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# Coral islands in West Papua: A model system for functional and taxonomic diversity and the resilience of isolated habitats

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“This gulf was studded along its shores with numbers of rocky islets, mostly mushroom shaped, from the water having worn away the lower part of the soluble coralline limestone, leaving them overhanging from ten to twenty feet. Every islet was covered will strange-looping shrubs and trees [...], forming one of the most singular and picturesque landscapes I have ever seen.”

**Alfred Russel Wallace** describing the small islands, subject of this thesis, around Gam island in the Raja Ampat Archipelago during his journey to New Guinea in 1860 (The Malay Archipelago 1869, pp. 464-465).

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# Abstract

Biological diversity on islands is shaped by an interplay of geo-environmental dynamics that are relatively easy to observe, as islands have distinct boundaries and are often small in size. These unique characteristics of islands have inspired naturalist to their use as research laboratories. Islands have therefore influenced many theories in ecology, evolution, and biogeography. Despite great scientific advances in island research, however, we still lack comprehensive understanding of numerous aspects in island ecology. Open research questions are related to the effects of spatial scales on biodiversity, community assembly processes, and diversity of species forms and functions on islands.

The central aim of my thesis, which consists of five research chapters that consecutively build on each other, was to investigate species diversity patterns and assembly processes on small islands. In chapter 2, I present a new method to measure leaf area, which was crucial for the plant trait analyses. In chapters 3-5, I sampled and analysed a dataset of tree communities on 60 small islands in the Raja Ampat Archipelago to gain detailed ecological knowledge of local patterns and processes of species diversity. In chapter 6, I compiled a global dataset that contains information on plant species occurrences and their respective growth forms for more than 5100 species on 700 small islands to test for global patterns in growth form species richness.

Based on the Raja Ampat dataset, I showed that the species-area relationship strongly depends on the applied sampling scale. In addition, environmental factors that determined species richness differed between scales. Species occurring on these islands have specific environmental requirements, are linked to island area and form island-specific species pools. Species communities on smaller islands had a lower community completeness than those on larger ones. This observation was likely rooted in local limiting processes, acting more severely on smaller islands and thus preventing many species of the pool to establish. These local limiting processes can be attributed to a combination of non-random dispersal and environmental filters operating simultaneously, but with different intensity on island communities. Species communities on smaller islands were shaped by dispersal constraints and limited niche space. In contrast, communities on larger islands were governed by niche partitioning related to nutrient, light, and resource acquisition strategies. At a global scale, species richness patterns dissected into growth forms varied

in their response to island area and were differentially affected by environmental factors and isolation.

My thesis provides new insights into the assembly of small islands communities. I show that small-island communities are shaped by a combination of environmental, population level, and species-level processes that differ in their intensity with island area. Functional trait-based approaches and species richness of plant growth forms better explained these processes than total measures of species richness. Global databases that cover species occurrences and functional traits can provide new insights into biogeographical patterns. Detailed ecological understanding of community assembly processes on islands is of paramount importance to conserve biodiversity in an increasingly fragmented natural world.

# Zusammenfassung

Biologische Diversität auf Inseln wird durch eine Vielzahl geo-ökologischer Dynamiken beeinflusst. Diese Dynamiken sind relativ einfach zu beobachten, da Inseln geographisch begrenzt und häufig von kleinem Ausmaß sind. Diese einzigartigen Eigenschaften machen Inseln zu idealen Forschungslaboren und haben seit jeher als Inspiration Naturwissenschaftlern gedient, und viele Theorien in Ökologie, Evolution und Biogeographie wurden durch Inselforschung entwickelt. Trotz großer wissenschaftlicher Fortschritte in der Erforschung von Inseln fehlt jedoch nach wie vor ein umfassendes Verständnis über die zahlreichen ökologischen Vorgänge auf Inseln. Vor allem wie sich Biodiversitätsmuster zwischen räumlichen Skalen unterscheiden, welche ökologischen Prozesse Pflanzengesellschaften prägen und wie sich die Vielfalt funktioneller Artenmerkmale auf Inseln zusammensetzt, stellen offene Forschungsfragen dar.

Zentrales Ziel meiner Dissertation war es, die Artenvielfalt und die ihr zugrundeliegenden Mechanismen auf kleinen Inseln zu untersuchen. Meine Dissertation besteht aus fünf thematisch aufeinander aufbauenden wissenschaftlichen Kapiteln. In Kapitel 2 stelle ich eine neue Methode zur Messung von Blattflächen vor, die für die Analyse funktioneller Pflanzenmerkmale von großer Bedeutung war. In den Kapiteln 3-5 habe ich einen Datensatz von Baumgesellschaften auf 60 kleinen Inseln im Raja Ampat Archipel gesammelt und analysiert, um detaillierte ökologische Kenntnisse über lokale Muster und Prozesse der Artenvielfalt zu gewinnen. In Kapitel 6 habe ich einen globalen Datensatz zusammengestellt, der Informationen über das Vorkommen von Pflanzenarten und deren jeweiligen Wuchsformen für mehr als 5100 Arten auf 700 kleinen Inseln enthält.

Basierend auf dem Datensatz aus dem Raja Ampat Archipel habe ich den Einfluss räumlicher Skalen auf Biodiversitätsmuster und Art-Areal-Kurven gezeigt. Umweltfaktoren, die den Artenreichtum bestimmen, variierten zwischen räumlichen Skalen. Darüber hinaus haben die auf den Inseln vorkommenden Arten individuelle Umweltanforderungen, die mit den Inselflächen korrelieren und dadurch inselspezifische Artenpools ergeben. Die Artengesellschaften auf kleineren Inseln waren stärker von lokalen Limitierungsprozessen beeinflusst als die Gesellschaften auf größeren Inseln. Die lokalen Limitierungsprozesse waren auf eine Kombination aus deterministischen Verbreitungs- und Umweltfiltern zurückzuführen, die gleichzeitig, aber mit

unterschiedlicher Intensität auf die Artengesellschaften wirken. Die Artengesellschaften auf kleineren Inseln waren geprägt durch Ausbreitungsbarrieren und begrenzte Verfügbarkeit von Nischen. Im Gegensatz dazu teilen sich die Arten auf größeren Inseln in eine Vielzahl verschiedener Nischen auf. Auf globaler Ebene variierte der Artenreichtum verschiedener Wuchsformen stark mit der Inselfläche und wurde zudem beeinflusst durch unterschiedliche Umweltfaktoren und die Isolation der Inseln.

In meiner Dissertation gebe ich neue Einblicke, die zeigen, wie sich Pflanzengesellschaften auf kleinen Inseln zusammensetzen. Pflanzengesellschaften auf kleinen Inseln werden durch eine Kombination verschiedener Selektierungsprozesse geprägt, die sich in ihrer Intensität zwischen den Inseln unterscheiden. Funktionale Merkmale der Arten und der Artenreichtum von Pflanzenwuchsformen erklären diese Prozesse besser als herkömmliche Diversitätsindices wie z.B. Gesamtmaße des Artenreichtums. Globale Datenbanken, die die Artverbreitung und funktionale Merkmale der Arten abdecken, können neue Erkenntnisse über biogeografische Muster liefern. Detaillierte Einblicke in die ökologischen Prozesse, welche Pflanzengesellschaften auf Inseln beeinflussen, ist von größter Bedeutung für den Erhalt der Biodiversität in einer zunehmend fragmentierten Umwelt.

# 1. Introduction

Islands have fascinated naturalists since Charles Darwin (1859) and Alfred R. Wallace (1880) contemplated how biodiversity assembled and evolved on islands. Since then, astonishing patterns in island biodiversity have been discovered (Carlquist 1965, 1974, Taylor et al. 2019), and the marked nature of islands have influenced many theories in ecology and evolution (Warren et al. 2015, Whittaker et al. 2017). Biodiversity on islands is shaped by an interplay of geoenvironmental dynamics that are relatively easy to observe as islands have distinct boundaries and are often small in size (Losos and Ricklefs 2009). Furthermore, groups of islands form replicates, which allow to test general ecological theories and patterns related to scale effects, colonisation and extinction dynamics, and assembly processes (Whittaker and Fernández-Palacios 2007, Losos and Ricklefs 2009). Despite great scientific advances in ecological island research, we still lack comprehensive understanding of many aspects in island ecology. Open research questions are related to effects of spatial scales on biodiversity, community assembly processes, and diversity of species forms and functions on islands (Patiño et al. 2017). However, due to the long tradition in island research, scientists can draw on a diverse portfolio of theories and concepts to answer open questions.

## 1.1 Island community assembly: Theories and concepts

Arguably the most influential work in island biogeography is the equilibrium theory (MacArthur and Wilson 1963, 1967), which provided the conceptual framework to quantitatively examine diversity patterns across islands (Warren et al. 2015). The equilibrium theory of island biogeography (hereafter ETIB) posits that species richness on islands is maintained by a dynamic equilibrium of random colonisation and extinction events, where larger and less isolated islands harbour more species than smaller and more isolated ones (MacArthur and Wilson 1963, 1967). According to the ETIB, species richness increases with island area, a pattern known as the species-area relationship (hereafter SAR; Rosenzweig 1995). Since its first conceptual description (Arrhenius 1921), the SAR has been reported in a wealth of studies and many mathematical models have been developed to describe the function between species richness and area (e.g. Tjørve

2003, Williams et al. 2009, Dengler 2010, Triantis et al. 2012, Chisholm et al. 2016). Despite the SAR having the reputation as being as close as possible to an ecological law (Rosenzweig 1995, Lomolino 2000), its underlying mechanisms are still poorly understood. The neutral assembly processes that form the basis of the ETIB have received considerable criticism (Simberloff 1976a, Gilbert 1980, Ricklefs 2001, Emerson and Gillespie 2008), but knowledge about non-random processes behind the SAR remains scarce. To date, it remains largely unknown to which degree neutral or non-neutral assembly processes explain the SAR in general and island community assembly in particular. In the following, I introduce concepts and theories of community assembly and drivers of species richness on islands in order to address pressing research questions that are in focus of the present thesis.

**Island area** is the strongest predictor of species richness on islands (Kreft et al. 2008, Triantis et al. 2012). However, direct influences of island area on species richness via neutral processes and indirect influences via niche availability are still debated (e.g. MacArthur and Wilson 1967, Hubbell 2001, Hortal et al. 2009). Direct effects of island area on species richness assume neutral assembly processes as larger islands support larger populations and receive more immigrants (Brown and Kodric-Brown 1977), which reduces the risk of stochastic extinctions (Coleman 1981, Pimm et al. 1988, Hubbell 2001). Larger islands may also support more habitats, thereby increasing niche availability and leading to increasing species numbers (Kohn and Walsh 1994, Hortal et al. 2009). Consequently, island area can also influence species richness indirectly via habitat diversity and the availability of different niches. Direct and indirect effects of area on species richness suggest that the assembly of island biota has multiple dimensions, that are often difficult to measure and disentangle (Simberloff 1976b, Kreft et al. 2008, Weigelt et al. 2015).

