Appendix 15: Potential apparent competition (PAC) imposed and experienced by bees in parks. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees..IX
Appendix 16: Heatmap representing the Potential apparent competition (PAC) imposed and experienced by bees in parks. Bee species on the x-axis (at the tip of the arrow) are experiencing competition by the bees on the y-axis (at the base of the arrow)...IX
Appendix 17: Flower-bee visitation network and associated indices - Islands.....................................X
Appendix 18: Potential apparent competition (PAC) imposed and experienced by bees in islands. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees..XI
Appendix 19: Heatmap representing the Potential apparent competition (PAC) imposed and experienced by bees in islands. Bee species on the x-axis (at the tip of the arrow) are experiencing competition by the bees on the y-axis (at the base of the arrow)...XI
Appendix 20: Flower-bee visitation network and associated indices - Wild sites...............................XII
Appendix 21: Potential apparent competition (PAC) imposed and experienced by bees in wild sites. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees...XIII
Appendix 22: Heatmap representing the Potential apparent competition (PAC) imposed and experienced by bees in wild sites. Bee species on the x-axis (at the tip of the arrow) are experiencing competition by the bees on the y-axis (at the base of the arrow)..XIII
Appendix 23: Flower-bee visitation network and associated indices - Manicured sites.....................XIV
Appendix 24: Potential apparent competition (PAC) imposed and experienced by bees in manicured sites. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees.. XV
Appendix 25: Heatmap representing the Potential apparent competition (PAC) imposed and experienced by bees in manicured sites. Bee species on the x-axis (at the tip of the arrow) are experiencing competition by the bees on the y-axis (at the base of the arrow)............................... XV
Appendix 26: Flower-bee visitation network and associated indices - Coney Island..........................XVI
Appendix 27: Land-use digitalisation - Coney Island...XVII
Appendix 28: Flower-bee visitation network and associated indices - Pulau Ubin...........................XVIII
Appendix 29: Land-use digitalisation - Pulau Ubin. XIX
Appendix 30: Flower-bee visitation network and associated indices - Hort Park............................... XX
Appendix 31: Land-use digitalisation - Hort Park...XXI
Appendix 32: Flower-bee visitation network and associated indices - Pasir Ris..............................XXII
Appendix 33: Land-use digitalisation - Pasir Ris. XXIII
Appendix 34: Betalink : habitats and management types networks' beta diversity. The value of these beta diversity components are useful to assess the dissimilarity of species interactions within the networks. β_S *= dissimilarity in the species composition of communities;* β_{WN} *= dissimilarity of interactions;* β_{OS} *= dissimilarity of interactions between species common to both networks;* β_{ST} *= dissimilarity of interactions due to species turnover... XXIV*
Appendix 35: Betalink : sites' beta diversity. The value of these beta diversity components are useful to assess the dissimilarity of species interactions within the networks. β_S *= dissimilarity in the species composition of communities;* β_{WN} *= dissimilarity of interactions;* β_{OS} *= dissimilarity of interactions between species common to both networks;* β_{ST} *= dissimilarity of interactions due to species turnover. For each index, values in yellow and blue highlight the sites with the greatest differences. .... XXIV*
Appendix 36: Local level: sites' specific richness, alpha diversity indices and local variables......... XXIV
Appendix 37: Landscape level: sites' specific richness, alpha diversity indices and land-use proportions. Three scales around sites are considered (250m, 500m and 1000m). XXV

Appendix 38: Landscape level: sites' specific richness, alpha diversity indices and land-use proportions: first aggregation. Land-use classes that can be considered as habitats are clustered together. Three scales around sites are considered (250m, 500m and 1000m). .... *XXV*
Appendix 39: Landscape level: sites' specific richness, alpha diversity indices and land-use proportions: second aggregation. Land-use classes that can be considered as impervious (water bodies, urbanized areas, etc.) are clustered together. Sites size is also tested. Three scales around sites are considered (250m, 500m and 1000m). .... *XXVI*
Appendix 40: List of bee species found in this study and their associated traits. .... *XXX*

1 INTRODUCTION

1.1 POLLINATING INSECTS: IMPORTANCE AND CURRENT SITUATION

The nineteenth, twentieth and twenty-first centuries can be seen as a turning point in the human and planet's history. The world ecosystems have been drastically modified in order to meet the ever-growing demand for water, food, raw materials and fossil fuels. The first observable impacts resulted in a global land use change, with the expansion of pastures, croplands and urban areas at the expense of the original natural forests and plains (Vitousek, 1997; Foley et al., 2005; Steffen et al., 2015). These global changes, their threats on natural ecosystems and human societies, and the time lapse in which they arise lead the scientific community to raise awareness on the potential major environmental, social and economic impacts in the next few decades (Millennium Ecosystem Assessment, 2005; Dryzek et al., 2011). The Earth may even have entered a new human-dominated geological epoch called the Anthropocene (Zalasiewicz et al., 2010; Lewis & Maslin, 2015).

These large-scale modifications of the natural environment lead to the irreversible loss of natural habitat through fragmentation and destruction and are known to be closely associated with pollinators decline (Winfree et al., 2009; Potts et al., 2010; Vanbergen, 2014). Pollinating insects like bees, wasps, butterflies, hoverflies and some coleopterans could provide valuable information about the impact of human disturbance (Kevan, 1999). But first and foremost, we need to address why pollinators, and bees in particular, are worth studying.

1.1.1 Pollination and bees associated services

The value of eusocial bees to humans is widely acknowledged due to their derived products (honey, wax, propolis) and their importance in pollinating various crops (Klein et al., 2007). Wild bees play an even greater role in pollination. Even if they are far less known and studied, wild bees have been globally recognized as important pollinators that provide ecological and economic benefits to native flora and agricultural crops (Greenleaf & Kremen, 2006; Brosi et al., 2007; Klein et al., 2007; Matteson et al., 2008; Bates et al., 2011; Ollerton et al., 2011).

Currently, about 20,000 wild bee species are identified in the world (Michez et al., 2011; Ascher & Pickering, 2018). Ollerton and colleagues (2011) estimate that 78% of plant species are animal-pollinated in temperate-zones, while this value may rise to 94% in the tropics. On a global scale, 85% of the known flowering plants are estimated to be pollinated. In terms of food security, among the one hundred crop species that provide 90% of world food supplies, seventy-one are bee-pollinated (Kluser & Peduzzi, 2007). It is thus safe to say that bees perform crucial ecological and economic functions through floral visitation. They have been regarded as the most ecologically important and efficient pollinators in various habitats (Roubik, 1989; Kearns & Inouye, 1997) thanks to their diet, flight capacities, physical, behavioural and sensory traits designed to collect pollen (Roubik, 1989; Pasquet et al., 2008). Singapore-wide, more than one hundred bee species can be found (Ascher & Pickering, 2018).

1.1.2 Wild bees decline and drivers

Recently, numerous reports have highlighted the increasing concern over the global decline in pollinators (Kluser & Peduzzi, 2007; Brittain et al., 2010; Potts et al., 2010; Cameron et al., 2011; Hallmann et al., 2017). However, these studies are often biased towards honey bees and bumble-bees, and with a stronger focus on Europe and North America (Ghazoul, 2015). Even in the best-sampled areas of the world such as Europe, there seems to be a major knowledge gap on the population trends of wild bees: among the 1,965 species recorded from the European continent, more than 50% are not monitored and are therefore considered as "data deficient" according to the IUCN standards (Nieto et al., 2014). This lack of available data might seriously restrain the implementation of conservation status and constitute an impediment to a more detailed, evidence-based evaluation of pollinators decline. That being said, it is not unreasonable to expect that pollinators decline is also occurring elsewhere across the globe (Goulson et al., 2015), such as in Africa, South America or Asia for example. As a matter of fact, if we exclude the 50% of data deficient bee evaluations, 9.2% of the European wild bee species are considered to be threatened (Nieto et al., 2014). This constitutes a worrying observation in view of the available data.

The on-going wild bees decline is ineluctably linked to anthropogenic activities. They induce a continuous loss of natural habitats, the rarefaction of food sources as well as nesting sites (Potts et al., 2010). The use of pesticides by individuals, cities and modern agriculture might play a potential role as well (Brittain et al., 2010; Goulson et al., 2015). But most of all, four key drivers might be suggested: urbanization, agricultural intensification, honey bees' domestication and climate change.

Firstly, urbanization involves radical modifications of the natural environment to suit human needs, leading to the irreversible loss of natural habitat through fragmentation and destruction (McKinney, 2002; Wastian et. al, 2016). However, the real effects of urbanization on biodiversity remain quite unpredictable, with cases of declines in specific richness (McKinney, 2006), declines in specimen abundance (Hernandez et al., 2009), but also reports of increases in specimen abundance (Fischer et al., 2016). Some recent studies have even shown a positive relation between urbanization and bumblebees pollination and reproductive success (Theodorou et al., 2016; Samuelson et al., 2018). In a particular way, urban areas could be considered as biodiversity hotspots thanks to their ecological niches diversity and hotter temperatures (Hall et al., 2017). Studies on urban bees facing major environmental stresses are still in their infancy and the coming years will undoubtedly see a dramatic increase of reports on urban bee diversity, their drivers and their patterns.

Secondly, rural landscape drastically changed after the Second World War. The reparcelling, mechanization, use of pesticides and chemical fertilizers along with the abandonment of traditional crops in the framework of the Green Revolution (industrialisation of agriculture) led to a loss of nesting sites, foraging sources and overuse of pesticides (Cariveau & Winfree, 2015; David et al., 2016; Goulson et al., 2018).

Thirdly, domesticated bees might be the cause of two main concerns for wild bees: domesticated species induce food competition and they can transmit diseases among domesticated colonies, and to the wild pollinators. With about 20,000 to 60,000 individuals per hive, domesticated bees gather huge quantities of pollen and nectar to ensure the colony survival and provide beekeepers the desired products (mainly honey, wax and propolis) (Vereecken et al., 2015). Domesticated species visit a taxonomical spectrum of plants that greatly overlaps with that of their wild counterparts. It is estimated that one single hive consumes the resources that could have been used for the development of 100,000 wild bees (Cane & Tepedino, 2017). Moreover, due to intensive breeding, domesticated bees have become sensitive to various diseases (Genersch, 2010) that are transmissible to wild bees (Fürst et al., 2014; Tehel al., 2016).

Finally, climate change is frequently mentioned as a cause of bee decline. Climate change is a complex issue, with direct and indirect effects and consequences that are difficult to predict and disentangle. The global temperature increase impacts wild bee communities, advancing their emergence proportionally to temperature increases (Bartomeus et al., 2011). Apart from its direct temperatures influence, climate change could also affect host plants by shifting blooming period or area of distribution (and thus create time-space mismatches) (Rasmont et al., 2015). Moreover, some wild bee species tend towards a new spatial distribution, becoming invasive to the communities originally present (Dellicour et al., 2014).

1.2 URBAN ECOSYSTEMS AND BIOGEOGRAPHY

Among the many anthropogenically disturbed environments, urban areas are considered as the most impacted ones. Often highly fragmented, with mosaic of buildings, built space, parks, gardens, and semi-natural areas, they offer to flora and fauna a limited spatial extent (Bates et al., 2011). Animal and plant species' habitats are generally isolated from each other in more or less impacted natural patches (Hennig & Ghazoul, 2011). In these ecosystems, decreases in several birds and mammals populations have been linked to the reduction of natural patches size. This might be partially explained by the lower opportunities to find resources or mates (McKinney, 2008; Seress & Liker, 2015). Impervious surfaces, that are characteristic to these areas, are known to negatively impact insect populations by suppressing potential nesting sites. This is especially true in urban cores, where impervious surfaces area great in number and scope (Martins et al., 2017). Also, the presence and type of foraging resources often differ from the habitat's climacic state : exotic or ornamental flower plots are mostly designed for cities' aesthetic and do not always take pollinators needs and requirements into account (Knapp et al., 2008).

Studying wild bee communities in heavily urbanised environments can provide researchers with insights on regional biogeography, species spatial replacement and species loss (these notions are detailed further in the *Beta (β) diversity and associated indices* section). As the isolation of habitat patches in urban areas may affect the abundance and diversity of insect species (Banaszak-Cibicka & Zmihorski, 2012), we could consider, to a certain extent, that the urban matrix consists of a set of island-like natural habitats. The patches inside this matrix would be more or less isolated from one another, enabling immigration and emigration flows or making them difficult to achieve. Just as MacArthur and Wilson postulate in their Theory of Island Biogeography (1967), the species richness inside fragmented habitats could depend on their size and isolation from source regions. However, many factors affect species richness and make the equilibrium theory only partly relevant (Kalmar & Currie, 2006; Spengler et al., 2011). In their study conducted in the Kepulauan Seribu Archipelago (Indonesia), Spengler and colleagues (2011) showed that isolation from a larger source (island of Java) was negatively correlated with bee and wasp species richness. However they found no species-area relationship. The most remote islands didn't show significant losses as compared with larger and less isolated areas. These observations imply that unique pollinators assemblages and endemic species could be found on remoted islands or isolated urban patches. As bee communities on Singapore's main and offshore islands are globally under-sampled (Ascher, personal communication, 2017), and as they play a key-role in ecological services, assessing their populations and species assemblages across parks and islands is essential for conservation purposes.

Despite facing habitat losses and resource degradation, many bee species persist in urban areas while substantially declining in rural landscapes (McFrederick & LeBuhn, 2006; Hall et al., 2017; Martins et al., 2017). For instance, bumble bees and cavity nester species appear to be well adapted to urban areas and thus induce changes in communities composition (Fortel et al., 2014; Geslin et al., 2017; Samuelson et al., 2018). Several factors could explain these findings (Martins et al., 2017): the continuous floral resource and nesting sites found in parks and gardens, the heat island effect providing warmer mean temperatures, habitats heterogeneity, and lower pesticide levels as compared to rural areas. It seems that moderate urbanisation doesn't have a net negative impact on species diversity but rather modifies species abundance and assemblages (Brosi et al., 2007; Bates et al., 2011).

In contrast to the highly fragmented habitats assumptions and the island-like isolation effect, bee communities occurring in Singapore parks are expected to be quite similar and homogenous. Thanks to several greening schemes (Auger, 2013), it is estimated that 56% of Singapore's land area is covered in secondary vegetation (Yee et. al, 2011). Often known as the "City in a garden" (Newman, 2014; Wen, 2014; National Parks Board, 2016), the city-sate counts numerous parks and gardens with a great variety of flowering plants, thus creating a global green web and an almost continuous vegetation cover. Nature reserves, nature parks, city parks, gardens, green rooftops and other public greeneries form a vegetal gradient that could facilitate bees immigration and emigration flows.

1.3 LANDSCAPE INFLUENCE ON BEE POPULATIONS

Studying bee populations and communities requires knowledge about the quality of their habitat and the structure of the surrounding landscape. Both habitat quality and landscape context might explain why a given species is present or absent and how it interacts with its environment and other species (Hennig & Ghazoul, 2011; Burkman & Gardiner, 2014).

For a given site, at the local scale, the two main factors influencing bee populations and species richness are their habitat's size and quality. Even if MacArthur & Wilson (1967) predict a direct positive influence of site size on species richness, Franzen & Nilsson (2010) state that habitat quality could play an even greater role. Wild bees habitat quality refers mostly to feeding and nesting resources. Floral quality, diversity and quantity are of major importance regarding wild bees' protein (ensured by the pollen) and carbohydrate (ensured by the nectar) feeding requirements. Müller and colleagues (2006) have estimated that some wild bee species needed to visit between 7,000 and 11,000 flowers to meet the development requirements of one single larva. When it comes to the nesting resources, wild solitary bees are manly ground and cavity nesters. Bare ground, wood, stems, walls and even empty snail shells are potential nesting habitats (Roubik, 1989). Wild bees nesting potential thus increase with habitat heterogeneity.

At a larger scale, the factors influencing wild bee communities are the landscape composition, the landscape configuration and the habitats' connectivity (Hopfenmüller et al., 2014). Landscape variables (or indices) are used to quantify landscape factors and will be detailed in the *Materials and methods* chapter. Landscape composition is determined by the different land-uses, their number and size. According to different studies (Burkman & Gardiner, 2014; Hopfenmüller et al., 2014), landscape composition affects pollinator communities and wild solitary bees in particular. The landscape configuration describes the spatial arrangement of surrounding patches. A complex configuration with numerous land-use classes and heterogenous habitats seems to positively impact wild bee communities. Finally, the landscape connectivity characterises the way that habitats enable or restrain wild bees flows between them. Few studies have tested the effect of habitats connectivity on wild bees. Until now, no significant influence has been detected (Jauker et al., 2013).

1.4 SINGAPORE: THE EVER GROWING "CITY IN A GARDEN"

Singapore is a densely-populated tropical city-state located at the southern tip of the Malaysian peninsula, near the equator (Figure 1). According to the Meteorological Service Singapore (MSS) (2018), the city-state has a tropical climate, with abundant rainfall, high and uniform temperatures, and high humidity all year round. Temperatures and relative humidity do not do not show large month-to-month variations, but rainfalls show diurnal variations (occurring more frequently in the afternoons when sun's heat is strongest) and a geographical distribution (being higher over the northern and western parts of Singapore, and lower in the

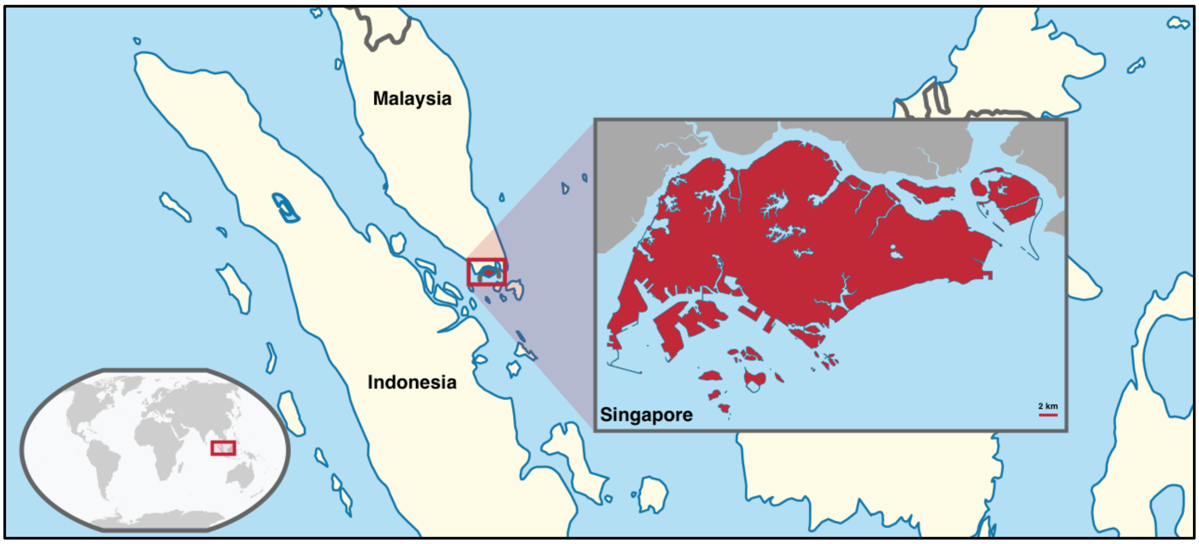


Figure 1: Geographic location of Singapore. Adapted from Mapsland (2018).

eastern part of the island). Singapore's climate is characterised by two main monsoon seasons (the Northeast Monsoon from December to early March and the Southwest Monsoon from June to September), separated by inter-monsoonal periods. It rains an average of 167 days per year, with mean annual rainfall of 2165.9 mm, most of them being heavy and accompanied by thunders. The daily temperatures usually range between 23-25°C during the night, and 31-33°C during the day.

Southeast Asia has rapidly urbanised in the last few decades, experiencing massive forest loss, reduced natural habitats and fragmented landscapes (Tan & Abdul Hamid, 2014). Singapore presents an interesting case for study of pollinators in urban habitats as only 0.28% of its current total land area (721.5 km^2) is left intact (Ng, Corlett, & Tan, 2011). This is the least amount of intact original forest as compared to other neighbouring countries (Tan & Abdul Hamid, 2014).

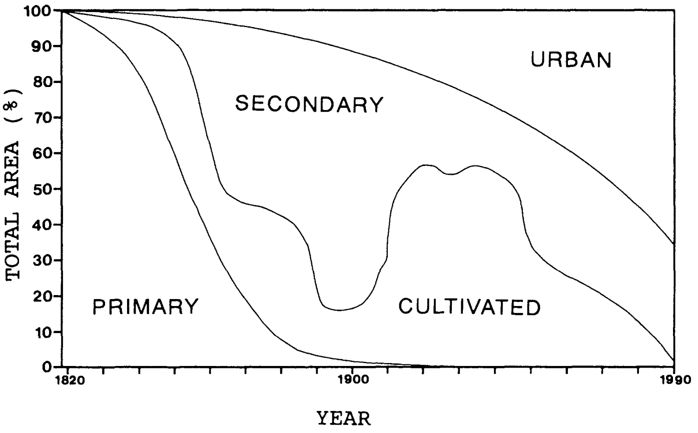


Figure 2 : Land use changes in Singapore, 1819-1990 (excluding offshore islands and reclaimed lands). PRIMARY = primary forest, CULTIVATED = cultivated land and tree crops; SECONDARY = secondary grass land and scrub land forest; URBAN = urban areas, parks and gardens (Chua, 2015)

As shown in Figure 2, Singapore has faced deforestation since the 1800s, when the native forests were cleared to make way for rubber plantations and several tropical crops. In a few decades only, up to 95% of primary lowland dipterocarp forest had already been lost (Corlett, 1992). By the 1990s, half of the island had been urbanised (Corlett, 1992) to meet demand in housing and infrastructures (Castelletta, Sodhi, & Subaraj, 2008). With its current population of 5,61 million people (Singapore Department of Statistics, 2017) that is set to rise to 6,24 million by 2030 (United Nations, 2017), Singapore's future land development is likely to place further pressure on the limited available green spaces. Consequently, Singapore would have lost up to 73% of its species since the 1890s (Brook et al., 2003).

Despite being the third most densely populated State in the world (Singapore Department of Statistics, 2017) and facing high urban development, Singapore is known as the "City in a garden". Since de 1960s, land planners have established several greening schemes (Auger, 2013), increasing green cover by 10.8% between 1986 and 2007 despite a 68% growth in population in the same period (National Parks Board, 2009). Numerous parks and gardens with a great variety of flowering plants can be seen across the city, attracting and supporting pollinator communities. In 2011, 56% of Singapore's land area was covered by vegetation, out of which 27% were actively managed parks, gardens and lawns while 29% were patches of spontaneous vegetation (Yee et al., 2011). Even if the managed vegetation accounts for 48% of total vegetation cover in Singapore (Yee et al., 2011), we can still find a few patches of mature primary forests, old secondary forests and large patches of secondary forests, as shown in Figure 3.

Due to Singapore's singular properties, green spaces are often close to urban and residential areas, vegetated patches tend to be small, fragmented and far from larger natural habitats such as forests and nature reserves. However, the recent greenery efforts have helped create a global green web across the city, thus enabling easier connexions between parks and natural habitats. The remaining green spaces along with newly planted vegetation are important to ensure the survival of the local flora and fauna.

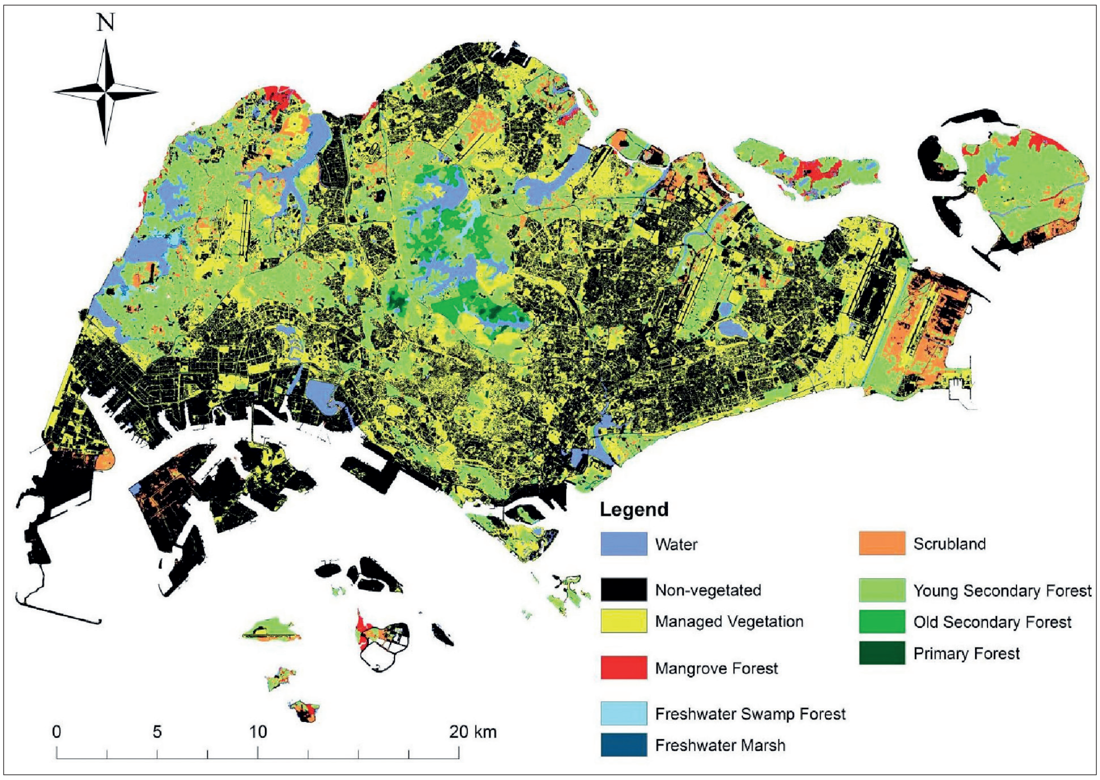


Figure 3: Distribution of vegetation types across Singapore. Retrieved from (Yee et al., 2011).

At first glance, providing a large diversity of flowering plants to flower-visiting insects seems highly beneficial under an ecological prism. However, very little is known about the real impact these urban gardens have on pollinators insects (Yee et al., 2011). According to the latest flora survey (Chong et al., 2011), 51% of vascular plant species are native to Singapore, 44% are exotic and the remaining 5% are weeds of uncertain origin. Unfortunately, recent greening efforts might not get the most out of their ecological potential (Chong et al., 2014) as nearly 50% of Singapore's green spaces are under some kind of management (mostly low biodiversity homogenous plant patches) (Yee et al., 2011). This managed vegetation represents a key land-use, holding a great potential for conservation. They do not only have an aesthetic value, but also attract and support communities of flower-visiting insects that feed on the floral resources (Wen et al., 2013). It is thus essential to understand flower-pollinator interactions in this particular urban setting, where managed vegetation could serve Singapore' conservation efforts. Despite the severe habitat degradations and species losses described above, Singaporean policy makers recognise the role of urban biodiversity strategies as essential conservation tools and incentives (National Parks Board, 2009, 2010, 2015).

1.5 PLANT-POLLINATOR NETWORKS

Plant-pollinator interactions play a key role in ecosystems. They are crucial to the reproduction of 85% of the known flowering plants species (Ollerton et al., 2011) and support pollinator communities that feed on these fundamental resources (Wen et al., 2013). However, these mutualistic networks could be jeopardized by anthropogenic disturbance, such as land use alteration, inappropriate agricultural practices, pathogens propagation or climate change consequences (Nieto et al., 2014). The interest in plant-pollinator networks studies is growing. They are easy to analyse and interpret, their related indexes seem to be linked to habitat stability, and observed interactions allow researchers to investigate species niches (Biella et al., 2017; Delmas et al., 2018). They represent a useful tool to understand bee ecological dynamics (Delmas et al., 2018), to address environmental perturbations (Vanbergen, 2014), anticipate species losses effects (Brosi et al., 2017), measuring species specialization (Blüthgen et. al, 2006) and thus choose the right conservation strategies accordingly.

Basically, ecological interaction networks are graphical representations of associations (links) between species (nodes). In plant-pollinator bipartite networks, the upper level usually represents the plant species whereas the lower one usually represents the pollinator insects (as shown in Figure 4). Their metrics are both qualitative (based on the presence or absence of a link) and quantitative (based on the number of links). Identifying trends among these networks can be useful to highlight patterns of community organization, trophic associations and realized interactions (Blüthgen et al., 2008).

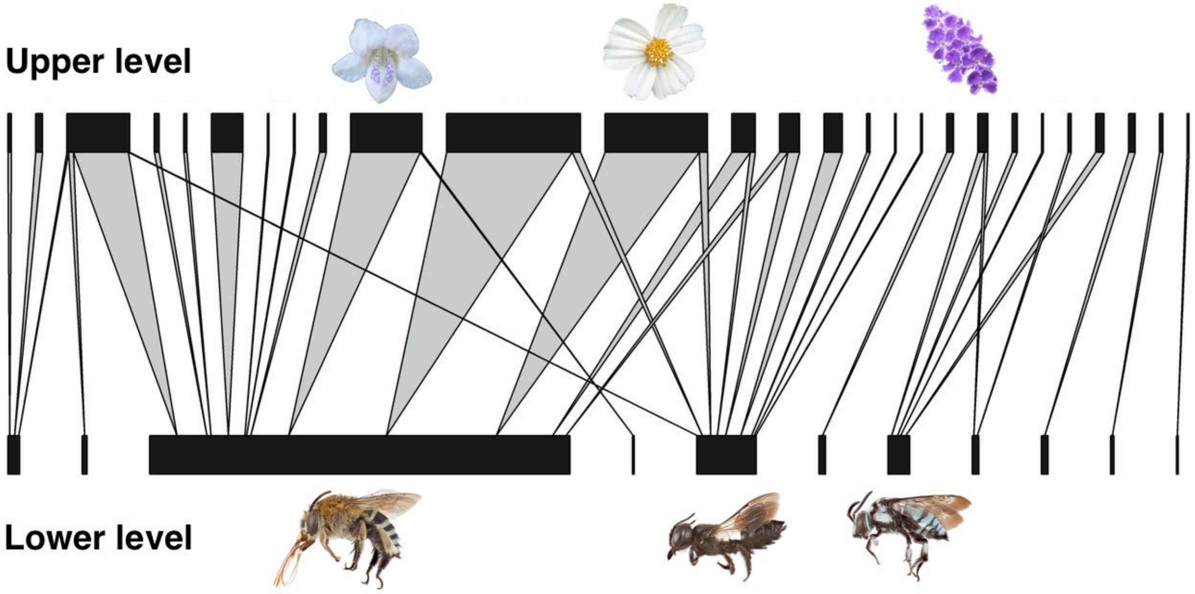


Figure 4: Example of a typical weighted two-level interaction network. The upper level represents the hosts whereas the lower one represents the visitors (flowers and bees from Singapore in this example). The boxes' width varies in proportion to the species abundance whereas the links' width varies in proportion to the number of interactions observed. Bee pictures courtesy of the Insect Diversity Lab (Department of Biological Sciences, National University of Singapore).

Plant and animal species are characterised by their ecological niche. A species' ecological niche describes how an individual or a population responds to the distribution of resources and competitors and how those species alters the same factors in return (Pocheville, 2015). More precisely, a distinction can be made between fundamental and realized niches. The first one describes the full range of resources, biotic and abiotic conditions in which a species could survive and reproduce. However, species are often more or less under pressure by interacting with other organisms and experiencing environmental stresses. Species are thus forced to occupy a narrower niche in which they are adapted. This second niche is the realized one (Griesemer, 1992). These niche concepts are useful to study the potential competition between two species or more. Two species are considered in competition if they are sharing the same niche or at least a part of it. The two species' respective realized niches will therefore represent their respective fundamental niches lowered by the part they covet (Hutchinson, 1957). A distinction can also be made between direct and indirect competition. Direct competition (or interference) is a quite rare phenomenon in pollinators behaviour (Nagamitsu & Inoue, 1997; Biesmeijer et al., 1999). Most of the time, pollinators compete by sharing a limited resource in the same area (nesting sites, floral patches, etc.) (Geslin et al., 2017).

Among the eight types of ecological interactions (cooperation, mutualism, commensalism, neutralism, parasitism, predation, amensalism and competition) (Moon et al., 2010), plant - pollinator networks can be qualified as mutualists. Both flowers and bees benefit from these interactions (Tylianakis et al., 2010). These precious ecological networks can experience deep topology modifications in the urban environment (Geslin et al., 2017). Baldock and colleagues (2015) suggest that network specialisation seems to decrease in urban areas compared to agricultural ones, diets are less diversified and interaction evenness increases (Geslin et al., 2013). However, it is important to keep in mind that, to date, little is known about how network structure exactly impacts ecosystem functioning and services. Most interaction networks are complex, many factors are involved and clear trends are not easily discerned.

In the tropics, and more particularly in Asia, very few plant-pollinator surveys focusing on bees have been conducted. We can mention studies in Brazil (Santos et al., 2010; Zotarelli et al., 2014), Costa Rica (Janzen, 1971; Brosi et al., 2007), Borneo (Momose et al., 1998), Laos (Kato et al., 2008), Indonesia (Spengler et al., 2011) and Singapore (Wen et al., 2013). These studies were often confined to forest landscapes, whereas tropical research on pollinators decline and response to land-use change in urban areas has been poorly studied. The present study modestly contributes to fill this knowledge gap.

1.6 PARKS DESIGN, MANAGEMENT AND PRACTICES

Considered as a completely urbanised country by the United Nations (2018), Singapore also ranks as the third most densely populated cities in the world. By combining colonial architecture, contemporary buildings and lush vegetation in a 721.5 km^2 surface, the city-state had to set up challenging planning and development strategies in order to support its ever-growing population.

Since the 1980's, Singapore authorities are implementing an island-wide network of green corridors connecting parks, nature reserves and various sites of interest (Figure 5) (Tan, 2006). Theses corridors aim to provide new pathways for weak road-users (cyclists and pedestrians) to get around Singapore, to serve as green linkages between habitats for fauna and thus enhance the city-state natural elements. Their design ranges from a several meters-wide asphalted or paved track with dense plantings of native and ornamental shrubs to dirt paths surrounded by spontaneous vegetation (Figure 6). Along the greenways, the trees are densely planted so as to form a continuous canopy. From an ecological perspective, Park Connector Networks could provide a protected vegetated path and cover for various species. They might facilitate immigration and emigration between habitats (Briffett et al., 1999) but their real contribution and effectiveness in the city-state have never been assessed and requires further investigations.

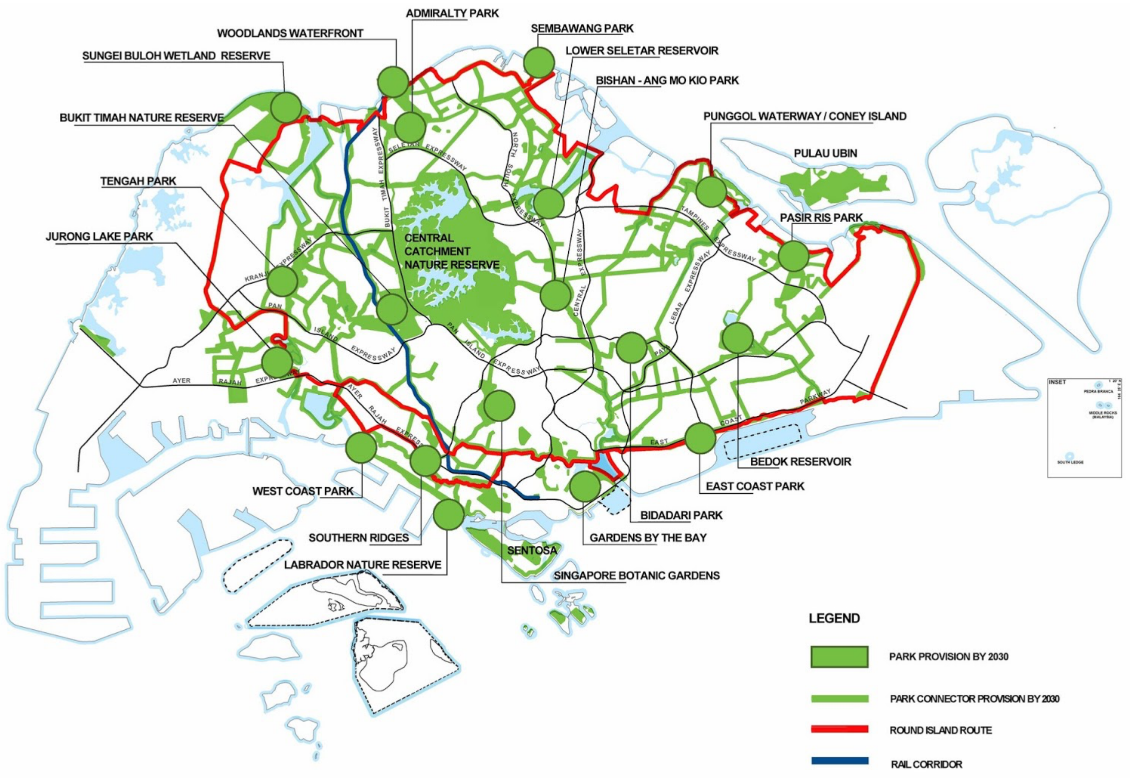


Figure 5: Park Connector Network (PCN) projections for 2030. This network aims to connect the parks, nature reserves and other green spaces thanks to vegetated pedestrian and cycle lanes (Ministry of National Development, 2013)

Figure 6: Connector Networks examples showing two radically different designs. The Punggol Park Connector (A) appears to be very neat and intensively managed whereas the Bukit Timah Rail Corridor (B) is basically a dirt path surrounded by spontaneous vegetation. Pictures copyrights Julien Clerbois.

On a smaller scale, parks are often valued by citizens for their recreational and leisure purpose. They provide important social and psychological benefits to human societies, and more particularly in large and dense urban areas. Several studies highlighted the beneficial services and the source of positive feelings arising from the experience of nature in urban environment (Chiesura, 2004; Peters et al., 2010). However, heavy utilization on a daily basis and high visitor traffic might constitute a source of conflicts. In Singapore parks and reserves, venomous, stinging and disease carrier species (like several snake, wasp and mosquito species) are monitored by scientists and park managers (Ooi et al., 2006; Burattini et al., 2008). Behaviour guidelines are also made available to the public in order to prevent any human - fauna conflict (National Environment Agency of Singapore, 2018; National Parks Board, 2018).

To many species, like pollinator insects, urban green spaces serve as an important refuge and source for food, shelter and nesting (Hall et al., 2017). Through human management and design, urban parks are often characterised by high degrees of concrete cover, unevenly distributed floral resources and tidy mown grass (Qiu et al., 2013). However, not all parks are built and managed equally. Their floral composition, level of greenery and management practices could have a great influence on pollinators communities and their biodiversity.

“Bee friendly” parks management should involve a judicious selection of nectar-producing plants species, allocate multiple patches of spontaneous vegetation and try to meet the local species’ nesting requirements. Parks’ design and management practices influence their effectiveness in providing a steady flow of resources and long-term nesting sites. The existing gap in knowledge for the conservation of wild bee species in Singapore lies in understanding the true value of its urban parks, nature reserves and offshore islands. Their effectiveness in providing a steady flow of resources and long-term nesting sites still need to be assessed. The present study modestly contributes to fill this knowledge gap by linking the land use and human management practices to the observed bee communities in urban parks and offshore islands.

2 AIMS OF THE MASTER THESIS

Despite being the third most densely populated State in the world (Singapore Department of Statistics, 2017) and facing high urban development, 56% of Singapore's land area is covered by vegetation (Yee, 2011). The recent greenery efforts have helped create a global green web across the city, thus enabling easier connexions between parks and natural habitats. The Park Connector Network implementation is a good example of this greenery effort (Tan, 2006). These serve as green linkages between habitats for fauna, forming a continuous vegetation cover and canopy. Even if their real contribution and effectiveness in the city-state have never been assessed and requires further investigations, we could expect very mobile species like bees to benefit from such infrastructures.

However, as managed vegetation accounts for 48% of total vegetation cover and green areas are often under some kind of management (mostly low biodiversity homogenous plant patches), Singapore might not get the most out of its ecological potential (Chong et al., 2014). To date, very little is known about the real impact these managed areas have on wild bee communities and it is of fundamental importance to understand the true value of Singapore green areas (urban parks, nature reserves and even offshore islands).