**Spatial scales** determine the number of species that can exist in a certain area. Spatial scales are composed of the grain size, i.e. the minimum scale sampled, and the spatial extent that describes the study region or distance between samples (Wiens 1989, Rosenzweig 1995). Larger scales support higher species richness, and thus, the relationship between scales and species richness is expressed by the SAR (Palmer and White 1994). Scale effects have been studied intensively on the mainland (e.g. Ricklefs 1987, Palmer and White 1994, Rahbek 2005), while islands have received less attention (but see Sfenthourakis and Panitsa 2012, Karger et al. 2014). However, especially for islands, scale effects can help to single out assembly processes of island communities and to identify the underlying mechanisms of the SAR. Indeed, island area strongly affects species richness and variation in species richness sampled at small grain sizes (Williamson et al. 2001, Sfenthourakis and Panitsa 2012). Species richness sampled at small grain sizes (plots or transects) increases with area for small islands but saturates on larger ones (Kohn and Walsh 1994). This suggests that small scale effects and stochasticity determine the number of species at small grain sizes (Chase 2014). Species richness at the island scale, in turn, depends on island area, habitat diversity, and isolation (MacArthur and Wilson 1967, Hortal et al. 2009). The strong dependency of biodiversity on spatial scales may impose great constraints for many island studies that use species richness sampled in plots or transects as estimates for total island richness to construct island SARs (Chase et al. 2019) and to refer to ecological processes on islands (e.g. Niering 1963, Kohn and Walsh 1994, Yu et al. 2012, Wang et al. 2015, Ibanez et al. 2018). Hence, a detailed understanding of the scale dependency of species richness patterns is of great importance to discern the drivers behind SAR. Biodiversity patterns at different spatial scales are especially important for small islands where an idiosyncratic phenomenon challenges our knowledge about island community assembly: the small-island effect.

**The small-island effect** (hereafter SIE) forms a notable exception to the ubiquitous form of the SAR. The SIE states that on very small islands, species richness displays high variation independently of island area (Lomolino and Weiser 2001), or increases at a lesser rate than on larger islands (Dengler 2010, Morrison 2014). The SIE was first explored by Niering (1963) who studied plant species on a remote Pacific atoll. While plotting island species richness against area, Niering observed that below a certain area threshold, species richness varied independently of area (Figure 1.1). MacArthur and Wilson (1967) explained that the SIE was part of the ETIB by hypothesising that, on small islands, extinction rates outnumber colonisation events, thus causing the independent variation of species richness with island area. However, the SIE remained largely unexplored thereafter (but see, e.g., Heatwole and Levins 1973, Woodroffe 1986, and Triantis et al. 2006 for review) until Lomolino and Weiser (2001) renewed the interest in the SIE by showing that 73-89 percent of worldwide archipelagos feature a SIE. Lomolino (2000) even suggested that the SIE reflects the sigmoidal shape of the SAR. Today, the interest in the SIE is steadily increasing (Figure 1.1b), and the SIE has been detected in different archipelagos (e.g. Triantis et al. 2006, Morrison 2014, Chisholm et al. 2016), island-like habitats (Wang et al. 2018), and across different taxonomic groups (Barrett et al. 2003, Qie et al. 2011, Gao and Perry 2016). In addition, numerous theories and concepts behind the SIE have been proposed. Spatial scales could cause the SIE, as small grain sizes inherently cause high species variability (Azovsky 2010). Other theories list environmental factors as causes of the SIE, such as less habitat diversity on small islands (Heatwole and Levins 1973, Triantis et al. 2003), greater differences in productivity between islands due to nutrient influxes (Anderson and Wait 2001), high levels of disturbance (Whittaker 1995), differential effects of isolation, topography, and geology (Triantis et al. 2006, Ackerman et al. 2007), or alternating effects of niche and neutral processes (Chisholm et al. 2016). In addition, species requirements and population level dynamics have been proposed to explain the SIE. These include species adapted to the harsh environmental conditions on small islands (Burns and Neufeld 2009, Sfenthourakis and Triantis 2009), high turnover rates (MacArthur and Wilson 1967, Heatwole and Levins 1973), or greater stochasticity (Qie et al. 2011). Also, mathematical constraints in the detection of the SIE have been identified, such as the log-transformation of island area or species numbers (Burns et al. 2009). Flawed application of statistical methods (Dengler 2010) questions its existence altogether (Tjørve and Tjørve 2011). However, most theories were developed based on descriptive studies, lacking mechanistic-based evidence (but see Chisholm et al. 2016), thereby not explaining why species occurrences vary independently with area on small islands. Detailed understanding of community composition, assembly processes, and species pools of small island biota could provide new insights to the underlying ecological mechanisms behind the SIE.

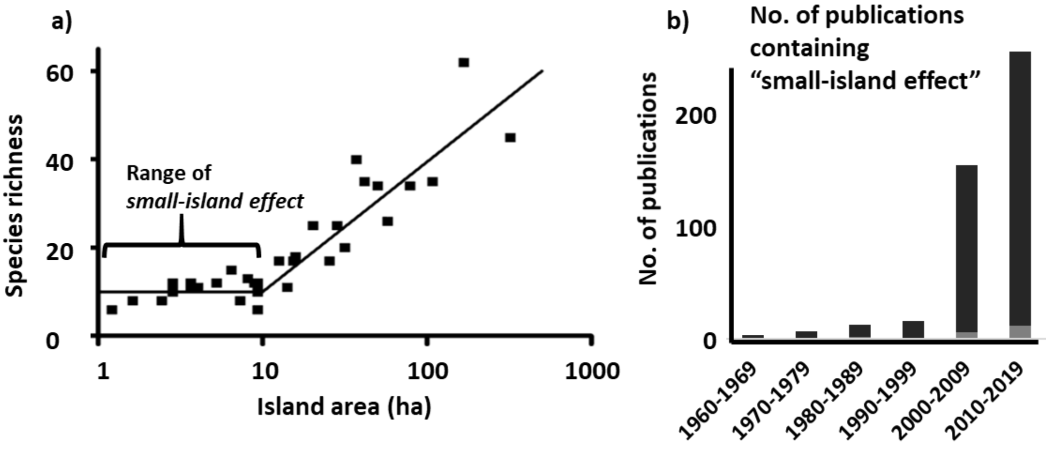

Figure 1.1 Island system featuring the small-island effect (SIE) and commonness of the SIE in the scientific literature. a) Species-area relationship of vascular plants on islands according to Niering (1963). The species-area relationship is best described by a breakpoint model indicating the presence of the SIE. b) Literature research (Google Scholar on Feb. 20. 2019) for the term *small-island effect* in the title (grey) and whole text (black) for six decades starting from 1960. The increased interest in the SIE from 2000 onwards was likely triggered by the seminal SIE-paper by Lomolino and Weiser in 2001.

**Species pools** describe the species in the region that can potentially inhabit a site, such as an island (Zobel 1997, Pärtel et al. 2011), and are central to understanding assembly processes. Small island communities often rely on constant immigrations from the species pool to maintain their low population densities (Brown and Kodric-Brown 1977, Pulliam 1988) and to compensate high species turnover rates (Heatwole and Levins 1973, Chiarucci et al. 2017). According to the ETIB, all species from the pool have identical probabilities to establish on an island (MacArthur and Wilson 1967, Hubbell 2001). Hence, the species pool should consist of the same set of species for all islands (at least within an archipelago). However, physical and ecological differences between islands lead to distinct species communities on small islands (Wardle et al. 1997). For instance, certain habitat types such as mountain tops or riverine systems are largely absent on small islands (Lovejoy et al. 1986, Ricklefs and Lovette 1999, Keppel et al. 2016). That indicates that (small) island communities likely recruit from a subset of the species pool that only includes species whose ecological requirements match the site-specific abiotic and biotic conditions. Despite the usefulness of species pools to understand community assembly processes (MacArthur and Wilson 1967, Ricklefs 1987, Cornell and Harrison 2014), species pools are rarely incorporated into island biogeography theory, likely due to constraints in the selection of incorporated taxa (Carstensen et al. 2013). New methods to estimate species pools for islands could help to indicate species that can become part of a community. These methods may consider species abiotic and biotic requirements and filtering processes on islands.

**Filtering** describes dispersal barriers and unfavourable abiotic and biotic requirements that prevent a species from becoming part of a community and that are commonly categorised as dispersal and environmental filters (Gillespie *et al.* 2012; Cadotte & Tucker 2017; but see Kraft *et al.* 2015). For plants, dispersal filters can act on species that have fleshy fruits and rely on bird dispersal and are thereby filtered from islands that are out of reach of the specific disperser (Carlquist 1974, Burns 2005, Gillespie et al. 2012). Environmental filters exclude species sensitive to prevailing abiotic and biotic conditions. For instance, salt-intolerant species are excluded from islands that feature high salinity due to frequent inundations or ocean-borne disturbances (Whitehead and Jones 1969, Whittaker 1995). Biotic interactions such as competition can also lead to exclusion of certain species (Abrams 1986, Chesson 2000, Levine and HilleRisLambers 2009). The concept of filtering is intuitively appealing due to the direct link of species (non-)adaptations to ecosystem properties. However, processes behind filtering are operationally difficult to separate (Violle et al. 2012) and should be interpreted with caution (Kraft et al. 2015).

**Functional traits** provide a useful framework to overcome the complexity of different filtering processes acting on a community (Cadotte and Tucker 2017). Functional traits describe morphological, physiological, or phenological features that can be measured at the level of an individual (Violle et al. 2007). Traits can directly be linked to dispersal ability and niche requirements (Díaz and Cabido 2001, Violle and Jiang 2009, Arjona et al. 2018), and are useful to describe species life-history characteristics (Westoby 1998, Reich 2014, Díaz et al. 2016). To test for filtering, particular trait values or groupings of traits that represent similar life-history strategies are compared against random trait samples from the species pool using null models (Mason et al. 2013). Underdispersed trait values may indicate trait clustering, e.g. co-occurrence of more similar traits than expected by chance. For island communities, underdispersed trait values could occur under high environmental stress, resulting in co-occurring species sharing similar strategies in regard to, e.g., resource acquisition (Astor et al. 2014). Overdispersed trait values indicate trait divergence where co-occurring species have more dissimilar trait values than expected by chance (Baraloto et al. 2012, Li et al. 2015, Cadotte and Tucker 2017). Overdispersed island communities could occur when high competition or absence of herbivory leads to the co-existence of many functionally different species (Schoener and Toft 1983, Weiher et al. 1998). Evenly dispersed trait values point towards neutral assembly processes (Kraft et al. 2007, Schamp et al. 2008) as assumed by the ETIB (MacArthur and Wilson 1967).

There is growing support for a functional perspective in island biogeography that considers species traits to explain assembly processes (Patiño et al. 2017). However, trait-based approaches were predominantly developed for mainland communities (e.g. Ackerly and Cornwell 2007, Lhotsky et al. 2016, Craven et al. 2018), and their applicability in island contexts remains limited. Only a few studies have investigated the scaling of functional diversity on islands (Ding et al. 2013, Whittaker et al. 2014, Karadimou et al. 2016, Si et al. 2016), but most have not identified the underlying mechanisms (but see Astor et al. 2014, Si et al. 2017).

Overall, multiple ecological and environmental dimensions act together on island communities. Classic neutral island biogeography theory, such as the ETIB, provide useful frameworks to quantitatively examine diversity patterns across islands. However, neutral colonisation and establishment dynamics are increasingly challenged in their ability to accurately describe assembly processes on islands. Influences of spatial scales on biodiversity, island-specific species pools, and filtering processes hint towards non-random community compositions on islands. These approaches have rarely been applied in island research, while the integration of multidimensional ecological processes becomes increasingly important to describe the underlying mechanisms behind island biodiversity.

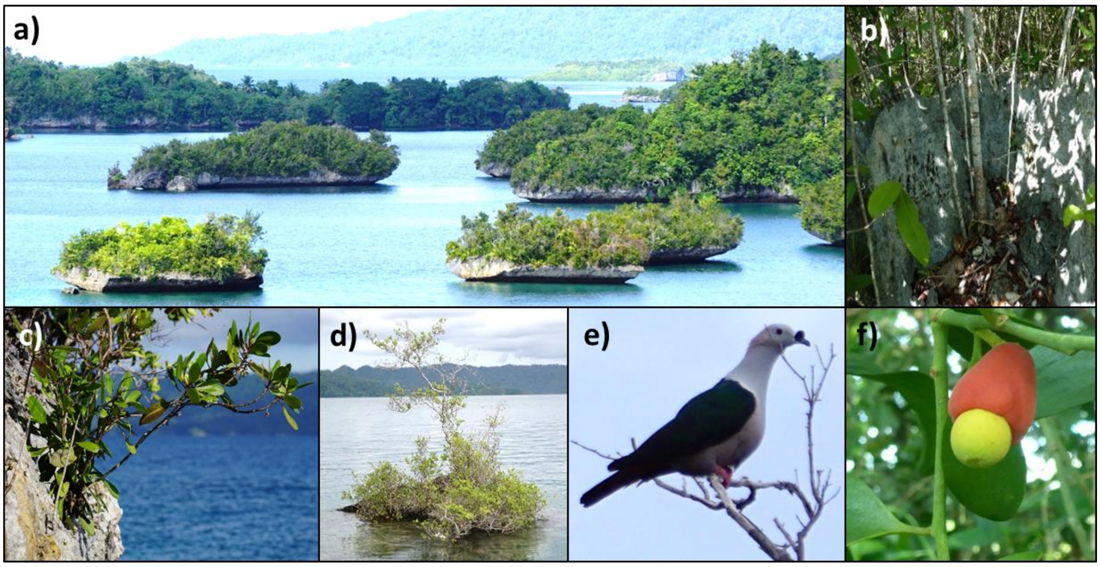

Figure 1.2 Small islands and their biota as model systems. a) Small-island system in the Raja Ampat Archipelago (Indonesia). b) Environmental factors, such as soil availability, are important to determine species richness at small scales. c) Many small-island species are adapted to extreme environmental conditions and d) small islands are often prone to ocean borne disturbances. e) Birds (here *Ducula myristicivora*) are important dispersers for many small-island species that f) often have fleshy fruits (here *Exocarpos latifolius*). (Pictures from Raja Ampat Archipelago, Indonesia. Photo credit: J. Schrader).

## 1.2 Small island research: Within and among archipelagos

Most studies that investigated diversity patterns on small islands have focused on within-archipelago dynamics, e.g. islands belonging to the same geographical system. Detailed understanding of local scale dynamics is important to gain in-depth knowledge of ecological processes, but large-scale patterns often remain concealed (Beck et al. 2012). The special case of the SIE serves as a good example to illustrate inconsistencies in findings between studies and how conflicting hypotheses can hamper the development of unifying frameworks. From the wealth of hypotheses that have been proposed to describe the SIE (see above and Triantis et al. 2006 for review), many have been only reported once to explain the SIE and seem unique to certain archipelagos. For instance, the Subsidized Island Biogeography Hypothesis attributes the SIE to greater nutrient influxes on small islands (Anderson and Wait 2001). However, this hypothesis has only been confirmed once for reptiles on small islands in the Caribbean (Barrett et al. 2003), and no other studies found nutrient influxes to have an impact on the SIE. Hu et al.

(2011) studied plants on small islands in a Chinese lake and proposed greater edge effects of small islands compared to larger ones to drive the SIE. But evidence from other archipelagos is scarce and the role of edge effects on the SIE remains to be tested. Such discrepancies among studies led to an intensive debate about how to detect the SIE altogether (Burns et al. 2009, Sfenthourakis and Triantis 2009, Dengler 2010), with the conclusion that the SIE is not a single-variable discipline (Triantis and Sfenthourakis 2012). Studies that go beyond the study of single archipelagos could provide fresh insights to the SIE debate by identifying consistent factors behind the SIE across archipelagos.

Methods to detect general biodiversity patterns across scales are developed in macroecology, which considers large spatiotemporal scales (Brown and Maurer 1989), and for islands, biogeographical patterns between islands, and archipelagos (Kreft et al. 2008, Weigelt 2015). Macroecological SIE studies used species richness data across archipelagos and reported new and intriguing patterns. For instance, Lomolino and Weiser (2001) found that the upper limit of the SIE (i.e. the maximum island area to which the SIE occurs) differs between taxonomic groups and is greater for more isolated archipelagos. Another example was presented by Wang et al. (2016), who reported that the inclusion and exclusion of empty islands affects the detectability of the SIE. Using a global island dataset, Chisholm et al. (2016) hypothesised that communities on small islands within the range of the SIE are governed by niche processes, whereas communities on larger islands assemble neutrally, shaped by random colonisations and extinctions. These patterns only become observable at macroecological scales. Indeed, there is a growing need to test existing hypotheses, such as for the SIE, at a global scale to identify consistent patterns.

## 1.3 Study outline

In my thesis, I use the flora of small islands as a model system to test and advance existing theories in island biogeography. I propose a conceptual framework and develop new methods to study the assembly of island floras. I put a special emphasis on exploring processes that shape the SAR in general and the SIE in particular. To achieve that, I combine taxonomic richness and functional diversity of plants on small islands using two distinct datasets: I compiled the first dataset at a regional scale in the Raja Ampat Archipelago (Indonesia): I collected detailed taxonomic and functional accounts on 57 tree species. I also sampled the species in standardised transects and a hierarchically nested sampling design on 60 small islands that vary in size by three orders of magnitude. For the second dataset, I collected species occurrence data for more than 700 small islands worldwide and collated information on species growth forms. I incorporated this dataset in the Global Inventory of Floras and Traits (GIFT; Weigelt et al. 2019).

Specifically, I used the two datasets to address the following questions:

- Does the shape of the SAR depend on the sampling scale, and which environmental factors shape species richness across spatial scales?
- Do species on small islands have requirements related to island area that determine island-specific species pools?
- Are small island communities shaped by dispersal and environmental filtering? Is filtering related to species life-history dimensions and, if so, does the filtering strength differ between islands?
- Does the shape of the SAR and the prevalence of the SIE differ between species richness of different plant functional types, and do functional types better predict the upper limit and prevalence of the SIE than measures of total species richness?

To answer these questions, I structured my thesis into five research chapters that consistently build on each other:

In chapter 2, I present Leaf-IT, a new smartphone application for measuring leaf area and other functional trait-related areas. I test the precision and accuracy of Leaf-IT and compare it against a well-established commercial software. I developed Leaf-IT as a free tool using smartphones as a platform to increase the portability. Leaf-IT provides the opportunity to measure leaf area under remote field conditions, which typically hamper the use of conventional methods that often rely on scanners and an electrical grid. I used Leaf-IT during my functional trait sampling on small islands in the remote Raja Ampat Archipelago.

In chapter 3, I investigate the effect of sampling scale on the SAR. I test whether local scale samples adequately predict richness at the island scale and then determine the importance of island area, isolation, shape, and habitat quality at each sampling scale on species richness. Therefore, I use the regional dataset of trees on 60 small islands in the Raja Ampat Archipelago to investigate species richness at different spatial scales. Specifically, I test whether different sampling scales affect the shape and function of the SAR, whether local species richness (within plots) is related to island area, and if small-scale habitat quality is important in explaining species richness at local sampling scales. Finally, I test whether richness sampled at a local scale resembles richness patterns typical for the SIE.

In chapter 4, I develop a novel method to estimate probabilistic island-specific species pools. I use the tree occurrences on 60 small islands in the Raja Ampat Archipelago to model the area requirements for each species and compare them against random colonisation models. Specifically, I test whether the species pool follows a similar SAR as the observed richness, whether the SIE found for observed richness originates already from the species pool, and whether species communities on small islands assemble randomly by testing observed species occurrences against null models.

Chapter 5 is closely linked to chapter 4, where I expand on the pattern of non-random community composition and provide further insights into its underlying processes. I propose a novel trait-based analytical framework to test for non-random community assembly and filtering processes on islands. I use the dataset from the Raja Ampat Archipelago that includes 11 plant functional traits representing major dimensions in plant form and function. I test whether species richness and abundance directly affect functional diversity on islands. Then, I use species life-history dimensions to test for non-random patterns in assembly processes related to dispersal and niche partitioning of light, nutrients, and resource acquisitions.

In chapter 6, I use the dataset on small islands implemented in the GIFT database to analyse the effects of plant growth form species richness on the SAR and the prevalence of SIE. Specifically, I test whether the shape of the SAR differs between plant richness dissected into herbs, shrubs, and trees, and whether the upper limit of the SIE differs between growth forms. Moreover, I investigate whether island area, isolation, topography, and environmental heterogeneity differently affect growth form species richness on small islands.

The last chapter 7 of my thesis summarises my work in form of a synopsis. I jointly discuss the research chapters to find general trends and patterns in island community assembly. I discuss the value of the SIE debate and point towards processes that shape the SAR. Moreover, I debate the significance of small islands as model systems and suggest future directions of exploration in the field of small island research.

# *Research chapters*

# 2. Leaf-IT: An Android application for measuring leaf area

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## 2.1 Abstract

1. The use of plant functional traits has become increasingly popular in ecological studies because plant functional traits help to understand key ecological processes in plant species and communities. This also includes changes in diversity, inter- and intra-specific interactions, and relationships of species at different spatio-temporal scales. Leaf traits are among the most important traits as they describe key dimensions of a plant's life history strategy. Further, leaf area is a key parameter with relevance for other traits such as specific leaf area, which in turn correlates with leaf chemical composition, photosynthetic rate, leaf longevity, and carbon investment. Measuring leaf area usually involves the use of scanners and commercial software and can be difficult under field conditions.

2. We present Leaf-IT, a new smartphone application for measuring leaf area and other trait-related areas. Leaf-IT is free, designed for scientific purposes and runs on Android 4 or higher. We tested the precision and accuracy using objects with standardised area and compared the area measurements of real leaves with the well-established, commercial software WinFOLIA using the Altman-Bland-Method.

3. Area measurements of standardised objects show that Leaf-IT measures area with high accuracy and precision. Area measurements with Leaf-IT of real leaves are comparable to those of WinFOLIA.

4. Leaf-IT is an easy-to-use application running on a wide range of smartphones. That increases the portability and use of Leaf-IT and makes it possible to measure leaf area under field conditions which are typical in remote locations. Its high accuracy and precision is similar to WinFOLIA. Currently, its main limitation is margin detection of damaged leaves or complex leaf morphologies.

**Key-words:** Functional trait, smartphone, App, leaf area, functional ecology, logical agent

## 2.2 Introduction

Plant functional traits describe ecologically relevant morphological, anatomical, biochemical, physiological, or phenological features of individuals and species and provide information about the environmental constraints a plant faces (Pérez-Harguindeguy et al. 2013). The study of functional traits allows, among others, to compare habitats with little taxonomic overlap and to gain better insights into ecosystem functions and processes (Díaz et al. 2004, Pérez-Harguindeguy et al. 2013, Cadotte 2017). Studying the variation in plant traits has become increasingly popular in ecology (Kattge et al. 2011a, Díaz et al. 2016). For a large number of plant species and from a huge number of studies and sites functional traits have been collated into large databases (Kühn et al. 2004, Kleyer et al. 2008, Kattge et al. 2011a) but glaring taxonomic and geographical gaps remain (Schrodt et al. 2015, Jetz et al. 2016), especially in tropical ecosystems and remote regions (Schrodt et al. 2015). A main limitation to fill these gaps is that measuring functional traits in the field is often laborious or requires expensive equipment.