From these few considerations, three key assumptions were made:

- Due to Singapore generalised greenery, wild bee communities are expected to be relatively homogenous across urban parks in terms of species composition;
- Bee communities occurring in islands are expected to be poorer in terms of species composition and relatively more nested than mainland sites. Moreover, distance from Singapore coastlines should influence this assumption;
- Wild bee populations are expected to be more generalist and vulnerable in manicured sites, as managed vegetation might be low in diversity, composed of homogenous plant patches, and heavily managed.

In summary, the global aim of this study was to investigate the diversity of wild bee communities across two habitats (parks vs. islands) and two management types (wild vs. manicured) in a highly urbanised tropical setting. The second and underlying aim was to review the implications of current park management practices and raise awareness about the value of such green spaces for wild bees conservation.

3 MATERIALS AND METHODS

3.1 STUDY AREA

The densely populated city-state of Singapore has lost up to 70% of its species since the 1890s (Brook et al., 2003). Despite having the least amount of its original forest left intact as compared to other neighbouring countries (approximately 2 km^2 (Ng et al., 2011) of its 721.5 km^2 land area recorded in 2016 by the Singapore Land Authority (2018)), authorities have increased green cover by 10.8% between 1986 and 2007 (National Parks Board, 2009). While urbanisation can be considered as the most significant cause of land use change in Singapore, remaining green areas (such as gardens, town parks, nature parks, forests, and green roofs) could be considered as islands alike. Urban parks could be seen as relatively small vegetation plots, more or less isolated from one another, characterised by singular flora and fauna assemblages. Their surface, structure, floral composition, degree of urbanisation, and many other local and landscape factors, are amongst the main characteristics impacting directly or indirectly pollinator communities.

For a comprehensive understanding of bee communities and their distribution in Singapore, specimens should be sampled across several vegetation types such as primary forests, old and young secondary forests, mangrove forests, freshwater swamp forests, and scrublands, (Yee et al., 2011). This includes parks and islands, that what we will split, in the context of this study, in two categories: **wild** sites (e.g. lands, scrublands, forests and mangroves covered in spontaneously growing vegetation, under minimal management and maintenance strategies) and **manicured** sites (that refers to orderly, neatly-planted, garden-like sites under heavy maintenance and management).

However, only six sites were covered during this study, for obvious constraints like time and manpower, but also limited personal travel funds (e.g. for expensive boat rides), restricted areas and accessibility, and necessary permits granted from the National Parks Board (the main competent authority) in order to visit some parks and islands. Out of these constraints, the sites selected, with different size scales and distinctive characteristics, were carefully chosen in order to provide the best representation of habitats and management types that can be found in Singapore. Sites location (Figure 7), details (Table 1), history, characteristics and specificities are set out below

A. **Dairy Farm Nature Park** is a 86 ha site located at the edge of an old secondary forest and in close proximity to the secondary and primary forests of Bukit Timah Nature Reserve. A notable Dairy Farm's feature is the presence of a relatively wide variety of cultivated exotics, naturalised exotics, and native flowering plants species (Wen et al., 2013). At the heart of the park, a former quarry provides a particularly interesting open space with numerous flowering trees. Illustrative photographs of both forested and open habitats can be found in Appendix 1.

B. **Hort Park** (short for Horticulture Park) is a 12 ha garden-themed park located in the southwestern part of Singapore. Opened in December 2007, its aims are to preserve nature, maintain biodiversity and engage citizens with nature through recreational, educational, research, commercial and natural activities and projects. This park counts numerous indigenous and exotic flower patches that are displayed very neatly in an ever-present landscape design concern. This park also features 21 themed gardens (Home Garden, Native Garden, Butterfly Garden, …), each of them being reflected by a careful selection of plant species (National Parks Board, 2018). This singular place is thus characterised by high density flower patches and heavy maintenance. Illustrative photographs can be found in Appendix 2.

C. **St John's Island** is a 122 ha island located approximately 6.5 km to the south of the singaporean coastline. Formerly used as quarantine station for cholera cases detected among immigrants in the late 1800's (Ong, 2017), it is now a low urbanized leisure island. Swimming lagoons, beaches, picnic grounds, trekking routes and sport amenities attracts tourists and citizens for weekend visits. Vegetation patches vary from heavily groomed ornamental flowers to regularly mowed lawns. Small young secondary forest patches still remain in certain parts of the island. Illustrative photographs can be found in Appendix 3.

D. **Coney Island** is a 102 ha island located off the northeastern coast of Singapore. Initially planned as an amusement park in the 1950's, the private island stayed untouched and have been sold to the singaporean government (Ghosh, 2016). Coney Island has underwent heavy land reclamation, with a tripled surface since the 1970's. Its habitats varies from vegeted beaches to coastal forests, grasslands and mangroves. This park is only opened to the public since October 2015 (National Parks Board, 2015). According to the Urban Redevelopment Authority plans, Coney Island is zoned for residential, sport and recreational uses but does not show immediate development (Wai, 2014). By its low urbanisation and maintenance, this site will be classified as "wild". Illustrative photographs can be found in Appendix 4.

E. **Pulau Ubin** is a 710 ha island located at the north east of Singapore. It is one of the few Singapore offshore islands that are relatively untouched by development and have a well preserved flora and fauna. Its wooden house villages, rich and preserved wildlife, abandoned quarries and plantations make it the last witness of the pre-colonial Singapore that existed before large-scale urban development (National Parks Board, 2017). With growing attention and interest in history and nature, visitors to Pulau Ubin have increased over the years. Despite growing concern to some environmentalists, leisure activities and their environmental impacts remain limited (Henderson, 2000). The island's vegetation patches consist in large young and old secondary forests, newly restored mangroves and tiny managed plots. Illustrative photographs can be found in Appendix 5.

F. **Pasir Ris Park** is a 90 ha coastal park located in the eastern part of Singapore. This green public space has recreational, aesthetical and conservation purposes as it counts many different habitats (mangrove forest, a rich community garden, several beaches, cycling tracks surrounded by ornamental flower patches and wide areas of mowed lawns) (National Parks Board, 2018). The “Kitchen Garden” is a noteworthy densely vegeted spot where culinary and medicinal plants are community gardened (National Parks Board, n.d.). This small spot attracts numerous pollinator insects. Illustrative photographs can be found in Appendix 6.

Site	Code	Coordinates		Surface (ha)	Site type	Site management
		Latitude	Longitude			
Coney Island	CI	1.402195	103.967882	102.4	Island	"Wild"
Dairy Farm	DF	1.361232	103.772621	86.2	Island	"Wild"
Hort Park	HP	1.278983	103.799729	12.3	Island	"Manicured"
Pasir Ris	PR	1.379202	103.950307	90.4	Park	"Wild"
Pulau Ubin	PU	1.402195	103.967882	708.5	Park	"Manicured"
St John's Island	SJ	1.220167	103.847000	122.1	Park	"Manicured"

Table 1: Site details. From left to right: full site name, code for in-text reference, site coordinates, study site area in hectares, site type (defines site habitat type, either park or island), and site management (“wild” defines sites covered in spontaneous vegetation, while “manicured” defines sites under heavy maintenance and management).

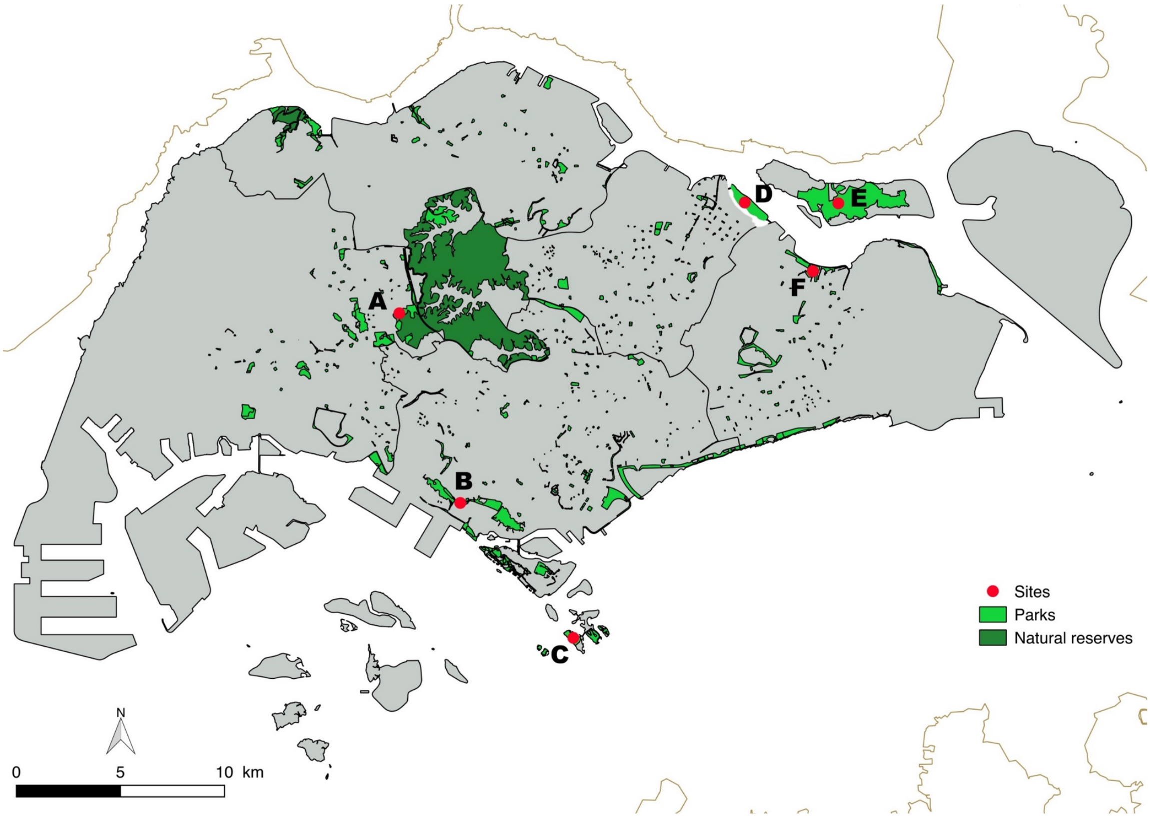
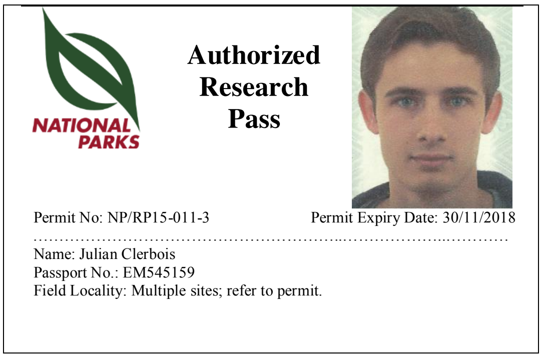


Figure 7 : Singapore map representing locality of sampled sites (red dots). (A) Dairy Farm, (B) Hort Park, (C) St. John’s Island, (D) Coney Island, (E) Pulau Ubin, (F) Pasir Ris. Singapore basemap and layers retrieved from the Urban Redevelopment Authority (2016). Forests and Nature reserves are represented in dark green, parks in light green.

3.2 METHODOLOGY

3.2.1 Data collection

Before starting any field work, we had to ensure that capture and killing authorisations were up-to-date. Permits for the collection of Hymenoptera were granted by the National Parks Board of Singapore (NParks). At least five days before each sampling session, sites managers had to be contacted and informed of the exact research location, date, time and logistics involved.



NATIONAL PARKS

Authorized Research Pass

Permit No: NP/RP15-011-3 Permit Expiry Date: 30/11/2018

Name: Julian Clerbois
Passport No.: EM545159
Field Locality: Multiple sites; refer to permit.

Figure 8 : NParks authorized research pass

3.2.1.1 Sampling protocol

A total of 180 hours of visitation survey was performed over 30 days, from November 2017 to January 2018. All six sites were surveyed twice a month on calm, sunny, or partly cloudy days (in order to reduce temporal variation in weather). In the event of unfavourable weather, the session was postponed, as heavy rains and high wind speeds could reduce bee activity. Each sampling session lasted for six hours, whenever possible between 9:00 AM and 3:00 PM (when pollinators' foraging activity is most active). That time included sampling and searching for samplable patches. A patch ranges from a flowering tree, a patch of flowers, or less commonly soil and sand where Hymenopteran insects fly around.

During a sampling session, each patch of flowers was sampled for approximately ten minutes. Hymenopteran flower-visiting insects and a few hover flies (Syrphidae) that were observed touching the reproductive parts of the plants were captured with a standard entomological net and transferred into Falcon™ tubes. This method prevents double counting and allows individuals to be quantified along with their floral associations. Netting was made to minimise direct sweeping at the flowers, in order to reduce the damage to the floral patch. Sampling was constrained by the maximum reach of the entomological net, thus specimens observed at higher levels (e.g. at the canopy level) were not collected. Honey bees (*Apis* genus) and non-Hymenopteran flower-visiting insects (excepting a few hover flies) were not collected either. Honey bees avoidance was chosen to optimise the number of species recorded, as some sites had a high abundance of them. Catching every honey bee would cause researchers to miss out on the other species of bees and wasps. According to (Gezon et al., 2015), the intensity of this method of capture affects neither the regeneration of wild bee populations, nor the abundance, diversity and composition of their functional groups.

Flowers that could not be identified on site were photographed, and insects captured from that unidentified plant were labelled correspondingly. Plants were later identified using the NParks flora and fauna website (https://florafaunaweb.nparks.gov.sg), guidebooks, and the expertise of the Insect Diversity Lab (NUS) assistants and students.

3.2.1.2 Strengths and weaknesses of the protocol

In order to maximise the sampling effort, different sampling methods can be used: sweep netting and pan trapping. When it comes to collecting flying insects, pan trapping is often seen as the most efficient method (Westphal et al., 2008; Wilson et al., 2008; Wilson et al., 2016; Prado et al., 2017). It is cost-effective, can be implemented by anyone, easy to set up and can be left alone once placed. This technique is also beneficial when manpower is limited and frequent visits to survey sites are difficult. However, a recent master thesis conducted in Singapore, submitted by Roscoe (2015), highlighted the fact that pan trapping, suggested by experts as a standard method around the globe, only caught one bee specimen during the four months long study. Attraction to these traps for tropical urban bees in Singapore (compared to other environmental conditions and geographical zones) yet remains to be clarified.

If pan trapping seems to be the most efficient one in European regions (Westphal et al., 2008), the sweep net is easier to use, portable, cost effective and does not require set up time. The discriminate sweep netting method (seeing the insect and actually catching it) allows researchers to link pollinators to floral hosts. However, according to Prado and colleagues (2017), there is no standard protocol for bee sampling using a sweep net in the tropics. The time spent sweep netting, the time of day, the number of aerial sweeps, the number of collectors per session, and the distance covered, can make comparing bee abundance and diversity between studies extremely difficult.

The combination of both morning and afternoon surveys at one site aimed to provide a broad representation of bees and wasps species that visit parks throughout a day. However, habitat characteristics, such as flower bloom and availability within these sites, tend to be spatially and temporally heterogeneous, making it difficult to obtain a representative sampling of a constant habitat character over the sampling period. A three-months sampling period might not be representative of the ground-level plant-pollinator associations occurring all year round. A longer period would be necessary to detect bee species which are seasonal, as *Megachile* bee species and others species associated with mass blooming events (Roubik et al., 2005; Ascher et al., 2016).

3.2.1.3 Supplementary data

To counterbalance the short sampling period and biases above-mentioned, Insect Diversity Lab's reference collection (courtesy of John Ascher, National University of Singapore) have supplemented personal collection conducted as part of this study. Specimens from the Singapore Mangrove Insect Project, a two-year survey performed from April 2012 to 2014, will be used in this project as well (Puniamoorthy et al., 2014). Gathering these additional data allows us to work with a nearly 2000 entries database, which should be sufficient for statistical analysis.

However, it is important to notice that sampling protocols and techniques might slightly differ between studies. Even if time spent on each floral patch remains constant for the sweep netting technique, sampling sessions time slots can vary between studies. Also, a few researchers focused on specific species or genera, perhaps leading to dissimilarities in the relative abundance of specimens collected. Finally, the Singapore Mangrove Insect Project has required Malaise trapping, which should — at least theoretically — be adequate to have an estimation of overall species richness locally across flying insect orders. All these characteristics should be considered when analysing the results.

3.2.2 Entomological collection preparation

3.2.2.1 Specimen conservation

The great majority of specimens captured during sampling sessions had to be killed and conserved. Most of the time, species identification requires a binocular examination, whereas field observations permit the identification to the genus level only. Moreover, the capture of bees creates an entomological collection of references which could be used as a scientifically robust dataset. This could be useful for our knowledge on species, as well as local and regional diversity, and conservation strategies. After capture, the specimens were stored in an ultra-low freezer (- 80°C) for at least one day. These ultra-low temperatures are highly recommended if future DNA barcoding studies are planned.

After being pinned and identified, specimens were recorded into the lab database and stored in wooden entomological boxes containing mothballs, in order to prevent the growth of mould and mildew.

3.2.2.2 Specimen pinning

Entomologic stainless-steel pins (n° 0 to 3, depending on the body size) were used to pin the specimens. Smaller ones were side-mounted using minutens (short pins used for very small insects). Pins were inserted perpendicularly to the body axis, in the middle right of the thorax, then pushed into a polystyrene plate in order to position the specimen between the upper two-thirds of the pin. For identification purpose, insects were preferably prepared so as to expose useful parts of the body (wings, legs, antennas, etc.). Afterwards, labels (annotated according to the Insect Diversity Lab collection standards : city, site, coordinates, collection date, collector, species and identifier) went in the lower third of the pin.

3.2.2.3 Specimen identification

Bee identifications were made or confirmed by Hymenoptera taxonomic specialist John S. Ascher (National University of Singapore) (see Acknowledgements). Bees were identified to the lowest taxonomic level possible, usually species, but for some taxa, morphospecies.

3.3 STATISTICAL ANALYSES

As a three-months long sampling period might not be representative of plant-pollinator associations occurring all year round, using the Insect Diversity Lab's reference collection is necessary in order to strengthen the database and the statistical analyses at the same time. If we limit the database to our six study sites, the first record dates back to 1972, when the latest dates back to early 2018. Over a 46-year period, especially given the significant urbanization history of Singapore, we should not expect a fair representation of current bee richness and their floral associations.

However, over 95 % of the 182 sampling sessions databased occurred between 2010 and 2018, which is a far more acceptable timescale. Most of these sessions were conducted as part of numerous bachelor thesis submitted to the Department of Biological Sciences (National University of Singapore) (Soh, 2014; Chua, 2015; Chui, 2015; Leem, 2015; Ng, 2015; Lai, 2016; Tjong, 2016; Chang, 2017; Tan, 2017; Tee, 2017; Teo, 2017) together with a checklist of flower-visiting insects in Singapore parks (Wen et al., 2013), and the Singapore Mangrove Insect Project (MIP) (Puniamoorthy et al., 2014). These documents allow us to verify protocols' similarities and dissimilarities, as well as noteworthy observations made during this period.

All statistical analyses run in this study were performed in R® version 3.3.3 (The R Foundation, 2018) with RStudio® version 1.1.423 (RStudio Team, 2018). Several statistical packages (detailed below) were used, depending on the statistical analyses performed.

3.3.1 Species diversity

What is diversity? Behind a question as simple as that lies fundamental terms, mechanisms and principles. Before going any further, for a better understanding of this study, let's clarify a few key concepts.

Study the **diversity** within and between **populations,** helps analysing wild bee **communities** structure. In ecology, a population defines a group of individuals from the same species, living in the same environment, whereas a community refers to a group of interacting species populations occurring together in a same area (Stroud et al., 2015). The diversity of a community describes the number of species present in the community (**species richness**) and the equity in the species distribution (**evenness**) (Gardener, 2014).

Diversity can also be analysed at different scales: at site or habitat level (**alpha diversity**), between sites or habitats (**beta diversity**) and at a broader scale, such a landscape made of multiple habitats (**gamma diversity**) (Gardener, 2014).

This study wil focus on the community and spatial aspects of biodiversity, discussing bee communities richness and composition, plant-pollinator associations, and landscape organisation around study sites. The indices of species diversity will be evaluated and compared between sites, habitats and management types using the six sites database (Coney Island, Dairy Farm, Hort Park, Pasir Ris, Pulau Ubin, and St John's Island).

3.3.1.1 Sampling effort evaluation and species richness

A sampling effort evaluation is necessary to verify the field work quality and the results robustness. Oliveira and colleagues (2017) showed that the perception of species richness is strongly influenced by the distribution of sampling effort. A positive correlation can be observed between local species richness and the number of records for various taxonomic groups. Since the relationship between sampling efforts and species richness may influence the results, sampling bias and their spatial distribution should be taken into account (Walther & Moore, 2005; Soria-Auza & Kessler, 2008).

In this study, accumulation curves and non-parametric methods will be used to evaluate the sampling effort. Accumulation curves give the sampling effort rate at which new species are still encountered (number of cumulated species encountered in ordinates, number of cumulated sampling sessions in abscises). If the curve reaches a plateau, the sampling effort can be considered as sufficient. It means that another sampling unit will not bring new species to the dataset anymore. A comparison between sites, habitats and management types was done to ensure the homogeneity of sampling efforts. Species accumulation curves were produced for the three subsets above-mentioned under 100 random permutations using the 'vegan' package (version 2.4-5) (Oksanen et al., 2018).

Based on observed species richness in the sites, habitats and management types subsets, extrapolated species richness was calculated using the 'specpool' function, and graphically depicted by using the 'poolaccum' function using the 'BiodiversityR' package (Kindt, 2018). Non-parametric estimators were used to evaluate the number of undetected species and add them to the observed species richness. On the one hand, the Chao1 index (Magurran, 2004) is a simple estimator of the absolute number of species in the assemblage. This estimator is based on the number of rare species present in the sample, increasing the ratio of singletons and doubletons until every species is represented by at least two individuals. The inventory can then be considered as complete. The Chao 2 index, on the other hand, is based on the species occurrence between samplings. Chao estimators were shown to be more precise and less biased than others estimators for mobile creatures like wild bees (Brose & Martinez, 2004; Fortel et al., 2014). Finally, the Jackknife and Bootstrap estimators are shown to reduce the bias although they underestimate the actual number of species if there is a large number of rare species in the dataset. (Smith & van Belle, 1984). Species richness estimator can be found in Appendix 7. However, this study will mainly focus on Chao1 and Jackknife1 estimators, as the abundance of each species is taken into account (Gotelli & Colwell, 2011).

Wild bee species abundances were aggregated by site and displayed as a heat map using the 'pheatmap' package (Kolde, 2018).

3.3.2 Alpha (α) diversity and associated indices

Biodiversity indices are of fundamental importance for environmental monitoring and conservation. They aim to describe general properties of communities, allowing us to compare different regions, taxa, and trophic levels (Morris et al., 2014). However, choosing the right index turns out to be tricky, because of the multitude of existing indices and the lack of consensus about which indices are more appropriate and informative.

The 'BiodiversityR' package (Kindt, 2018) was used to produce Simpson (D) and Shannon's (H) diversity indices, as well as Pielou's evenness index (J). Analysis of variance (AOV) was carried out on the indices to assess if differences were significant between sites, habitats and management types. Indices values are reported in Appendix 7Appendix 8.

3.3.2.1 Simpson's indices

Two of the most commonly used indices in ecology are Simpson (1949) and Shannon (1949) diversities. Both Shannon and Simpson diversities increase as richness and evenness increases (for a given pattern of evenness and richness). However, communities are not always ranked in the same order: Simpson diversity is less sensitive to richness and more sensitive to evenness than Shannon diversity, which, in turn, is more sensitive to evenness than is a simple count of species (Morris et al., 2014).

Simpson's index (S) uses the proportion (abundance) of each species within the population. It is determined by calculating the probability that two randomly selected individuals in the community belong to the same species. The higher the value is (ranging between 0 and 1), the less diversified the community is. This relatively counterintuitive index has led to the classic Simpson's index (D). It characterises the probability that two randomly selected individuals belong to two different species. The higher the value is, the more diversified the community is.

3.3.2.2 Shannon's index

Shannon's index (H) is based on the same principle as Simpson's index, but uses a different algorithm. The relative proportion of a species is not squared but multiplied by its own logarithm. Unlike Simpson's indexes, Shannon's index is less sensitive to the variation of the abundance of the rarest (Colwell, 1988).

3.3.2.3 Piélou evenness index

Piélou evenness index (J) (1975) characterises the distribution of specimens among the different species, independently of the species richness (Help, Herman, & Soetaert, 1998). The J value ranges between 0 and 1. The closer the index is to 1, the less difference there is between species' relative abundances.

3.3.3 Beta (β) diversity and associated indices

Despite the plurality of the beta diversity concept and the lack of overall consensus about which approach is the most appropriate for addressing particular ecological questions (Anderson et al., 2011), we will define beta diversity as a measure of the similarity (in the species composition) between sites. This is used as a global indicator to characterise the level of differentiation between sites by comparing them pairwise (Baselga, 2010). For a given regional species richness, if beta diversity increases, the species structure of each community compared differs more from the others and covers a lower species proportion of the region (Villebrun, 2016).

The beta diversity index underlines two distinct processes: the species turnover (or spatial replacement) and nestedness (or species loss). The species nestedness appears when the sites with lower species richness are subgroups of the sites with a higher number of different species. The species turnover can be described as a simultaneous gain and loss of species due to environmental filtering, competition and historical events along spatial or environmental gradients (Legendre, 2014).

For this study, the Sørensen's index was used (Dice, 1945; Sørensen, 1948) to compute the beta diversity between sites, habitats and management types. The closer the index is to 0, the less difference there is between species' composition. However, this index does not distinguish the turnover form the nestedness.

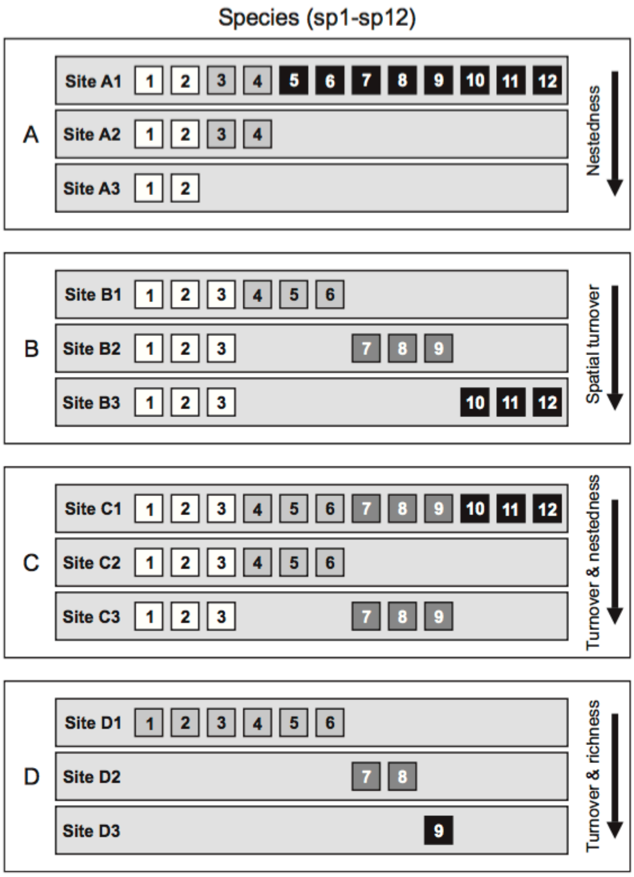


Figure 9 : Graphical illustration of turnover and nestedness involving four island communities (A–D) and three sites in each island (Baselga, 2010)

In order to differentiate the two components, Sørensen's index ($\beta_{s\O r}$) can be decomposed as follows :

$$\beta_{s\O r} = \beta_{repl} + \beta_{rich} = \beta_{turnover} + \beta_{nestedness}$$

Beta diversity analyses were carried out using the 'BAT' (Cardoso et. al, 2017) and 'betapart' (Baselga et al., 2018) packages, using the 'beta.multi' function and specifying Sørensen similarity index. The diversity partitioning (turnover and nestedness) results were graphically depicted for parks, islands, manicured and wild sites. Numeric results are reported in the legend.

3.3.4 Species diversity between habitats and management types

Species diversity was compared between habitat types (parks and islands) and management types (wild and manicured) by assessing species richness, specimen abundance, alpha diversity indexes (Simpson, Shannon and Piélou's indexes) and beta diversity index.

To assess if there are significant differences in species counts per habitat and management types, we checked the homogeneity of variances (thanks to the Levene's test) and the normality (thanks to the Shapiro-Wilk's test for multivariate normality). When both

Levene and Shapiro-Wilk's p values were above 0.05, a One-way ANOVA was performed. If at least one of the homogeneity or normality tests p values was below 0.05 (indicating a non-homogeneity of the variances or a non-normality), the Mann-Withney test was performed.

The One-way ANOVA, Levene, Shapiro-Wilk and Mann-Withney's tests were carried out using the 'stats' (R Core Team, 2018), 'car' (Fox et al., 2018) and 'mvnormtest' (Jarek, 2012) packages.

3.3.5 Spatial auto-correlation between sites

Since some sites were quite close one another (like Pulau Ubin, Coney Island and Pasir Ris), the reduced distance between sites could hypothetically influence bee communities. It is thus important to address the following question: are neighbouring sites more likely to harbour more similar communities of wild bees? The spatial auto-correlation was tested between sites using a matrix of Euclidean distance between the communities of sites and a matrix of geographical distance between sites (based on the sites coordinates). A Mantel test was then realised to test the correlation between both matrices in order to determine if the geographical distance between sites influence the communities' specific diversity. The Mantel test carried out using the 'ade4' package (Dray et al., 2018).

3.4 FLOWER-BEE VISITATION NETWORKS

Floral visitation data for bees were used to construct visitation networks for each site. Those networks are bipartite webs with two trophic levels, the higher level representing the flowers, and the lower one representing the bee species. Each bee species is linked to the flower they have visited, proportionately to the number of interactions observed. The 'bipartite' package (Dormann et al., 2017) was used to generate the visitation networks and compute the following informative and quantitative metrics (Ballantyne et al., 2015): **network specialisation (H2')**, **connectance**, **nestdeness**, **interaction evenness** and **generality/vulnerability**.

The **network specialisation** is an index describing the level of selectiveness of the visitation network. The more selective a species, the larger is H2' for the web analysed (Dormann et al., 2017). It ranges from 0 (extreme generalisation) to 1 (perfect specialisation). The **connectance** is a qualitative index representing the interactions actually observed within a network, among all the possible ones (Dunne et al., 2002). It ranges from 0 (low connectance) to 1 (high connectance). The **nestedness** measures the structure and temperature of the matrix. It ranges between 0 for a perfectly nested matrix and 100 for a "chaotic" unnested matrix (Rodriguez-Girones & Santamaria, 2006). Nestedness increases with the complexity of the network: for a given number of species, communities with more interactions are generally more nested (Bascompte et al., 2003). The **interaction evenness**, based on Shannon's diversity, characterizes the homogeneity in the interaction frequencies (Allesina & Tang, 2012). A network in which each bee species has equal and uniform interactions with host flowers has high evenness; where a network with unequal and heterogeneous interactions has low evenness (Smith & Wilson, 1996). Interaction evenness ranges from 0 (unequal distribution) to 1 (uniform distribution). In a bipartite network with two trophic levels, where the higher level is represented by the flowers species (F) and the lower one represented by the bee species (B), the mean number of flowers species (links or L) per bee species is termed **generality** ($G = L / B$) and the mean links per flower species **vulnerability** ($V = L / F$) (Blüthgen et al., 2008). Schoener (1989) suggests that web vulnerability does not vary with food-web size. For a constant number of links per web species, and a constant fraction of flowers species, the web vulnerability must be constant.

The standardized specialization index of bees and plants (d'), deriving from Shannon's entropy index, describes the degree of interaction specialization at the species level. This index can be seen as a comparison between the interaction frequencies actually observed and the theoretical use of all partners in proportion to their availability. This index, that can be used to analyse the variation within networks, ranges from 0 (for the most generalized communities) to 1 (for the most specialized communities) (Blüthgen et al., 2006). The standardized specialization index (d') was computed thanks to the dfun function of the 'bipartite' package.

Finally, we will discuss the species interspecific interactions thanks to the potential for apparent competition index (PAC). Holt (1977) defines two species in apparent competition whenever the presence of either species leads to a reduced population density for the other species at equilibrium. Two species could be subject to apparent competition because of direct competition, a shared a predator, or being linked through the food web by some other indirect causal chain. The potential for one species to influence indirectly another species from the same trophic level via shared interaction partners will depend on the presence and the strength of each interaction link. In plant-pollinator networks, the potential for an influence between plant species may lead to facilitation (when the presence of one plant species increases the visitation of effective pollinators for other plant species) or competition (when the presence of one plant species attracts effective pollinators away from other plan species) (Carvalheiro et al., 2014). Carvalheiro and colleagues showed that floral resource abundance, accessibility and phylogenetic distance are many factors that may influence the potential for apparent competition and should be taken into account when analysing plant-pollinator networks. The PAC index was computed for both bees and flowers thanks to the PAC function of the 'bipartite' package. This function quantifies, for each pair of lower trophic level species, the potential for showing apparent competition with another species, mediated through the higher trophic level. The PAC imposed by bee species on other bee species and experienced by bees from other bee species was then computed thanks to the colSums et rowSums functions and graphically depicted thanks to the barplot function.

3.5 SPATIAL ANALYSIS: SITES OBSERVATIONS AND CHARACTERISATION

3.5.1 Local factors

At the local scale, wild bees' communities are influenced by the size and quality of their habitat. The number and quality of nesting sites, the abundance and quality of floral patches and the degree of human disturbance are valuable indicators to assess habitat quality. In this study, three variables were taken into account: the site size (ha), green cover (%) and degree of urbanization (%) within the sites. Aside from these quantitative variables, a series of on-site qualitative observations were made. Criteria such as observed management practices, sites purpose (recreational, conservation, aesthetics, …) and non-quantifiable features (personal observations and remarks) were useful to highlight and interpret the quantitative data gathered at the local scale.

3.5.2 Landscape factors

At a larger scale, wild bees' communities are influenced by the composition and configuration of the landscape. Numerous landscape variables (or indices) can be analysed depending on the studied topic (Uuemaa et al., 2009). In this study, the landscape composition was characterised by the number of different habitats and land-use classes. The landscape configuration, describing the spatial arrangement of habitats, was characterised by the density of green and urbanised patches in the landscape. Those variables are commonly used in wild bees' studies focusing on the landscape effects and influences (Banaszak-Cibicka & Zmihorski, 2012; Burkman & Gardiner, 2014; Fortel et al., 2014; Hopfenmüller et al., 2014).

Type of variable	Variabe
Local factor	Site size (ha)
	Management type
	Green cover (%)
	Urbanized (%)
Landscape factor	Site size (ha)
	Parks (%)
	Reserves (%)
	Mixed vegetation (%)
	Residential (%)
	Water (%)
	Urbanized (%)
	Green patches density (/km2)
	Urbanized patches density (/km2)

Table 2: Summary of the variables used in both aggregations.

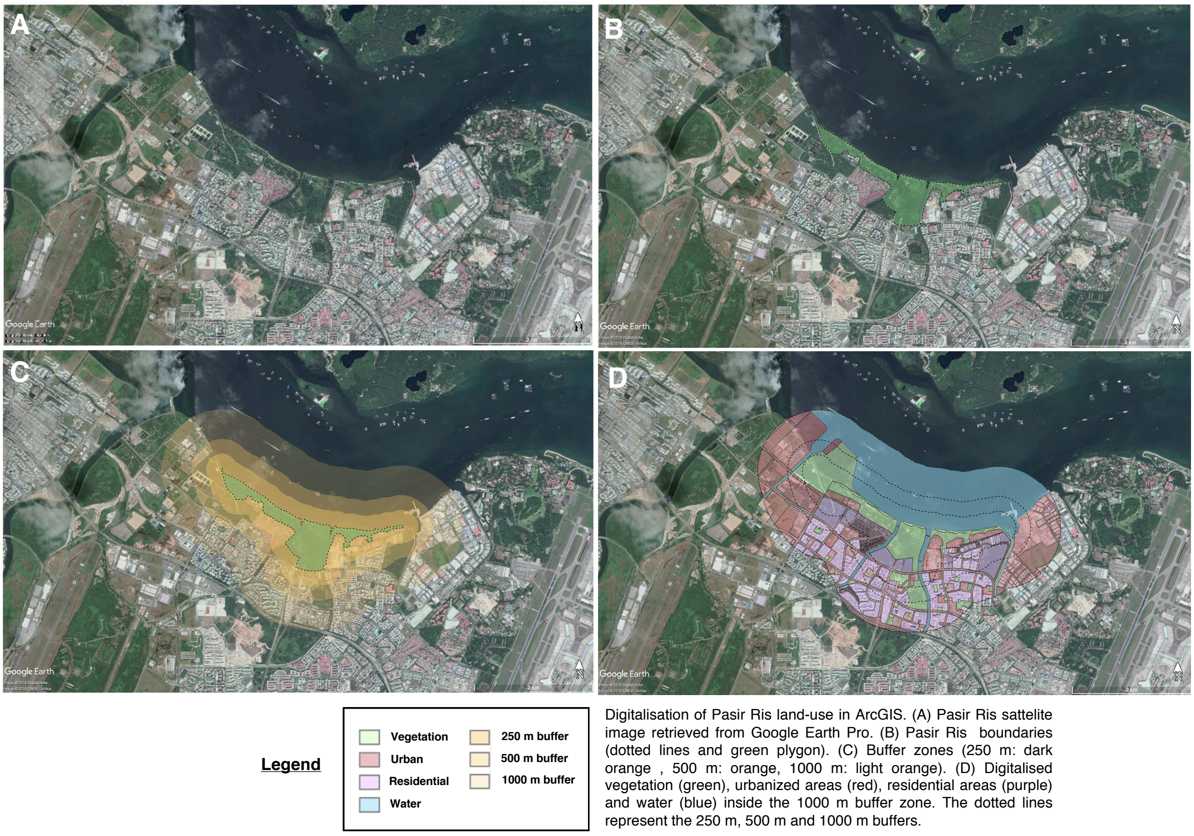
3.5.3 Land-use digitalisation and map making

The local and landscape variables were analysed thanks to ArcGIS® version 1.4 (Esri, 2015), a geographic information system (GIS) software. From the official *Master Plan 2014 Land Use* file (Urban Redevelopment Authority, 2017), land-use classes were clustered in eight sub-groups: parks, reserves, mixed vegetation, water, business, residential, transportation and other. From these sub-groups, a first aggregation was created to assess the influence of theoretical nesting and foraging habitats. This aggregation includes parks, reserves, mixed vegetation, residential areas and green patches density. The second aggregation was created to assess the influence of sites size and impermeable surfaces. This aggregation includes sites size, water bodies, urbanized areas and urbanized patches density.

Each landscape variable was analysed along three buffer zones: 250m, 500m and 1000m around the sites limits. It is important to note that each buffer zone analysed covers the site area as well. A multi-scale spatial analysis is necessary because of the mobile nature of wild bees. Their flying distance and foraging range can vary from a few hundred meters to several kilometres depending on the species considered and its traits (e.g. body size and intertegular distance) (Roubik, 1989; Gathmann & Tscharntke, 2002; Cariveau et al., 2016).

Firstly, satellite images were retrieved from Google Earth Pro® and spatially referenced, constituting the base layer. Sites limits were manually edited in order to generate polygons as close as possible to reality. Form each polygonised site, three buffers were generated and intersected with the Singapore's *Master Plan 2014 Land Use* file. In total, eighteen land-use layers (three per site) were generated and analysed in order to determine the relative proportion of each land-use class and the density of green and urbanized patches.

Stages of land-use digitalisation in ArcGIS



Digitalisation of Pasir Ris land-use in ArcGIS. (A) Pasir Ris sattelite image retrieved from Google Earth Pro. (B) Pasir Ris boundaries (dotted lines and green plygon). (C) Buffer zones (250 m: dark orange , 500 m: orange, 1000 m: light orange). (D) Digitalised vegetation (green), urbanized areas (red), residential areas (purple) and water (blue) inside the 1000 m buffer zone. The dotted lines represent the 250 m, 500 m and 1000 m buffers.

Figure 10: Stages of land-use digitalisation in ArcGIS : Pasir Ris.