Leaf area is among the most important plant traits (Wilson et al. 1999, Violle et al. 2007, Pérez-Harguindeguy et al. 2013, Díaz et al. 2016) and can be regarded as key trait relevant to other traits like the specific leaf area. Specific leaf area in turn is often used in growth form analyses (Evans and Poorter 2001, Pérez-Harguindeguy et al. 2013). It is also a key trait in the leaf economics spectrum (Wright et al. 2004), linked to differences in plant life strategies (Wilson et al. 1999), and correlates positively with photosynthetic rate, leaf nitrogen concentration, light interception, and relative growth rate and negatively with leaf longevity and carbon investment (Pérez-Harguindeguy et al. 2013). Other important ecophysiological attributes of plants including leaf phosphorous capacity, dark respiration, chemical composition, and evapotranspiration are often expressed per leaf area (Reich et al. 1999, Wright et al. 2004, Garnier et al. 2017), emphasising the importance of leaf area in plant ecology.

Measuring leaf area can be difficult under field conditions as standard protocols require a scanner, computer, and digital image processing by sophisticated and often expensive software to obtain accurate and reliable results (e.g: *Delta-T Devices* (Cambridge, UK), *LI-COR* (Lincoln, NE, USA), *WinFOLIA* (Regent Instruments Canada Inc.)). This often restricts analyses of leaf area to laboratories with connection to electricity and computers (but see Pérez-Harguindeguy *et al.* (2013) for low-tech options for the measurement of leaf area).

Smartphones have a high potential for science (Welsh and France 2012) as they are widespread, have strong computing power (Lane et al. 2010), and include a wide range of accurate tools like GPS, camera, and different types of sensors (e.g. acceleration sensors, gyroscopes, magnetic field sensors, light sensors, barometers, thermometers, and air humidity sensors). Smartphone applications using this set of sensors can be well suited to assist within fieldwork (Welsh and France 2012), especially, as many applications are free of charge. Despite the many accurate sensors in smartphones, surprisingly few applications have been designed as tools for ecology and evolution (but see Teacher *et al.* 2013) and are an underexploited resource. Also, the use of smartphones for plant functional ecology is highly undervalued. Only a few recent developments have been made to use smartphones for measuring plant traits like leaf area index (e.g. *PocketLA*I (Confalonieri *et al.* 2014), *VitiCanopy* (De Bei et al. 2016)) and leaf area (*Petiole* (http://petioleapp.com/), *Easy Leaf Area* (Easlon and Bloom 2014)).

Here, we present Leaf-IT, a new smartphone application to measure leaf area as well as other trait-related areas accurately under field conditions which are typical in remote locations.

Leaf-IT uses a margin detection algorithm that is highly robust against unwanted shadows and impurities, which may interfere with area measurement. This makes Leaf-IT fundamentally different to other area-analysing software and applications based on threshold-based pixel count measurement (Easlon and Bloom 2014). Leaf-IT is specifically designed to measure area under challenging field conditions, includes easy-to-use features for area measurement and data output and can be used freely for ecological research and teaching. We tested the accuracy and precision of Leaf-IT using real leaves as well as objects with standardised area and compared the results with the well-established, commercial software WinFOLIA.

## 2.3 Methods

### Technical details of the application and margin detection

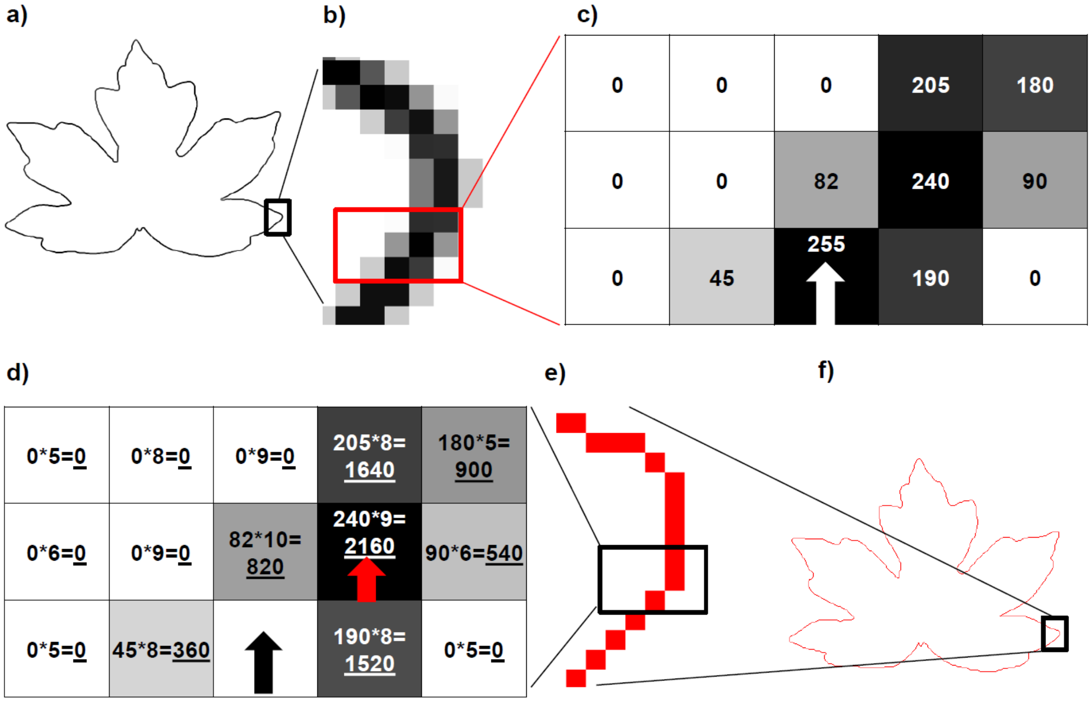
Leaf-IT runs on smartphones with Android 4 (or higher) operating systems and does not require connection to the internet or databases. Images of leaves or other objects are taken by the internal smartphone camera. After image acquisition, Leaf-IT uses digital image processing for area measurement and proceeds in three steps: i) margin detection of the leaf or any desired object that has clearly defined margins, ii) pixel count, and iii) comparison with a reference object with a known area. For best results, the leaf should be placed on a background with a high contrast to the leaf. A white background works best for darker leaves. For lighter objects such as flower petals, a black background might be more suitable. After image acquisition, Leaf-IT conducts three steps of image processing: (1) converting the image to grayscales, (2) highlighting the margins by increasing the contrast, blurring weak margins, and enhancing strong margins, and (3) calculating the light gradients and displaying the light gradients (Figure 2.1 c), so that the image only retains the margins (Figure 2.1 a, b). Light gradients are calculated by comparing the contrast between neighbouring pixels and by assigning values between 0 and 255 to each pixel. Neighbouring pixels with high contrast get high values (e.g. from white pixel to black pixel: value of 255) and neighbouring pixels with low contrast (e.g. light grey pixel to grey pixel: value of 50; white pixel to white pixel: value of 0, etc.) get low values. Light values are later displayed as pixels ranging from white to black, whereas pixels with low light values are displayed brighter (value of 0 equals white) and pixels with high values are displayed darker (value of 255 equals black). This procedure reduces the effects of distortions from e.g. unwanted shadows or lines on a background paper that become weaker or even vanish and interfere less with the margin detection of the leaf.

During calculation of the light gradients, the pixel with the highest gradient in the image, which is normally part of the leaf margin, is stored. A logical agent (Wooldridge and Jennings 1995), specially designed for margin detection, is placed on the pixel with the highest light gradient and traces the margin step by step by drawing a line which is one pixel strong until it reaches its starting point again. The agent is based on the concept of a robot following a line (Barraquand et al. 1992). During each step along the margin, the agent conducts four tasks (according to Russell & Norvig 2016). First, the agent creates a viewing area of three times five pixels, where the agent occupies one pixel in the centre of a five-pixel-long margin (Figure 2.1 b). The direction from the pixel occupied by the agent towards the centre of the viewing area is the viewing direction (Figure 2.1 c & d). In the second step, the agent calculates weighted light values for each pixel in its viewing area. The values for each pixel of the light gradients are multiplied with a value depending on the location of the pixel within the viewing area (Figure 2.1 d). Pixels located closer to the position of the agent and located closer to the viewing direction get the highest multiplier (based on the *inverse-square law*; Figure 2.1 d). Thus, pixels directly in front of the agent and in line with the viewing direction are considered more likely to be part of the leaf margin and get higher multipliers (Figure 2.1 d). In the third step, the agent moves to the position of the pixel with the highest weighted light level (Figure 2.1 d). In the fourth step, the agent verifies if it moved at all (in case its former path led to a dead end) and if it reached the starting position again. Each time the agent moves, it indicates the covered way as a one-pixel strong red line (Figure 2.1 e, f). The user can view the red line encircling the object for verification whether the agent encircled the leaf correctly (Figure 2.1 f).

Defined rules are provided for the agent (following Russell & Norvig 2016) for the evaluation of its last actions and to undo its last moves in case of errors. The rules provide guidelines for the agent how to proceed if it reaches the margin of the images or if it ran into a dead end (in this case the agent goes back one step and proceeds to the pixel with the second highest weighted light value). The agent also contains exit commands to avoid endless searches and loops in path finding. In this case, an error message appears for the user and area measurement stops.

### Area measurement

After finishing the leaf margin detection, the area is measured. All pixels encircled by the one-pixel strong red line are counted and compared with the amount of pixel of a reference object of a known length or area. Two different methods are available in Leaf-IT for setting a reference object. The first method (in Leaf-IT: S*et size of leaf manually*; from now *set size*) allows the user to place an object of a known length (e.g. a ruler or any other defined object; compare Figure 2.2 c) next to the leaf. By manually drawing a rectangle around the reference object, it is spared from image processing to not interfere with the margin detection. After margin detection, the user can adjust a digital ruler (which starts automatically; compare with Figure 2.2 d) to the reference object and enter the length in mm. Next, the area of one pixel is calculated by counting the number of pixel of the digital ruler and set against the measured length. This allows the measurement of leaf area by comparing the numbers of pixels from the digital ruler and the leaf. The second method (in Leaf-IT: *Use reference object*; from now *reference object*) allows the user to place an object with a known area (e.g. a coin or a printed rectangle; compare with Figure 2.2 f) next to the leaf. Both reference object and leaf are processed separately (again by placing a digital rectangle around the reference object). After the image is processed, the user enters the area of the reference object. Leaf-IT then compares the number of pixel of the reference object and the leaf and measures the area in cm$^2$ as describe above.



|  |  |  |  |  |
|---|---|---|---|---|
| 0 | 0 | 0 | 205 | 180 |
| 0 | 0 | 82 | 240 | 90 |
| 0 | 45 | 255 | 190 | 0 |

|  |  |  |  |  |
|---|---|---|---|---|
| 0*5=0 | 0*8=0 | 0*9=0 | 205*8=1640 | 180*5=900 |
| 0*6=0 | 0*9=0 | 82*10=820 | 240*9=2160 | 90*6=540 |
| 0*5=0 | 45*8=360 |  | 190*8=1520 | 0*5=0 |

Figure 2.1 Details of image processing and pathway of the logical agent in Leaf-IT. (a) Image of leaf after three steps of image processing and calculation of light gradients. Only the margin remains, shown as several- pixel- strong line (b). (c) The logical agent starts at the pixel with highest light gradient (white arrow) and evaluates all pixels in its viewing area (five times three pixels). Light gradient values (ranging from 0 to 255) of pixels, position of agent and its viewing direction (white arrow) are shown. (d) The agent multiplies the light gradient values (first factor) with values depending on the distance from the agent's position (second factor). Highest product (products are underlined) indicates the pixel where the agent moves next (pixel with red arrow). After each step, the agent starts again with the evaluation of its viewing area. The path of the agent is indicated as one- pixel- strong red line (e) until it has circled the whole margin of the leaf (f) and reaches its starting point again.

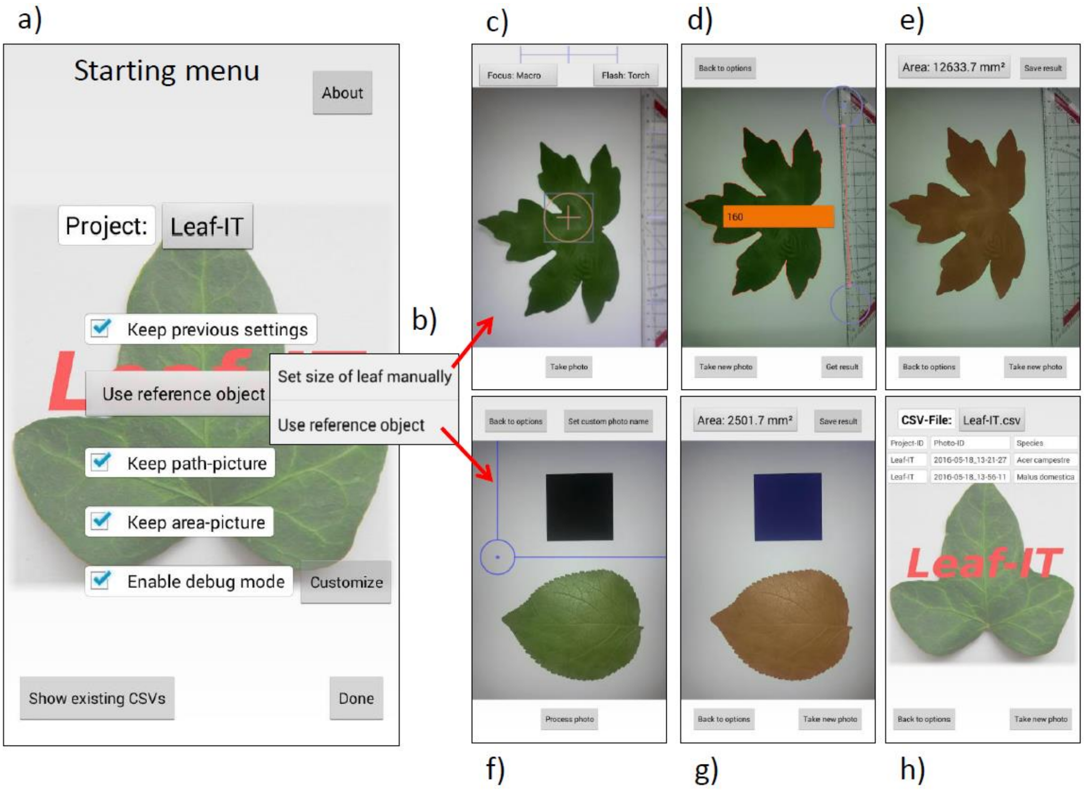


Figure 2.2 Starting menus, methods, and options in Leaf-IT. (a) Starting menu with all relevant options displayed. (b) Options to choose between the two main methods (set size and reference object) for measurement leaf area and the non-destructive method. (c), (d), and (e) the different steps during the set size method, and (f) and (g) during the reference object method. (h) The output of Leaf-IT can be exported as .csv- file.

## Tools, options, and data output

Leaf-IT offers intuitive tools for data management, export, and image acquisition. All options can be selected and viewed in the start menu (Figure 2.2 a). The *Project*-menu allows the user to create own projects. A project can be, for instance, a measurement series of a certain plant individual or species, a field site, or a sampling day. Each project can be exported as .csv-file (Figure 2.2 h). All area measurements within a project are saved in the same .csv-file where also species names and image IDs can be edited or deleted (Figure 2.2 h). The *set reference*-menu contains the two methods how to define the reference object as described above (Figure 2.2 b). Here, the user can select between *set size* (Figure 2.2 c-e) and *reference object* (Figure 2.2 f, g). After choosing the appropriate settings, Leaf-IT opens the camera mode (Figure 2.2 c). When the image mode is displayed, a level appears. Provided that the photographed object is in level, optimised set up for highest accuracy can thus be created (90° angle from camera lens to object; Figure 2.1 c). After the image has been taken, the user defines the area where the reference object is located and proceeds to the image analysis as described above (Figure 2.2 d, f). The detected margin is displayed in red with the image in the background (Figure 2.2 d), allowing the user to evaluate the accuracy of the margin detection procedure before proceeding to area measurement. Here, the user defines length (method: *set size*) or area (method: *reference object*) of the reference object on the smartphone display (Figure 2.2 d). The measured area of the leaf (Figure 2.2 e, g) can be saved to a .csv-file. The file also automatically includes the date and time of area measurement and image ID. All images as well as area and path images measured by Leaf-IT (when requested in the *customise*-option; Figure 2.2 a) can be saved as .png in the Leaf-IT folder or project subfolder on the smartphone where also the .csv-file is saved.

## Assessing accuracy and precision

Precision and accuracy are two important metrics for validating new measurement methods (Westgard et al. 1974). Precision describes the random analytic error (distribution of the individual measurements around a mean value), while accuracy describes the systematic analytic error (difference between the mean of the measured values and the *true* value) (Westgard et al. 1974). We estimated both precision and accuracy of Leaf-IT using standardised objects with known area. This allowed us to assess how accurate and precise Leaf-IT reproduced the area and to compare measured and true leaf area.

For testing the accuracy of the *set size* method, we designed 22 shapes with different shapes and sizes (shapes are shown in Figure A 1): eight different shapes with 1 cm$^2$ and 10 cm$^2$, respectively, and six different shapes with 100 cm$^2$. Different shapes and areas were created in black colour on white background with the software Microsoft PowerPoint Version 10 and printed out using a high-resolution printer (Xerox Colour 550, 2.400 dpi x 2.400 dpi) on 160 g/m$^2$ paper. Precision and accuracy of the *reference object* method was measured on the same 22 objects as for the *set size* method. We only added a square of the same area next to the other object as reference area.

Subsequently, we compared the area match of real leaves of different sizes and morphologies between Leaf-IT (*reference object* method) and the computer software WinFOLIA (Version: 2016b Pro; Regent Instruments Canada Inc., 2016). WinFOLIA is an established standard software for leaf area measurements.

## Precision of Leaf-IT

We measured the precision of Leaf-IT using the *reference object* method (described above). Therefore, we took an image of the same object (a square) of the area classes of 1 cm$^2$, 10 cm$^2$, and 100 cm$^2$ under optimised conditions (levelled smartphone with 90° angle between object and camera lens) ten times, respectively. Measured area was standardised for better comparison between the three area classes by dividing the measured area by ten for 10 cm$^2$ and by 100 for 100 cm$^2$. Thus, the true mean always equalled one. We calculated the precision for the three area classes (1 cm$^2$, 10 cm$^2$, and 100 cm$^2$) separately. We indicated the precision (in %) by calculating the range between the lower and the upper confidence interval (CI; upper CI minus lower CI).

## Accuracy of Leaf-IT

To test the accuracy of Leaf-IT, we used the methods *set size* and *reference object* separately under optimised conditions (levelled smartphone, object in 90° angle from the lens) and handheld to simulate field conditions (four runs in total). All standardised objects were photographed and analysed by Leaf-IT (n = 22). Area values from each run were divided by 100 for 1 cm$^2$, by 1,000 for 10 cm$^2$, and by 10,000 for 100 cm$^2$ for analysing the three area classes together. We provided the accuracy (in %) by subtracting the calculated mean by the true mean (always one).

## Comparison between Leaf-IT and WinFOLIA

To test Leaf-IT on real leaves, we compared the area measurements of Leaf-IT with WinFOLIA. Therefore, we photographed 25 leaves of different size (from 1.88 cm$^2$ to 115 cm$^2$) and shape of 18 European plant species (species list and area values are provided in Table A 1). The same photographs taken and analysed by Leaf-IT were also analysed by WinFOLIA for direct comparison.

## Statistical analyses

For testing the accuracy of Leaf-IT, we compared the mean of the true area values of standardised objects with the area measured by Leaf-IT. We calculated the differences (in %) and 95% CI of the area measured by Leaf-IT towards the true area for all measurements of the same run respectively (methods *set size*, *reference object*, and both methods combined under optimised conditions and handheld). For the precision, we calculated the mean and the 95% CI of ten measurements repeated on the same standardised object with the area of 1 cm$^2$, 10 cm$^2$, and 100 cm$^2$, respectively. We used the Altman-Bland-Method (Altman and Bland 1983, Bland and Altman 1986) to compare area measurements of Leaf-IT and WinFOLIA. This allowed us to investigate the relationship between the measurement error and the true value. However, since the true value was unknown the mean of both measurements was the best estimate of the true value provided (Bland and Altman 1986). We calculated the mean difference between both methods by subtracting the mean of the WinFOLIA measurements by the mean of the Leaf-IT measurements. The mean difference indicated the bias of Leaf-IT compared with WinFOLIA. The critical difference (in $cm^2$) between both methods is expressed as the difference from the mean (of both methods) to the upper or lower 95% CI. All statistical analyses were done in the statistical software *R* (version 3.3.1, R Core Team 2014).

## 2.4 Results

### Precision of Leaf-IT

For the smallest object size (1 $cm^2$), the mean leaf area as measured by Leaf-IT was exactly 1 (rounded by three decimal figures) showing that true and Leaf-IT-measured area values were virtually identical. The 95% CI was between 0.990 to 1.009 (n = 10) resulting in a precision of 98.1%. For the intermediate area class (10 $cm^2$), the mean calculated from Leaf-IT was 1.005, which differed from the true value by 0.5%. The 95% CI ranged from 1.001 to 1.009 (n = 10) with a precision of 99.2%. The largest area class (100 $cm^2$) revealed a mean of 1.004, i.e. 0.4% higher than the true value, and 95% CI ranged from 0.999 to 1.009 (n = 10) giving a precision of 99% (Figure 2.3 a). All area measurements are provided in Table A 2.

### Accuracy of Leaf-IT

We measured the accuracy of both Leaf-IT methods (*reference object* and *set size*) under optimised conditions and under simulated field conditions. Using the *set size* method under optimised conditions, the mean was 1 (true mean also 1) with the 95% CI ranging from 0.996 to 1.005 (n = 22). Taking images under simulated field conditions, the calculated mean was 1.001, which gives a deviation of 0.1% from the true mean for the *set size* method. The 95% CI was between 0.997 and 1.005 (n = 22). Under optimised conditions the method *reference object* produced a mean of 0.990 which deviated 1% from the true value. The 95% CI ranged between 0.986 and 0.995 (n = 22). The mean of simulating field conditions of the *reference object* method was 0.999 (0.1% off the true mean) with a 95% CI of 0.993 to 1.006 (n = 22; Figure 2.3 b). All area measurements for the accuracy measurements are given in Table A 3.