3.5.4 Local and landscape factors' statistics

The effects of local and landscape factors on the diversity of wild bees' communities were tested with a series of simple linear regressions. Due to the limited number of sites, General Linear Models (GLM) could not be used. For each site, and each spatial scale, the correlation between landscape variables and response variables (observed species richness, Jackknife1, Shannon's index and Piélou's index) was tested.

4 RESULTS

4.1 SAMPLING EFFORT: ACCUMULATION CURVES

As a reminder, sites, habitats and management types were compared using data collected over the last eight years (2010 – 2018 period). During this period, 1789 specimens belonging to 94 species were captured. The accumulation curves shown below then represent the whole database (Figure 11 and Figure 12).

The species accumulation curves for the whole database, parks, manicured sites and wild sites seem to reach a plateau, suggesting a quite exhaustive sampling effort. The islands' species accumulation curve, however, is quite difficult to assess. A species accumulation curve reaching a plateau means that a new sampling unit wouldn't be more representative of the population. In order words, additional sampling sessions would not be useful to discover new species. As a visual evaluation often results in approximations, the species richness was extrapolated thanks to the Chao, Jackknife1, Jackknife2 and Bootstrap estimators. Those are helpful to compare the observed species richness with the extrapolated one.

Results suggest that we have captured between 79% and 91% of the total number of bee species potentially present in our study sites. Parks, islands and manicured sites show an extrapolated species richness comprised between 72% and 90% whereas wild sites seem to have the most potential for progress with an estimated richness comprised between 68% and 88%. Data relating to the comparison between the observed and extrapolated species richness can be found in appendixes (Appendix 7).

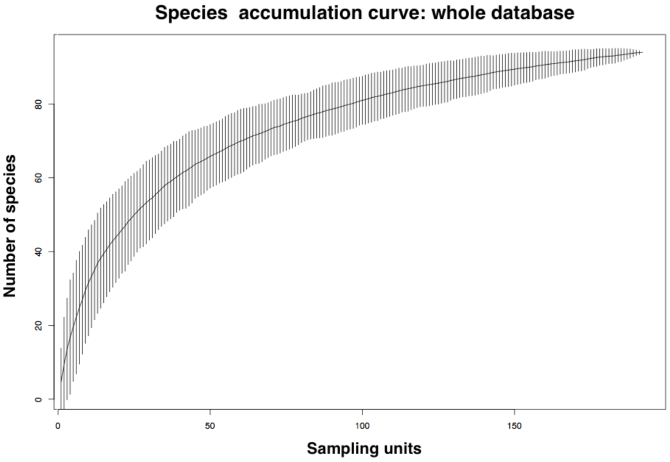


Figure 11: Species accumulation curve for the whole database. One sampling unit equals one sampling session at a given sampling date in a given sampling site.

Observed and extrapolated species richness were evaluated for the whole dataset, each habitat and each management type thanks to the Chao, Jackknife1, Jackknife2 and Bootstrap non-parametric estimators (Appendix 7Appendix 8).

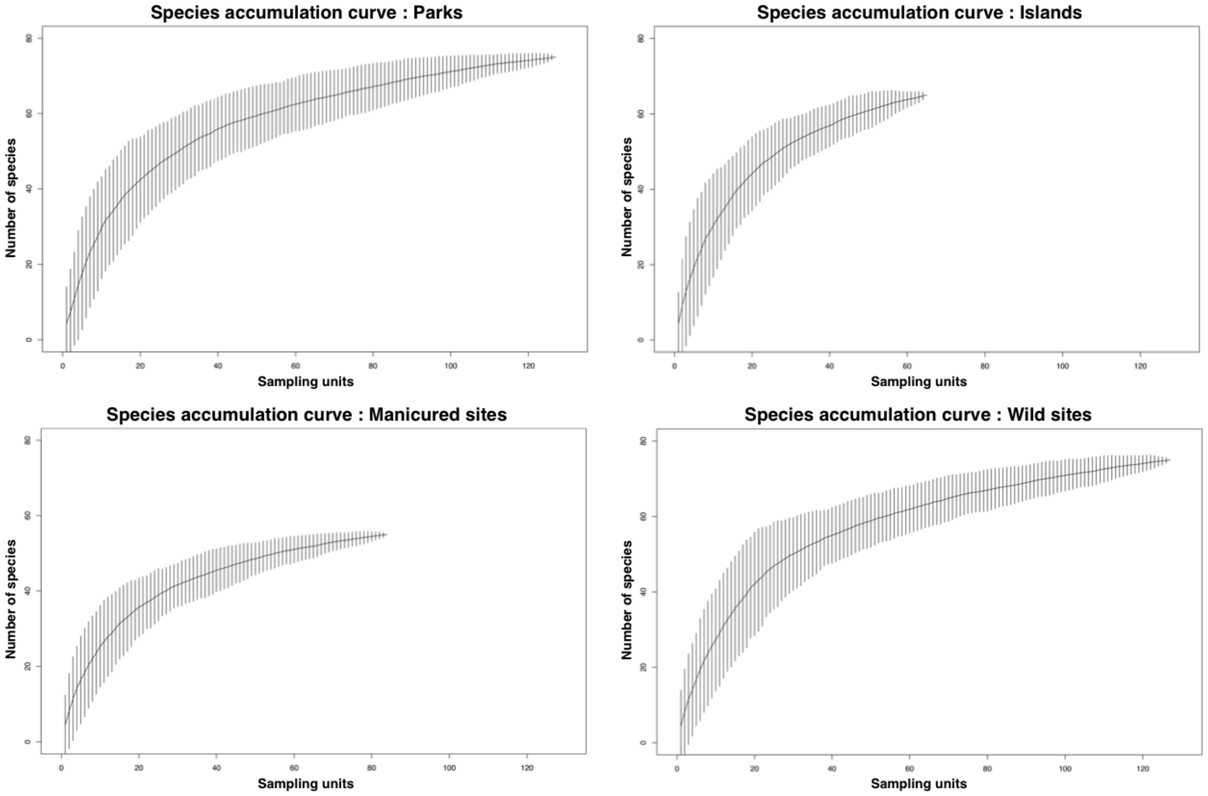


Figure 12: Species accumulation curves for each habitat and management type. One sampling unit equals one sampling session at a given sampling date in a given sampling site.

4.2 SPECIES DIVERSITY

4.2.1 Species richness and specimen abundance

As shown by the Figure 13, the Apidae family is the most represented one in terms of specimens and species collected. Among Apidae, two species are highly abundant (over 50 specimens): *Tetragonula laeviceps* (a highly eusocial species) and *Ceratina collusor*. The Halictidae and Megachilidae families are quite equally represented in terms of specimens and species collected. The Colletidae, representing the fourth and last bee family found in Singapore, are relatively scarse. Only 5 species and a few specimens were recorded in our study.

Figure 14 shows the number of specimens collected per study site. As it may be observed, great disparities exist between the number of specimens collected in our study sites. Two factors may explain this observation: the site-specific specimen abundance and the number of sampling sessions conducted. The site-specific specimen abundance is subject to variation due to many factors, such as habitat quality and site surface. In this study, the second factor must be highlighted. Sites like Dairy Farm and Pulau Ubin are heavily sampled because of their well-preserved natural state and singular characteristics. Conversely, sites like Coney Island and St John’s Island are either recently open to researchers and citizens or not easily accessible due to their location and travelling costs (mostly islands). This factor must be weighted and taken into account when analysing specimen abundance across sites.

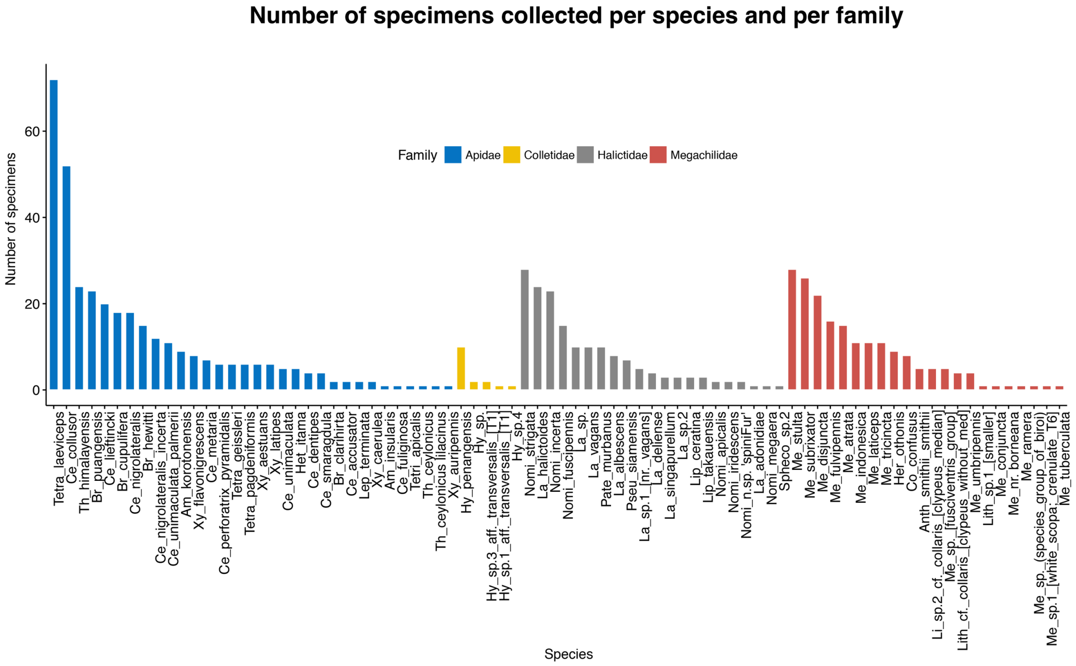


Figure 13: Number of specimens collected per species (ordered by family).

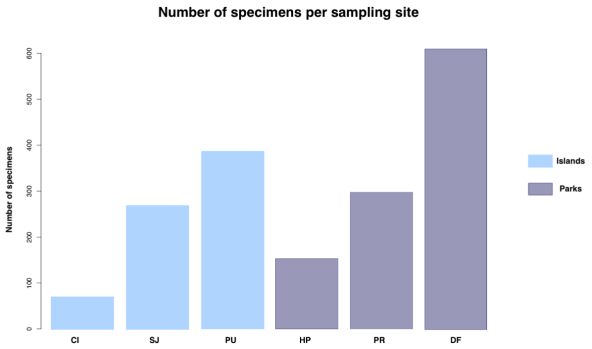


Figure 14: Number of specimens collected in each sampling site.

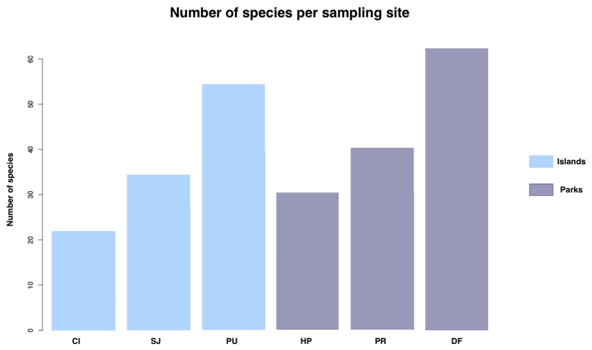


Figure 15: Number of species per sampling site.

Site	Species richness
CI	30.99
SJ	31.07
PU	42.56
HP	30.55
PR	38.68
DF	45.52

Table 3: Number of species per site when we rarefy the community to 100 specimens per site.

Figure 15 shows the number of identified bee species per site. As we can see, the same disparities exist between the number of specimens collected and the number of species identified in our study sites. The specimen abundance and sampling intensity may cause a severe imbalance between sites in terms of observed species richness. To overcome these disparities, species richness can be simulated among a rarefied community composed of 100 theoretical specimens.

The results of rarefaction (shown in Table 3) smooth Coney Island (CI), Hort Park (HP) and SJ (St John's Island) data. They all show a new specific richness around 30 species, representing a significant gain of species in Coney Island (the least well sampled island). Dairy Farm (DF), Pulau Ubin (PU) and Pasir Ris (PR) stay the richest sites in terms of specific species richness. These results suggest that the species richness in our least well sampled sites could increase, even if the species accumulation curves analysed above suggest that the sampling effort was quite exhaustive.

The heatmap shown in Figure 16 gives a visual representation of the species abundance and repartition between sites. By a quick visual overview, we can notice that some species are highly dominant in the sites surveyed (e.g. *Ceratina collusor* in Dairy Farm, *Ceratina lieftincki* in Pulau Ubin or *Tetragonula laeviceps* in St John's Island).

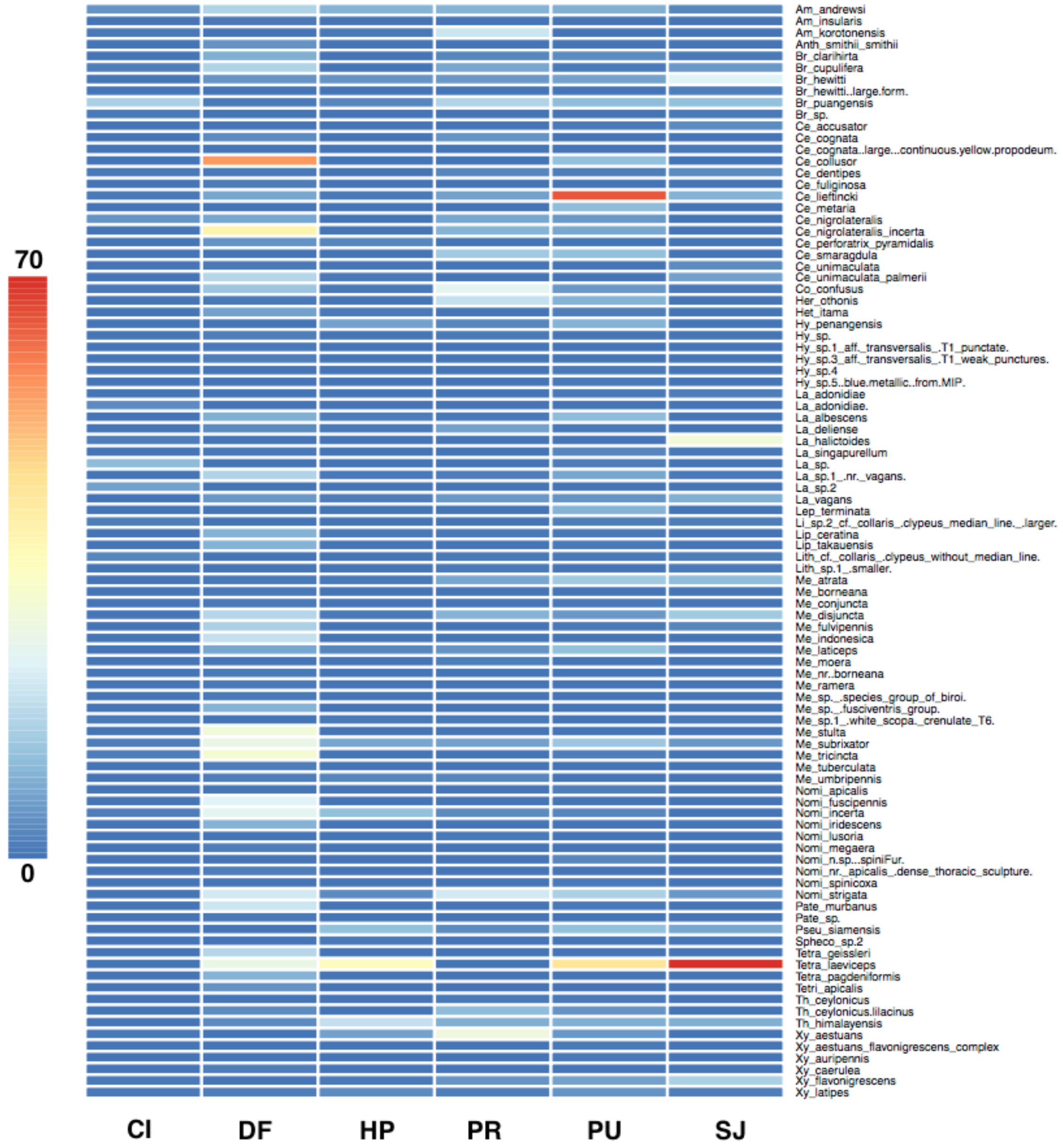


Figure 16: Heatmap giving the species density in each site.

The Figure 17 is another way to visualize the abundance of each species in our dataset. As we can see, the abundance of species present in islands and manicured sites are not equally distributed. A few species represent the majority of the specimens collected. Species abundance in parks and wild sites seem to be more equally distributed, with several abundant, moderately and poorly represented species.

The Venn diagrams (Figure 18) allows us to compare the species composition between habitats and management types. It can be observed that islands and parks respectively have 19 and 29 proper species (in a total pool of 94 species). In the same pool of species, manicured sites only have 6 proper species whereas wild ones have 39 unshared species.

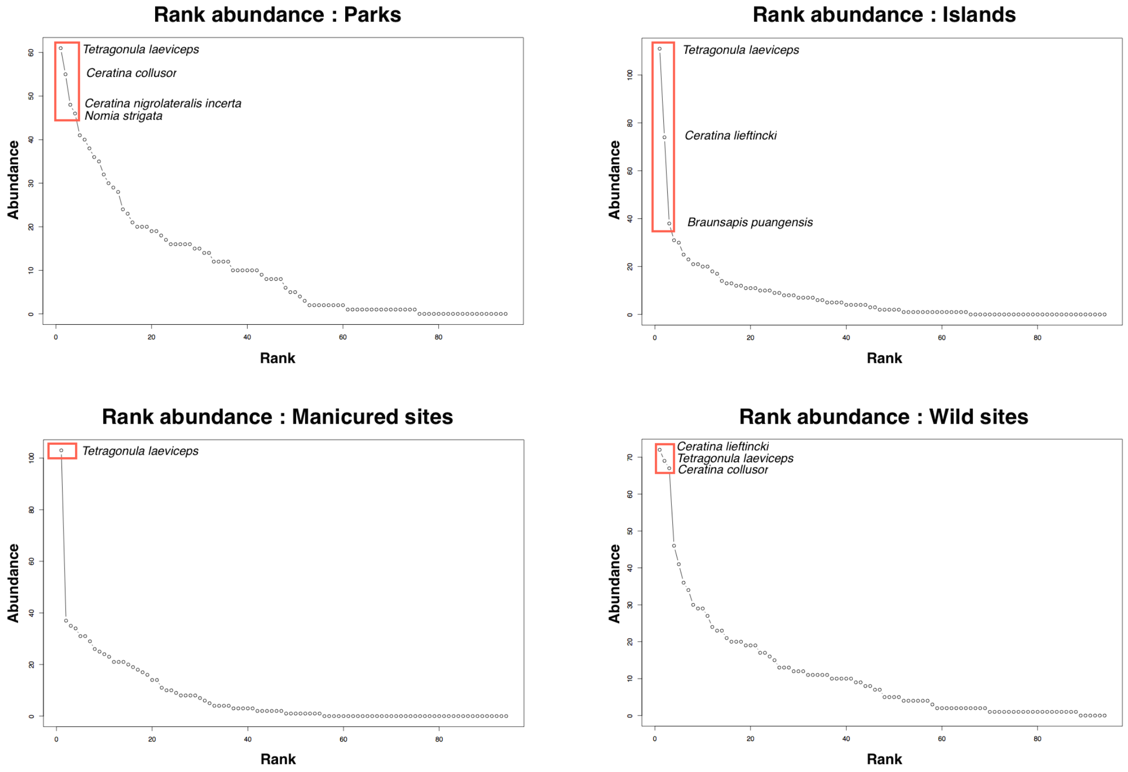


Figure 17: Species abundance rank, in descending order, for each habitat and management type.

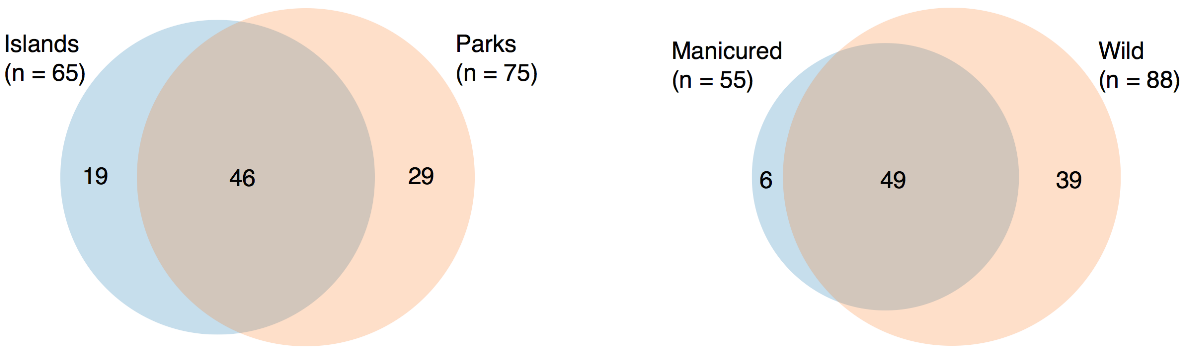


Figure 18: Venn diagrams showing the number of shared and unshared species between habitats and management types.

The Figure 19 compare the species richness between habitats and management types. In this case, there does not appear to be a clear effect of habitat or management type on species richness. Further statistical analyses confirm this assumption.

When comparing habitats together, the homogeneity of variances (Levene's test) and data normality (Shapiro-Wilk's test) need to be tested in a first place. As they were not statistically significant, a One-way ANOVA (parametric test) was used and showed that the differences in species composition between habitats were not statistically significant (*p-value* = 0.61). When comparing management types together, the Shapiro-Wilk's test showed a *p-value* of 0.02. Since one of the two preliminary tests was statically significant, we have used a non-parametric approach: the Kruskal-Wallis's test. With a Kruskal-Wallis *p-value* of 0.51, we can say that the differences in species composition between management types are not statistically significant. Species richness values among habitats and management types can be found in Appendix 7.

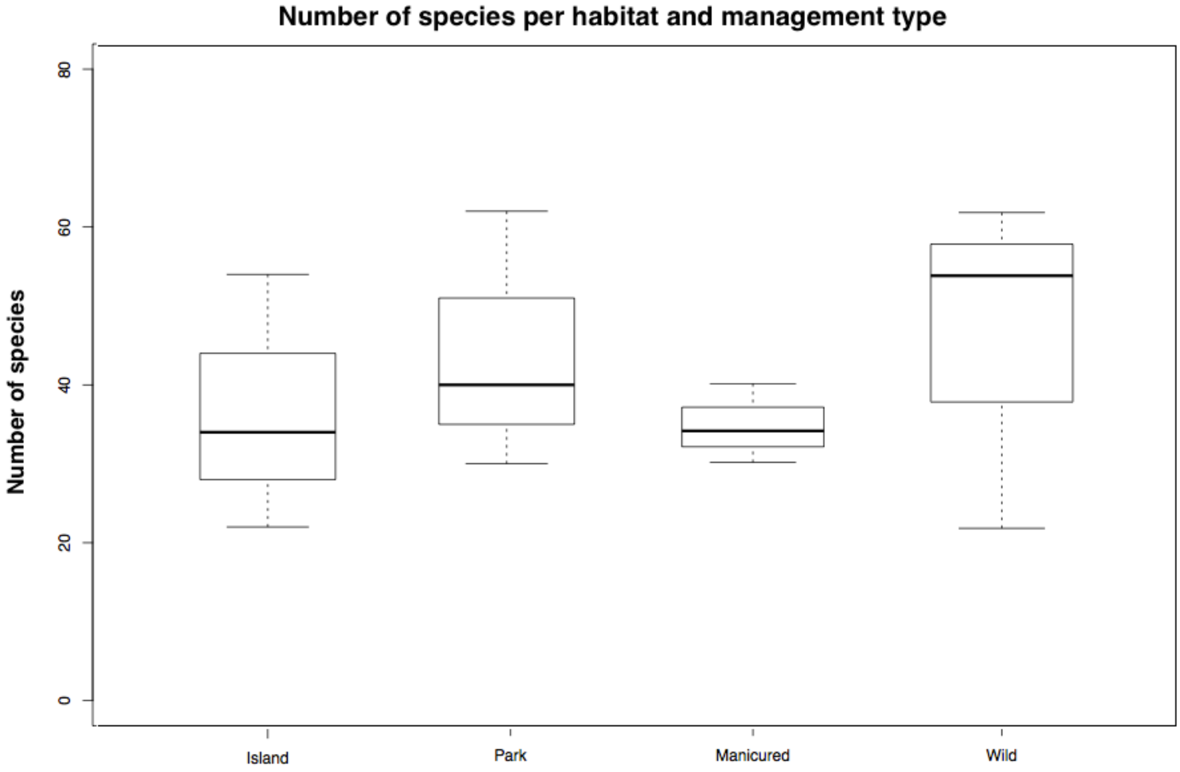


Figure 19: Number of species per habitat and management type.

4.2.2 Alpha diversity

The Table 4 summarises the indices used in this study to characterise alpha diversity across sites, habitats and management types. Simpson's classic index (D) (Figure 20), Shannon's diversity index (H) (Figure 21) and Piélou's evenness index (J) (Figure 20) values will be useful to assess communities' diversity and species evenness.

Among sites, Dairy Farm has the highest couple of Simpson – Shannon's values whereas Coney Island has the lowest one. This result indicate that Dairy Farm's community might be more diversified than Coney Island's. Piélou's evenness index is at its highest in Hort Park and at its lowest in Coney Island, suggesting that there is less differences between species' relative abundances in Hort Park than Coney Island.

Among habitats, parks have the highest of Simpson – Shannon and Piélou's values, indicating that parks' communities might be more diversified and evenly distributed than islands' ones. However, the One-Way ANOVA performed on these data does not show any statistically significant difference (Table 5).

Among management types, wild sites have the highest of Simpson – Shannon and Piélou's values, indicating that wild sites' communities might be more diversified and evenly distributed than manicured' ones. However, the One-Way ANOVA performed on these data does not show any statistically significant difference (Table 5).

		Simpson (D)	Shannon (H)	Piélou (J)
Habitat	**Parks**	0.97	3.86	0.89
	Islands	0.95	3.52	0.84
Management	**Wild**	0.97	3.91	0.87
	Manicured	0.95	3.46	0.86
Site	**CI**	0.9	2.66	0.86
	SJ	0.9	2.84	0.96
	PU	0.94	3.39	0.91
	HP	0.9	2.77	0.99
	PR	0.95	3.31	0.72
	DF	0.97	3.63	0.88

Table 4: Summary of alpha diversity indices per site, habitat and management type. Highlighted values represent the highest results per index inside each category.

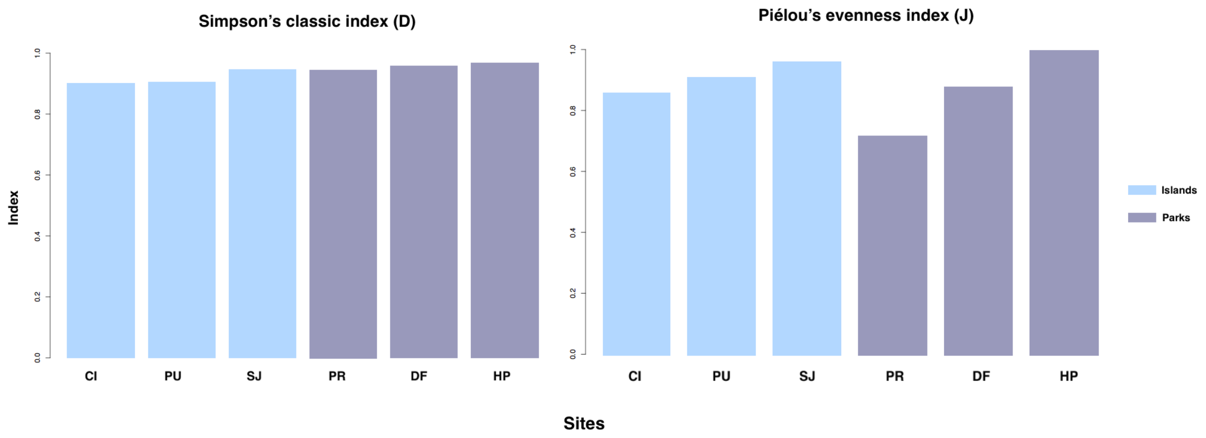


Figure 20: Simpson and Piélou's indices for each site.

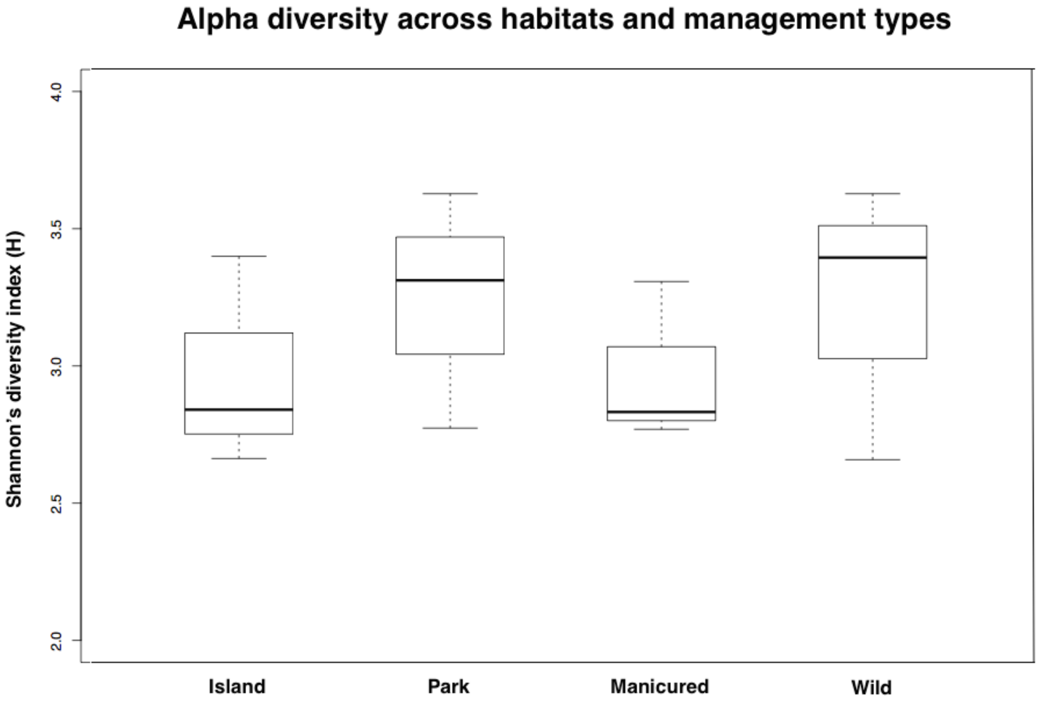


Figure 21: Alpha diversity across habitats and management types characterized by the Shannon's diversity index.

	Index	Statistic test	*p-value*
Habitat	**Species richness**	Levene	0.9866
		Shapiro	0.9683
		ANOVA	0.61
	Simpson	levene	0.78924
		Shapiro	0.31969
		ANOVA	0.3506
	Shannon	levene	0.8712
		Shapiro	0.7143
		ANOVA	0.4571
	Piélou	levene	0.31328
		Shapiro	0.84556
		ANOVA	0.6284

	Index	Statistic test	*p-value*
Management	**Species richness**	Levene	0.3641
		Shapiro	0.0166
		ANOVA	0.4179
	Simpson	levene	0.8665
		Shapiro	0.60742
		ANOVA	0.5357
	Shannon	levene	0.61508
		Shapiro	0.4432
		ANOVA	0.4956
	Piélou	levene	0.37331
		Shapiro	0.73936
		ANOVA	0.9064

Table 5: Results of the Levene's test, Shapiro-Wilk's test and One-way ANOVA on habitats and management types' alpha diversity indices.

4.2.3 Beta diversity

The Table 6 sums up the beta diversity values for habitats, management types and sites. The total beta diversity (beta.SOR) is decomposed into its species turnover (beta.SIM) and nestedness (beta.SNE) components (as a reminder, see the formula below). Results show that the total beta diversity is slightly higher among sites than habitats. The Soerensen index's partitioning allows is to notice that the

	β diversity		
	beta.SIM	**beta.SNE**	**beta.SOR**
Habitat	0.49315068	0.164	0.65661253
Management	0.49315068	0.164	0.65661253
Sites	0.501	0.163	0.66431925

Table 6: Differentiation of beta diversity index among habitats, management types and sites.

differentiation degree among habitats, management types and sites is mainly attributable to species turnover (beta.SIM). Across habitats and management types, 49.3% of species are replaced against 16.4% of species nested. Across sites, 50.1% of species are replaced against 16.3% of species nested. These results allow us to make a first preliminary assumption: our surveyed sites seem to have distinctive bee communities with specific bee assemblages. The processes and factors behind this phenomenon (e.g. gain or loss of species, environmental filters or competition) still need to be investigated.

$$\beta_{sØr} = \beta_{repl} + \beta_{rich} = \beta_{turnover} + \beta_{nestedness}$$

Sørensen's index ($\beta_{sØr}$) decomposition

4.3 HIERARCHICAL CLUSTERING AND *K-MEANS* ON CLUSTERING DATA

The dendrogram depicted in Figure 22 is useful to group the surveyed sites according to their communities' species composition. This method seems to sort surveyed sites in four groups: (1) Coney Island, (2) Dairy Farm, (3) Pasir Ris and Pulau Ubin, (4) Hort Park and St John's Island. To confirm this assumption, we will use the *k-means* method (Figure 23). Groups are formed by identifying high-density regions in the data. The best sites partition should match the highest "SSI" (simple structure index) criterion (Borcard et al., 2011). As we can see, the *K-means* cascade plot classify our sites the same way as the dendrogram does.

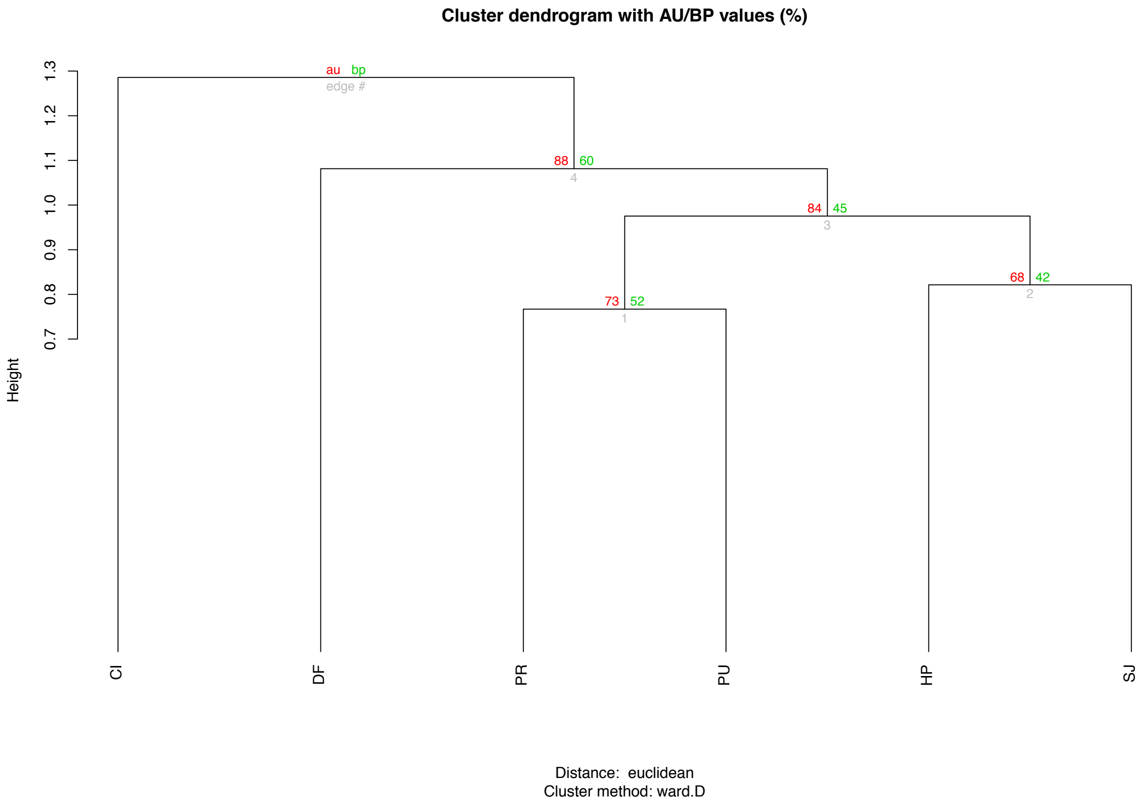


Figure 22: Hierarchical clustering of sites based on bootstrapping of a Hellinger distance matrix of bee species abundances. The dendrogram is clustered using the Ward's (minimum variance) method and based on Euclidean distances. AU (approximately unbiased) and BP (bootstrap probability) values (%) are highlighted in red and green respectively.

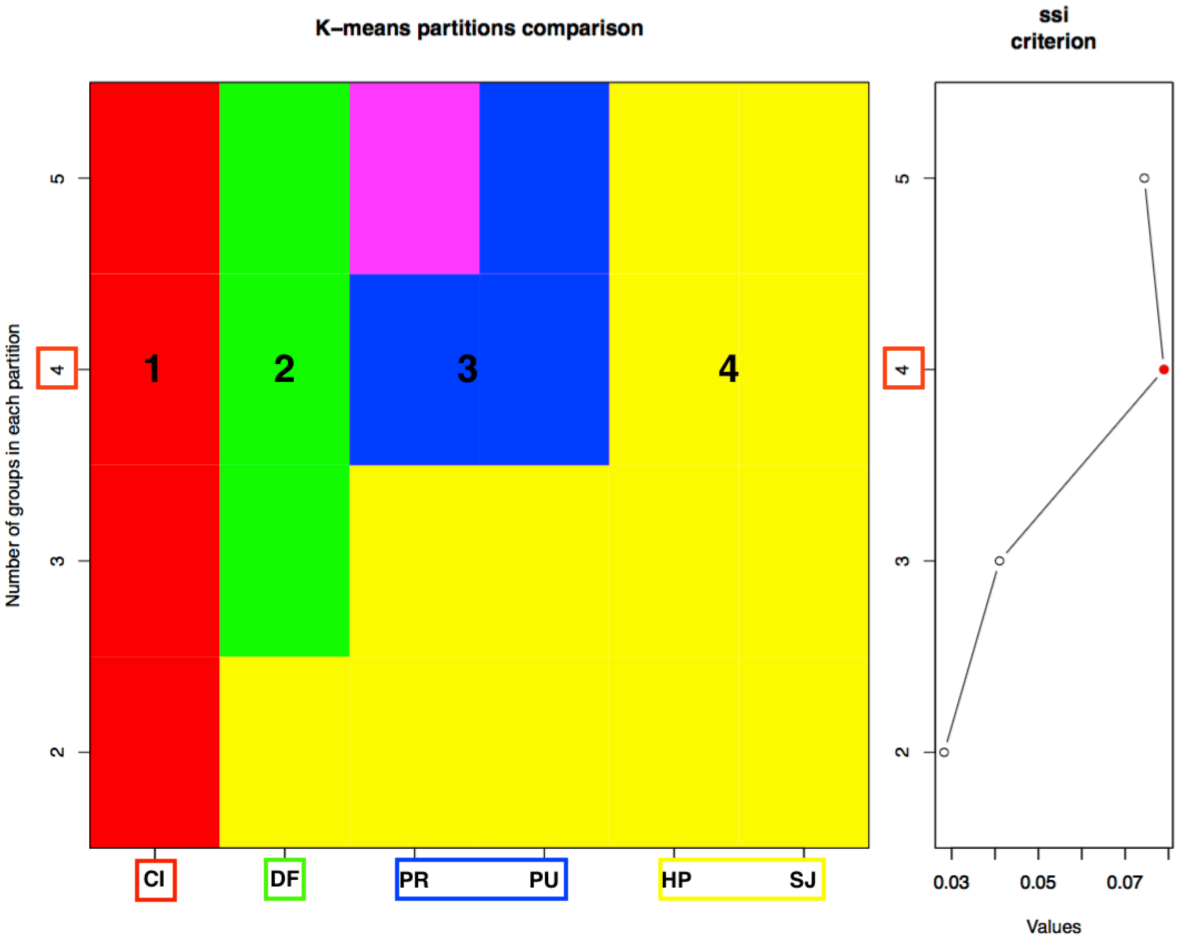


Figure 23: K-means cascade plot showing the group attributed to each site for each partition.

4.4 MANTEL TEST

The mantel test (Figure 24) is useful to investigate if neighbouring sites are more likely to harbour more similar communities of wild bees. With a simulated *p-value* of 0.63, we can't conclude that the distance between sites constitutes a factor explaining bee communities.