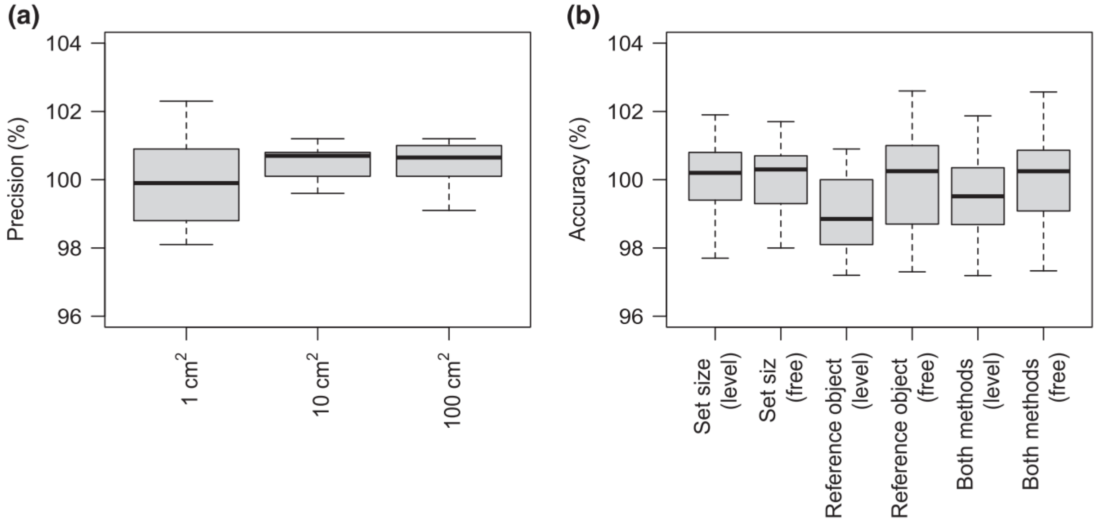


Figure 2.3 Precision and accuracy of Leaf-IT. (a) Precision for reference objects of three area classes. The same area was measured ten times per class. (b) Accuracy of two methods IT (set size and reference object) for area measurement under optimized condition (level) and field conditions (free). Twenty- two objects with known area were measured. In all cases, the true area equals 100%.

## Leaf-IT compared to WinFOLIA

Area measured with Leaf-IT was on average 0.1% (0.132 cm$^2$) higher than of WinFOLIA. The 95% CI ranged between -0.389 cm$^2$ and +0.653 cm$^2$ with a critical difference (half the difference from lower to upper CI) of 0.521 cm$^2$. However, the highest mean difference was recoded for area values above 100 cm$^2$. Smaller area values did not show larger difference than -0.203 cm$^2$ and +0.463 cm$^2$. The highest difference between two measured values was -3.6% and +1.5%. The mean difference between Leaf-IT and WinFOLIA was +0.1% (Figure 2.4). Area measurements for different plant species estimated by Leaf-IT and WinFOLIA are provided in Table A 1.

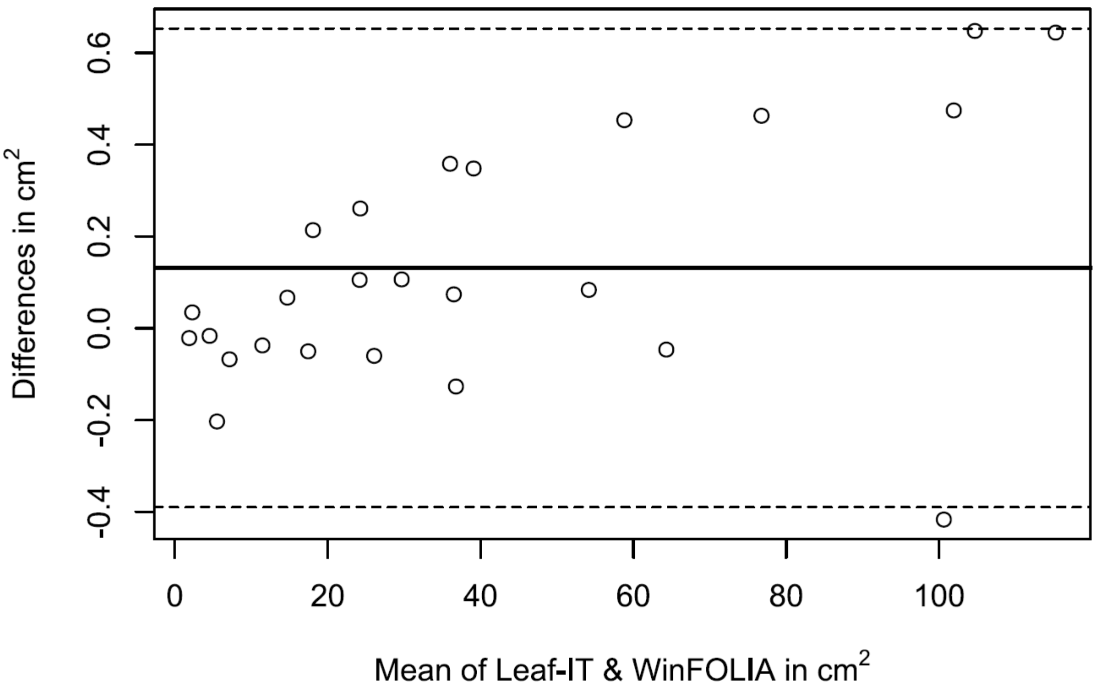


Figure 2.4 Bland–Altman plot showing the mean difference in leaf area measurements between Leaf-IT and the commercial software WinFOLIA. Twenty- five leaves of different sizes and shapes were measured by Leaf-IT and WinFOLIA. The mean of area values for each leaf measured by WinFOLIA and Leaf-IT is shown on the x- axis. The y- axis indicates the difference of each measurement of Leaf-IT compared with WinFOLIA. Mean difference of all 25 measurements (solid line; 0.132 cm$^2$) between both methods and 95% confidence intervals (dashed lines; 0.653 and −0.389 cm$^2$) are shown.

## 2.5 Discussion

Leaf-IT is a new, easy-to-use, and free of charge application licenced under creative commons (licence: CC BY-NC-SA 4.0) that produces sufficiently accurate and precise area measurements. Due to its intuitive graphical user interface and high portability Leaf-IT is useful for a wide range of applications in ecological research and teaching.

The logical agent and the option to choose between two different methods for area measurements make Leaf-IT fundamentally different to other software programs that evaluate each pixel individually (e.g. WinFOLIA, Easy Leaf Area; Easlon & Bloom, 2014), or need elaborate image calibration (e.g. Petiole). Instead, Leaf-IT encircles the leaf and rates each pixel equally within the enclosed area making Leaf-IT more robust against shadows and other artefacts on the background. At the same time, Leaf-IT currently has limitations in assessing leaf area of species with complex leaf morphologies (e.g. pinnate and fern leaves) and damaged leaves.

## The *set size* method

The method *set size* yielded highly accurate results with a mean accuracy of less than 0.5%. The accuracy did not decrease when taking the image by handholding the smartphone, which conforms to challenging condition during field work. Accuracy mainly depended on the accurate measurement of the reference object and the user skills to set the length on the smartphone display perfectly. Here, we recommend training before proceeding to real leaves by using a ruler as reference and a known area as object. The *set size* method, however, is more time consuming (about 40 seconds for a trained user from taking the image to obtaining the result) then the method *reference object* (about 30 seconds). Four separate manual steps are involved: (1) taking the image, (2) defining the patch where the reference object is located in the image, (3) measuring a distance on the reference object (can be simplified by using a ruler as reference), and (4) setting the length of the measured distance on the smartphone screen.

## The reference object method

The method *reference object* by Leaf-IT is also highly accurate (<1.5% deviation) and precise (2% deviation) under both optimised and field conditions. Based on our experience, highest accuracy can be achieved when camera lens and object are in perpendicular direction to each other. Furthermore, it should be avoided to fill out the whole image range provided by the camera with the reference object and the leaf. The closer the margins of the images lie to the object the higher the image distortion becomes and increases the inaccuracy of the depicted objects. Different camera lenses and image sensors produced similar results in area measurements. We achieved reliable results by leaving blank about one third from the image margins towards the centre. The method is, compared to the *set size* method, faster and more users friendly. Three manual steps are involved from taking the image to the results: (1) taking the image, (2) defining the patch where the reference object is located in the image, and (3) typing in the area of the reference object. For easy use, we recommend to use a printout (white paper) with a black square with known area in one corner (e.g. side length of 5 x 5 cm) serving as a reference object. The leaf can then be placed next to the reference object and both photographed together. The reference object and the unknown object should be roughly of the same size. During tests of the application in the field, it proved successful to have printouts prepared with reference objects ranging in area from the smallest to the highest leaf area expected.

## Leaf-IT compared to WinFOLIA

Leaf area measured in Leaf-IT and WinFOLIA yielded similar results. The maximum difference between both methods was -3.6% and +1.5% and the difference between the mean from Leaf-IT and WinFOLIA was 0.132 cm$^2$. These low values indicate that no method is biased towards the other and that both method measure area equally well (Bland and Altman 2003). For smaller leaves (< 100 cm$^2$), the difference of the means was < 0.5 cm$^2$ and decreased with leaf size. That means, that the critical difference (0.521 cm$^2$) was only recorded for the biggest leaves. When comparing area measurements of both methods for each leaf individually the difference was always < 4%. In 19 of 25 leaves it was even smaller than 1%. When images showed shadows or the background had impurities Leaf-IT measured leaf area more reliable than WinFOLIA, which often had problems to distinguish between artefacts and real leaves. We choose for comparison only leaves which had simple margin morphologies and were undamaged. Here, Leaf-IT detected the margin very accurately. However, when using damaged leaves or complex margin morphologies (e.g. ferns) Leaf-IT may not have detected the margin correctly or detected at all.

## Strengths and limitations of Leaf-IT

All features in Leaf-IT are specially designed for scientific use. Export of data comes as .csv-file which can be imported to most common software programs for further data analyses. The option to choose between two methods (*set size* and *reference object*) allows the user to assess leaf area with minimal effort and preparation. Its high accuracy and precision is similar to those of other well established software (e.g. WinFOLIA). Different smartphone types can produce reliable results as we did not find great dissimilarities in area measurements related to lenses and image sensors. Its major limitation, however, is the margin detection of complicated leaf morphologies. Serrated, compound, pinnate, and strongly pilose or lobed leaves often cause problems for Leaf-IT. This is for instance the case for some herbs (like many species from the families Apiaceae, Geraniaceae, Ranunculaceae, and Fabaceae) as well as ferns and plant species with similar leaf morphologies. Also holes (as in *Monstera deliciosa* Liebm.) and herbivore damage within leaves cannot be detected by Leaf-IT and are included in the overall leaf area.

## Conclusion

In summary, Leaf-IT is easy to use and applicable on all smartphones operating on Android 4 or higher. Android is the most widely used operation systems found on the widest range of smartphones (Teacher et al. 2013) increasing the portability and use of Leaf-IT. Besides leaf area, all objects can be measured given a high light contrast of object and background. However, its main limitation is the area measurement of complex leaf morphologies. Here, further effort is needed to improve the performance with complex leaf morphologies. Collaborative testing of interested users could improve Leaf-IT and provide more detailed suggestions and recommendation about strength and limitations of the application as well as to compile guidelines for future improvements on Leaf-IT. We hope that Leaf-IT motivates ecologists to use free smartphone applications designed for assessing functional traits in particular and for ecological data acquisition in general.

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# 3. Plants on small islands revisited: the effects of spatial scale and habitat quality on the species-area relationship

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## 3.1 Abstract

Understanding how species diversity is related to sampling area and spatial scale is central to ecology and biogeography. Small islands and small sampling units support fewer species than larger ones. However, the factors influencing species richness may not be consistent across scales. Richness at local scales is primarily affected by small-scale environmental factors, stochasticity, and the richness at the island scale. Richness at whole-island scale, however, is usually strongly related to island area, isolation, and habitat diversity. Despite these contrasting drivers at local and island scales, island species-area relationships (SARs) are often constructed based on richness sampled at the local scale. Whether local scale samples adequately predict richness at the island scale and how local scale samples influence the island SAR remains poorly understood. We investigated the effects of different sampling scales on the SAR of trees on 60 small islands in the Raja Ampat archipelago (Indonesia) using standardised transects and a hierarchically nested sampling design. We compared species richness at different grain sizes ranging from single (sub)transects to whole islands and tested whether the shape of the SAR changed with sampling scale. We then determined the importance of island area, isolation, shape, and habitat quality at each scale on species richness. We found strong support for scale dependency of the SAR. The SAR changed from exponential shape at local sampling scales to sigmoidal shape at the island scale indicating variation of species richness independent of area for small islands and hence the presence of a small-island effect. Island area was the most important variable explaining species richness at all scales, but habitat quality was also important at local scales. We conclude that the SAR and drivers of species richness are influenced by sampling scale, and that the sampling design for assessing the island SARs therefore requires careful consideration.

**Key words:** Species-area relationship, sampling scale, spatial scale, grain size, species richness, habitat quality, small-island effect, woody plants

## 3.2 Introduction

The number of species that can exist in an area increases with spatial scale and sampling effort (Chase et al. 2019). The rate at which the number of species changes with spatial scales is described by the species-area relationship (SAR; Palmer and White 1994, Rosenzweig 1995, Triantis et al. 2012). Both, spatial scales and the SAR, are among the most intensively studied patterns in ecology and have been the focus of many studies about islands and island-like habitats, with great influence on the fields of conservation biology and the ecology of fragmented landscapes (Lomolino 2000, Whittaker and Fernández-Palacios 2007). Effects of spatial scales are also of great importance in many ecological studies investigating species richness sampled at small spatial grains to estimate diversity patterns for larger spatial units (e.g. plots or transects to estimated diversity at the extent of the overall study area or whole island area). However, the factors determining species richness may also change greatly between small and larger scales (Wiens 1989, Rahbek 2005, Chase and Knight 2013).

Whereas local-regional scale effects have been studied more intensively on the mainland (e.g. Ricklefs 1987, Palmer and White 1994, Rahbek 2005), spatial scales within islands have received less attention (but see Sfenthourakis and Panitsa 2012, Karger et al. 2014). Islands constitute great model systems to study the effects of different sampling scales on richness patterns and the SAR as they show great variety in sizes and other ecological conditions and often have clearly defined species pools (Warren et al. 2015, Whittaker et al. 2017). Indeed, some island studies have shown that island area strongly affects the species richness and the variation in richness sampled at local scales (Williamson et al. 2001, Sfenthourakis and Panitsa 2012, Karger et al. 2014). Kohn and Walsh (1994) found that plot-level plant species richness generally increased with island area for small islands, but saturated with larger island area (see also Karger et al. 2014). Processes determining species richness patterns at local scales (i.e. sampling units) have been attributed to small-scale environmental factors, stochasticity, and the size of the regional species pool

(MacArthur and Wilson 1967, Zobel 1997, Rahbek 2005, Karger et al. 2014, Ibanez et al. 2018). At the regional scale (hereafter for islands referred to as island scale), main drivers of species richness are linked to direct effects of area *per se*, habitat diversity, isolation, and island age (MacArthur and Wilson 1967, Whittaker et al. 2008, Hortal et al. 2009, Keppel et al. 2016) and at larger spatial extent, to differences in climate (Field et al. 2008, Kreft et al. 2008, Ibanez et al. 2018).

Understanding the relationship between species richness sampled at local and island scale may help understanding how island communities assemble (Karger et al. 2014). Moreover, a better understanding of this relationship may also guide protocols for estimating species richness on islands, as many studies use species richness sampled at local scales (plots/transects) regressed against island area to attain island SARs (e.g. Niering 1963, Kohn and Walsh 1994, Yu et al. 2012, Wang et al. 2015). Using island scale species richness estimates derived from these local scales is potentially problematic because biodiversity is multi-dimensional and scale dependent (Chase et al. 2018). Furthermore, estimates of species richness obtained at local scales are often highly variable (see data in Kohn and Walsh 1994, Sfenthourakis and Panitsa 2012). Therefore, a SAR attained by local sampling may not correctly describe the relationship between species richness and island area (see also Chase and Knight 2013, Chase et al. 2019).

Small islands are particularly suited for studying the effects of local and island scales on the SAR (e.g. Burns 2005, Sfenthourakis and Panitsa 2012), as the local scale (e.g. sampling unit) can be held constant while the island scale varies between islands. Further, for very small islands, the local sampling scale approaches the extent of the island scale, whereas on larger islands diversity patterns across different sampling units can be investigated. However, small islands may deviate from the SAR, a pattern called the small-island effect (SIE; Niering 1963), which states that species richness on smaller islands varies independent of area and is hence difficult to predict (Lomolino and Weiser 2001, Triantis et al. 2006). This phenomenon has been attributed to smaller islands having limited habitat diversity (Connor and McCoy 1979, Triantis et al. 2003), higher levels of disturbance (Whittaker 1995), or greater turnover and stochasticity (Heatwole and Levins 1973, Morrison 2010) than larger islands.

Lower environmental heterogeneity and greater stochasticity would also be relevant for local scales (plots/transects), suggesting higher variability in species richness at these scales (see also Azovsky 2010). However, not all factors believed to be creating the SIE are applicable to local scales. Especially factors like disturbance (Whittaker 1995), isolation

(Lomolino and Weiser 2001), and rapid colonisation and extinction events (MacArthur and Wilson 1967) may be unique to the SIE.

Here, we investigate patterns of species richness sampled at local plot scale and at island scale on 60 small islands in the Raja Ampat archipelago, Indonesia. We tested whether different sampling scales affect the shape and function of the SAR and whether local species richness (within plots) was related to island area, and if small-scale habitat quality was important in explaining species richness at local sampling scales. Finally, we tested whether richness sampled at local scale resembles richness patterns of the SIE.

## 3.3 Methods

### Study system

We studied the woody vegetation on 60 small islands in the Raja Ampat archipelago, Indonesia (Figure 3.1 a). Islands were located in a sheltered bay of Gam island protected from the open ocean (130°34'E; 0°31'S, for coordinates of individual islands see Table B 1). Islands ranged from 3 $m^2$ to 11,806 $m^2$ in size. Climate in the region is tropical and mostly calm without the occurrence of strong storms. Mean annual precipitation is around 2768 mm, being highest in June (366 mm) and lowest in November (154 mm), and mean annual temperature is 27.4 °C (weather station Sorong/Jefman; http://www.worldclimate.com).

The islands consist of ultrabasic limestone, and are characterized by their rugged surface (Figure 3.1 f). Litter, when existing, represent the only basis for soil development on the islands. The stages of litter decomposition depend on accumulation depth, and humus and mull only occur when litter depth is > 3 cm. Soil depth is highly variable, ranging from 0 to > 1 m. Woody vegetation with canopies reaching up to 15 m dominates on all islands and non-native plant species are absent (Takeuchi 2003).

### Sampling design

Fieldwork was conducted from November 2017 to February 2018. Only islands with primary vegetation and without any signs of anthropogenic use or disturbance were included in this study. On each island, we established transects of 2 x 10 m. Each transect was divided into five subtransects of equal size (2 x 2 m). Transects were aligned at the longest extension of the island from one side to the other. Two transects oriented towards the island centre were established on the opposite sides of the island. The other transects were placed at the centre of the island in perpendicular orientation to edge transects (Figure 3.1 b).

The number of transects per island was roughly proportional to island area: one transect was placed on islands < 500 m$^2$ (n=40 islands); two transects on islands between 500 m$^2$ and 750 m$^2$ (n=2); three transects on island between 750 m$^2$ and 1,000 m$^2$ (n=2); four transects on islands between 1,000 m$^2$ and 3,000 m$^2$ (n=9); five transects on islands between 3,000 m$^2$ and 5,000 m$^2$ (n=3); six transects on islands > 5,000 m$^2$ (n=4). The distance between transects on islands with multiple transects was held constant but it was related to the longest extension of an island, and hence varied among islands. For 36 islands < 10 m (equivalent to the length of one transect), we placed as many subtransects as possible on islands at their longest extension (Figure 3.1 b, for more information on the study design see Schrader et al. 2019a).

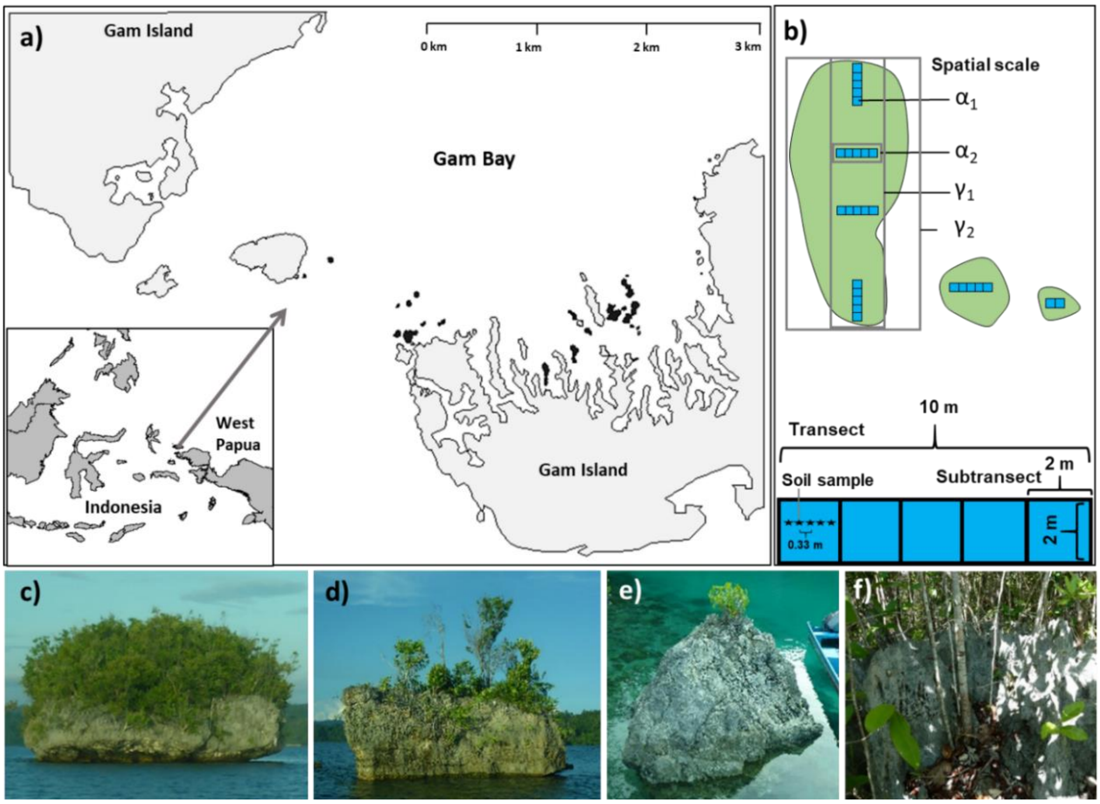

Figure 3.1 Study region (a), study design (b), and representative islands (c - f). Sampled islands are highlighted in dark grey (a). b) Transects were aligned at the longest extension of the island from one edge to the other edge. Numbers of transects on the islands were attributed to island area. Spatial grain is divided into $\alpha_1$: size of a single subtransect, $\alpha_2$: size of a single transect, $\gamma_1$: observed species richness on a given island, and $\gamma_2$: estimated species richness (Jackknife 1) (Photos: J. Schrader).