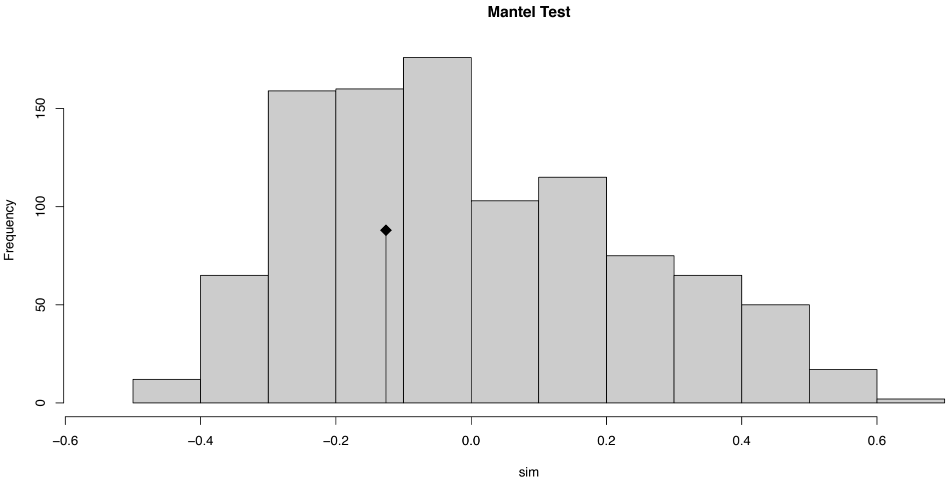


Figure 24: Graphical representation of the Mantel test assessing if neighbouring sites are more likely to harbour more similar communities of wild bees.

4.5 PLANT-POLLINATOR NETWORKS

4.5.1 Global network

In total, across our six surveyed sites, 748 interactions were observed between flowers and wild bee species. Because of the high number of species in the network (76 flower and 81 bee species), the interactions actually observed among all the possible ones (connectance index) are quite low (C = 0.049). In this global network, a mean number of 6.56 links per species is observed (linkage density index). On average, each bee species is linked to 7.14 flower species (generality index) whereas each flower species is linked to 5,98 bee species (vulnerability index). When analysing the presence / absence matrix (Figure 25), the network's nestedness is relatively high (η = 3.33). However, if we consider the interaction frequencies (weighted nestedness index), communities are moderately nested (η_w = 0.47). When it comes to the network's evenness, the global network shows a moderately heterogeneous distribution with a value of 0.61.

The five bee species with the highest number of bee-flower interactions are (in descending order) : *Tetragonula laeviceps*, *Ceratina collusor*, *Amegilla andrewsi*, *Megachile stulta* and *Nomia strigata*. They represent 27.94% of the observed interactions within our global network. These five species are also among the ten most competitive ones, with values of potential apparent competition (PAC) up to 2 (Appendix 10). As mentioned earlier, this study excludes honey bees (*Apis* genus) as some sites had an overabundance of them. However, despite the uncertainty of their role in pollination, cleptoparasitic species such as *Thyreus himalayensis* were not excluded from the plant-pollinator networks. By a quick visual analysis of the cumulative distributions graph (Figure 26), we can estimate that 50% of bees species are linked to three flowers at most whereas 5% are linked to twelve flower species at most. It is important to note that the most specialized bee species are not among the species experiencing the strongest competition (Appendix 11).

The five most visited flowers are (in descending order): *Melastoma malabathricum*, *Cratoxylum cochinchinense*, *Bidens pilosa*, *Asystasia gangetica ssp. micrantha* and *Asystasia gangetica*. Together, they represent 33,69% of the observed interactions within our global network. As is the case for bee species, these five flowers are also among the ten most competitive ones, with values of potential apparent competition (PAC) up to 3 (apart from *Cratoxylum cochinchinense* with a PAC value slightly below 3) (Appendix 12). The cumulative distribution distributions graph (Figure 26) indicates that 50% of flower species are visited by two bee species at most whereas 10% are visited by twelve bee species at most. Like bee species, it is important to note that the most specialized flower species are not among the species experiencing the strongest competition (Appendix 13).

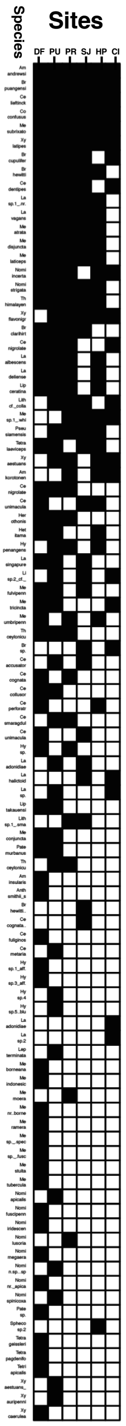


Figure 25: Presence / absence visitation web for all sites.

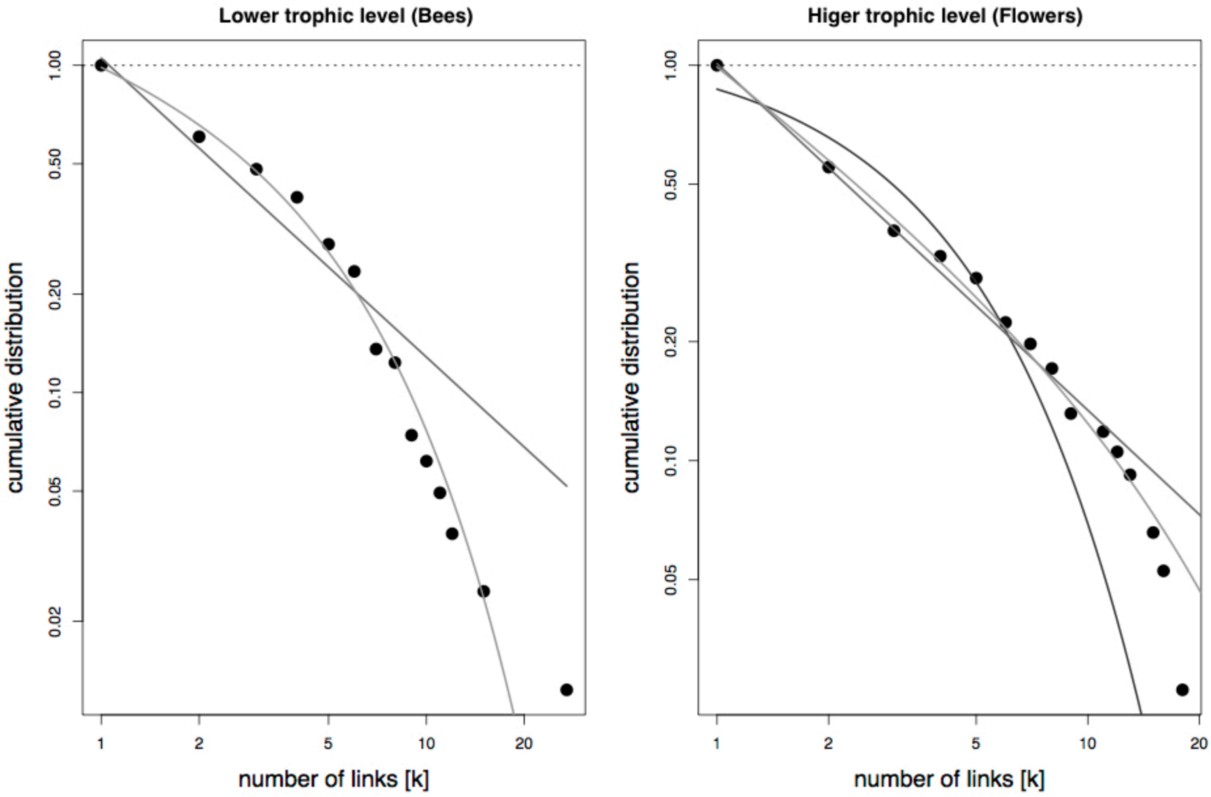


Figure 26: Graphical representation of the cumulative degree distributions of both trophic levels. This graph is generated thanks to the 'degreedistr' function of the 'bipartite' package in R (Dormann et al., 2017) : "The function first calculates degrees for each species, then constructs a cumulative distribution with them, and finally fits three different functions to these distributions: exponential, power law and truncated power law".

4.5.2 Habitats and management types networks

After examining the global flower-bee visitation network and its associated indices, we will focus on habitats and management types networks. Parks, islands, wild sites and manicured sites networks can be found in Appendix 14Appendix 17Appendix 20 andAppendix 23 along with their associated indices.

Let's first compare habitats together. As shown in Figure 27, island networks seem to be more specialised, connected and nested than park networks. With a network specialisation index (H2') of 0.53, island networks stay averagely specialised despite being slightly above parks' H2' (0.49). Among all possible interactions in both habitats, islands are the most connected ones with a connectance value of 0.07. Park networks seem to be more nested than island ones (the closer the value to 0, the more nested the network). Both habitats have moderately uniform interactions with evenness values of 0.60 and 0.59. While flower species are visited by an average of 4 bee species in both habitats, bee species visit more flower species in parks (6.29) than islands (4.97).

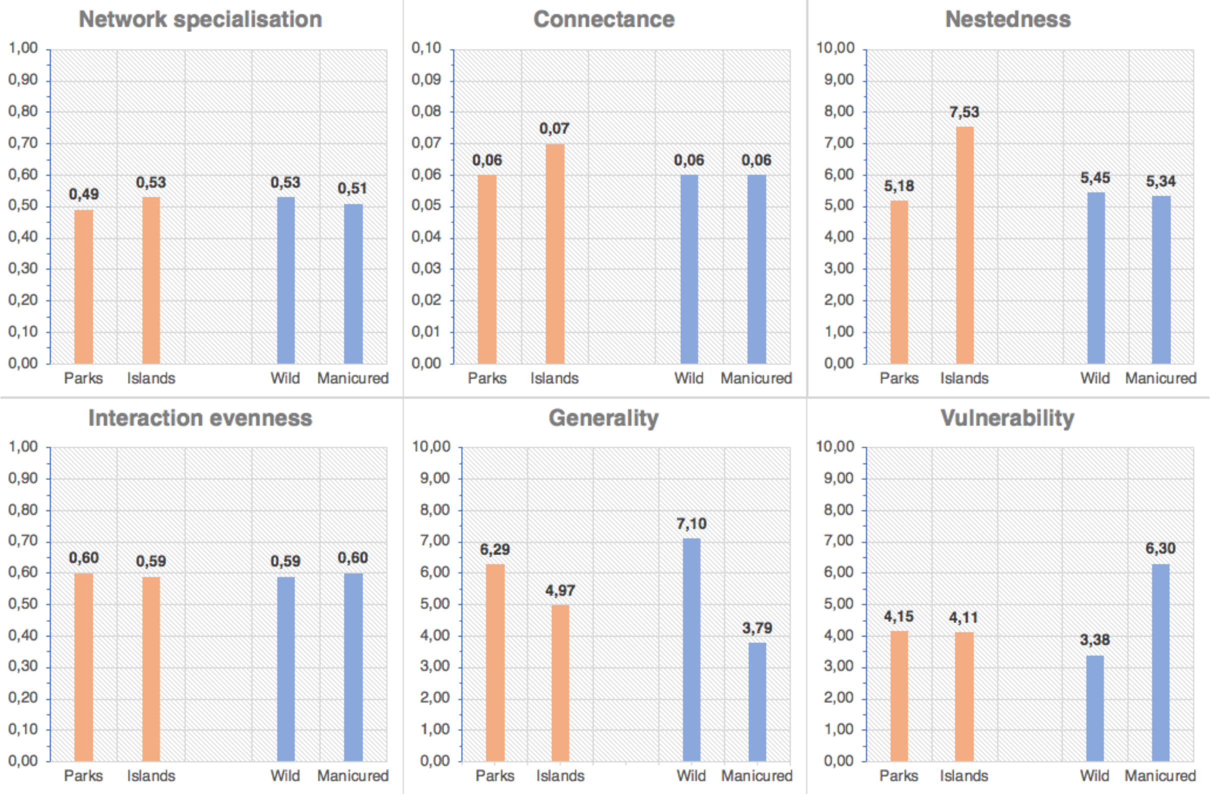


Figure 27: Parks, islands, wild sites and manicured sites' visitation networks indices.

When comparing management types together, wild networks seem to be slightly more specialised and nested than manicured ones. However, the differences between indexes are too weak to be taken into account. With a network specialisation index (H2') of 0.53, island networks stay averagely specialised despite being slightly above parks' H2' (0.49). Both management types show the same connectance value (0.06) and have moderately uniform interactions with evenness values of 0.59 and 0.60. However, we can observe significant disparities between wild and manicured sites generality, as bee species visit 7.10 flower species on average in wild sites against 3.79 in manicured ones. The same disparities can be observed for the vulnerability index, as flower species are visited by an average of 3.38 bee species in wild sites against 6.30 species in manicured sites.

Disparities between habitats and management types in terms of species composition inside our visitation networks is another useful analysis to make. This beta analysis takes species composition and species interactions into account. The β_{S} index (dissimilarity in the species composition of communities) is slightly higher between habitats ($\beta_{S} = 0.554$) than management types ($\beta_{S} = 0.495$), which might indicate greater dissimilarities between habitats in terms of species composition. The β_{WN} index (dissimilarity of interactions) is slightly higher between habitats ($\beta_{WN} = 0.881$) than management types ($\beta_{WN} = 0.869$), which might indicate greater dissimilarities between habitats in terms of species interactions. The β_{WN} index can be decomposed into β_{OS} (dissimilarity of interactions between species common to both networks) and β_{ST} (dissimilarity of interactions due to species turnover). In both habitats and management types, the dissimilarity of interactions between shared species is significantly higher than the dissimilarity of interactions due to species turnover (see Appendix 34).

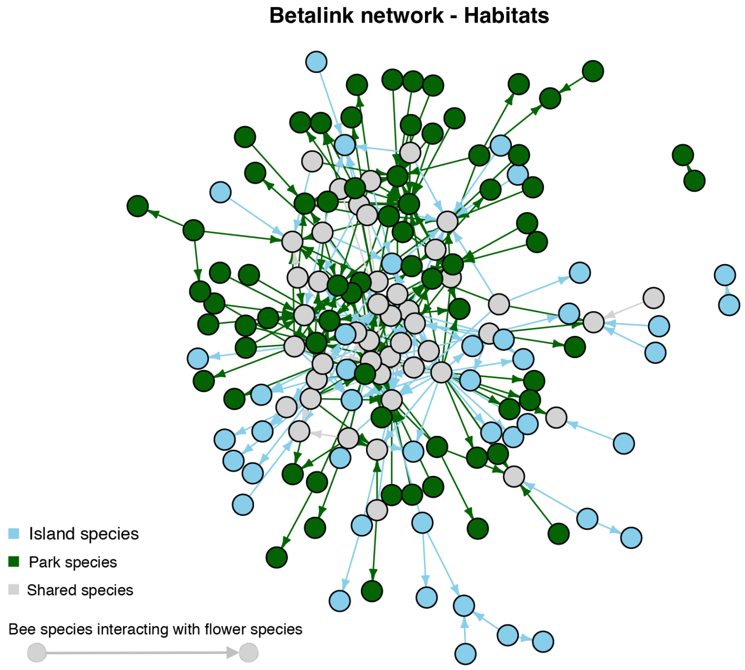


Figure 28: Betalink interactions network between islands and parks. Each dot represents a bee (at the base of the arrow) or a flower (at the tip of the arrow) species. The arrow represents the interaction between the two species. Closer dots are more likely to share the same links. Blue dots represent species that are only found in islands, green dots represent species that are only found in parks and grey dots represent species that are common to both habitats.

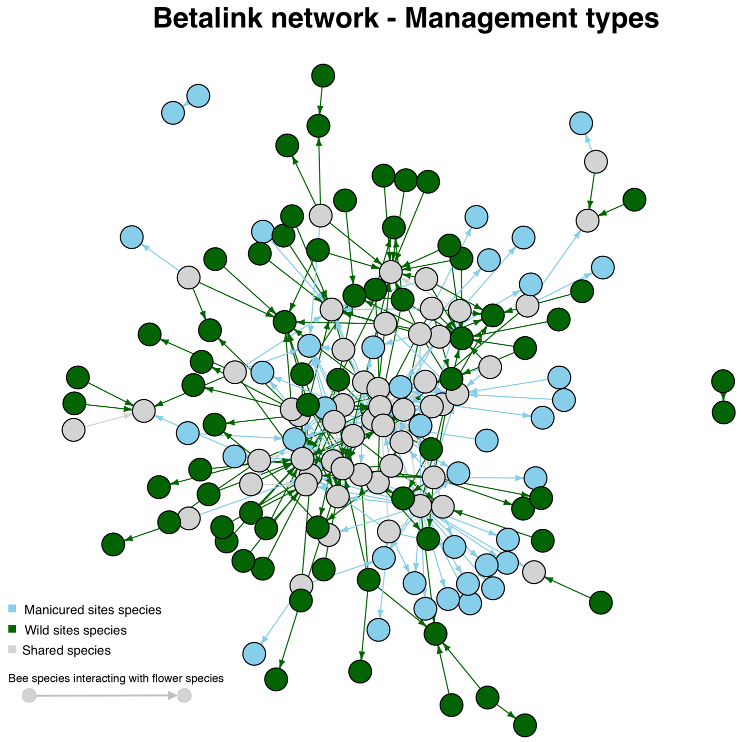


Figure 29: Betalink interactions network between manicured sites and wild sites. Each dot represents a bee (at the base of the arrow) or a flower (at the tip of the arrow) species. The arrow represents the interaction between the two species. Closer dots are more likely to share the same links. Blue dots represent species that are only found in manicured sites, green dots represent species that are only found in wild sites and grey dots represent species that are common to both management types.

4.5.3 Sites networks

Now that habitats and management types networks are assessed along with their associated indices, let's scale down to the site level. In order to illustrate our results and visually understand the networks indices, St John's Island and Dairy Farm's cases will be displayed below. These two sites were highlighted because of their singular characteristics. Dairy Farm is a massively forested nature park located at the heart of Singapore. This site is connected to the two largest natural areas found in Singapore : the Bukit Timah Nature Reserve (a 163 ha primary lowland dipterocarp forest) and the Central Catchment Nature Reserve (a 2880 ha mixture of young and mature secondary forests with virgin primary forest surrounding the reservoirs). At the opposite, St John's Island is located approximately 6.5 km to the south of the singaporean coastline. Formerly used as a quarantine station for cholera cases detected among immigrants, it is now a non-urbanized leisure island of 122 ha under management. The remaining four sites' networks (Coney Island, Pulau Ubin, Hort Park and Pasir Ris) will of course also be assessed and can be found in Appendix 26Appendix 28Appendix 30Appendix 32.

As shown in Figure 30, St John's Island and Pasir Ris seem to have the most specialised networks, whereas Coney Island and Hort Park seem to have the least specialised ones. When it comes to networks' connectance, all six sites seem to be poorly connected (with values under 0.10), even if Coney Island has a connectance above average (C = 0.15). While all sites are quite evenly distributed (homogenous interaction frequencies), St John's Island, Hort Park and Dairy Farm seem to be more nested than Coney Island, Puau Ubin and Pasir Ris. Across all sites, bee species visit 2.75 to 3.76 flower species on average except in Dairy Farm, where bee species visit 6.87 flowers on average (generality index). Flower species are visited by an average of 1.93 to 2.33 bee species in Coney Island, Pulau Ubin and Pasir Ris whereas more visitations are observed in St John's island and Hort Park (respectively 3.88 and 4.22).

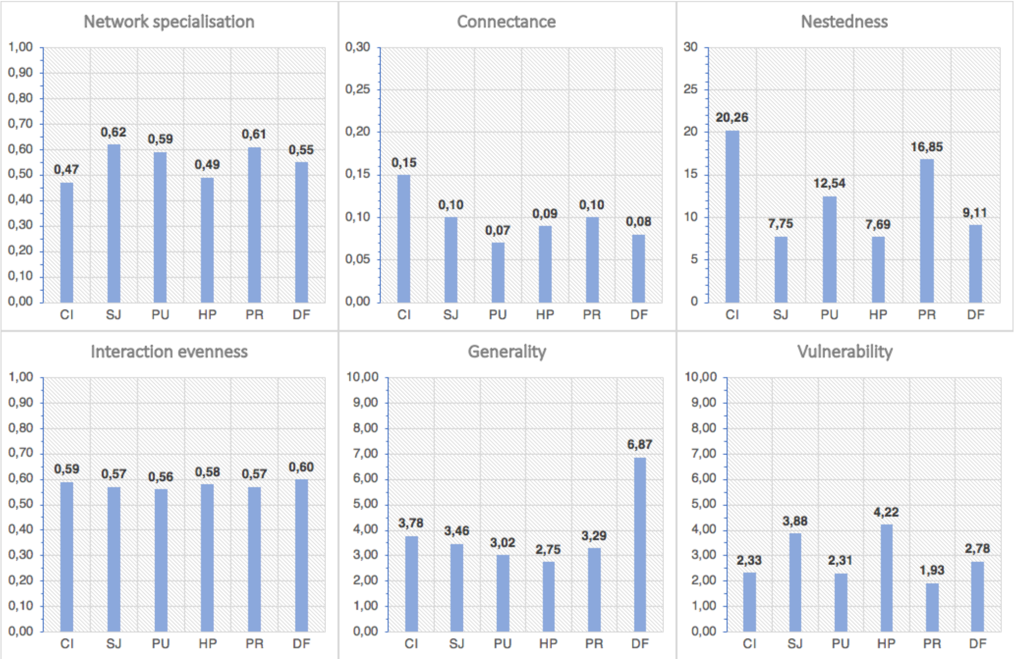


Figure 30: Sites' flower-bee visitation networks associated indices.

St John’s Island and Dairy Farm’s visitation networks (Figure 31 and Figure 32) illustrate quite well some of the results exposed above. As we can see in St John’s network, many bee species are specialists of one or two flower species whereas very few bee species are visiting a wide spectrum of flower species. Even if many specialists can be found in Dairy Farm’s network too, a larger proportion of the bee species visit a high number of flower species. These observations partially explain why Dairy Farm’s network is slightly less specialised than St John’s while having a generality index twice as high.

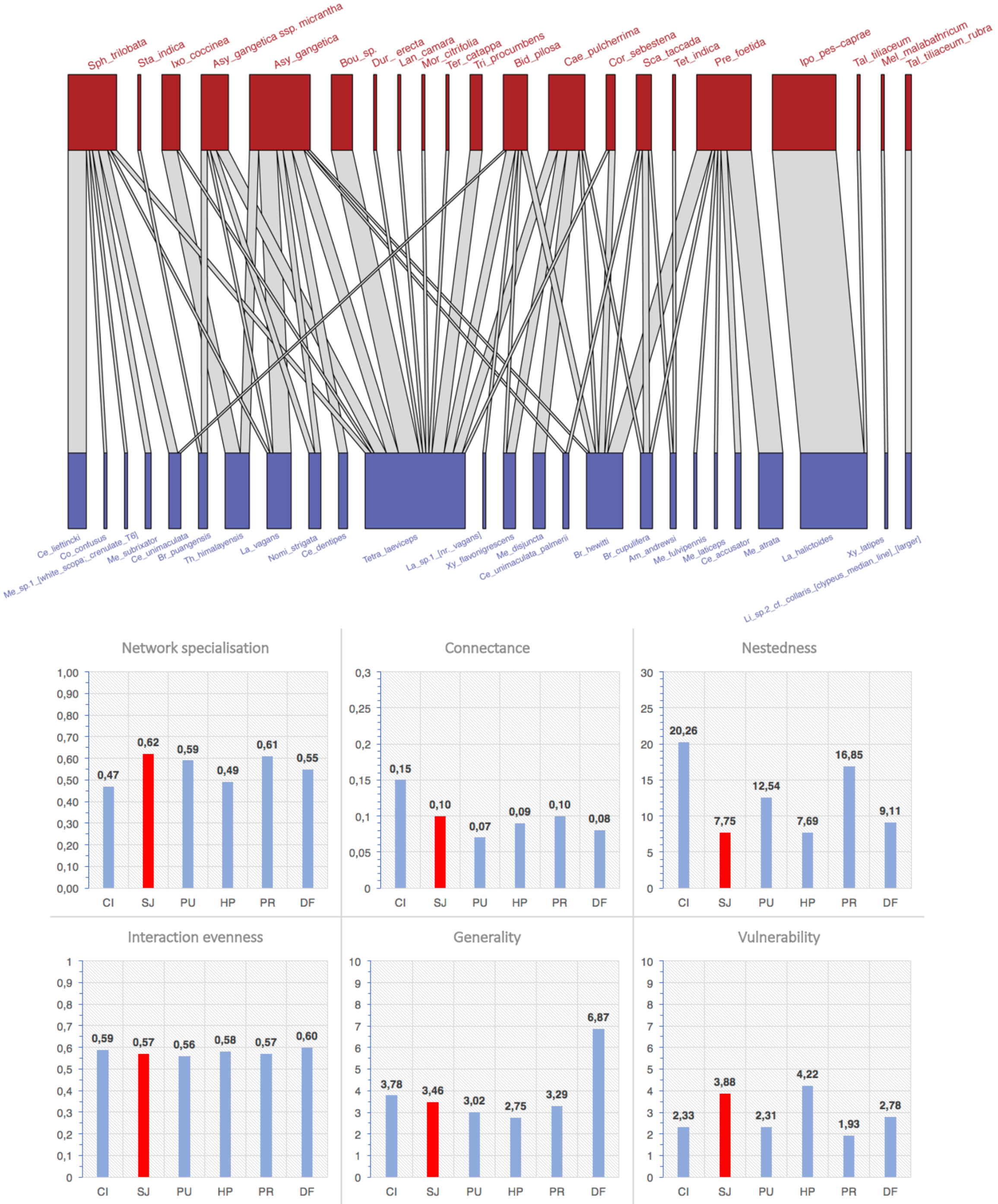


Figure 31: Flower-bee visitation network and associated indices - St John's Island.

Another interesting feature to highlight lies in the vulnerability index. The number of flower species' visitors is higher in St John's network than Dairy Farm's. Even if Dairy Farm's network is more complex and counts numerous interactions, flower species host less visitors on average (2.78 in Dairy Farm compared to 3.88 in St John's). A small fraction of flower species are visited by many bee species while several flower species are linked to one or two bee species at most. St John's flower species are, in general, better connected and thus less vulnerable.

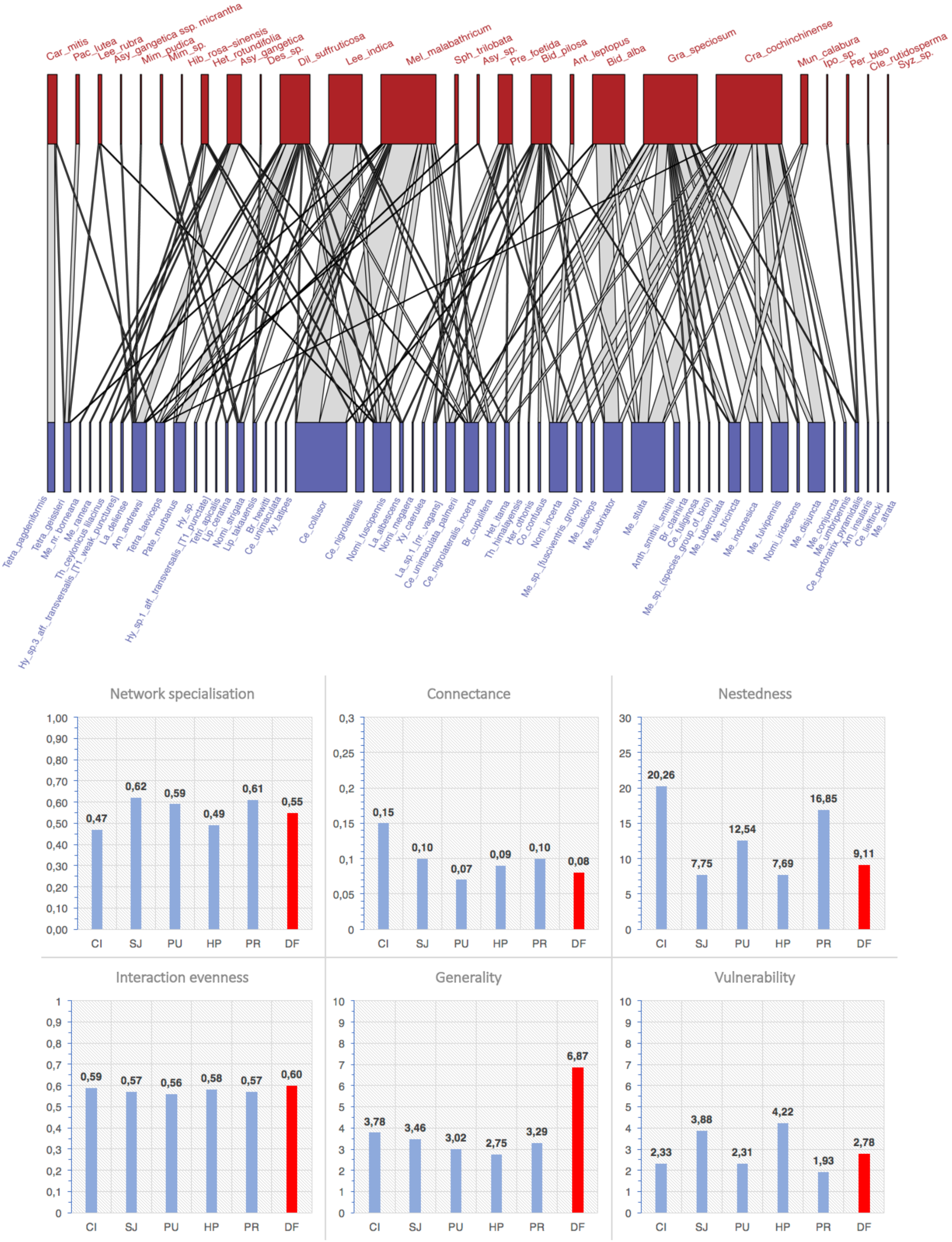


Figure 32: Flower-bee visitation network and associated indices - Dairy Farm

4.6 SITES CHARACTERISATION: LOCAL AND LANDSCAPE FACTORS

4.6.1 Local factors

At the local scale, none of the four variables that were taken into account (the site size, green cover and degree of urbanization) showed a significant response to the observed species richness, Jackknife1, Shannon and Piélou's indices. The simple linear regressions results are displayed in Table 7 .

	Site size	Manag. Type	Green cover	Urbanized
Species richness	0,449	-0,411	0,885	-0,885
Jacknife 1	0,504	-0,449	0,897	-0,897
Shannon	0,371	-0,351	0,899	-0,899
Piélou	0,068	0,038	-0,307	0,307

Table 7: Linear regression results on the local variables.

4.6.2 Landscape factors

At the landscape level, two aggregations were tested. The first one, created to assess the influence of potential habitats, includes parks, reserves, mixed vegetation, residential areas and green patches density. The second one, created to assess the influence of sites size and impermeable surfaces, includes sites size, water bodies, urbanized areas and urbanized patches density.

Inside these two aggregations, none of the landscape variable showed a significant response to the observed species richness, Jackknife1, Shannon and Piélou's indices at the three scales studied (250m, 500m and 1000m). The simple linear regressions results for both aggregations and each spatial scale are displayed in Table 8 and Table 9.

250 m

	Parks	Reserves	Mixed vegetation	Residential	Green patches density
Species richness	-0,686	0,373	0,898	-0,356	0,053
Jacknife 1	-0,672	0,325	0,924	-0,330	0,078
Shannon	-0,497	0,374	0,778	-0,225	0,005
Piélou	-0,379	0,046	0,114	-0,199	0,296

500 m

	Parks	Reserves	Mixed vegetation	Residential	Green patches density
Species richness	-0,622	0,090	0,901	-0,197	0,092
Jacknife 1	-0,594	0,083	0,930	-0,179	0,103
Shannon	-0,470	0,124	0,783	-0,070	0,083
Piélou	-0,242	0,070	0,111	-0,214	0,130

1000 m

	Parks	Reserves	Mixed vegetation	Residential	Green patches density
Species richness	-0,345	0,069	0,925	-0,101	0,008
Jacknife 1	-0,297	0,085	0,948	-0,079	0,023
Shannon	-0,281	0,077	0,816	-0,006	0,028
Piélou	0,029	0,173	0,084	-0,122	0,027

Table 8: Linear regression results on the first aggregation.

250 m

	Site size	Management type	Water	Urbanized	Urbanized patches density
Species richness	0,449	-0,411	-0,392	-0,323	0,288
Jacknife 1	0,504	-0,449	-0,431	-0,286	0,216
Shannon	0,371	-0,351	-0,426	-0,242	0,516
Piélou	0,068	0,038	0,038	0,011	-0,744

500 m

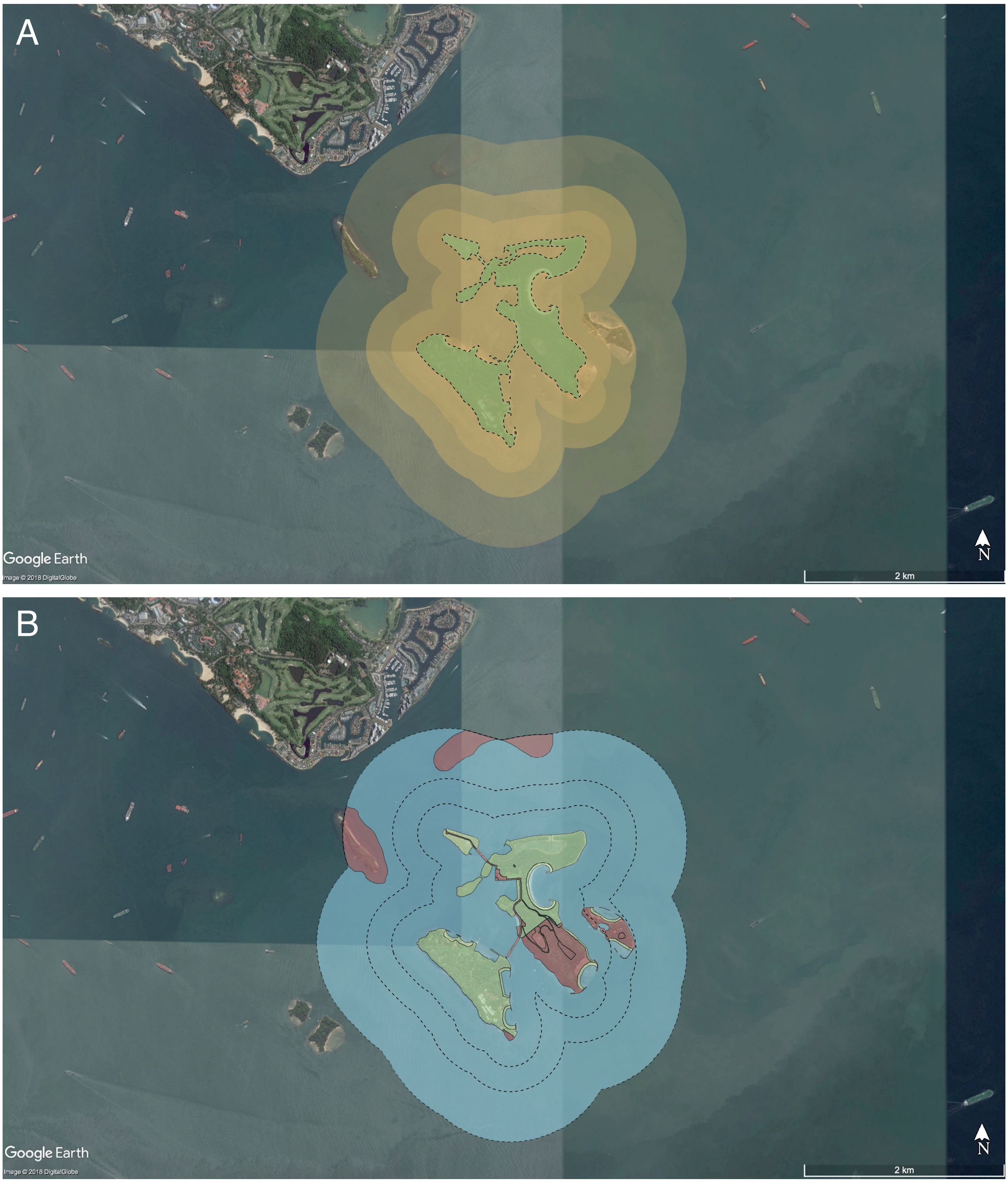
	Site size	Management type	Water	Urbanized	Urbanized patches density
Species richness	0,449	-0,411	-0,493	-0,319	0,288
Jacknife 1	0,504	-0,449	-0,547	-0,281	0,216
Shannon	0,371	-0,351	-0,405	-0,156	0,314
Piélou	0,068	0,038	0,036	-0,097	-0,394

1000 m

	Site size	Management type	Water	Urbanized	Urbanized patches density
Species richness	0,449	-0,411	-0,493	-0,319	0,288
Jacknife 1	0,504	-0,449	-0,547	-0,281	0,216
Shannon	0,371	-0,351	-0,283	-0,163	0,417
Piélou	0,068	0,038	0,072	-0,168	-0,021

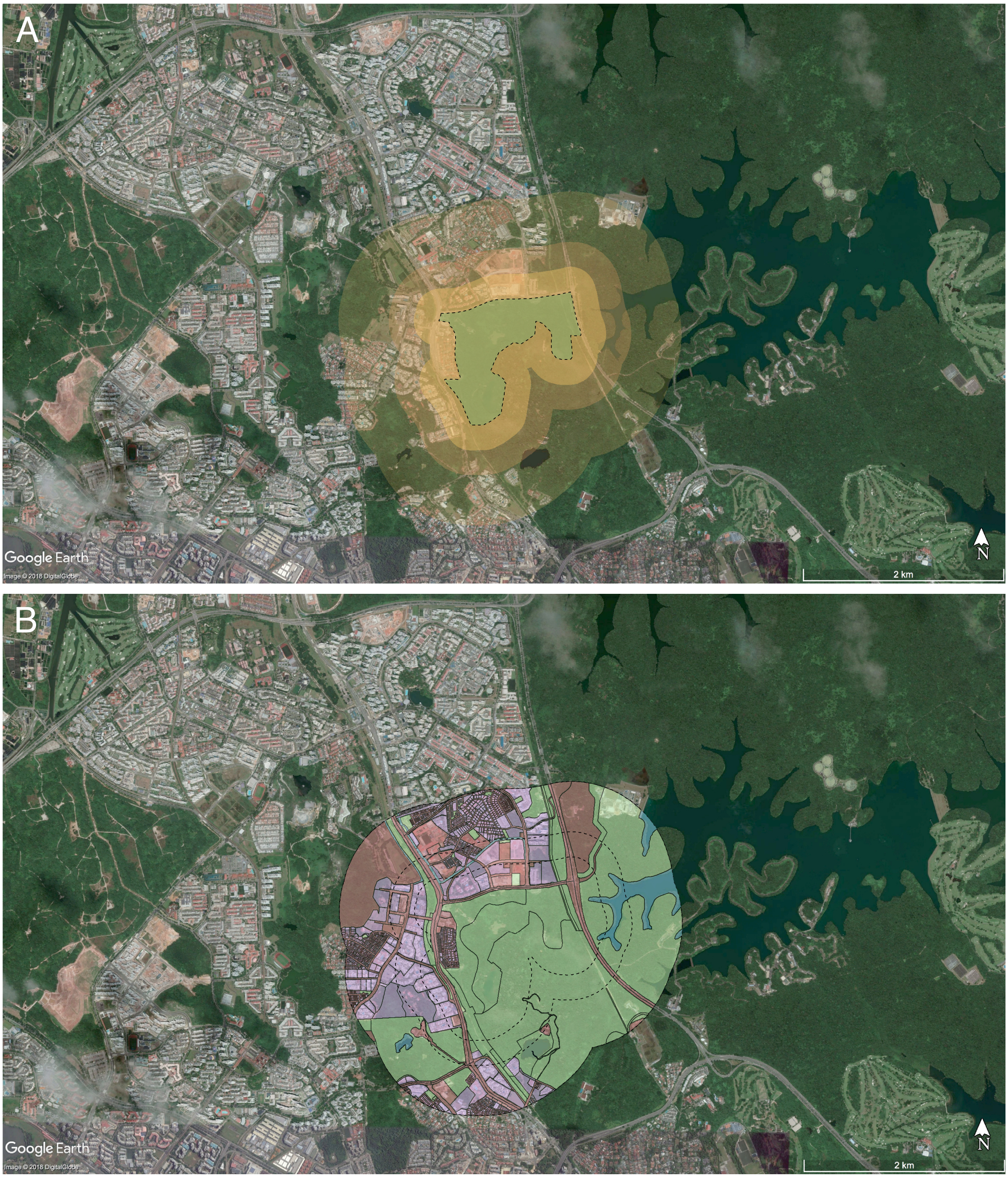
Table 9: Linear regression results on the second aggregation.

To ensure the continuity of St John's island and Dairy Farm's case example, the land-use digitalisation and geographic information processing of both sites will be displayed below (Figure 33Figure 34). The remaining four sites' land-use digitalisation (Coney Island, Pulau Ubin, Hort Park and Pasir Ris) can be found in Appendix 27Appendix 29, Appendix 31, Appendix 33.



Digitalisation of St John's Island landuse in ArcGIS. (A) St John's Island boundaries (dotted lines) with three buffer zones (250 m: dark orange , 500 m: orange, 1000 m: light orange). (B) Digitalised vegetation (green), urbanized areas (red), residential areas (purple) and water (blue) inside the 1000 m buffer zone. The dotted lines represent the 250 m, 500 m and 1000 m buffers.

Figure 33: Land-use digitalisation - St John's Island.



Legend

🟩	**Vegetation**	🟧	**250 m buffer**
🟥	**Urban**	🟨	**500 m buffer**
🟪	**Residential**	⬜	**1000 m buffer**
🟦	**Water**		

Digitalisation of Dairy Farm landuse in ArcGIS. (A) Dairy Farm boundaries (dotted lines) with three buffer zones (250 m: dark orange , 500 m: orange, 1000 m: light orange). (B) Digitalised vegetation (green), urbanized areas (red), residential areas (purple) and water (blue) inside the 1000 m buffer zone. The dotted lines represent the 250 m, 500 m and 1000 m buffers.

Figure 34: Land-use digitalisation - Dairy Farm.

5 DISCUSSION

5.1 SAMPLING EFFORT

When considering the whole database, this study covers an eight-year long sampling effort (2010-2018). This represents the capture of 1789 specimens that belong to 4 families, 20 genus and 94 species. Currently, about 130 bee species and morphospecies are recorded in Singapore (100 described/identifiable species and 30 unidentifiable to the species level). It is noteworthy that some species like *Geniotrigona thoracica, Homotrigona fimbriate*, *Lophotrigona canifrons* or *Tetragonula atripes* are believed to be extinct in Singapore (this is mostly true for the Meliponini tribe) (Ascher et al., 2018). That being said, across the six sites surveyed, about 72% of the bee species recorded in Singapore were caught.

A closer look to the sampling results highlights significant disparities between sites in terms of specimens and species counts. If these disparities can partially be attributed to environmental characteristics, uneven sampling efforts across sites should be taken into account as well. Sites recently opened to the public, like Coney Island in 2015, are inherently less sampled than sites like Dairy Farm or Pulau Ubin, opened for years and recognised as a true natural heritage. To counteract these limitations, bee communities have been virtually rarefied by simulating a random 100 specimens community. Results show that the three least sampled sites (in that eight-year period), namely Coney Island (7 sessions), St John's Island (14 sessions) and Hort Park (26 sessions), would be equally rich in species in this rarefied community. This simulation emphasises the need for several new sampling sessions, especially in Coney Island.

Using non-parametric richness estimators and accumulation curves is another way to assess the quality of our sampling effort. Overall, between 79% (with the Jackknife2 estimator) and 91% (with the bootstrap estimator) of the potential species that could be found across our six sites are assumed to be caught. This estimation confirms the global species accumulation curve that seems to reach a plateau. When scaling down to the habitat and management type levels, parks and wild sites seem to have the most potential for progress, with respectively 72% to 91% and 68% to 89% of the potential species assumed to be caught. At the site level, quite surprisingly, Coney Island doesn't have the biggest potential for progress. Instead, Hort Park comes first with 51% to 83% of the potential species occurring in it assumed to be caught. This might be explained by the fact that Hort Park is the second least sampled site after Coney Island in terms of specimens collected. In light of these results, future studies should focus on both Coney Island and Hort Park. Aside from being under sampled, these two sites have unique characteristics that could hold a great potential for less common wild bee species. For instance, Coney Island and its preserved coastal habitats could host sand nesting species or mangroves specialists. In contrast, by its heavily diverse and managed vegetation and its heterogenous habitat, Hort park could host numerous bee species with totally opposite requirements.

5.2 ABUNDANCE ACROSS SITES, BETWEEN HABITATS AND MANAGEMENT TYPES

Bearing in mind the sampling effort considerations above mentioned, species abundance across sites seems to be quite evenly distributed (Figure 16). However, we can notice that some species like *Tetragonula laeviceps* are particularly abundant in sites like Dairy Farm, Hort Park, Pulau Ubin and St John's Island. That might be due to the fact that these stingless bees have an advanced social behaviour (Chui, 2015), are generalists and tend to forage in large numbers. Along with *Ceratina collusor*, *Ceratina lieftincki*, *Ceratina nigrolateralis incerta* and *Braunsapis puangensis*, both habitat types and management types are dominated by *Tetragonula laeviceps*. Islands and manicured sites seem to be less evenly distributed than parks and wild sites, as very few species rank as highly abundant and numerous species are represented by small populations. It is interesting to link this observation to the potential apparent competition (PAC) results. As we can see in Appendix 10, the influence of *Tetragonula laeviceps* is much higher than other species. As Roubik postulated in his work on the ecology and natural history of tropical bees (1989), each highly eusocial species could occupy the role of several solitary species in an ecological hierarchy of food resource usage. This is especially true and relevant for isolated sites like St John's Island. However, islands and manicured sites' PAC heatmaps (aAppendix 19 Appendix 25) suggest that the competition they impose is fairly distributed among other species. In contrast, parks and wild sites seem to be more equally distributed, with several abundant, moderately and less represented populations. The parks PAC heatmap shows that species of the *Megachile* genus are slightly in competition with each other. This might be due to their seasonality (Ascher, 2016) (unlike most of the species in Singapore), constraining them to share limited resources over a limited time lapse.

5.3 SITES DIVERSITY ASSESSMENT

Regarding species richness across sites, Dairy Farm and Pulau Ubin are the richest surveyed sites with 62 and 54 species recorded respectively. These two highly preserved natural areas are, with Bukit Timah Nature Reserve, among the least impacted ones across Singapore. Despite being eight times smaller than Pulau Ubin, more species are recorded in Dairy Farm. Its location, close to the old secondary and primary forests of Bukit Timah Nature Reserve, makes this site a precious hotspot for Singapore wild bees diversity. A notable Dairy Farm's feature is the presence of a relatively wide variety of cultivated exotics, naturalised exotics, and native flowering plants species (Wen, 2013). Among the 62 species recorded over the last eight years in Dairy Farm, more than one third are not encountered in the other sites surveyed. This site also seems to be the most diversified one as having the highest Simpson and Shannon's alpha diversity values. Moreover, in a recent study on the impact of urbanisation on bee and wasp diversity in Singapore, Lai (2016) has recorded the presence of *Amegilla insularis* in Dairy Farm. According to the NUS Insect Diversity Lab historical database, this rare forest-associated bee has fewer than ten specimen records in Singapore and is known to be associated with good forest habitat. The number of Dairy Farm exclusive species and the presence of *Amegilla insularis* highlights the quality and importance of this singular habitat and reaffirms the need for nature parks biodiversity conservation efforts.

If less bee species are recorded in Pulau Ubin, nine species are exclusive to this site. Due to its location, wide area, preserved and heterogenous habitats, species are not expected to regularly emigrate to the mainland. About 1 km separates Pulau Ubin from the Malay coast, and flying not much further is required to join Singapore coastlines. However, if the smallest species could be constrained to thrive on the island (Wright et al., 2015), medium to large species (i.e. from the *Xylocopa* genus) could easily fly from one side to another as the flying distance can go up to several kilometres depending on the species traits (e.g. body size and intertegular distance) (Roubik, 1989; Gathmann & Tscharntke, 2002; Cariveau et al., 2016). The foraging distances of wild bees in Singapore are yet to be estimated. However, John Ascher and his team (Ascher, personal communication, 2017) have recorded the intertegular distances (ITDs) (measurement of the shortest linear distance between bees' wing tegulae) of all bee species occurring in Singapore. ITDs are shown to be related with bees' body size (Cane, 1987), which can be used to estimate the species flight distance (Araújo et al., 2004; Greenleaf et al., 2007). Further studies could make use of these precious measurements, i.e. by linking bees occurrences and diversity across sites to their functional traits. As the Pulau Ubin's vegetation consists in large young and old secondary forests, newly restored mangroves and tiny managed plots, Pulau Ubin's potential for floral resource and nesting sites can be considered as high. Flower-bee visitation networks and their associated indexes show that Pulau Ubin has, among the six surveyed sites, the lowest connectance and the second lowest generality and vulnerability values. The low connectance value can partially be explained by the numerous bee species specialized on one or two flower species. This observation is confirmed by the generality index, as bee species visit an average of 3.02 flower species. This highly contrasts with Dairy Farm results where bee species were nearly visiting twice as many flower species than Pulau Ubin's does. This is valuable information given the fact that a loss in flowers richness could cause a loss of their specific associated hosts as well. However, we must keep in mind that their fundamental niche may be wider than it appears, as a vast majority of bees found in Singapore are known to be polylectic (see Appendix 40). Further research need to be done in order to fully assess this issue. The same remarks apply for the vulnerability index, as flower species doesn't host many bee species (2.31).

The sites' hierarchical clustering displayed in Figure 22 (based on the species abundances) suggests that Pasir Ris and Pulau Ubin could be grouped together. At first glance, these two sites have nothing in common: Pulau Ubin is a wild island about eight times larger than Pasir Ris whereas Pasir Ris is a small beach park under heavy management. However, we must comment this result given the potential similarities between the two sites. Firstly, Pasir Ris isn't a strictly manicured site, as hosting a restored 6 ha mangrove forest. This feature is also found in Pulau Ubin, where the 100 ha Chek Jawa wetlands hold preserved mangroves and coastal forests (National Parks Board, 2018). Pulau Ubin's Butterfly Hill constitutes another noteworthy wildlife spot. About the size of a football field, it is one of the very few managed / garden-like areas found in Pulau Ubin. It attracts over 80 species of butterflies (Teo, 2012) and constitutes therefore a rich foraging spot for bees (as floral species implemented for butterflies also benefit to bees, at least for the nectar reward) (Herrera, 1990). An equally interesting feature can be found in Pasir Ris: the Kitchen Garden. This densely vegeted spot, where culinary and medicinal plants are community gardened, attracts numerous pollinator insects. Finally, the Serangoon Harbour separates Pulau Ubin from Pasir Ris by an approximate distance of 2 km. If large species could easily cover the distance, smaller ones are not expected to emigrate from Pasir Ris to Pulau Ubin. Without rushing to any conclusion, it would be it would be worth considering to link these observations with Pulau Ubin's slightly higher nestedness values.

When taking into consideration the sampling effort disparities (thanks to the simulated rarefaction of communities), Coney Island, St John's Island and Hort Park appear to be the least diversified sites in terms of species richness. Communities rarefaction shows that these three sites would be 30% less diversified than Dairy Farm and Pulau Ubin in terms of species counts. These three sites are also the less diversified ones, having the lowest Simpson and Shannon's alpha diversities values. Flower-bee visitation networks and their associated indexes show that Coney Island's network is the least specialized, the least nested and the most connected one. This site, freshly opened to the public in 2015, has some interesting features. Despite being dominated by a young secondary forest and having globally homogenous floral patches (mainly composed by *Asystasia gangetica spp. micrantha* and *Biden pilosa*), Coney Island's coastal forests and restored mangroves are of particular interest. Moreover, as only 59% to 82% of its bee species richness is estimated to be discovered, the implementation of new studies on this site would ensure new species discoveries. At the opposite, St John's Island has the most specialized and the second most nested network after Hort Park. It is interesting to note that the hierarchical clustering performed on our sites (Figure 22) groups St John's Island and Hort Park together. This means that at some extent, the two sites are relatively similar. Despite being both classified as manicured, these two sites doesn't have much in common. Hort Park is garden-themed park about ten times smaller than St John's Island. The park counts numerous indigenous and exotic flower patches that are displayed very neatly and under heavy maintenance. St John's Island vegetation, on the other hand, vary from heavily groomed ornamental flowers to regularly mowed lawns. Small young secondary forest patches still remain in certain parts of the island. We will not go any further about these two sites similarities, but it was interesting to note that such contrasting settings could host communities that are one way or another quite alike.

5.4 LOCAL AND LANDSCAPE FACTOR ASSESSMENT

At the local scale, the site size and its quality are two key factors that could affect wild bee communities. In this study, habitat quality was assessed at the site level thanks to four parameters : site size, management type, green covers percentage and urbanized areas percentage. However, none of the response variables (species richness and alpha diversity indices) were shown to be significantly affected. In order to fully assess wild bee communities response to local factors, further studies should particularly focus on quantitative and qualitative floral surveys as well as nesting sites availability according to specific species requirements.

At the landscape scale, the influences of potential habitats, sites size and impervious surfaces have not shown any significant response to the observed species richness, Jackknife1, Shannon and Piélou's indices at the three scales studied (250m, 500m and 1000m). However, we must draw attention to the very limited number of sites surveyed, making landscape analyses tricky to interpret. From these results, we cannot conclude that landscape factors have (or do not have) an influence on bee communities.

5.5 HABITATS DIVERSITY ASSESSMENT: PARKS VS. ISLANDS

At the habitat level, parks and islands share a common pool of 46 species when having respectively 29 and 19 exclusive species. When comparing parks and islands together, the number of species encountered in parks were slightly higher but the differences in species composition were not statistically significant.

The Simpson, Shannon and Piélou's indexes values are higher in parks than islands, suggesting that parks communities are more diversified and the species more evenly distributed. However, when assessed statistically, the differences were not significant.

As we examine habitats flower-bee visitation networks, it can be observed that the island network seems to be more specialised, nested and connected. Also, while flower species are visited by the same number of bees in both habitats, bee species visit more flower species in parks than islands. On the one hand, this could mean that bee species are more specialised in islands networks. On the other hand, if island networks were poorer in floral species, the same result could be displayed while observing the most generalist bee species in this particular setting. That being said, the only non-speculative comment we could make would be as follow: bee species in the island network are, on average, linked to less flower species when compared to the park network. This network seems thus more vulnerable.

5.6 MANAGEMENT TYPES DIVERSITY ASSESSMENT: WILD VS. MANICURED

When focusing on management type, manicured and wild sites share a common pool of 49 species when having respectively 6 and 39 exclusive species. When comparing manicured and wild sites together, the number of species encountered in wild sites is higher but subject to large variations. Further statistical analyses have confirmed that the differences in species composition were not statistically significant.

The Simpson, Shannon and Piélou's indexes values are higher in wild sites than the manicured ones, suggesting that communities occurring in unmanaged settings are more diversified and the species more evenly distributed. However, when assessed statistically, the differences were not significant.

As we examine wild and manicured networks, it can be observed that the wild network seem slightly more specialised and nested than the manicured one. However, the differences observed between them are too weak to be taken into account. If wild and manicured networks are both equally connected and have moderately uniform interactions, we can highlight the significant disparities between networks generality, as bee species visit twice as much flower species in wild sites than they do in manicured ones. The same (but reversed) disparities can be observed for the vulnerability index, as flower species in wild networks are visited by twice as less bee species than they are in manicured ones.

The betadiversity analyses applied to habitats and management types networks show that bigger dissimilarities in terms of species composition can be found between habitats than management types. The same observation applies for the dissimilarities for interactions.

6 CONCLUSIONS, LIMITATIONS AND PROSPECTS

The findings from this study suggest that each site surveyed has specific features that are particularly suited for a community of species that possibly might not have occurred together somewhere else. As these communities are composed by unique species assemblages, habitat losses could have tremendous consequences on species richness and diversity. However, we must keep in mind that species realised niche may be narrower than it appears, and especially in the tropics where most of bee species are polylectic. These results must be interpreted with care, as species considered as "specialists" in a particular setting could, under specific environmental conditions, be subject to unusual behaviour change. To understand the species' fundamental and realised niches in these particular settings is of decisive importance in view of their conservation. It could also help researchers to better understand and asses tropical urban settings.

While the landscape context does not explain species richness and diversity in this study, it is interesting to observe that contrasting sites in terms of size, habitat, management type or location could host wild bee communities with quite similar characteristics, but unique species assemblages at the same time. Having regard to these observations, Singapore environmental gradient is of particular interest. Its habitats mosaic made of parks, islands, reserves, forests, community gardens, green rooftops and numerous urban greeneries, holds a great potential towards wild bee species conservation and diversity. At the site level, further investigations are needed, as habitat quality and distinctive features could better explain communities similarities, variations and strengths.

To conclude, our results suggest that unmanaged preserved parks and islands could serve as refuge for rare bee species while managed parks and islands could support pollinator species richness and abundance. This study must draw attention to the importance of preserving both wild untouched habitats and managed floral-rich urban parks in order to enhance bee diversity while maintaining ecologically stable networks.

7 BIBLIOGRAPHY

Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, *483*(7388), 205–208. http://doi.org/10.1038/nature10832

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., … Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, *14*(1), 19–28. http://doi.org/10.1111/j.1461-0248.2010.01552.x

Araújo, E. D., Costa, M., Chaud-Netto, J., & Fowler, H. G. (2004). Body size and flight distance in stingless bees (Hymenoptera: Meliponini): inference of flight range and possible ecological implications. *Brazilian Journal of Biology*, *64*(3b), 563–568. http://doi.org/10.1590/S1519-69842004000400003

Ascher, J. S., & Pickering, J. (2018). Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila).

Ascher, J. S., Risch, S., Soh, Z. W. W., Lee, J. X. Q., & Soh, E. J. Y. (2016). Megachile leaf-cutter and resin bees of Singapore (Hymenoptera: Apoidea: Megachilidae). *Raffles Bulletin of Zoology*, *2016*, 33–55.

Ascher, J. S., Soh, Z. W. W., Ho, B. M., Lee, R. Y. Y., Leong, A. Q. E., Chui, S. X., … Soh, E. J. Y. (2018). *Bees of the Bukit Timah Nature Reserve and vicinity*. Singapore.

Auger, T. (2013). Living In A Garden: The Greening Of Singapore. *Mygreenspace*, *3*(18).

Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Osgathorpe, L. M., … Memmott, J. (2015). Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1803), 20142849–20142849. http://doi.org/10.1098/rspb.2014.2849

Ballantyne, G., Baldock, K. C. R., & Willmer, P. G. (2015). Constructing more informative plant–pollinator networks: visitation and pollen deposition networks in a heathland plant community. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151130. http://doi.org/10.1098/rspb.2015.1130

Banaszak-Cibicka, W., & Zmihorski, M. (2012). Wild bees along an urban gradient: Winners and losers. *Journal of Insect Conservation*, *16*(3), 331–343. http://doi.org/10.1007/s10841-011-9419-2

Bartomeus, I., Ascher, J. S., Wagner, D., Danforth, B. N., Colla, S., Kornbluth, S., & Winfree, R. (2011). Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences*, *108*(51), 20645–20649. http://doi.org/10.1073/pnas.1115559108

Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences*, *100*(16), 9383–9387. http://doi.org/10.1073/pnas.1633576100

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. http://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., & Leprieur, F. (2018). Package 'betapart' : Partitioning Beta Diversity into Turnover and Nestedness Components.

Bates, A. J., Sadler, J. P., Fairbrass, A. J., Falk, S. J., Hale, J. D., & Matthews, T. J. (2011). Changing Bee and Hoverfly Pollinator Assemblages along an Urban-Rural Gradient. *PLoS ONE*, *6*(8), e23459. http://doi.org/10.1371/journal.pone.0023459

Biella, P., Ollerton, J., Barcella, M., & Assini, S. (2017). Network analysis of phenological units to detect important species in plant-pollinator assemblages: can it inform conservation strategies? *Community Ecology*, *18*(1), 1–10. http://doi.org/10.1556/168.2017.18.1.1

Biesmeijer, J. C., Richter, J. A. P., Smeets, M. A. J. P., & Sommeijer, M. J. (1999). Niche differentiation in nectar-collecting stingless bees: the influence of morphology, floral choice and interference competition. *Ecological Entomology*, *24*(4), 380–388. http://doi.org/10.1046/j.1365-2311.1999.00220.x

Blüthgen, N., Fründ, J., Vázquez, D. P., & Menzel, F. (2008). What do interaction network metrics tell us about specialization and biological traits? *Ecology*, *89*(12), 3387–3399. http://doi.org/10.1890/07-2121.1

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*. http://doi.org/10.1186/1472-6785-6-9

Borcard, D., Gillet, F., & Legendre, P. (2011). Numerical Ecology with R. *Media*, 1–306. http://doi.org/10.1007/978-1-4419-7976-6

Briffett, C., Kong, L., Yuen, B., & Sodhi, N. (1999). Nature in urban areas: the planning and ecology of green corridor systems in Singapore. *National University of Singapore*.

Brittain, C. A., Vighi, M., Bommarco, R., Settele, J., & Potts, S. G. (2010). Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology*, *11*(2), 106–115. http://doi.org/10.1016/j.baae.2009.11.007

Brook, B. W., Sodhl, N. S., & Ng, P. K. L. (2003). Catastrophic extinctions follow deforestation in Singapore. *Nature*, *424*(6947), 420–423. http://doi.org/10.1038/nature01795

Brose, U., & Martinez, N. (2004). Estimating the richness of species with variable mobility. *Oikos*, *105*(2), 292–300. http://doi.org/10.1111/j.0030-1299.2004.12884.x

Brosi, B. J., Daily, G. C., & Ehrlich, P. R. (2007). Bee community shifts with landscape context in a tropical countryside. *Ecological Applications : A Publication of the Ecological Society of America*, *17*(2), 418–30. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/17489249

Brosi, B. J., Niezgoda, K., & Briggs, H. M. (2017). Experimental species removals impact the architecture of pollination networks. *Biology Letters*, *13*(6), 20170243. http://doi.org/10.1098/rsbl.2017.0243

Burattini, M. N., Chen, M., Chow, A., Coutinho, F. A. B., Goh, K. T., Lopez, L. F., … Massad, E. (2008). Modelling the control strategies against dengue in Singapore. *Epidemiology and Infection*, *136*(03). http://doi.org/10.1017/S0950268807008667

Burkman, C. E., & Gardiner, M. M. (2014). Urban greenspace composition and landscape context influence natural enemy community composition and function. *Biological Control*, *75*, 58–67. http://doi.org/10.1016/j.biocontrol.2014.02.015

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*, *108*(2), 662–667. http://doi.org/10.1073/pnas.1014743108

Cane, J. H. (1987). Estimation of Bee Size Using Intertegular Span (Apoidea). *Journal of the Kansas Entomological Society*, *60*(1), 145–147. http://doi.org/10.1098/rstb.2011.0050

Cane, J. H., & Tepedino, V. J. (2017). Gauging the Effect of Honey Bee Pollen Collection on Native Bee Communities. *Conservation Letters*, *10*(2), 205–210. http://doi.org/10.1111/conl.12263

Cardoso, P., Rigal, F., & Carvalho, J. C. (2017). Package 'BAT' : Biodiversity Assessment Tools.

Cariveau, D. P., Nayak, G. K., Bartomeus, I., Zientek, J., Ascher, J. S., Gibbs, J., & Winfree, R. (2016). The allometry of bee proboscis length and its uses in ecology. *PLoS ONE*, *11*(3). http://doi.org/10.1371/journal.pone.0151482

Cariveau, D. P., & Winfree, R. (2015). Causes of variation in wild bee responses to anthropogenic drivers. *Current Opinion in Insect Science*, *10*, 104–109. http://doi.org/10.1016/j.cois.2015.05.004

Carvalheiro, L. G., Biesmeijer, J. C., Benadi, G., Fründ, J., Stang, M., Bartomeus, I., … Kunin, W. E. (2014). The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecology Letters*, *17*(11), 1389–1399. http://doi.org/10.1111/ele.12342

Castelletta, M., Sodhi, N. S., & Subaraj, R. (2008). Heavy Extinctions of Forest Avifauna in Singapore: Lessons for Biodiversity Conservation in Southeast Asia. *Conservation Biology*, *14*(6), 1870–1880. http://doi.org/10.1111/j.1523-1739.2000.99285.x

Chang, J. Y. A. (2017). *Population genomics of the stingless bee, Tetragonula laeviceps in Singapore*. NATIONAL UNIVERSITY OF SINGAPORE.

Chiesura, A. (2004). The role of urban parks for the sustainable city. *Landscape and Urban Planning*, *68*(1), 129–138. http://doi.org/10.1016/j.landurbplan.2003.08.003

Chong, K. Y., Tan, H. T. W., & Corlett, R. T. (2011). A summary of the total vascular plant flora of Singapore. *Gardens' Bulletin Singapore*, *63*, 197–204.

Chong, K. Y., Teo, S., Kurukulasuriya, B., Chung, Y. F., Rajathurai, S., & Tan, H. T. W. (2014). Not all green is as good: Different effects of the natural and cultivated components of urban vegetation on bird and butterfly diversity. *Biological Conservation*, *171*, 299–309. http://doi.org/10.1016/j.biocon.2014.01.037

Chua, S. H. (2015). *Population genomics of Amegilla blue-banded bees and their Thyreus*. National University of Singapore.

Chui, S. X. (2015). *A Conservation Assessment of Stingless Bees (Apidae: Meliponini) in Singapore*. National University of Singapore.

Colwell, R. K. (1988). Biodiversity: Concepts, Patterns, and Measurement. *Communities and Ecosystems*, 257–264. http://doi.org/10.1111/j.1442-9993.2012.02436.x

Corlett, R. T. (1992). The Ecological Transformation of Singapore, 1819-1990. *Journal of Biogeography*, *19*(4), 411. http://doi.org/10.2307/2845569

David, A., Botías, C., Abdul-Sada, A., Nicholls, E., Rotheray, E. L., Hill, E. M., & Goulson, D. (2016). Widespread contamination of wildflower and bee-collected pollen with complex mixtures of neonicotinoids and fungicides commonly applied to crops. *Environment International*, *88*, 169–178. http://doi.org/10.1016/j.envint.2015.12.011

Dellicour, S., Mardulyn, P., Hardy, O. J., Hardy, C., Roberts, S. P. M., & Vereecken, N. J. (2014). Inferring the mode of colonization of the rapid range expansion of a solitary bee from multilocus DNA sequence variation. *Journal of Evolutionary Biology*, *27*(1), 116–132. http://doi.org/10.1111/jeb.12280

Delmas, E., Besson, M., Brice, M.-H., Burkle, L., Riva, G. V. D., Fortin, M.-J., … Poisot, T. (2018). Analyzing ecological networks of species interactions. *BioRxiv*, 112540. http://doi.org/10.1101/112540

Dice, L. R. (1945). Measures of the Amount of Ecologic Association Between Species. *Ecology*, *26*(3), 297–302. http://doi.org/10.2307/1932409

Dormann, C. F., Fruend, J., Gruber, B., Devoto, M., Iriondo, J., Strauss, R., & Vazquez, D. (2017). Visualising Bipartite Networks and Calculating Some (Ecological) Indices : Package 'bipartite.'

Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, *5*(1), 90–98. http://doi.org/10.1111/2041-210X.12139

Dray, S., Dufour, A.-B., & Thioulouse, J. (2018). Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences : Package 'ade4.'

Dryzek, J. S., Norgaard, R. B., & Schlosberg, D. (2011). *Climate Change and Society: Approaches and Responses*. Oxford University Press. http://doi.org/10.1093/oxfordhb/9780199566600.003.0001

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences*, *99*(20), 12917–12922. http://doi.org/10.1073/pnas.192407699

Esri (Environmental Systems Research Institute). (2015). ArcGIS 10.4 for Desktop.

Fischer, L. K., Eichfeld, J., Kowarik, I., & Buchholz, S. (2016). Disentangling urban habitat and matrix effects on wild bee species. *PeerJ*, *4*, e2729. http://doi.org/10.7717/peerj.2729

Foley, J. a, Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., … Snyder, P. K. (2005). Global consequences of land use. *Science (New York, N.Y.)*, *309*(5734), 570–4. http://doi.org/10.1126/science.1111772

Fortel, L., Henry, M., Guilbaud, L., Guirao, A. L., Kuhlmann, M., Mouret, H., … Vaissière, B. E. (2014). Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. *PLoS ONE*, *9*(8), e104679. http://doi.org/10.1371/journal.pone.0104679

Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-Bovy, G., … R Core Team. (2018). Companion to Applied Regression : Package 'car.'

Franzen, M., & Nilsson, S. G. (2010). Both population size and patch quality affect local extinctions and colonizations. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1678), 79–85. http://doi.org/10.1098/rspb.2009.1584

Fürst, M. A., McMahon, D. P., Osborne, J. L., Paxton, R. J., & Brown, M. J. F. (2014). Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature*, *506*(7488), 364–366. http://doi.org/10.1038/nature12977

Gardener, M. (2014). *Community ecology: analytical methods using R and Excel*. Pelagic Publishing

Ltd.

Gathmann, A., & Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, *71*(5), 757–764. http://doi.org/10.1046/j.1365-2656.2002.00641.x

Genersch, E. (2010). Honey bee pathology: current threats to honey bees and beekeeping. *Applied Microbiology and Biotechnology*, *87*(1), 87–97. http://doi.org/10.1007/s00253-010-2573-8

Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., … Vereecken, N. J. (2017). Massively Introduced Managed Species and Their Consequences for Plant–Pollinator Interactions (pp. 147–199). http://doi.org/10.1016/bs.aecr.2016.10.007

Geslin, B., Gauzens, B., Thébault, E., & Dajoz, I. (2013). Plant Pollinator Networks along a Gradient of Urbanisation. *PLoS ONE*, *8*(5), e63421. http://doi.org/10.1371/journal.pone.0063421

Gezon, Z. J., Wyman, E. S., Ascher, J. S., Inouye, D. W., & Irwin, R. E. (2015). The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology and Evolution*, *6*(9), 1044–1054. http://doi.org/10.1111/2041-210X.12375

Ghazoul, J. (2015). Qualifying pollinator decline evidence. *Science*, *348*(6238), 981–982. http://doi.org/10.1126/science.348.6238.981-b

Ghosh, P. (2016). The History Of Singapore’s Coney Island.

Gotelli, N., & Colwell, R. (2011). Estimating species richness. In *Biological Diversity: Frontiers in Measurement and Assessment* (pp. 39–54). http://doi.org/10.2307/3547060

Goulson, D., Nicholls, E., Botias, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957–1255957. http://doi.org/10.1126/science.1255957

Goulson, D., Thompson, J., & Croombs, A. (2018). Rapid rise in toxic load for bees revealed by analysis of pesticide use in Great Britain. *PeerJ*, *6*, e5255. http://doi.org/10.7717/peerj.5255

Greenleaf, S. S., & Kremen, C. (2006). Wild bees enhance honey bees’ pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences*, *103*(37), 13890–13895. http://doi.org/10.1073/pnas.0600929103

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589–596. http://doi.org/10.1007/s00442-007-0752-9

Griesemer, J. R. (1992). Niche: historical perspectives. *Keywords in Evolutionary Biology*, 231–240.

Hall, D. M., Camilo, G. R., Tonietto, R. K., Ollerton, J., Ahrné, K., Arduser, M., … Threlfall, C. G. (2017). The city as a refuge for insect pollinators. *Conservation Biology*, *31*(1), 24–29. http://doi.org/10.1111/cobi.12840

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., … De Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, *12*(10). http://doi.org/10.1371/journal.pone.0185809

Help, C. H. R., Herman, P. M. J., & Soetaert, K. (1998). Indices of diversity and evenness. *Oceanis*, *24*(4), 61–87. http://doi.org/10.1016/j.hal.2004.08.006

Henderson, J. C. (2000). Managing tourism in small islands: The case of pulau ubin, Singapore. *Journal of Sustainable Tourism*, *8*(3), 250–262. http://doi.org/10.1080/09669580008667361

Hennig, E. I., & Ghazoul, J. (2011). Plant-pollinator interactions within the urban environment. *Perspectives in Plant Ecology, Evolution and Systematics*, *13*(2), 137–150. http://doi.org/10.1016/j.ppees.2011.03.003

Hernandez, J. J. L., Frankie, G. W., & Thorp, R. W. (2009). Ecology of Urban Bees: A Review of Current Knowledge and Directions for Future Study. *Cities and the Environment*, *2*(1), 1–15. http://doi.org/http://escholarship.bc.edu/cate/vol2/iss1/3

Herrera, C. M. (1990). Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. *Oikos*, *58*, 277–288. http://doi.org/10.2307/3545218

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, *12*(2), 197–229. http://doi.org/10.1016/0040-5809(77)90042-9

Hopfenmüller, S., Steffan-Dewenter, I., & Holzschuh, A. (2014). Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLoS ONE*, *9*(8). http://doi.org/10.1371/journal.pone.0104439

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. http://doi.org/10.1101/SQB.1957.022.01.039

Janzen, D. H. (1971). Euglossine Bees as Long-Distance Pollinators of Tropical Plants. *Science*, *171*(3967), 203–205. http://doi.org/10.1126/science.171.3967.203

Jarek, S. (2012). Normality test for multivariate variables : Package ‘mvnormtest.’

Jauker, B., Krauss, J., Jauker, F., & Steffan-Dewenter, I. (2013). Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landscape Ecology*, *28*(1), 107–120. http://doi.org/10.1007/s10980-012-9820-6

Kalmar, A., & Currie, D. J. (2006). A global model of island biogeography. *Global Ecology and Biogeography*, *15*(1), 72–81. http://doi.org/10.1111/j.1466-822X.2006.00205.x

Kato, M., Kosaka, Y., Kawakita, A., Okuyama, Y., Kobayashi, C., Phimminith, T., & Thongphan, D. (2008). Plant-pollinator interactions in tropical monsoon forests in Southeast Asia. *American Journal of Botany*, *95*(11), 1375–1394. http://doi.org/10.3732/ajb.0800114

Kearns, C. A., & Inouye, D. W. (1997). Pollinators, Flowering Plants, and Conservation Biology. *BioScience*, *47*(5), 297–307. http://doi.org/10.2307/1313191

Kevan, P. G. (1999). Pollinators as bioindicators of the state of the environment: species, activity and diversity. In *Invertebrate Biodiversity as Bioindicators of Sustainable Landscapes* (pp. 373–393). Elsevier. http://doi.org/10.1016/B978-0-444-50019-9.50021-2

Kindt, R. (2018). Package ‘BiodiversityR’ : Package for Community Ecology and Suitability Analysis.

Klein, A.-M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 303–313. http://doi.org/10.1098/rspb.2006.3721

Kluser, S., & Peduzzi, P. (2007). Global pollinator decline: a literature review. *UNEP/GRID Europe*, (September), 10 pp. http://doi.org/10.1007/s00442-010-1809-8

Knapp, S., Kühn, I., Wittig, R., Ozinga, W. A., Poschlod, P., & Klotz, S. (2008). Urbanization causes shifts in species' trait state frequencies. *Preslia*, *80*(4), 375–388. http://doi.org/10.1677/J0E-09-0034

Kolde, R. (2018). Pretty Heatmaps : Package 'pheatmap.'

Lai, J. L. (2016). *The impact of urbanisation on bee and wasp diversity & their interaction with floral communities*. National University of Singapore.

Leem, J. M. C. (2015). *Exploring a new world of bee and wasp diversity with next-gen sequencing*. National University of Singapore.

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, *23*(11), 1324–1334. http://doi.org/10.1111/geb.12207

Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, *519*(7542), 171–180. http://doi.org/10.1038/nature14258

MacArthur, R. ., & Wilson, E. . (1967). The Theory of Island Biogeography. *Princeton University Press*, *1*, 202. http://doi.org/10.1086/282697

Magurran, A. E. (2004). Measuring Biological Diversity. *Measuring Biological Diversity*, 256. http://doi.org/10.1017/CBO9781107415324.004

Mapsland. (2018). Large location map of Singapore.

Martins, K. T., Gonzalez, A., & Lechowicz, M. J. (2017). Patterns of pollinator turnover and increasing diversity associated with urban habitats. *Urban Ecosystems*, *20*(6), 1359–1371. http://doi.org/10.1007/s11252-017-0688-8

Matteson, K. C., Ascher, J. S., & Langellotto, G. A. (2008). Bee Richness and Abundance in New York City Urban Gardens. *Annals of the Entomological Society of America*, *101*(1), 140–150. http://doi.org/10.1603/0013-8746(2008)101[140:BRAAIN]2.0.CO;2

McFrederick, Q. S., & LeBuhn, G. (2006). Are urban parks refuges for bumble bees Bombus spp. (Hymenoptera: Apidae)? *Biological Conservation*, *129*(3), 372–382. http://doi.org/10.1016/j.biocon.2005.11.004

McKinney, M. L. (2002). Urbanization, Biodiversity, and ConservationThe impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience*, *52*(10), 883–890.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. http://doi.org/10.1016/j.biocon.2005.09.005

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, *11*(2), 161–176. http://doi.org/10.1007/s11252-007-0045-4

Meteorological Service Singapore (MSS). (2018). Climate of Singapore. *Weather.Gov.Sg*.

Michez, D., Vanderplanck, M., & Engel, M. S. (2011). Fossil bees and their plant associates. In *The Systematics Association Special Volume 81: Evolution of Plant-Pollinator Relationships* (pp. 103–164). http://doi.org/10.1017/CBO9781139014113.006

Millennium Ecosystem Assessment. (2005). *Ecosystems and Human Well-being: Biodiversity Synthesis*. *Ecosystems* (Vol. 86). http://doi.org/10.1088/1755-1307/6/3/432007

Ministry of National Development. (2013). Land Use Plan to Support Singapore's Future Population.

Momose, K., Yumoto, T., Nagamitsu, T., Kato, M., Nagamasu, H., Sakai, S., … Inoue, T. (1998). Pollination biology in a lowland dipterocarp forest inSarawak, Malaysia. I. Characteristics of the plant-pollinator communityin a lowland dipterocarp forest. *American Journal of Botany*, *85*(10), 1477–501. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/21684899

Moon, D. C., Moon, J., & Keagy, A. (2010). Direct and Indirect Interactions. *Nature Education Knowledge*, *3*(10), 50. Retrieved from https://www.nature.com/scitable/knowledge/library/direct-and-indirect-interactions-15650000

Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., … Rillig, M. C. (2014). Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, *4*(18), 3514–3524. http://doi.org/10.1002/ece3.1155

Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., & Dorn, S. (2006). Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee-flower relationships. *Biological Conservation*, *130*(4), 604–615. http://doi.org/10.1016/j.biocon.2006.01.023

Nagamitsu, T., & Inoue, T. (1997). Aggressive foraging of social bees as a mechanism of floral resource partitioning in an Asian tropical rainforest. *Oecologia*, *110*(3), 432–439. http://doi.org/10.1007/s004420050178

National Environment Agency of Singapore. (2018). Pest Control : Mosquito Control. *Ministry of the Environment and Water Resources*.

National Parks Board. (n.d.). Pasir Ris Park - Guide. Retrieved from https://www.nparks.gov.sg/-/media/nparks-real-content/gardens-parks-and-nature/diy-walk/diy-walk-pdf-files/pasir_ris_park_guide.pdf

National Parks Board. (2009). Conserving Our Biodiversity : Singapore's National Biodiversity Strategy and Action Plan. Retrieved from https://www.nparks.gov.sg/biodiversity/our-national-plan-for-conservation//~/media/nparks-real-content/biodiversity/national-plan/nbsap_2009.pdf

National Parks Board. (2010). Forth National Report to the Convention on Biological Diversity (CBD).

National Parks Board. (2015). Coney Island Park opens to the public.

National Parks Board. (2015). Fifth National Report to the Convention on Biological Diversity (CBD) (2010 - 2014).

National Parks Board. (2016). City in a Garden. Retrieved from https://www.nparks.gov.sg/about-us/city-in-a-garden

National Parks Board. (2017). Kampong Life. Retrieved from https://www.nparks.gov.sg/gardens-parks-and-nature/parks-and-nature-reserves/kamponglife

National Parks Board. (2018). Chek Jawa Wetlands. Retrieved from https://www.nparks.gov.sg/gardens-parks-and-nature/parks-and-nature-reserves/chekjawawetlands

National Parks Board. (2018). Do's and Don'ts : Animal Advisories. *Ministry of National Development*.

National Parks Board. (2018). Hort Park. Retrieved from https://www.nparks.gov.sg/gardens-parks-and-nature/parks-and-nature-reserves/hortpark

National Parks Board. (2018d). Pasir Ris Park.

Newman, P. (2014). Biophilic urbanism: a case study on Singapore. *Australian Planner*, *51*(1), 47–65. http://doi.org/10.1080/07293682.2013.790832

Ng, K. Y. (2015). *Population genomics of cryptic carpenter bee species (Hymenoptera: Apidae: Xylocopa) in Singapore*. National University of Singapore.

Ng, P. K. L., Corlett, R., & Tan, H. T. W. (2011). *Singapore biodiversity: an encyclopedia of the natural environment and sustainable development*. Editions Didier Millet.

Nieto, A., Roberts, S. P. M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., … Michez, D. (2014). European Red List of bees. *Luxembourg: Publication Office of the European Union*.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2018). Package 'vegan': Community Ecology Package. Retrieved from https://cran.r-project.org/package=vegan

Oliveira, U., Brescovit, A. D., & Santos, A. J. (2017). Sampling effort and species richness assessment: a case study on Brazilian spiders. *Biodiversity and Conservation*, *26*(6), 1481–1493. http://doi.org/10.1007/s10531-017-1312-1

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. http://doi.org/10.1111/j.1600-0706.2010.18644.x

Ong, T. (2017). Beneath St. John's Island's tranquility is a past linked to drugs, diseases, & political detainees. *Mothership*.

Ooi, E.-E., Goh, K.-T., & Gubler, D. J. (2006). Dengue Prevention and 35 Years of Vector Control in Singapore. *Emerging Infectious Diseases*, *12*(6), 887–893. http://doi.org/10.3201/10.3201/eid1206.051210

Pasquet, R. S., Peltier, A., Hufford, M. B., Oudin, E., Saulnier, J., Paul, L., … Gepts, P. (2008). Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. *Proceedings of the National Academy of Sciences*, *105*(36), 13456–13461. http://doi.org/10.1073/pnas.0806040105

Peters, K., Elands, B., & Buijs, A. (2010). Social interactions in urban parks: Stimulating social cohesion? *Urban Forestry & Urban Greening*, *9*(2), 93–100. http://doi.org/10.1016/j.ufug.2009.11.003

Piélou, E. C. (1975). Ecological Diversity (Wiley.). *New-York*.

Pocheville, A. (2015). The Ecological Niche: History and Recent Controversies. In *Handbook of Evolutionary Thinking in the Sciences* (pp. 547–586). Dordrecht: Springer Netherlands. http://doi.org/10.1007/978-94-017-9014-7_26

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology and Evolution*. http://doi.org/10.1016/j.tree.2010.01.007

Prado, S. G., Ngo, H. T., Florez, J. A., & Collazo, J. A. (2017). Sampling bees in tropical forests and agroecosystems: a review. *Journal of Insect Conservation*. http://doi.org/10.1007/s10841-017-0018-8

Puniamoorthy, J., Grootaert, P., Foo, M., Ascher, J., & Meier, R. (2014). *Mangrove Insect Project (MIP): species discovery, inventory and habitat assessment*. Singapore.

Qiu, L., Lindberg, S., & Nielsen, A. B. (2013). Is biodiversity attractive?-On-site perception of recreational and biodiversity values in urban green space. *Landscape and Urban Planning*, *119*, 136–146. http://doi.org/10.1016/j.landurbplan.2013.07.007

R Core Team. (2018). The R Stats Package.

Rasmont, P., Franzén, M., Lecocq, T., Harpke, A., Roberts, S. P. M., Biesmeijer, J. C., … others. (2015). *Climatic risk and distribution atlas of European bumblebees* (Vol. 10). Pensoft Publishers.

Rodriguez-Girones, M. A., & Santamaria, L. (2006). A new algorithm to calculate the nestedness temperature of presence-absence matrices. *Journal of Biogeography*, *33*(5), 924–935. http://doi.org/10.1111/j.1365-2699.2006.01444.x

Roscoe, C. (2015). *Supporting pollinator communities and supported by stakeholders ? Measuring the ecological and social values of green roofs in Singapore*. Free University of Brussels.

Roubik, D. W. (1989a). Foraging and pollination. In *Ecology and natural history of tropical bees* (pp. 25–160). Cambridge: Cambridge University Press. http://doi.org/10.1017/CBO9780511574641.002

Roubik, D. W. (1989b). Nesting and reproductive biology. In *Ecology and natural history of tropical bees* (pp. 161–312). Cambridge: Cambridge University Press. http://doi.org/10.1017/CBO9780511574641.003

Roubik, D. W., Sakai, S., & Karim, A. A. H. (2005). Pollination ecology and the rain forest: Sarawak studies. *Ecological Studies*. http://doi.org/10.1007/b138701

RStudio Team. (2018). RStudio : Open source and enterprise-ready professional software for R.

Samuelson, A. E., Gill, R. J., Brown, M. J. F., & Leadbeater, E. (2018). Lower bumblebee colony reproductive success in agricultural compared with urban environments. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1881), 20180807. http://doi.org/10.1098/rspb.2018.0807

Santos, G. M. de M., Aguiar, C. M. L., & Mello, M. A. R. (2010). Flower-visiting guild associated with the Caatinga flora: trophic interaction networks formed by social bees and social wasps with plants. *Apidologie*, *41*(4), 466–475. http://doi.org/10.1051/apido/2009081

Schoener, T. W. (1989). Food Webs From the Small to the Large: The Robert H. MacArthur Award Lecture. *Ecology*, *70*(6), 1559–1589. http://doi.org/10.2307/1938088

Seress, G., & Liker, A. (2015). Habitat urbanization and its effects on birds. *Acta Zoologica Academiae Scientiarum Hungaricae*, *61*(4), 373–408. http://doi.org/10.17109/AZH.61.4.373.2015

Shannon, C. E. (1949). Communication theory of secrecy systems. *Bell System Technical Journal*, *28*(4), 656 – 715.

Simpson, E. H. (1949). Measurement of species diversity. *Nature (Lond)*, *163*(688).

Singapore Department of Statistics (DOS). (2017). Population and Population Structure.

Singapore Land Authority. (2018). Total Land Area of Singapore. *Data.Gov.Sg*. Retrieved from https://data.gov.sg/dataset/total-land-area-of-singapore

Smith, B., & Wilson, J. B. (1996). A Consumer's Guide to Evenness Indices. *Oikos*, *76*(1), 70. http://doi.org/10.2307/3545749

Smith, E. P., & van Belle, G. (1984). Nonparametric Estimation of Species Richness. *Biometrics*, *40*(1), 119. http://doi.org/10.2307/2530750

Soh, J. Y. E. (2014). *Diversity and trap-nesting studies of Singaporean Megachile bees to inform monitoring and management of tropical pollinators*. National University of Singapore.

Sørensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter / Kongelige Danske Videnskabernes Selskab*, *5*(4), 1 – 34.

Soria-Auza, R. W., & Kessler, M. (2008). The influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia. *Diversity and Distributions*, *14*(1), 123–130. http://doi.org/10.1111/j.1472-4642.2007.00433.x

Spengler, A., Hartmann, P., Buchori, D., & Schulze, C. H. (2011). How island size and isolation affect bee and wasp ensembles on small tropical islands: a case study from Kepulauan Seribu, Indonesia. *Journal of Biogeography*, *38*(2), 247–258. http://doi.org/10.1111/j.1365-2699.2010.02395.x

Steffen, W., Richardson, K., Rockstrom, J., Cornell, S. E., Fetzer, I., Bennett, E. M., … Sorlin, S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, *347*(6223), 1259855–1259855. http://doi.org/10.1126/science.1259855

Stroud, J. T., Bush, M. R., Ladd, M. C., Nowicki, R. J., Shantz, A. A., & Sweatman, J. (2015). Is a community still a community? Reviewing definitions of key terms in community ecology. *Ecology and Evolution*, *5*(21), 4757–4765. http://doi.org/10.1002/ece3.1651

Tan, K. W. (2006). A greenway network for singapore. *Landscape and Urban Planning*, *76*(1–4), 45–66. http://doi.org/10.1016/j.landurbplan.2004.09.040

Tan, P. Y., & Abdul Hamid, A. R. bin. (2014). Urban ecological research in Singapore and its relevance to the advancement of urban ecology and sustainability. *Landscape and Urban Planning*, *125*, 271–289. http://doi.org/10.1016/j.landurbplan.2014.01.019

Tan, Y. G. (2017). *Island biogeorgaphy of bees and wasps on Singapore's offshore islands*. National University of Singapore.

Tee, Y. X. (2017). *Integrating Morphology and Next-generation Sequencing (NGS) for Understanding Bee Species in Singapore*. NATIONAL UNIVERSITY OF SINGAPORE.

Tehel, A., Brown, M. J., & Paxton, R. J. (2016). Impact of managed honey bee viruses on wild bees. *Current Opinion in Virology*, *19*, 16–22. http://doi.org/10.1016/j.coviro.2016.06.006

Teo, A. Y. L. (2017). *Park type predicts flower-visiting insect assemblages in a tropical asian city*. NATIONAL UNIVERSITY OF SINGAPORE.

Teo, R. (2012). Butterfly Hill - Where Tigers Fly! *Mygreenspace - A Quarterly Newsletter by NParks on Conservations Issues, Lifestyle and Gardening Tips*, *1*(12).

The R Foundation. (2018). The R Project for Statistical Computing.

Theodorou, P., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T. E., & Paxton, R. J. (2016). Pollination services enhanced with urbanization despite increasing pollinator parasitism. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1833), 20160561. http://doi.org/10.1098/rspb.2016.0561

Tjong, F. A. (2016). *Genomic Exploration of native stingless bees (Apidae: Meliponini) in Singapore*. National University of Singapore.

Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, *143*(10), 2270–2279. http://doi.org/10.1016/j.biocon.2009.12.004

United Nations. (2017). World Population Prospects 2017. *United Nations, Department of Economic and Social Affairs, Population Division*.

United Nations. (2018). World Urbanization Prospects: The 2018 Revision. *United Nations, Department of Economic and Social Affairs, Population Division*.

Urban Redevelopment Authority. (2016). Master Plan 2014 Region Boundary. *Data.Gov.Sg*.

Urban Redevelopment Authority. (2017). Master Plan 2014 Land Use.

Uuemaa, E., Antrop, M., Marja, R., Roosaare, J., & Mander, Ü. (2009). Landscape Metrics and Indices : An Overview of Their Use in Landscape Research. *Living Reviews in Landscape Research*, *3*, 1–28.

Vanbergen, A. J. (2014). Landscape alteration and habitat modification: Impacts on plant-pollinator systems. *Current Opinion in Insect Science*. http://doi.org/10.1016/j.cois.2014.09.004

Vereecken, N. J., Dufrêne, E., & Aubert, M. (2015). Rapport de synthèse sur les risques liés à l'introduction de ruches de l'abeille domestique (Apis mellifera) vis-à-vis des abeilles sauvages et de la flore. Sur la coexistence entre l'abeille domestique et les abeilles sauvages.

Villebrun, M. (2016). *Investigating wild bee community structure at the landscape scale to evaluate the ecological performance of a permaculture micro-farm in a comparative approach*. ULiège.

Vitousek, P. M. (1997). Human Domination of Earth's Ecosystems. *Science*, *277*(5325), 494–499. http://doi.org/10.1126/science.277.5325.494

Wai, L. K. (2014). Coney Island to open to public in 2015.

Walther, B. A., & Moore, J. L. (2005). The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography*, *28*(6), 815–829. http://doi.org/10.1111/j.2005.0906-7590.04112.x

Wastian, L., Unterweger, P. A., & Betz, O. (2016). Influence of the reduction of urban lawn mowing on wild bee diversity (Hymenoptera, Apoidea). *Journal of Hymenoptera Research*, *49*, 51.

Wen, J. N. (2014). Singapore, A City in a Garden : Enhancing Greenery and Biodiversity.

Wen, Z., Soh, W., Wen, R., & Ngiam, R. (2013). Flower-visiting bees and wasps in Singapore parks (Insecta: Hymenoptera), *6*, 153–172.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., … Steffan-Dewenter, I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, *78*(4), 653–671. http://doi.org/10.1890/07-1292.1

Wilson, J. S., Griswold, T., & Messinger, O. J. (2008). Sampling Bee Communities (Hymenoptera: Apiformes) in a Desert Landscape: Are Pan Traps Sufficient? *Journal of the Kansas Entomological Society*, *81*(3), 288–300. http://doi.org/10.2317/JKES-802.06.1

Wilson, J. S., Jahner, J. P., Starley, L., Calvin, C. L., Ikerd, H., & Griswold, T. (2016). Sampling bee communities using pan traps: alternative methods increase sample size. *Journal of Insect Conservation*, *20*(5), 919–922. http://doi.org/10.1007/s10841-016-9914-6

Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G., & Aizen, M. A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, *90*(8), 2068–76. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/19739369

Wright, I. R., Roberts, S. P. M., & Collins, B. E. (2015). Evidence of forage distance limitations for small bees (Hymenoptera: Apidae). *European Journal of Entomology*. http://doi.org/10.14411/eje.2015.028

Yee, A. T. K., Corlett, R. T., Liew, S. C., & Tan, H. T. W. (2011). The vegetation of Singapore — an updated map. *Gardens' Bulletin Singapore*, *63*(1&2), 205–212.

Zalasiewicz, J., Williams, M., Steffen, W., & Crutzen, P. (2010). The New World of the Anthropocene. *Environmental Science & Technology*, *44*(7), 2228–2231. http://doi.org/10.1021/es903118j

Zotarelli, H. G. S., Evans, D. M., Bego, L. R., & Sofia, S. H. (2014). A Comparison of Social Bee–Plant Networks between Two Urban Areas. *Neotropical Entomology*, *43*(5), 399–408. http://doi.org/10.1007/s13744-014-0227-8

8 APPENDIXES

Dairy Farm (DF)

© Julien Clerbois

© Julien Clerbois

© Julien Clerbois

© Dairy Farm natural rock climbing

Appendix 1: Photographs of Dairy Farm's habitats and distinctive features.

Hort Park (HP)

© Julien Clerbois

© Landscape Engineering Pte Ltd

© Landscape Engineering Pte Ltd

© Julien Clerbois

Appendix 2: Photographs of Hort Park's habitats and distinctive features.

St John’s Island (SJ)

Appendix 3: Photographs of St John’s Island’s habitats and distinctive features.

Coney Island (CI)

Appendix 4: Photographs of Coney Island’s habitats and distinctive features.

Pulau Ubin (PU)

Appendix 5: Photographs of Pulau Ubin's habitats and distinctive features.

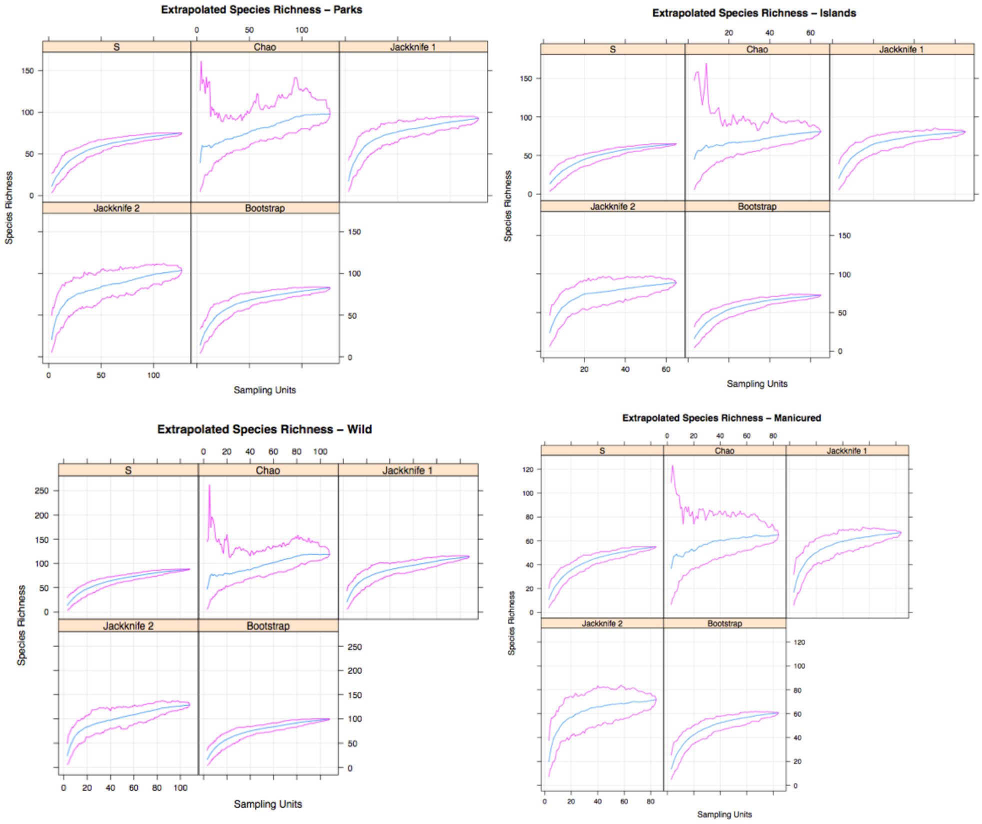
Pasir Ris (PR)

Appendix 6: Photographs of Pasir Ris' habitats and distinctive features.

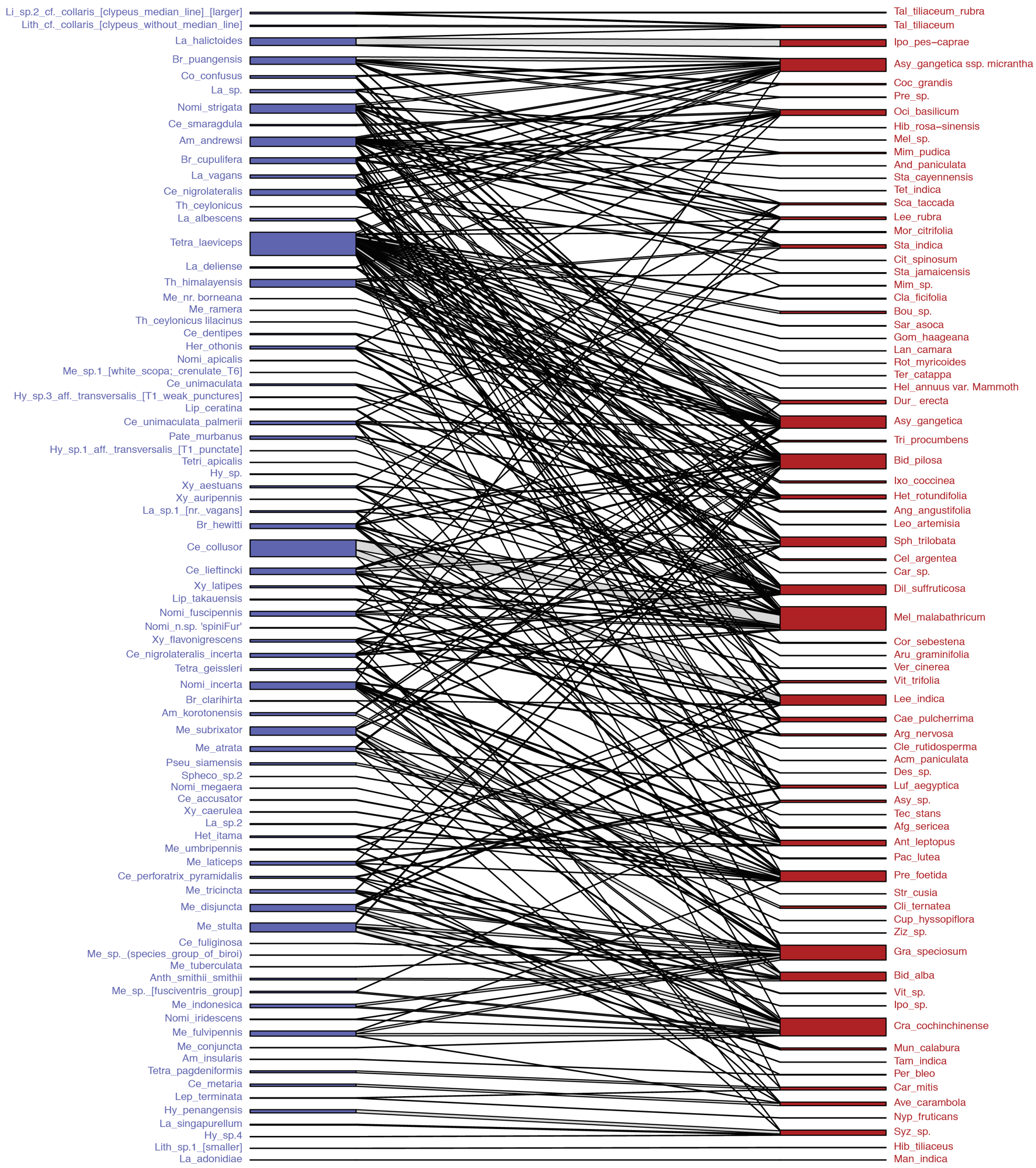
		Observed SR	Extrapolated SR				Obs.SR / Extrap.SR min (%)	Obs.SR / Extrap.SR max (%)	Obs.SR / Extrap.SR mean (%)
			Chao	Jackknife1	Jackknife2	Bootstrap			
Habitat	**Parks**	75	97,96	92,86	103,74	82,8	72,30	90,58	81,44
	Islands	65	80,75	80,75	88,63	72,33	73,34	89,87	81,60
Management	**Wild**	88	118,44	113,76	128,58	99,27	68,44	88,65	78,54
	Manicured	55	65,16	66,86	71,82	60,73	76,58	90,56	83,57
Site	**CI**	22	32,29	32,29	37,29	26,71	59,00	82,37	70,68
	SJ	34	43,36	44,21	48,9	38,88	69,53	87,45	78,49
	PU	54	81,92	73,55	86,11	62,45	62,71	86,47	74,59
	HP	30	53,87	45,38	58,38	36,16	51,39	82,96	67,18
	PR	40	49,85	50,75	55,66	45,03	71,86	88,83	80,35
	DF	62	84,74	79,68	90,42	69,83	68,57	88,79	78,68

Appendix 7: Observed and extrapolated species richness (SR) in each habitat (yellow), management type (blue) and site (green). Chao, Jackknife1, Jackknife2 and Bootstrap are non-parametric species richness estimators. Site names: CI = Coney Island, SJ = St John's Island, PU = Pulau Ubin, HP = Hort Park, PR = Pasir Ris, DF = Dairy Farm.

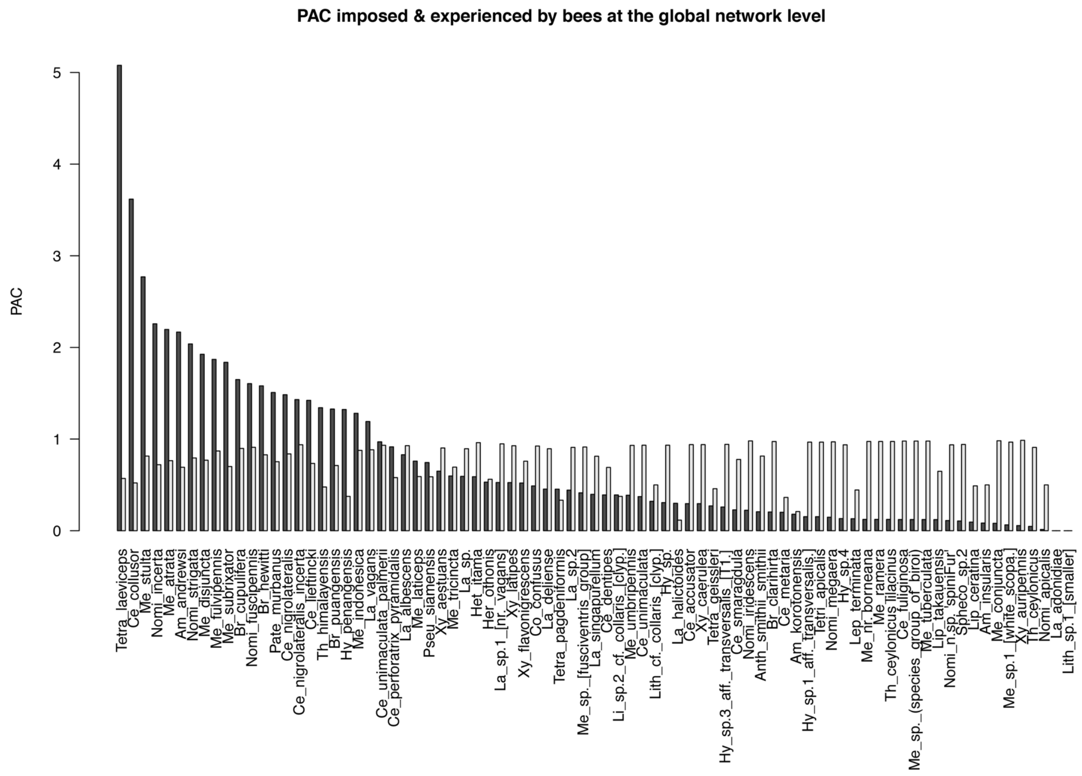
Extrapolated species richness - Habitats and management types



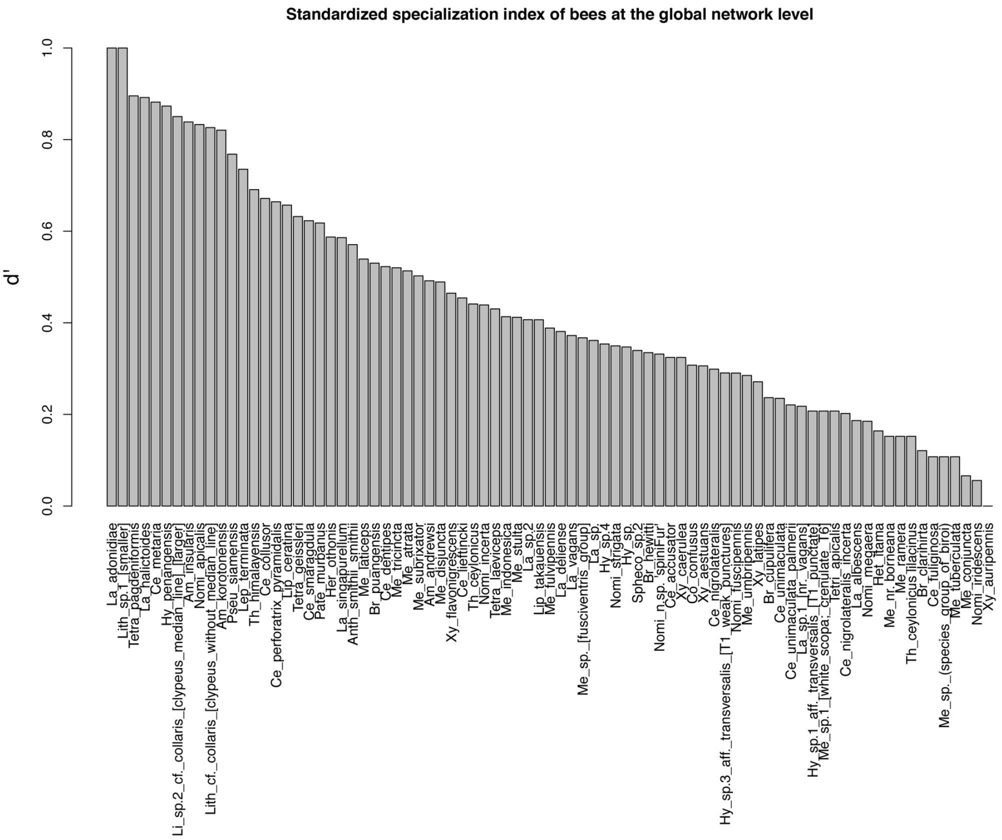
Appendix 8: Habitats and management types' extrapolated species richness with non-parametric estimators (Chao, Jackknife1, Jackknife2 and Bootstrap).



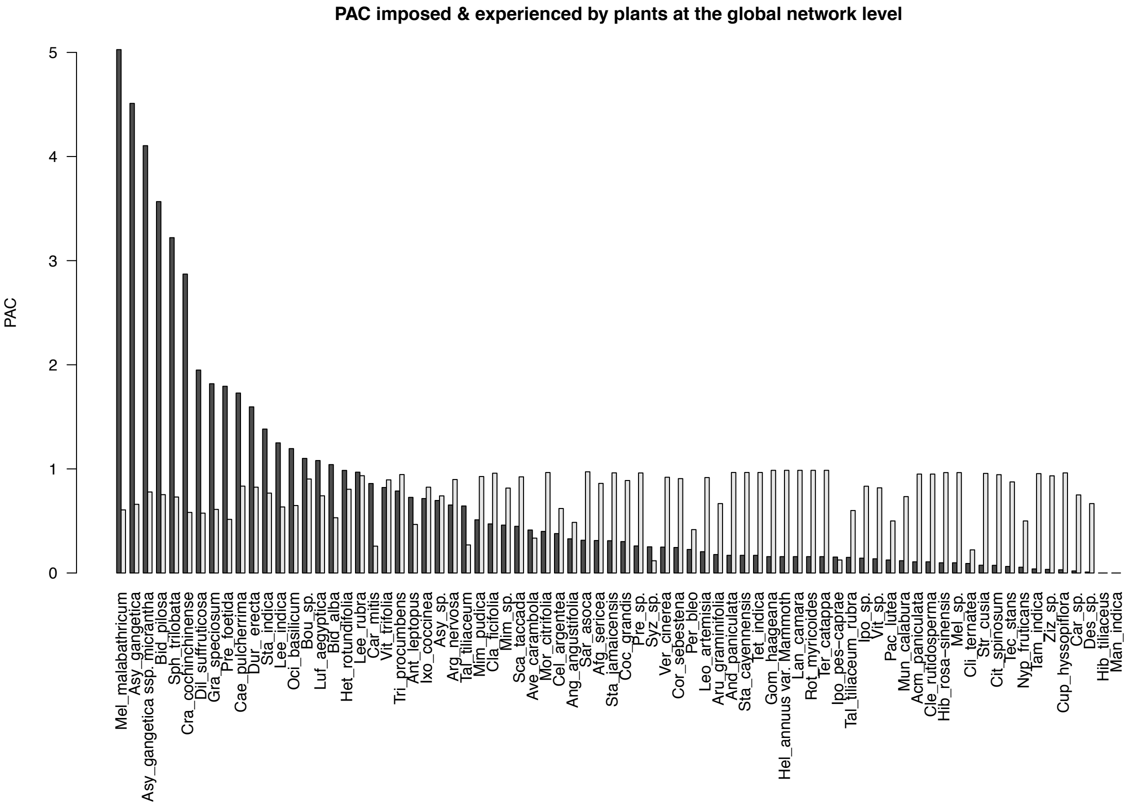
Appendix 9: Global flower-bee visitation network. The upper level represents the flower species (red), the lower level represents the bee species (blue). Boxes' width varies in proportion to the species abundance whereas the links' width varies in proportion to the number of interactions observed.



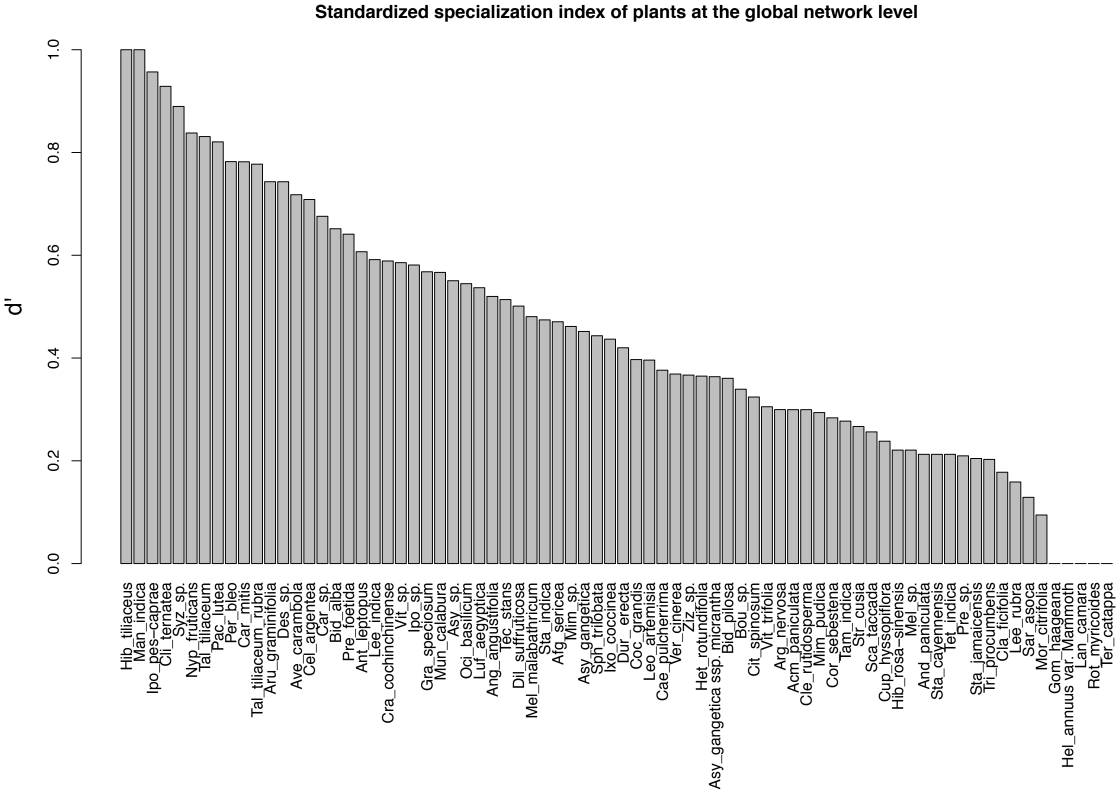
Appendix 10: Potential apparent competition (PAC) imposed and experienced by bees at the global network level. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees.



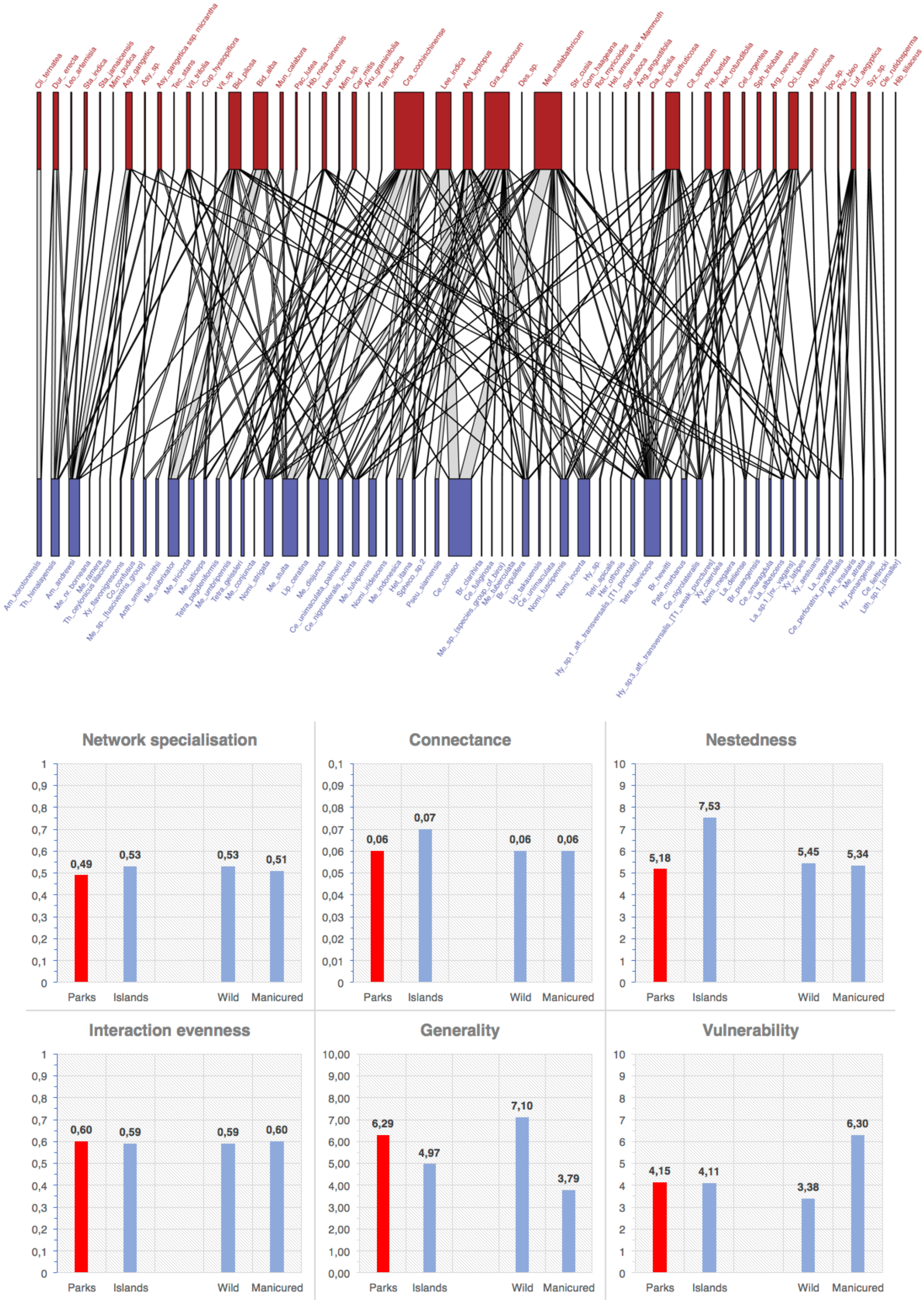
Appendix 11: Standardized specialization index (d') of bees at the global network level.



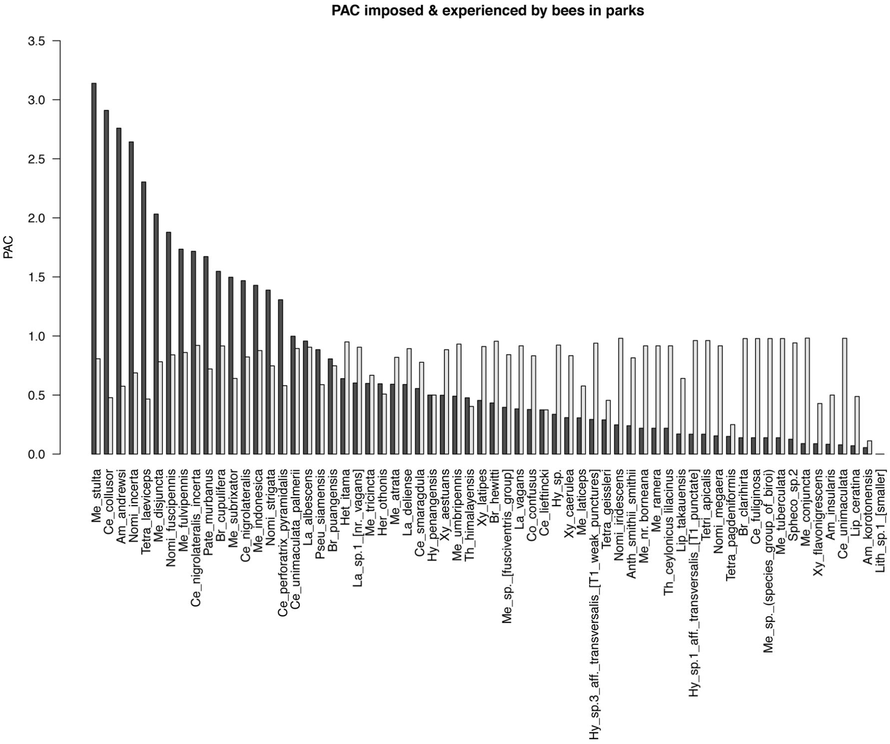
Appendix 12: Potential apparent competition (PAC) imposed and experienced by plants at the global network level. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees.



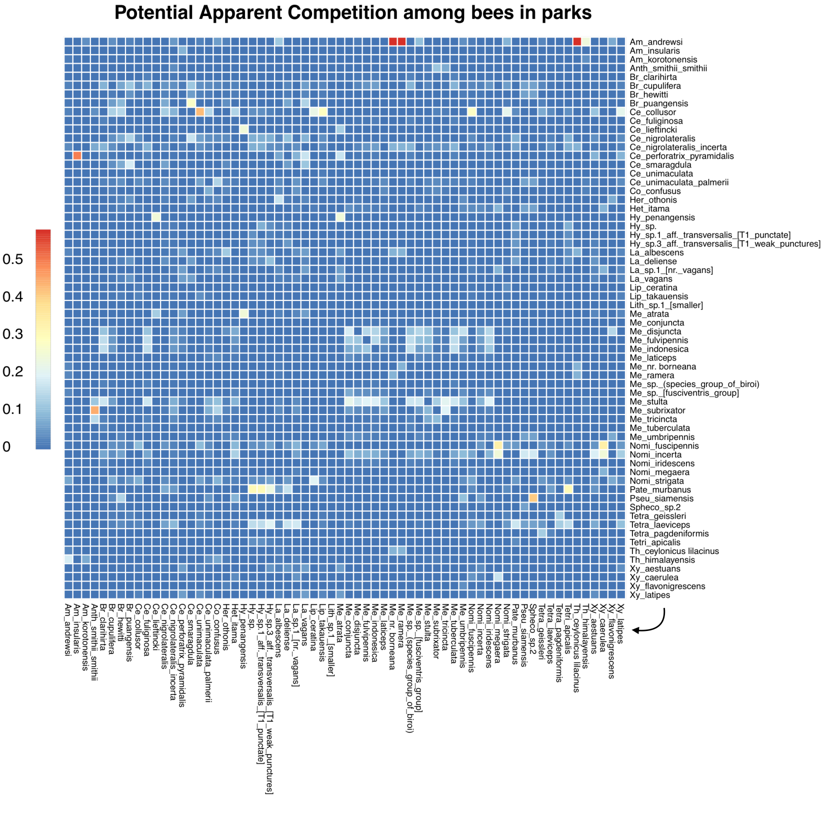
Appendix 13: Standardized specialization index (d') of plants at the global network level.



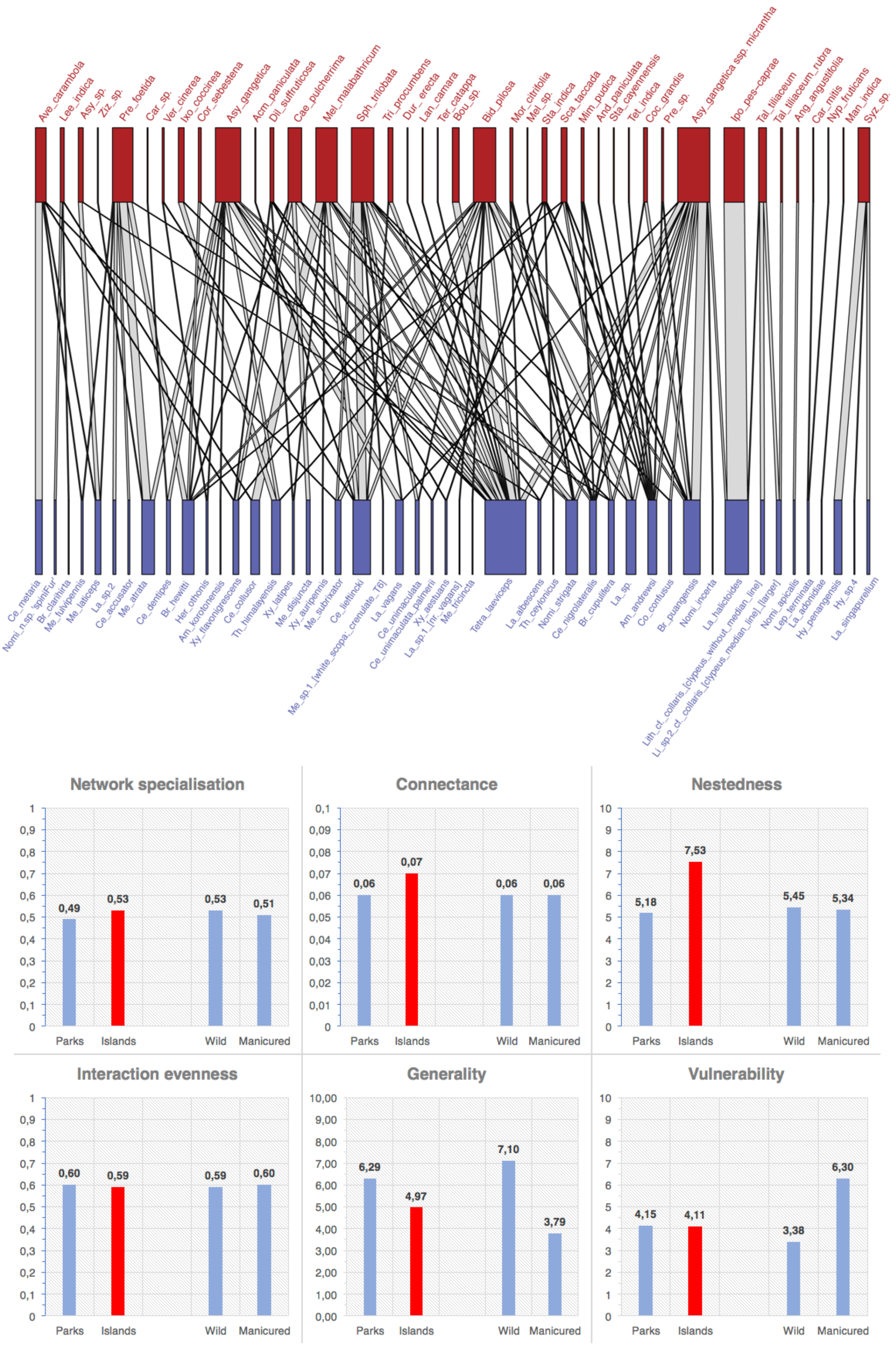
Appendix 14: Flower-bee visitation network and associated indices - Parks.



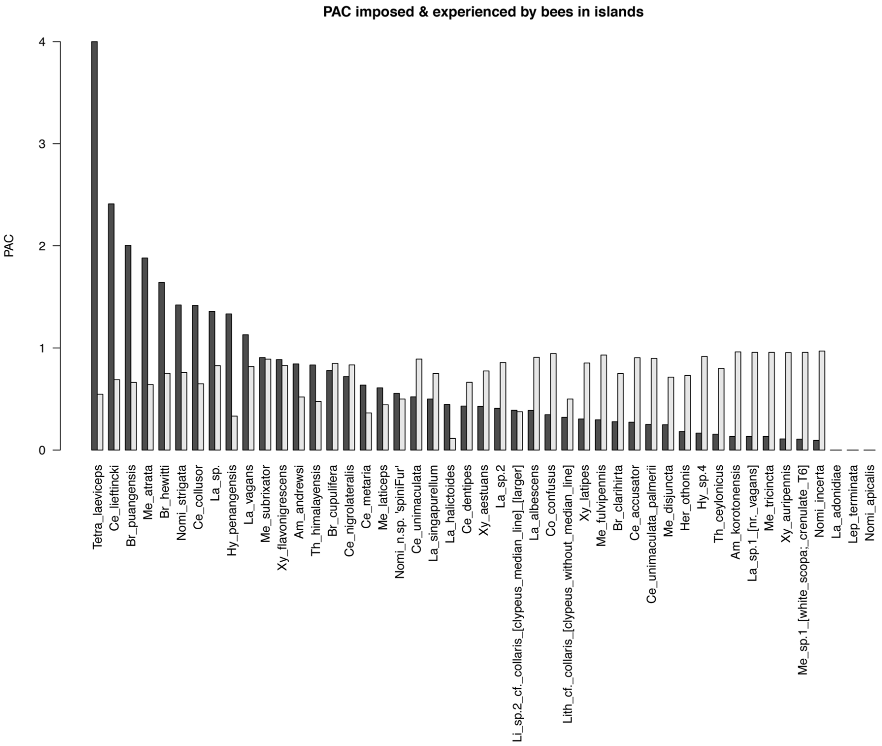
Appendix 15: Potential apparent competition (PAC) imposed and experienced by bees in parks. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees.



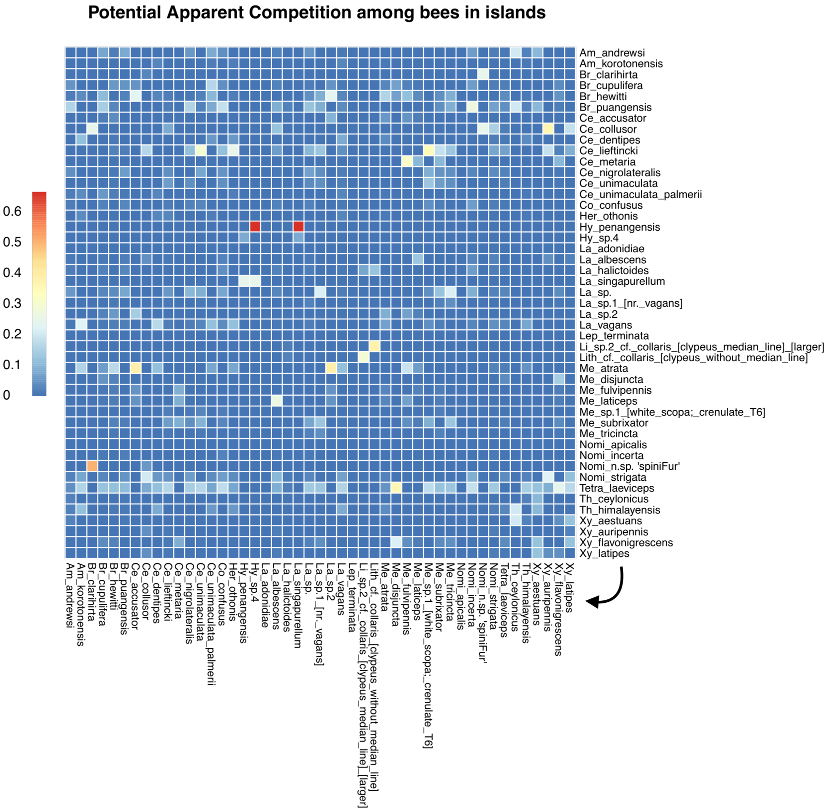
Appendix 16: Heatmap representing the Potential apparent competition (PAC) imposed and experienced by bees in parks. Bee species on the x-axis (at the tip of the arrow) are experiencing competition by the bees on the y-axis (at the base of the arrow).



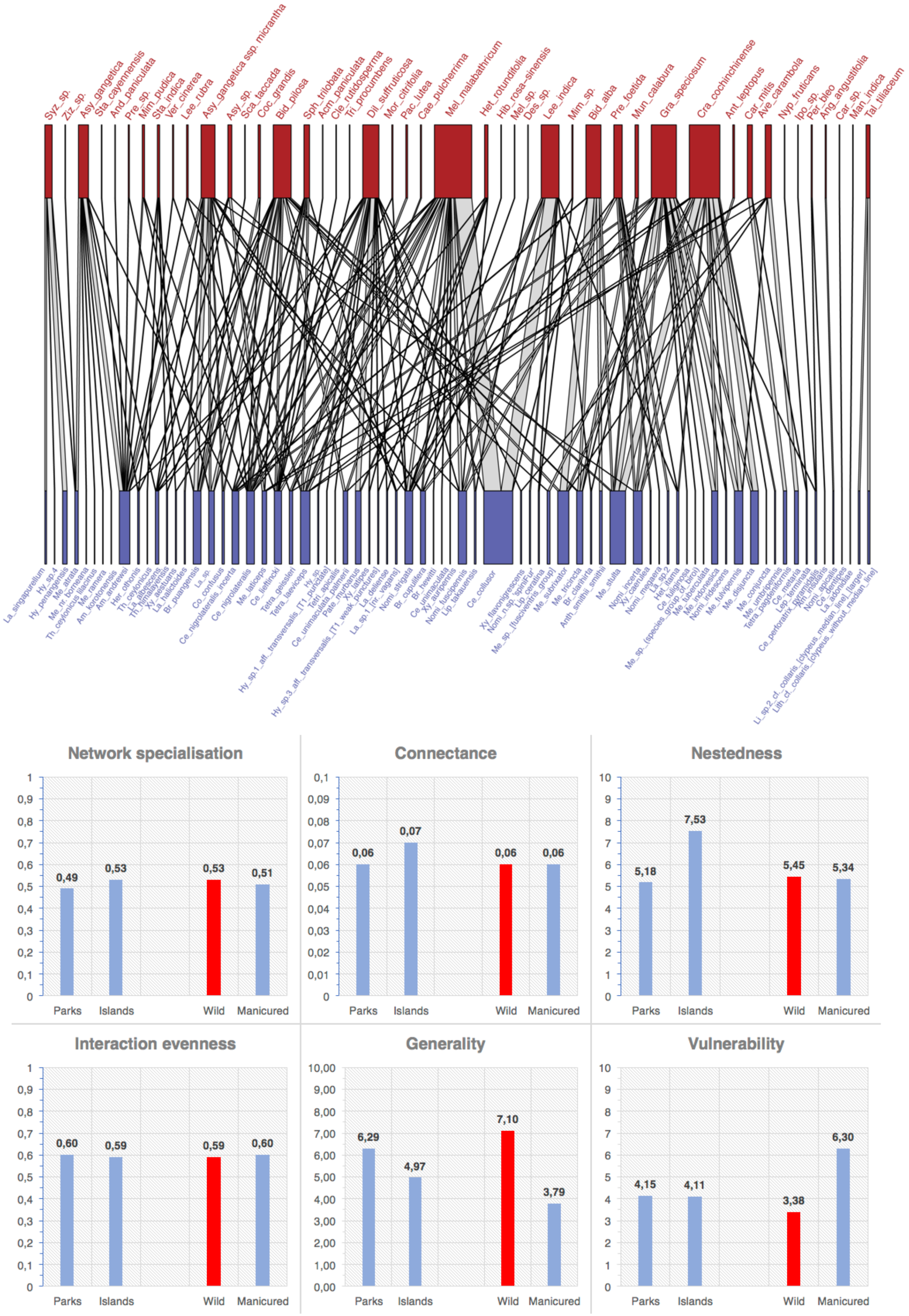
Appendix 17: Flower-bee visitation network and associated indices - Islands.



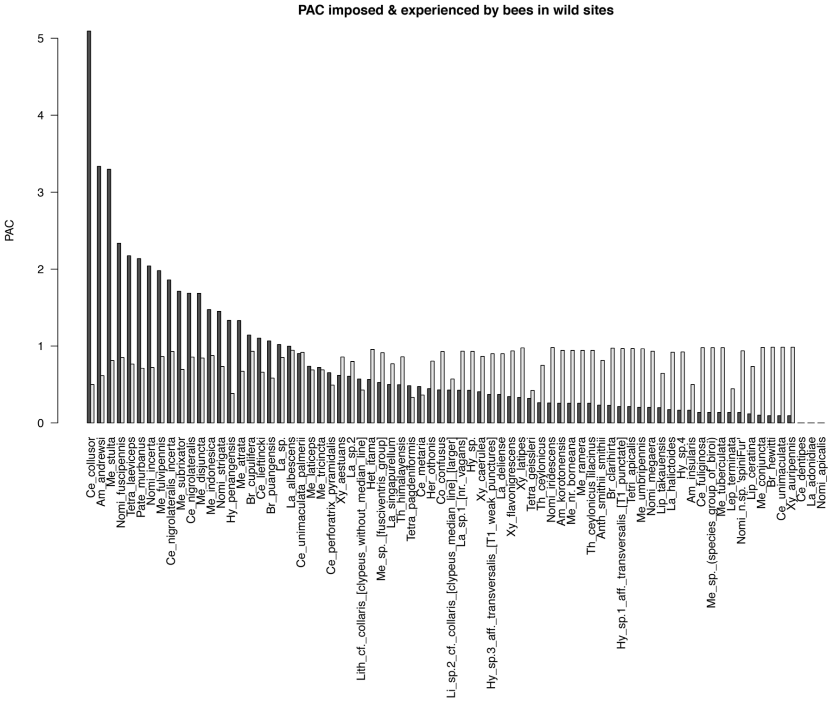
Appendix 18: Potential apparent competition (PAC) imposed and experienced by bees in islands. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees.



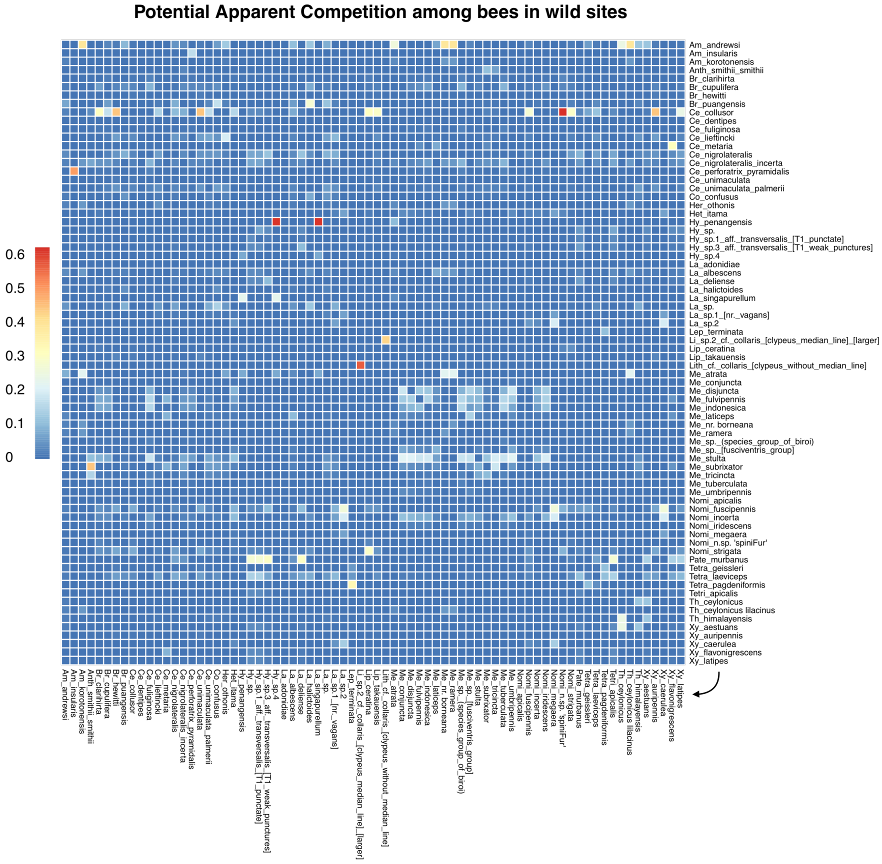
Appendix 19: Heatmap representing the Potential apparent competition (PAC) imposed and experienced by bees in islands. Bee species on the x-axis (at the tip of the arrow) are experiencing competition by the bees on the y-axis (at the base of the arrow).



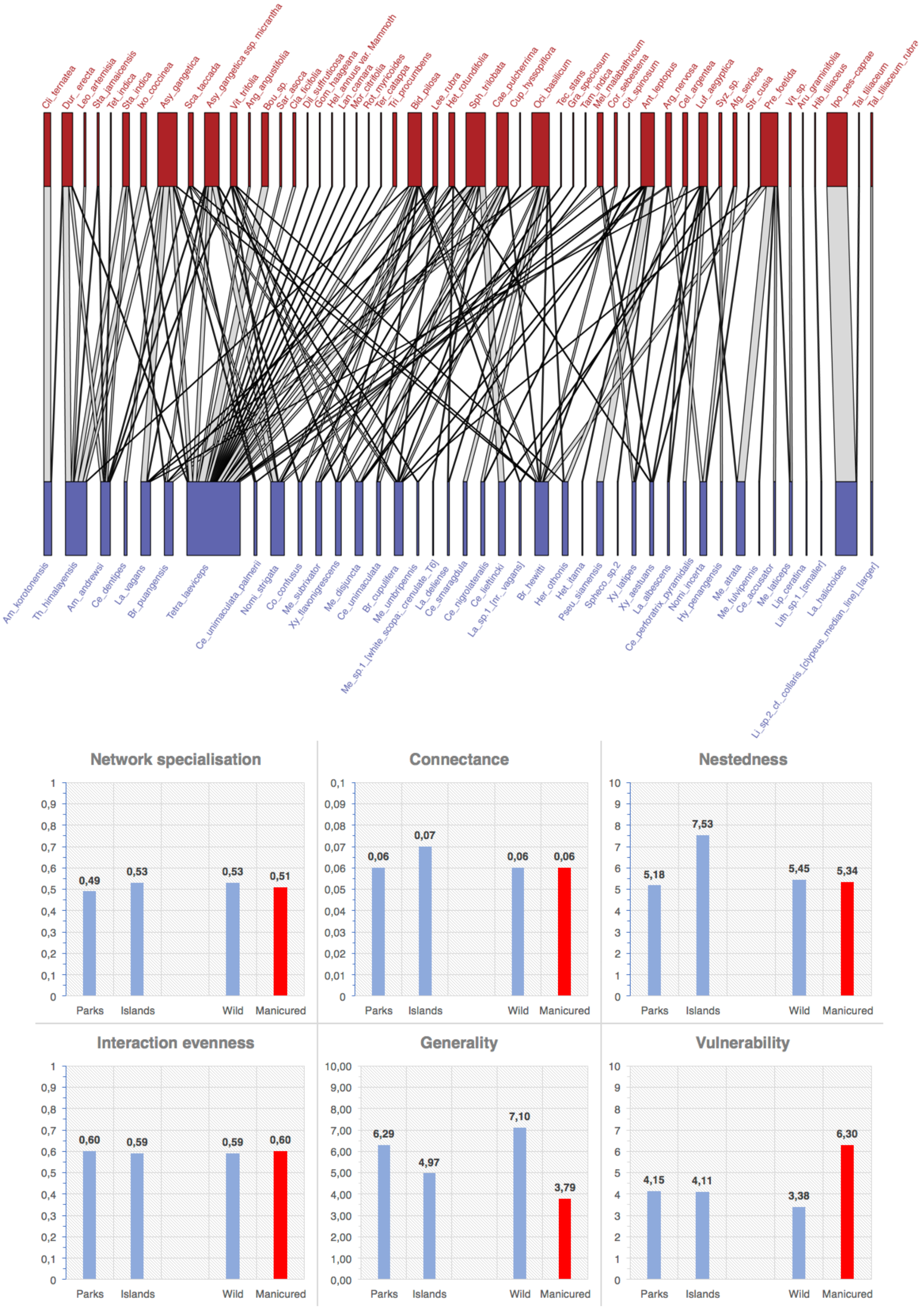
Appendix 20: Flower-bee visitation network and associated indices - Wild sites.



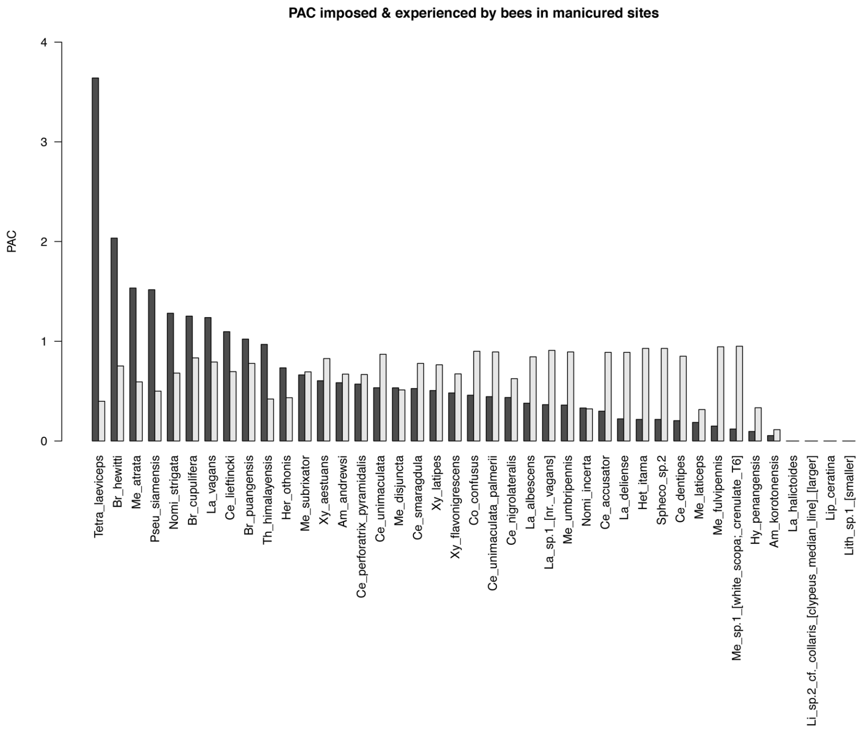
Appendix 21: Potential apparent competition (PAC) imposed and experienced by bees in wild sites. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees.



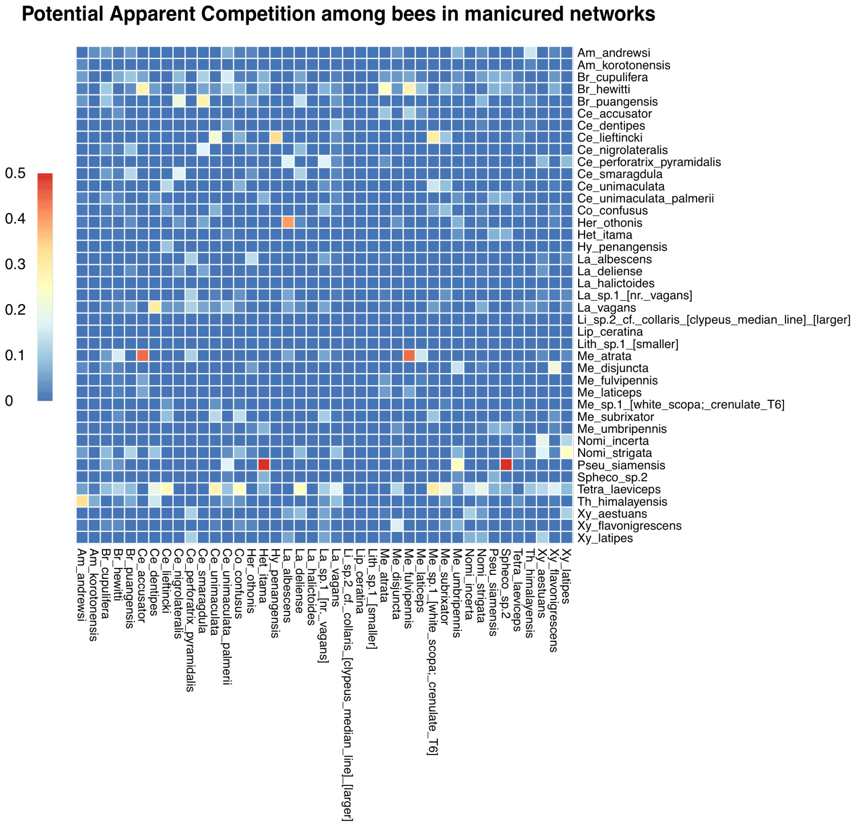
Appendix 22: Heatmap representing the Potential apparent competition (PAC) imposed and experienced by bees in wild sites. Bee species on the x-axis (at the tip of the arrow) are experiencing competition by the bees on the y-axis (at the base of the arrow).



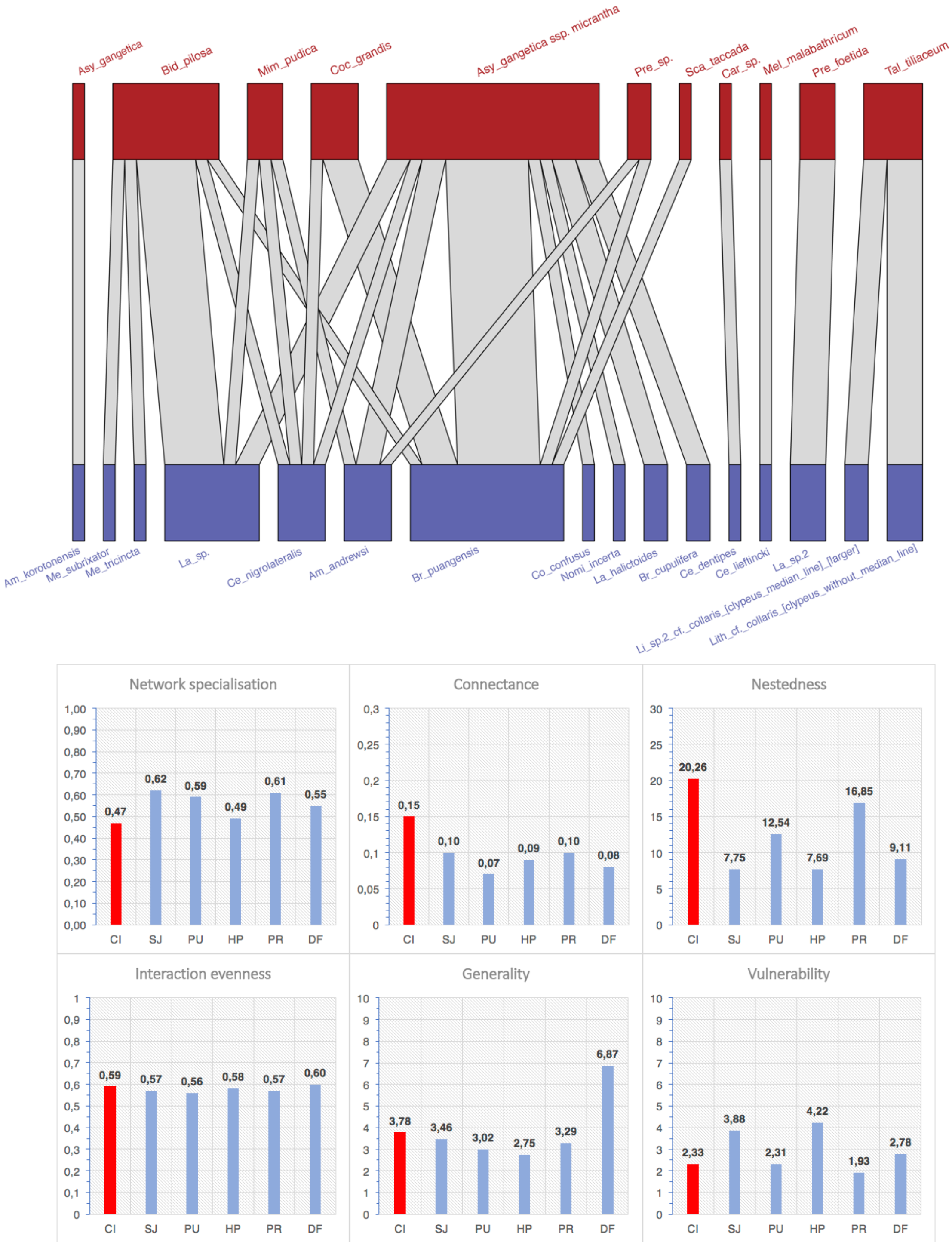
Appendix 23: Flower-bee visitation network and associated indices - Manicured sites.



Appendix 24: Potential apparent competition (PAC) imposed and experienced by bees in manicured sites. For each species, the black barplot refers to the competition imposed to other bees whereas the grey one refers to the competition experienced by other bees.



Appendix 25: Heatmap representing the Potential apparent competition (PAC) imposed and experienced by bees in manicured sites. Bee species on the x-axis (at the tip of the arrow) are experiencing competition by the bees on the y-axis (at the base of the arrow).



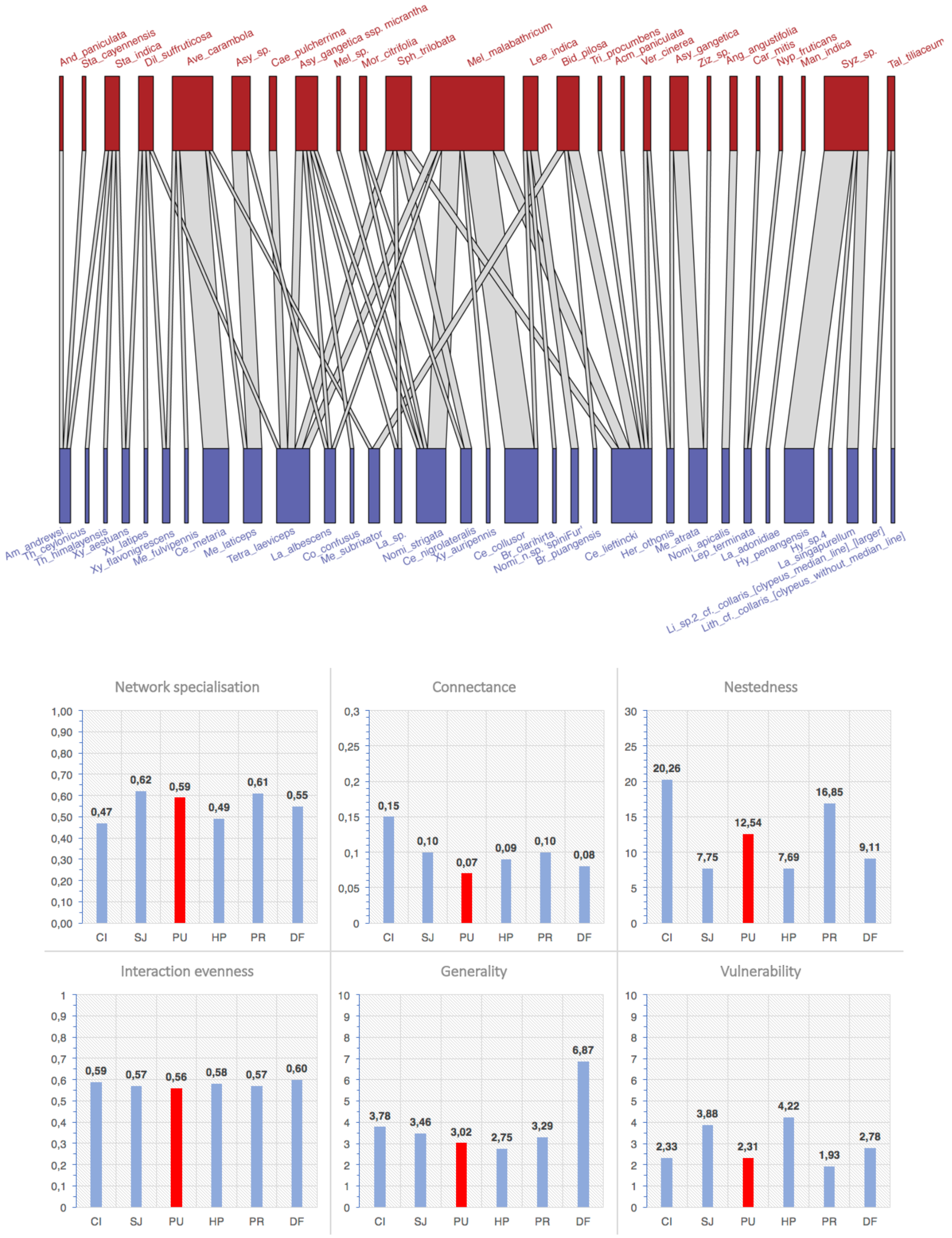
Appendix 26: Flower-bee visitation network and associated indices - Coney Island.

Legend

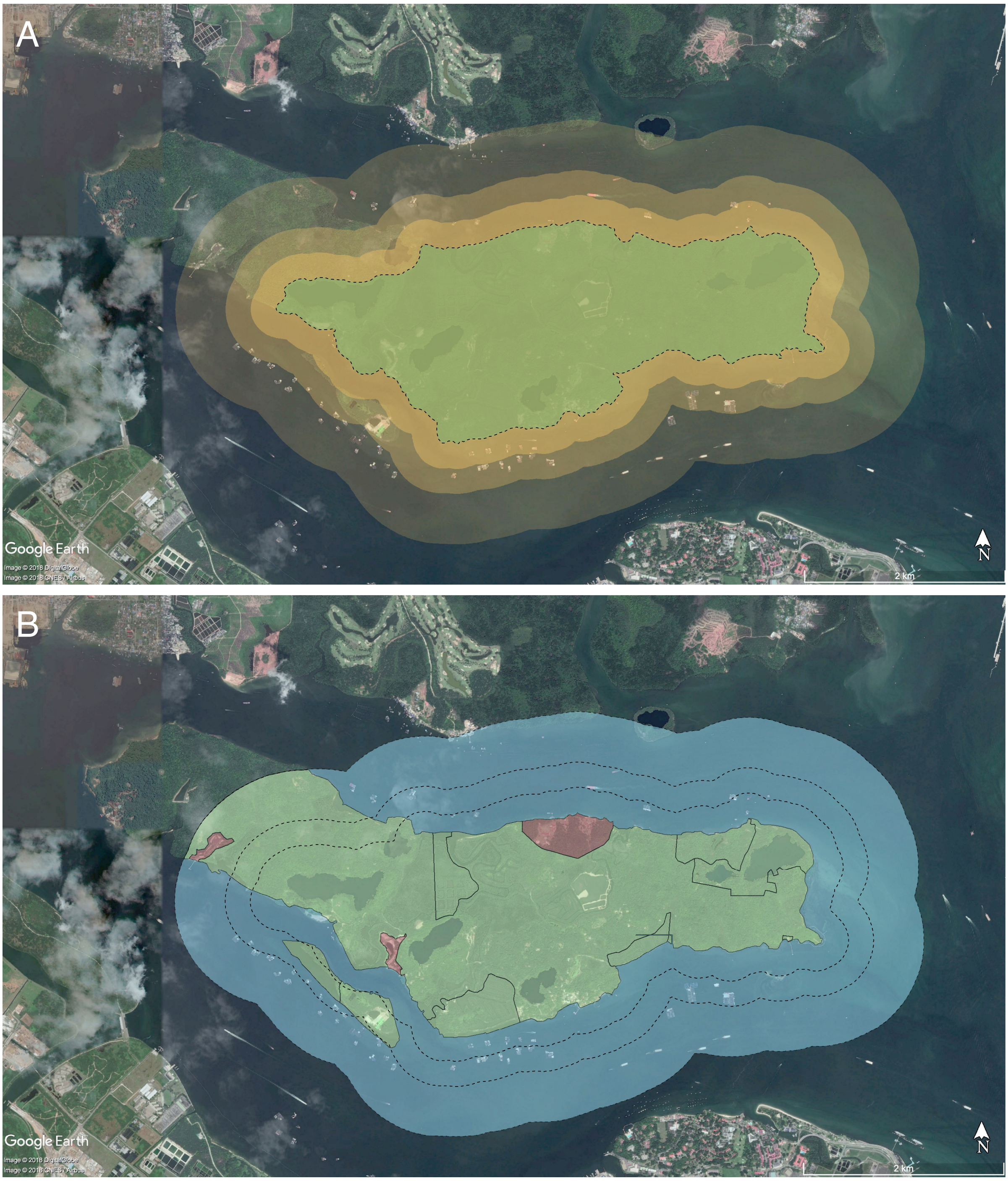
🟩	**Vegetation**	🟧	**250 m buffer**
🟥	**Urban**	🟨	**500 m buffer**
🟪	**Residential**	⬜	**1000 m buffer**
🟦	**Water**		

Digitalisation of Coney Island landuse in ArcGIS. (A) Coney Island boundaries (dotted lines) with three buffer zones (250 m: dark orange , 500 m: orange, 1000 m: light orange). (B) Digitalised vegetation (green), urbanized areas (red), residential areas (purple) and water (blue) inside the 1000 m buffer zone. The dotted lines represent the 250 m, 500 m and 1000 m buffers.

Appendix 27: Land-use digitalisation - Coney Island.



Appendix 28: Flower-bee visitation network and associated indices - Pulau Ubin.

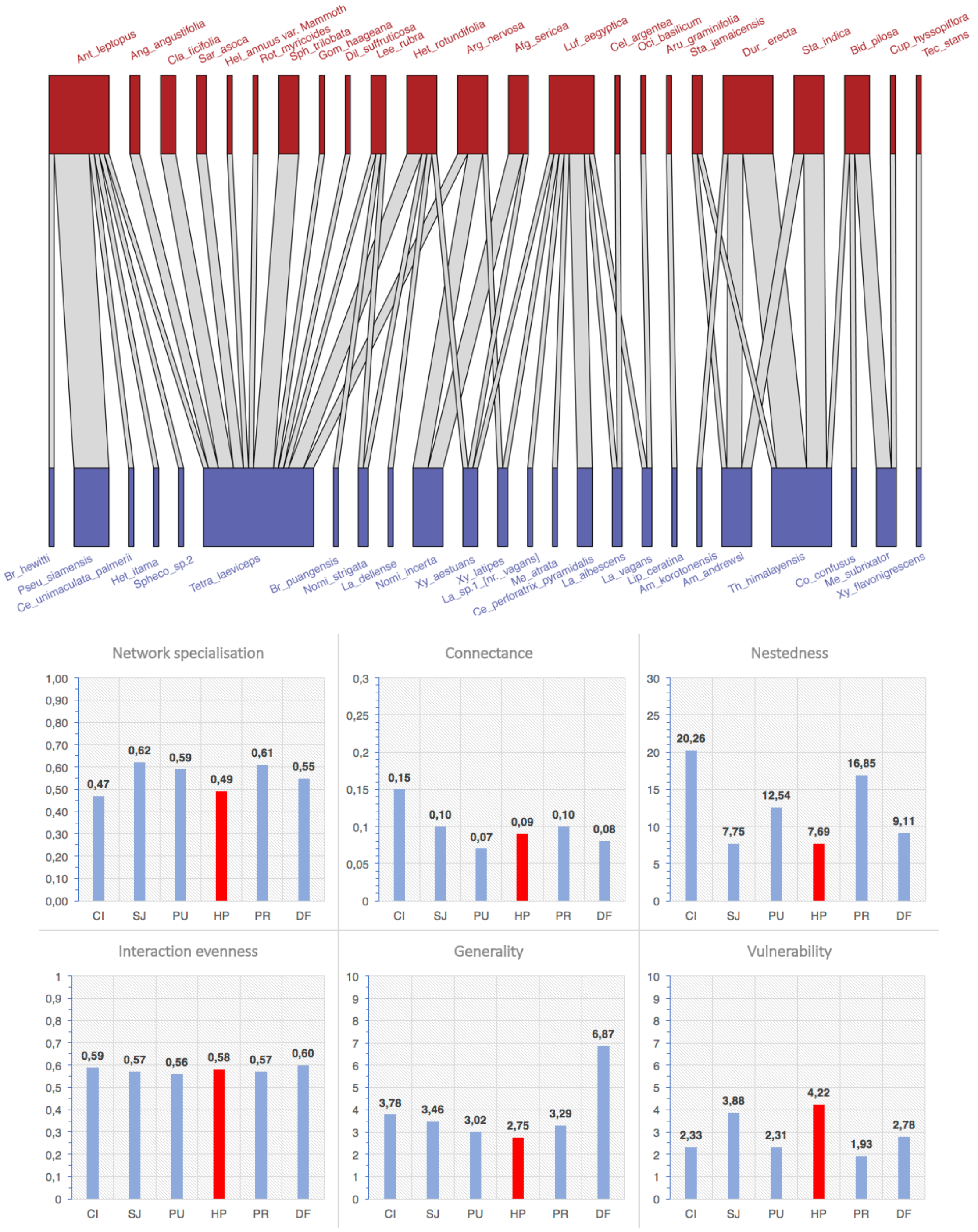


Legend

🟩 Vegetation
🟥 Urban
🟪 Residential
🟦 Water
🟧 250 m buffer
🟧 500 m buffer
🟨 1000 m buffer

Digitalisation of Pulau Ubin landuse in ArcGIS. (A) Pulau Ubin boundaries (dotted lines) with three buffer zones (250 m: dark orange , 500 m: orange, 1000 m: light orange). (B) Digitalised vegetation (green), urbanized areas (red), residential areas (purple) and water (blue) inside the 1000 m buffer zone. The dotted lines represent the 250 m, 500 m and 1000 m buffers.

Appendix 29: Land-use digitalisation - Pulau Ubin.



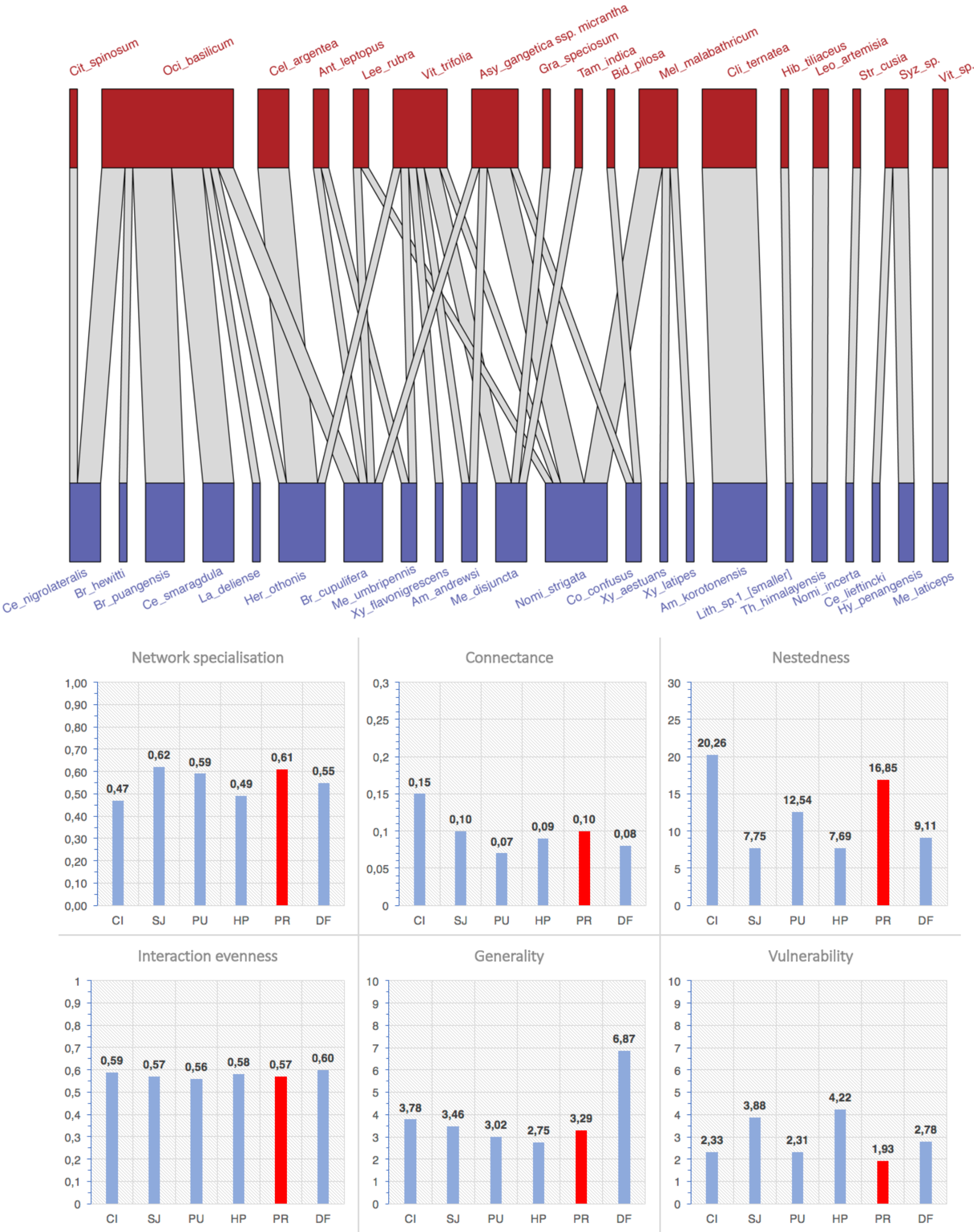
Appendix 30: Flower-bee visitation network and associated indices - Hort Park.

Legend

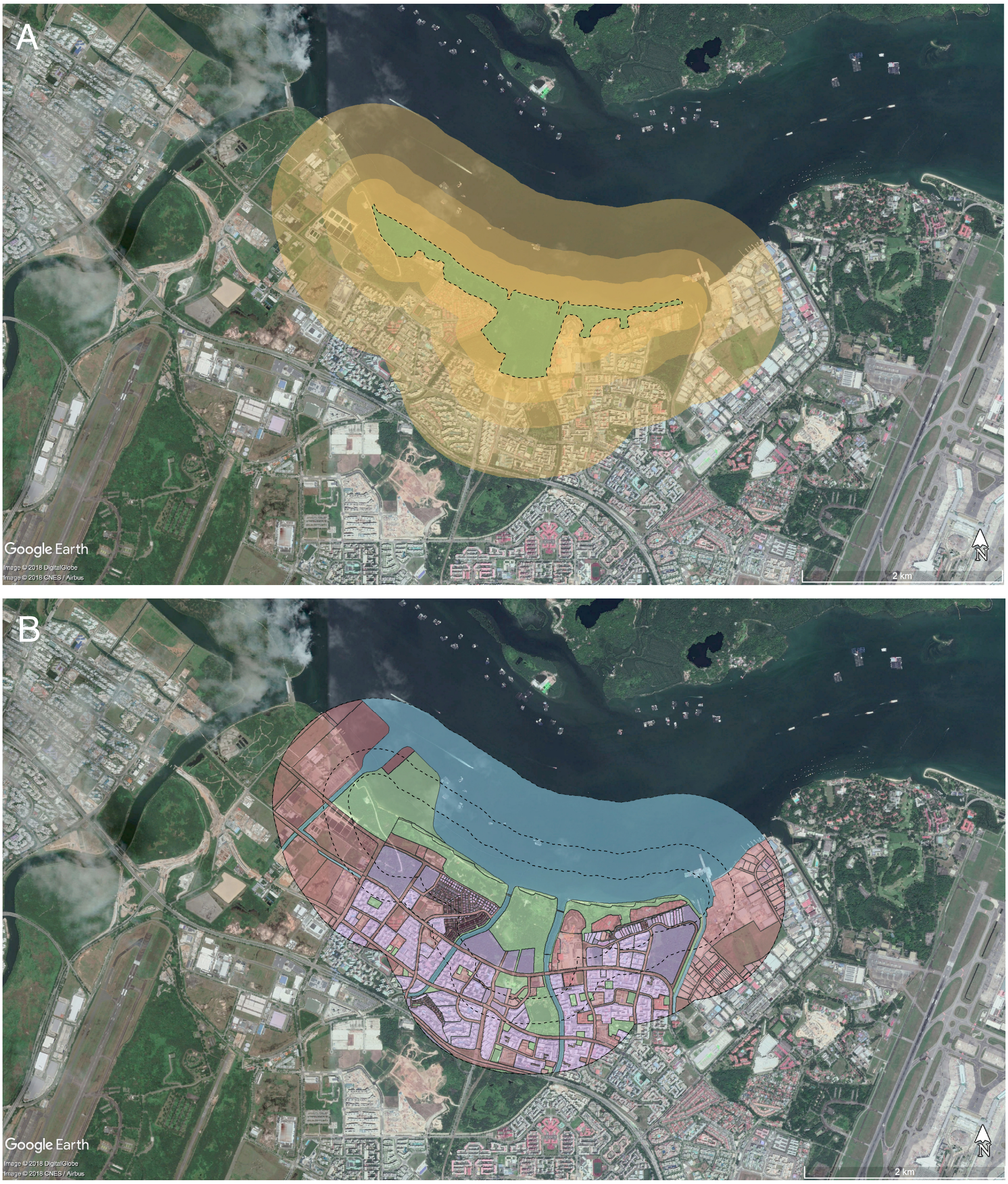
🟩	**Vegetation**	🟧	**250 m buffer**
🟥	**Urban**	🟧	**500 m buffer**
🟪	**Residential**	☐	**1000 m buffer**
🟦	**Water**		

Digitalisation of Hort Park landuse in ArcGIS. (A) Hort Park boundaries (dotted lines) with three buffer zones (250 m: dark orange , 500 m: orange, 1000 m: light orange). (B) Digitalised vegetation (green), urbanized areas (red), residential areas (purple) and water (blue) inside the 1000 m buffer zone. The dotted lines represent the 250 m, 500 m and 1000 m buffers.

Appendix 31: Land-use digitalisation - Hort Park.



Appendix 32: Flower-bee visitation network and associated indices - Pasir Ris.



Digitalisation of Pasir Ris landuse in ArcGIS. (A) Pasir Ris boundaries (dotted lines) with three buffer zones (250 m: dark orange , 500 m: orange, 1000 m: light orange). (B) Digitalised vegetation (green), urbanized areas (red), residential areas (purple) and water (blue) inside the 1000 m buffer zone. The dotted lines represent the 250 m, 500 m and 1000 m buffers.

Appendix 33: Land-use digitalisation - Pasir Ris.

	β_S	β_{WN}	β_{OS}	β_{ST}
Habitat	0,554	0,881	0,667	0,214
Management	0,495	0,869	0,700	0,169

Appendix 34: Betalink : habitats and management types networks' beta diversity. The value of these beta diversity components are useful to assess the dissimilarity of species interactions within the networks. β_S = dissimilarity in the species composition of communities; β_{WN} = dissimilarity of interactions; β_{OS} = dissimilarity of interactions between species common to both networks; β_{ST} = dissimilarity of interactions due to species turnover.

βS

Sites	CI	DF	HP	PR	PU	SJ
CI		0,738	0,811	0,667	0,667	0,562
DF	0,738		0,638	0,630	0,620	0,635
HP	0,811	0,638		0,605	0,673	0,613
PR	0,667	0,630	0,605		0,646	0,647
PU	0,667	0,620	0,673	0,646		0,534
SJ	0,562	0,635	0,613	0,647	0,534	

βWN

Sites	CI	DF	HP	PR	PU	SJ
CI		0,932	0,973	0,905	0,835	0,975
DF	0,932		0,929	0,949	0,933	0,966
HP	0,973	0,929		0,952	0,906	0,980
PR	0,905	0,949	0,952		0,915	0,956
PU	0,835	0,933	0,906	0,915		0,911
SJ	0,975	0,966	0,980	0,956	0,911	

βOS

Sites	CI	DF	HP	PR	PU	SJ
CI		0,545	0,500	0,538	0,300	0,875
DF	0,545		0,586	0,724	0,750	0,850
HP	0,500	0,586		0,600	0,444	0,889
PR	0,538	0,724	0,600		0,500	0,667
PU	0,300	0,750	0,444	0,500		0,722
SJ	0,875	0,850	0,889	0,667	0,722	

βST

Sites	CI	DF	HP	PR	PU	SJ
CI		0,387	0,473	0,366	0,535	0,100
DF	0,387		0,342	0,225	0,183	0,116
HP	0,473	0,342		0,352	0,461	0,092
PR	0,366	0,225	0,352		0,415	0,289
PU	0,535	0,183	0,461	0,415		0,188
SJ	0,100	0,116	0,092	0,289	0,188	

Appendix 35: Betalink : sites' beta diversity. The value of these beta diversity components are useful to assess the dissimilarity of species interactions within the networks. β_S = dissimilarity in the species composition of communities; β_{WN} = dissimilarity of interactions; β_{OS} = dissimilarity of interactions between species common to both networks; β_{ST} = dissimilarity of interactions due to species turnover. For each index, values in yellow and blue highlight the sites with the greatest differences.

Site	Habitat	Manag. type	Species richness	Jacknife 1	Shannon	Piélou	Site size (ha)	Green cover (%)	Urbanized (%)
CI	**Island**	**Wild**	22	32	2,66	0,86	102,4	82,30	17,70
SJ		**Manicured**	34	44	2,84	0,96	122,1	76,33	23,67
PU		**Wild**	54	74	3,39	0,91	708,5	95,39	4,61
HP	**Park**	**Manicured**	30	45	2,77	0,99	12,3	79,43	20,57
PR		**Manicured**	40	51	3,31	0,72	90,4	86,68	13,32
DF		**Wild**	62	80	3,63	0,88	86,2	97,67	2,33

Appendix 36: Local level: sites' specific richness, alpha diversity indices and local variables.

250 m

Site	Habitat	Manag. type	Species richness	Jacknife 1	Shannon	Piélou	Site size (ha)	Parks (%)	Reserves (%)	Mixed veget. (%)	Water (%)	Business (%)	Resid. (%)	Transport (%)	Other (%)	Green patches density	Urbanized patches density
CI	Island	Wild	22	32	2,66	0,86	102,4	21,99	0,79	0,00	53,59	0,55	18,55	2,69	1,83	4,98	8,71
SJ		Manicured	34	44	2,84	0,96	122,1	0,00	12,13	11,96	68,12	0,00	0,00	1,02	6,77	4,20	4,69
PU		Wild	54	74	3,39	0,91	708,5	0,00	4,20	63,71	29,10	0,00	0,00	0,00	2,99	1,30	0,37
HP	Park	Manicured	30	45	2,77	0,99	12,3	20,06	13,90	0,00	0,80	26,02	28,53	10,71	0,00	11,97	50,28
PR		Manicured	40	51	3,31	0,72	90,4	21,02	12,95	2,52	24,87	1,08	20,66	6,47	10,43	4,63	182,86
DF		Wild	62	80	3,63	0,88	86,2	1,59	16,35	54,36	0,69	0,00	15,27	11,64	0,11	11,18	108,83

500 m

Site	Habitat	Manag. type	Species richness	Jacknife 1	Shannon	Piélou	Site size (ha)	Parks (%)	Reserves (%)	Mixed veget. (%)	Water (%)	Business (%)	Resid. (%)	Transport (%)	Other (%)	Green patches density	Urbanized patches density
CI	Island	Wild	22	32	2,66	0,86	102,4	13,86	1,45	0,00	53,64	6,30	16,89	5,95	1,91	4,53	12,39
SJ		Manicured	34	44	2,84	0,96	122,1	0,00	7,64	7,79	78,61	0,00	0,00	0,64	5,31	2,65	3,11
PU		Wild	54	74	3,39	0,91	708,5	0,00	3,07	51,66	43,07	0,00	0,00	0,00	2,19	0,89	0,27
HP	Park	Manicured	30	45	2,77	0,99	12,3	15,47	15,20	0,49	0,58	21,87	30,90	13,17	2,30	7,90	110,04
PR		Manicured	40	51	3,31	0,72	90,4	12,10	11,52	1,51	29,21	5,65	23,41	7,27	9,33	3,97	131,29
DF		Wild	62	80	3,63	0,88	86,2	3,96	10,59	45,35	2,68	0,35	20,68	10,13	6,26	8,86	98,66

1000 m

Site	Habitat	Manag. type	Species richness	Jacknife 1	Shannon	Piélou	Site size (ha)	Parks (%)	Reserves (%)	Mixed veget. (%)	Water (%)	Business (%)	Resid. (%)	Transport (%)	Other (%)	Green patches density	Urbanized patches density
CI	Island	Wild	22	32	2,66	0,86	102,4	7,77	0,75	0,03	50,76	8,33	14,16	7,47	10,73	5,71	16,17
SJ		Manicured	34	44	2,84	0,96	122,1	0,00	4,05	4,13	85,26	0,00	0,00	0,34	6,22	1,40	1,98
PU		Wild	54	74	3,39	0,91	708,5	0,00	1,92	35,52	61,00	0,00	0,00	0,00	1,56	0,51	0,21
HP	Park	Manicured	30	45	2,77	0,99	12,3	13,54	10,51	0,42	0,78	13,58	32,73	18,78	9,64	7,51	151,62
PR		Manicured	40	51	3,31	0,72	90,4	6,45	6,43	1,03	31,42	15,35	21,71	8,18	9,44	3,83	89,30
DF		Wild	62	80	3,63	0,88	86,2	6,94	6,58	39,01	3,59	0,22	23,25	9,40	11,02	8,64	209,40

Appendix 37: Landscape level: sites' specific richness, alpha diversity indices and land-use proportions. Three scales around sites are considered (250m, 500m and 1000m).

250 m

Site	Habitat	Manag. type	Species richness	Jacknife 1	Shannon	Piélou	Parks (%)	Reserves (%)	Mixed vegetation (%)	Residential (%)	Green patches density (/km2)
CI	Island	Wild	22	32	2,66	0,86	21,99	0,79	0,00	18,55	4,98
SJ		Manicured	34	44	2,84	0,96	0,00	12,13	11,96	0,00	4,20
PU		Wild	54	74	3,39	0,91	0,00	4,20	63,71	0,00	1,30
HP	Park	Manicured	30	45	2,77	0,99	20,06	13,90	0,00	28,53	11,97
PR		Manicured	40	51	3,31	0,72	21,02	12,95	2,52	20,66	4,63
DF		Wild	62	80	3,63	0,88	1,59	16,35	54,36	15,27	11,18

500 m

Site	Habitat	Manag. type	Species richness	Jacknife 1	Shannon	Piélou	Parks (%)	Reserves (%)	Mixed vegetation (%)	Residential (%)	Green patches density (/km2)
CI	Island	Wild	22	32	2,66	0,86	13,86	1,45	0,00	16,89	4,53
SJ		Manicured	34	44	2,84	0,96	0,00	7,64	7,79	0,00	2,65
PU		Wild	54	74	3,39	0,91	0,00	3,07	51,66	0,00	0,89
HP	Park	Manicured	30	45	2,77	0,99	15,47	15,20	0,49	30,90	7,90
PR		Manicured	40	51	3,31	0,72	12,10	11,52	1,51	23,41	3,97
DF		Wild	62	80	3,63	0,88	3,96	10,59	45,35	20,68	8,86

1000 m

Site	Habitat	Manag. type	Species richness	Jacknife 1	Shannon	Piélou	Parks (%)	Reserves (%)	Mixed vegetation (%)	Residential (%)	Green patches density (/km2)
CI	Island	Wild	22	32	2,66	0,86	7,77	0,75	0,03	14,16	5,71
SJ		Manicured	34	44	2,84	0,96	0,00	4,05	4,13	0,00	1,40
PU		Wild	54	74	3,39	0,91	0,00	1,92	35,52	0,00	0,51
HP	Park	Manicured	30	45	2,77	0,99	13,54	10,51	0,42	32,73	7,51
PR		Manicured	40	51	3,31	0,72	6,45	6,43	1,03	21,71	3,83
DF		Wild	62	80	3,63	0,88	6,94	6,58	39,01	23,25	8,64

Appendix 38: Landscape level: sites' specific richness, alpha diversity indices and land-use proportions: first aggregation. Land-use classes that can be considered as habitats are clustered together. Three scales around sites are considered (250m, 500m and 1000m).

250 m

Site	Habitat	Management type	Species richness	Jacknife 1	Shannon	Piélou	Site size (ha)	Water (%)	Urbanized (%)	Urbanized patches density (/km2)
CI	**Island**	Wild	22	32	2,66	0,86	102,4	53,59	23,62	8,71
HP	**Park**	Manicured	30	45	2,77	0,99	12,3	0,80	65,25	50,28
SJ	**Island**	Manicured	34	44	2,84	0,96	122,1	68,12	7,79	4,69
PR	**Park**	Manicured	40	51	3,31	0,72	90,4	24,87	38,64	182,86
PU	**Island**	Wild	54	74	3,39	0,91	708,5	43,07	2,19	0,37
DF	**Park**	Wild	62	80	3,63	0,88	86,2	0,69	27,01	108,83

500 m

Site	Habitat	Management type	Species richness	Jacknife 1	Shannon	Piélou	Site size (ha)	Water (%)	Urbanized (%)	Urbanized patches density (/km2)
CI	**Island**	Wild	22	32	2,66	0,86	102,4	53,64	31,05	12,39
HP	**Park**	Manicured	30	45	2,77	0,99	12,3	0,58	68,25	110,04
SJ	**Island**	Manicured	34	44	2,84	0,96	122,1	78,61	5,95	3,11
PR	**Park**	Manicured	40	51	3,31	0,72	90,4	29,21	45,66	131,29
PU	**Island**	Wild	54	74	3,39	0,91	708,5	43,07	2,19	0,27
DF	**Park**	Wild	62	80	3,63	0,88	86,2	2,68	37,43	98,66

1000 m

Site	Habitat	Management type	Species richness	Jacknife 1	Shannon	Piélou	Site size (ha)	Water (%)	Urbanized (%)	Urbanized patches density (/km2)
CI	**Island**	Wild	22	32	2,66	0,86	102,4	50,76	40,70	16,17
HP	**Park**	Manicured	30	45	2,77	0,99	12,3	0,78	74,75	151,62
SJ	**Island**	Manicured	34	44	2,84	0,96	122,1	85,26	6,56	1,98
PR	**Park**	Manicured	40	51	3,31	0,72	90,4	31,42	54,67	89,30
PU	**Island**	Wild	54	74	3,39	0,91	708,5	61,00	1,56	0,21
DF	**Park**	Wild	62	80	3,63	0,88	86,2	3,59	43,88	209,40

Appendix 39: Landscape level: sites' specific richness, alpha diversity indices and land-use proportions: second aggregation. Land-use classes that can be considered as impervious (water bodies, urbanized areas, etc.) are clustered together. Sites size is also tested. Three scales around sites are considered (250m, 500m and 1000m).

Name	Sociality	Nesting	Pollen Transport	Lecty	Origin	Mean ITD (mm)
Amegilla (Glossamegilla) insularis	Solitary	Soil	Hindleg	Polylectic	Native	4,90
Amegilla (Zonamegilla) andrewsi	Solitary	Soil	Hindleg	Polylectic	Native	4,51
Amegilla (Zonamegilla) korotonensis	Solitary	Soil	Hindleg	Polylectic	Native	3,50
Anthidiellum (Pycanthidiellum) smithii smithii	Solitary	Cavity	Abdomen	Polylectic	Native	1,42
Apis (Apis) cerana	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	3,01
Apis (Megapis) dorsata dorsata	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	4,11
Apis (Micrapis) andreniformis	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	2,05
Apis (Micrapis) florea	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Exotic	2,56
Braunsapis breviceps	[Social parasite]	[Pithy stems or cavity]	Uncertain	Uncertain	Native	0,80
Braunsapis clarihirta	Primitively social	Pithy stems or cavity	Hindleg	Polylectic	Native	1,30
Braunsapis cupulifera	Primitively social	Pithy stems or cavity	Hindleg	Polylectic	Native	0,95
Braunsapis hewitti	Primitively social	Pithy stems or cavity	Hindleg	Polylectic	Native	1,06
Braunsapis hewitti [large form]	Primitively social	Pithy stems or cavity	Hindleg	Polylectic	Native	1,24
Braunsapis philippinensis	Primitively social	Pithy stems or cavity	Hindleg	Polylectic	Native	1,31
Braunsapis puangensis	Primitively social	Pithy stems or cavity	Hindleg	Polylectic	Native	1,09
Ceratina (Catoceratina) perforatrix pyramidalis	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	2,07
Ceratina (Ceratinidia) accusator	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,22
Ceratina (Ceratinidia) cognata	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,80
Ceratina (Ceratinidia) collusor	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,56
Ceratina (Ceratinidia) lieftincki	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,58
Ceratina (Ceratinidia) nigrolateralis	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	N.A
Ceratina (Ceratinidia) nigrolateralis incerta	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,74
Ceratina (Lioceratina) ridleyi	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,86
Ceratina (Neoceratina) dentipes	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,11
Ceratina (Pithitis) smaragdula	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,62
Ceratina (Pithitis) unimaculata palmerii	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,63
Ceratina (Xanthoceratina) fuliginosa	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,60
Ceratina (Xanthoceratina) fuliginosa ['sayang' form]	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	1,48
Ceratina (Xanthoceratina) metaria	Subsocial	Pithy stems or cavity	Hindleg	Polylectic	Native	0,98
Ceylalictus (Ceylalictus) communis	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	0,88
Ceylalictus (Ceylalictus) malayensis	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	1,16
Coelioxys (Allocoelioxys) sp. 2	[Solitary]	[Cavity]	Uncertain	Uncertain	Native	2,70
Coelioxys (Allocoelioxys) sp.1 'basalis' [probably misdetermined]	[Solitary]	[Cavity]	Uncertain	Uncertain	Native	2,00
Coelioxys (Callosarissa) confusus	[Solitary]	[Cavity]	Uncertain	Uncertain	Native	2,24
Coelioxys (Torridapis) n.sp. 'leo'	[Solitary]	[Cavity]	Uncertain	Uncertain	Native	2,25
Euaspis n. sp. 1	[Solitary]	[Cavity]	Uncertain	Uncertain	Native	1,63
Euaspis polynesia	[Solitary]	[Cavity]	Uncertain	Uncertain	Native	2,18
Eupetersia (Nesoeupetersia) yanegai	[Solitary, could be communal]	[Soil]	Uncertain	Uncertain	Native	1,05
Geniotrigona thoracica	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,83
Heriades (Michenerella) othonis	Solitary	Cavity	Abdomen	Polylectic	Native	1,15

Heterotrigona (Heterotrigona) itama	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,54
Heterotrigona (Sundatrigona) moorei	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	0,96
Homotrigona fimbriata	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,85
Hylaeus (Gephryrohylaeus) sandacanensis	Solitary	Cavity	Crop	Polylectic	Native	0,63
Hylaeus (Indialeus) sp. (large) [continuous yellow propodeum]	Solitary	Cavity	Crop	Polylectic	Native	1,38
Hylaeus (Nesoprosopis) penangensis	Solitary	Cavity	Crop	Polylectic	Native	1,03
Hylaeus (Nesoprosopis) sp. 1 aff. transversalis [T1 punctate]	Solitary	Cavity	Crop	Polylectic	Native	1,43
Hylaeus (Nesoprosopis) sp. 2 aff. transversalis [reduced prop. yellow; T1 not punctate]	Solitary	Cavity	Crop	Polylectic	Native	1,38
Hylaeus (Nesoprosopis) sp. 3 aff. transversalis [T1 weak punctures]	Solitary	Cavity	Crop	Polylectic	Native	1,20
Hylaeus (Nesoprosopis) sp.4 [like 1 but propodeum closely spaced transverse lines]	Solitary	Cavity	Crop	Polylectic	Native	1,13
Hylaeus (new subgenus nr. Prosopisteron) sp.5 [blue metallic, from MIP]	Solitary	Cavity	Crop	Polylectic	Native	0,95
Lasioglossum (Ctenonomia) albescens	[Solitary, communal, or primitively eusocial]	Soil	Hindleg	Polylectic	Native	1,89
Lasioglossum (Ctenonomia) deliense	[Solitary, communal, or primitively eusocial]	Soil	Hindleg	Polylectic	Native	1,58
Lasioglossum (Ctenonomia) halictoides	[Solitary, communal, or primitively eusocial]	Soil	Hindleg	Polylectic	Native	1,79
Lasioglossum (Ctenonomia) semirussatum	[Solitary, communal, or primitively eusocial]	Soil	Hindleg	Polylectic	Native	2,00
Lasioglossum (Ctenonomia) sp. 1 [nr. vagans]	[Solitary, communal, or primitively eusocial]	Soil	Hindleg	Polylectic	Native	1,43
Lasioglossum (Ctenonomia) sp.2	[Solitary, communal, or primitively eusocial]	Soil	Hindleg	Polylectic	Native	1,56
Lasioglossum (Ctenonomia) vagans	[Solitary, communal, or primitively eusocial]	Soil	Hindleg	Polylectic	Native	1,28
Lasioglossum (Homalictus) adonidiae	[Solitary, communal, or primitively eusocial]	Soil	Hindleg,Abdomen	Polylectic	Native	1,32
Lasioglossum (Homalictus) latitarse	[Solitary, communal, or primitively eusocial]	Soil	Hindleg,Abdomen	Polylectic	Native	1,08
Lasioglossum (Homalictus) singapurellum	[Solitary, communal, or primitively eusocial]	Soil	Hindleg,Abdomen	Polylectic	Native	0,98
Lepidotrigona nitidiventris	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,48
Lepidotrigona terminata	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,30
Lipotriches (Austronomia) goniognatha	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	1,75
Lipotriches (Austronomia) takauensis	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	1,80

Lipotriches (Rhopalomelissa) ceratina	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	1,56
Lipotriches (Rhopalomelissa) minutula	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	1,43
Lithurgus cf. collaris [clypeus without median line]	Solitary	Wood	Abdomen	Mesolectic?	Native	3,00
Lithurgus sp.1 [smaller]	Solitary	Wood	Abdomen	Mesolectic?	Native	2,86
Lithurgus sp.2 cf. collaris [clypeus median line] [larger]	Solitary	Wood	Abdomen	Mesolectic?	Native	3,09
Lophotrigona canifrons	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,90
Megachile (Aethomegachile) borneana	Solitary	Cavity	Abdomen	Polylectic	Native	2,55
Megachile (Aethomegachile) conjuncta	Solitary	Cavity	Abdomen	Polylectic	Native	3,64
Megachile (Aethomegachile) laticeps	Solitary	Cavity	Abdomen	Polylectic	Exotic?	3,64
Megachile (Aethomegachile) nr. borneana	Solitary	Cavity	Abdomen	Polylectic	Native	2,88
Megachile (Aethomegachile) ramera	Solitary	Cavity	Abdomen	Polylectic	Native	4,16
Megachile (Aethomegachile) sp. [fusciventris group]	Solitary	Cavity	Abdomen	Polylectic	Native	3,76
Megachile (Anodonteutricharea) tricincta	Solitary	Cavity	Abdomen	Polylectic	Native	2,72
Megachile (Callomegachile s.l.) ornata	Solitary	Cavity	Abdomen	Polylectic	Native	5,50
Megachile (Callomegachile s.l.) tuberculata	Solitary	Cavity	Abdomen	Polylectic	Native	5,70
Megachile (Callomegachile) disjuncta	Solitary	Cavity	Abdomen	Polylectic	Exotic?	3,86
Megachile (Callomegachile) fulvipennis	Solitary	Cavity	Abdomen	Polylectic	Native	4,99
Megachile (Callomegachile) indonesica	Solitary	Cavity	Abdomen	Polylectic	Native	5,14
Megachile (Callomegachile) sp. (species-group of biroi)	Solitary	Cavity	Abdomen	Polylectic	Exotic?	3,41
Megachile (Callomegachile) umbripennis	Solitary	Cavity	Abdomen	Polylectic	Exotic?	3,24
Megachile (Carinula) sp. aff. butteli	Solitary	Cavity	Abdomen	Polylectic	Native	2,44
Megachile (Carinula) stulta	Solitary	Cavity	Abdomen	Polylectic	Exotic?	2,29
Megachile (Chelostomoda) moera	Solitary	Cavity	Abdomen	Polylectic	Native	2,20
Megachile (Creightonella) atrata	Solitary	Soil[lined with leaves]	Abdomen	Polylectic	Native	4,68
Megachile (Eutricharaea) sp.1 [white scopa; crenulate T6]	Solitary	Cavity	Abdomen	Polylectic	Native	2,33
Megachile (Eutricharaea) subrixator	Solitary	Cavity	Abdomen	Polylectic	Native	2,26
Nomada aff. polyodonta	[Solitary]	[Soil]	Uncertain	Uncertain	Native	0,95
Nomada malayana	[Solitary]	[Soil]	Uncertain	Uncertain	Native	1,05
Nomada penangensis	[Solitary]	[Soil]	Uncertain	Uncertain	Native	0,68
Nomada sandacana	[Solitary]	[Soil]	Uncertain	Uncertain	Native	1,03
Nomia (Acunomia) iridescens	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	2,11
Nomia (Acunomia) lusoria	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	2,28
Nomia (Acunomia) strigata	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	2,11
Nomia (Gnathonomia) thoracica	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	2,50
Nomia (Hoplonomia) incerta	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	2,40

Nomia (Maculonomia) apicalis	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	3,22
Nomia (Maculonomia) elegans	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	2,25
Nomia (Maculonomia) fuscipennis	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	2,52
Nomia (Maculonomia) n.sp. 'spinifemur'	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	2,71
Patellapis (Pachyhalictus) intricata	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	1,70
Patellapis (Pachyhalictus) murbanus	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	1,52
Pseudapis (Pseudapis) siamensis	Solitary [could be communal]	Soil	Hindleg	Polylectic	Native	1,44
Sphecodes duplex	[Solitary, could be communal or primitively eusocial]	[Soil]	Uncertain	Uncertain	Native	1,15
Sphecodes sp.2	[Solitary, could be communal or primitively eusocial]	[Soil]	Uncertain	Uncertain	Native	1,48
Sphecodes sp.3	[Solitary, could be communal or primitively eusocial]	[Soil]	Uncertain	Uncertain	Native	0,84
Sphecodes sp.4	[Solitary, could be communal or primitively eusocial]	[Soil]	Uncertain	Uncertain	Native	1,72
Sphecodes sp.5	[Solitary, could be communal or primitively eusocial]	[Soil]	Uncertain	Uncertain	Native	N.A
Sphecodes sp.6	[Solitary, could be communal or primitively eusocial]	[Soil]	Uncertain	Uncertain	Native	0,98
Tetragonula (Tetragonilla) atripes	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,30
Tetragonula fuscobalteata	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	0,90
Tetragonula geissleri	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,30
Tetragonula laeviceps	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,20
Tetragonula pagdeni	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,08
Tetragonula pagdeniformis	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,03
Tetrigona apicalis	Eusocial (Advanced)	Hive	Corbicula	Polylectic	Native	1,46
Thyreus [abdominalis rostratus, or decorus]	[Solitary]	[Soil]	Uncertain	Uncertain	Native	3,28
Thyreus ceylonicus lilacinus	[Solitary]	[Soil]	Uncertain	Uncertain	Native	2,90
Thyreus himalayensis	[Solitary]	[Soil]	Uncertain	Uncertain	Native	2,83
Thyreus novaehollandiae signatus	[Solitary]	[Soil]	Uncertain	Uncertain	Native	2,50
Xylocopa (Biluna) auripennis iridipennis	Subsocial	Bamboo	Hindleg	Polylectic	Native	6,78
Xylocopa (Koptortosoma) aestuans	Subsocial	Wood	Hindleg	Polylectic	Native	6,64
Xylocopa (Koptortosoma) caerulea	Subsocial	Wood	Hindleg	Polylectic	Native	7,59
Xylocopa (Koptortosoma) flavonigrescens	Subsocial	Wood	Hindleg	Polylectic	Native	7,05
Xylocopa (Koptortosoma) insularis	Subsocial	Wood	Hindleg	Polylectic	Native	5,55
Xylocopa (Nyctomelitta) myops	Subsocial	Wood	Hindleg	Polylectic	Native	6,86
Xylocopa (Platynopoda) latipes	Subsocial	Wood	Hindleg	Polylectic	Native	12,40
Xylocopa (Zonohirsuta) dejeanii	Subsocial	Wood	Hindleg	Polylectic	Native	6,40

Appendix 40: List of bee species found in this study and their associated traits.

UNIVERSITÉ LIBRE DE BRUXELLES

ULB

FACULTÉ DES SCIENCES ET ÉCOLE POLYTECHNIQUE DE BRUXELLES
ÉCOLE INTERFACULTAIRE DE BIOINGÉNIEURS
Ecologie du Paysage & Systèmes de Production Végétale
Avenue F.D. Roosevelt 50, CP 264/2
B-1050 BRUXELLES

Tel: +32 (0)2 650 63 44
Email: nicolas.vereecken@ulb.ac.be

Agroecology
& Pollination

Brussels (Belgium), 5.ix.2017

To whom it may concern,

I am pleased to support the research project of Mr Julien Clerbois who will work under my supervision and the co-supervision of Prof. John S. Ascher (National University of Singapore) on the community structure of wild bees in Singapore and on neighbouring islands.

Prof. John. S. Ascher will host Mr Julien Clerbois in his lab during his short stay in Singapore (October 25, 2017 – January 19, 2018) and will provide access to the insect collection, as well laboratory and office space. Upon his return in Belgium, Mr Julien Clerbois will be hosted in my department (Landscape Ecology & Plant Production Systems, Agroecology & Pollination group) where he will be in charge of the statistical analyses of wild bees community structure under my supervision.

Collectively, his results will constitute the core of Mr Julien Clerbois' MSc thesis which will be submitted in August 2018 for the degree of "Environmental Science Management" at the Université libre de Bruxelles (ULB, Belgium).

On behalf of all research partners, I would be very grateful if you could facilitate Mr Julien Clerbois' administrative procedures to ease his research efforts and make his research stay in Singapore more scientifically productive and enjoyable.

Thank you very much in advance for your collaboration,

Best regards,

FACULTE DES SCIENCES

Prof. N.J. Vereecken
Agroecology & Pollination Group
Ecologie du Paysage & Systèmes de Production Végétale
Campus de la Plaine CP 264/2 - Building NO
Université Libre de Bruxelles (ULB)
Blvd. du Triomphe
B-1050 Bruxelles, Belgique

Amegilla andrewsi visiting *Stachytarpheta jamaicensis* – Pulau Ubin (2017)

Apis cerana visiting ornamental flowers – Dairy Farm Nature Reserve (2017)