We inventoried all woody plants with a diameter at breast height ≥ 2 cm rooted within the transects. A diameter at breast height ≥ 2 cm is a commonly used threshold in tropical vegetation (e.g. Molino and Sabatier 2001, Brambach et al. 2017), and we expected species $\geq 2$ cm to be well established in the community and to not reflect spontaneous shifts in species composition. Soil depth was recorded in each subtransect at five spots with equal distance to each other (33 cm) and spaced along the central axis of the transect (Figure 3.1 b). Soil depth was measured to a maximum depth of 35 cm using a metal wire. Beyond that, measurements were impracticable due to the rugged surface of the coralline rock.

## Island metrics and isolation

All islands in Gam Bay (Figure 3.1 a) were georeferenced in ArcGIS (Version: 10.3) using high-resolution satellite images (World Imagery, Esri 2017). The length and width of small islands < 100 $m^2$ were additionally measured in the field, and matched with georeferenced shape. For all islands, we calculated island area (in $m^2$), island perimeter (in m), and the shape index. The shape index is an indicator of relative shape complexity of an island and positively correlates with the proportion of edge habitat. The shape index was calculated according to Patton (1975) as shape index = $P / [2 * (\pi * A)^{0.5}]$, where P is the perimeter and A is the island area.

We tested two alternative metrics describing island isolation. First, we calculated the closest distance to the island of Gam, which is by far the largest neighbouring landmass (area = 195 $km^2$) surrounding all focal islands (Figure 3.1 a) and the nearest major source. Second, we calculated the area of surrounding landmass (following Weigelt & Kreft 2013). This metric also considers the spatial arrangement and neighbouring islands, and was calculated as the total landmass within a buffer of 1000 m around each focal island.

## Sampling scales and species richness

Our study design allowed us to investigate the scaling of species richness at four different sampling scales (from local to island scale), here referring to grain size of sampling units used to quantify species richness (according to Whittaker et al., 2001; Rahbek, 2005). As local scale, we considered two grain sizes, at the level of subtransects ($\alpha_1$) and transects ($\alpha_2$, Figure 3.1 b). Grain sizes at the island scale were all transects of an island combined ($\gamma_1$) and estimated diversity for the whole island ($\gamma_2$). Note that $\gamma_1$ could also be interpreted as transect scale because this grain size consists of multiple transects. However, as grain size of transects increased proportionally with island area, we considered $\gamma_1$ at the island scale.

At the smallest grain size ($\alpha_1$; 4 $m^2$; size of a single subtransect), species richness was calculated as mean richness of all subtransects of a particular island. Five islands had a total area < 4 $m^2$. In these cases, species richness recorded for $\alpha_1$ equalled the total species richness of the islands. The second local scale grain size ($\alpha_2$; 20 $m^2$; size of a single transect) was the mean species richness of all transects of an island. On 27 islands we could place only one subtransect due to their limited area size. Here, species richness was the same for $\alpha_2$ and $\alpha_1$.

Species richness at the island scale was calculated as all species sampled in all transects ($\gamma_1$) and estimated species richness ($\gamma_2$) for that island. Grain size of the scales $\gamma_1$ and $\gamma_2$ was always equal to island area. In 27 cases, $\gamma_1$ equalled $\alpha_1$ and in 39 cases $\gamma_1$ equalled $\alpha_2$ due to islands allowing only for a single subtransect or transect, respectively. $\gamma_2$ represented the total species richness expected to occur on an island and was calculated using the Jackknife 1 estimator in the *vegan* package (Oksanen et al. 2018), based on species recorded in subtransects. Jackknife 1 is considered a reliable estimator for small sample sizes (Gotelli and Colwell 2011).

## Statistical analyses

All analyses were performed in the statistical software R (v. 3.4.4.; R Core Team, 2018). We expected unequal variation in species richness at the local scale (see also Figure 4a in Kohn & Walsh, 1994). Therefore, we used quantile regression, which is a particularly powerful model when analysing data with unequal variation (Cade and Noon 2003), as quantile regression can estimate multiple slopes relating to minimum and/or maximum responses. To this end, we calculated the linear regression line of the lower (0.05) and the upper (0.95) quantile of observed species richness for all islands (empty islands included) at each sampling scale at island area (log-transformed) by using the R package *quantreg* (Koenker 2015). We inspected the slope coefficients of both quantiles to test whether they differed significantly and calculated adjusted $R^2$ (Koenker 2015). Significant differences between the slope estimates indicate that species richness in the lower quantile increased at a lower rate than species richness in the upper quantile. The adjusted $R^2$ indicates the relative difference of slopes between the four sampling scales.

Different mathematical approaches and functions have been proposed for modelling the SAR of small islands and for testing for the presence of a SIE. Most previous studies have used break-point regression models and tested whether they provide a better fit to the data than simple linear models (e.g., Lomolino & Weiser, 2001; Morrison, 2014; Wang et al., 2016). Lomolino (2000) suggested that sigmoidal models are better suited as they test for the presence of the SIE while allowing a smooth transition between the range of the SIE and the linear phase of the SAR. Smooth transitions often provide more realistic representations of natural phenomena than sharp transitions (Toms and Lesperance 2013), such as the SIE (see also Chisholm et al. 2016; Schrader et al. 2019a). Most authors agree that multiple alternative SAR models should be fitted and compared (Lomolino and Weiser 2001, Dengler 2010).

We therefore compared a total of 11 different species-area relationship (SAR) models (according to Lomolino & Weiser, 2001; Dengler, 2010; Guilhaumon et al., 2010; see Table B 2 for model shapes and functions), at each sampling scale. Note that local-scale species richness regressed against island area does not show a SAR in the strict sense, but rather describes a species-density island-area relationship (Giladi et al. 2014). We fitted one linear and two breakpoint models using linear regression on log-transformed island area. For the first breakpoint model, we calculated a horizontal line before the breakpoint (´zero model´, left-horizontal function according to Lomolino & Weiser, 2001). The second breakpoint model was a continuous two-slope function (´non-zero´ following Dengler, 2010). Breakpoint models were calculated with the package *segmented* (Muggeo 2008). The remaining eight models consisted of five convex (power, exponential, negative exponential, Monod, rational), and three sigmoidal models (logistic, Lomolino, cumulative Weibull), and were fitted on untransformed island area using the *mmSAR* package (Guilhaumon et al. 2010). As axis transformation can have great effect on the detectability of the SIE (Matthews et al. 2014), we applied a null model for incidence data proposed by Burns et al. (2009) on our island dataset (for detailed description of the model see Figure B 3).

Dengler (2010) and Wang et al. (2015, 2016) showed that the inclusion or exclusion of islands with zero species may affect the SAR and the detection of a SIE. These authors recommended that empty islands should be included when studying small islands. Therefore, we fitted and compared all 11 SAR models at the four sampling scales with all empty islands included (60 islands in total), with all empty islands excluded (40 islands), and with only empty islands included larger than the smallest populated island (52 islands). We detected no major differences in the best supported SAR model for any sampling scale (Figure B 2) and thus opted to focus on the full set of islands including all empty islands in all further analyses.

SAR models at each grain size were compared using Akaike-weights derived from second-order information criterion corrected for small sample size (AICc, Hurvich and Tsai 1989, Burnham and Anderson 2002). Following previous studies (e.g. Lomolino & Weiser, 2001; Morrison, 2014; Wang et al., 2016), we considered data to support the presence of the SIE, if breakpoint models performed better than the linear model based on $\Delta$AICc $\leq$ 2. Following Lomolino (2000), we also considered a SIE to be present, if a sigmoidal model performed best. To test if a SIE can be reproduced by small sample areas in general, we randomly subsampled 30 subtransects 1000 times for the four largest islands and compared SARs for plot sizes ranging from 4 $m^2$ to 80 $m^2$ ($n = 20$).

To identify the best predictors of species richness, we used generalised linear models (GLMs) with Gaussian distribution. Explanatory variables were island area (log-transformed), shape index, distance to Gam island, surrounding landmass, and soil depth (Table B 1, Table B 3 & Table B 4 for Pearson correlation and spatial autocorrelation of explanatory variables). Collinearity among the explanatory variables was weak except for soil depth and island area ($r = 0.75$; see Table B 3 for Pearson correlation matrix of all variables). We identified minimum adequate models at each sampling scale based on lowest AICc from all possible candidate models. We considered all models as equally well supported when $\Delta$AICc $\leq$ 2 (Burnham and Anderson 2002). We used the relative variable importance (RVI) to determine the importance of each variable in explaining species richness, and this was calculated by examining all candidate models (Johnson and Omland 2004). Model selection and RVI were calculated using the package *MuMIn* (Bartoń 2018).

## 3.4 Results

We recorded a total of 57 woody plant species (64 species estimated with Jackknife 1 estimator; SE = ±2.0) on the 60 islands. Twenty islands had no plant species. On one island (5,526 $m^2$), we recorded a maximum of 26 species (38.6 species estimated; SE = ±3.5 species) with mean species richness of 6.5 (SE = ±0.9, max = 26) at the $\gamma_1$ and 9.3 (SE = ±1.3, max = 38.6) at the $\gamma_2$ grain size. The mean species richness was 1.5 (SE = ±0.2; max = 3.4) at the $\alpha_1$ (4 $m^2$ subtransects) and 3.7 (SE = ±0.5, max = 10.2) at the $\alpha_2$ (20 $m^2$ transects) grain size.

Quantile regression indicated that the slope coefficients of the upper and lower quantile differed significantly for all grain sizes (Figure 3.2, see Table B 5 for detailed results of quantile regression and Figure B 2 for quantile regression with empty islands excluded). Differences between slopes were larger at the local than at the island scale ($\gamma_1$: $R^2 = 0.91$, p = 0.013; $\gamma_2$: $R^2 = 0.91$, p = 0.014; $\alpha_1$: $R^2 = 0.16$, p < 0.001 $\alpha_2$: $R^2 = 0.71$, p < 0.001, note that greater difference between slopes is indicated by a lower p-value and that lower $R^2$ values indicate greater difference between the slopes). This indicates that species richness showed more unequal variation with island area at the local than the island scale.

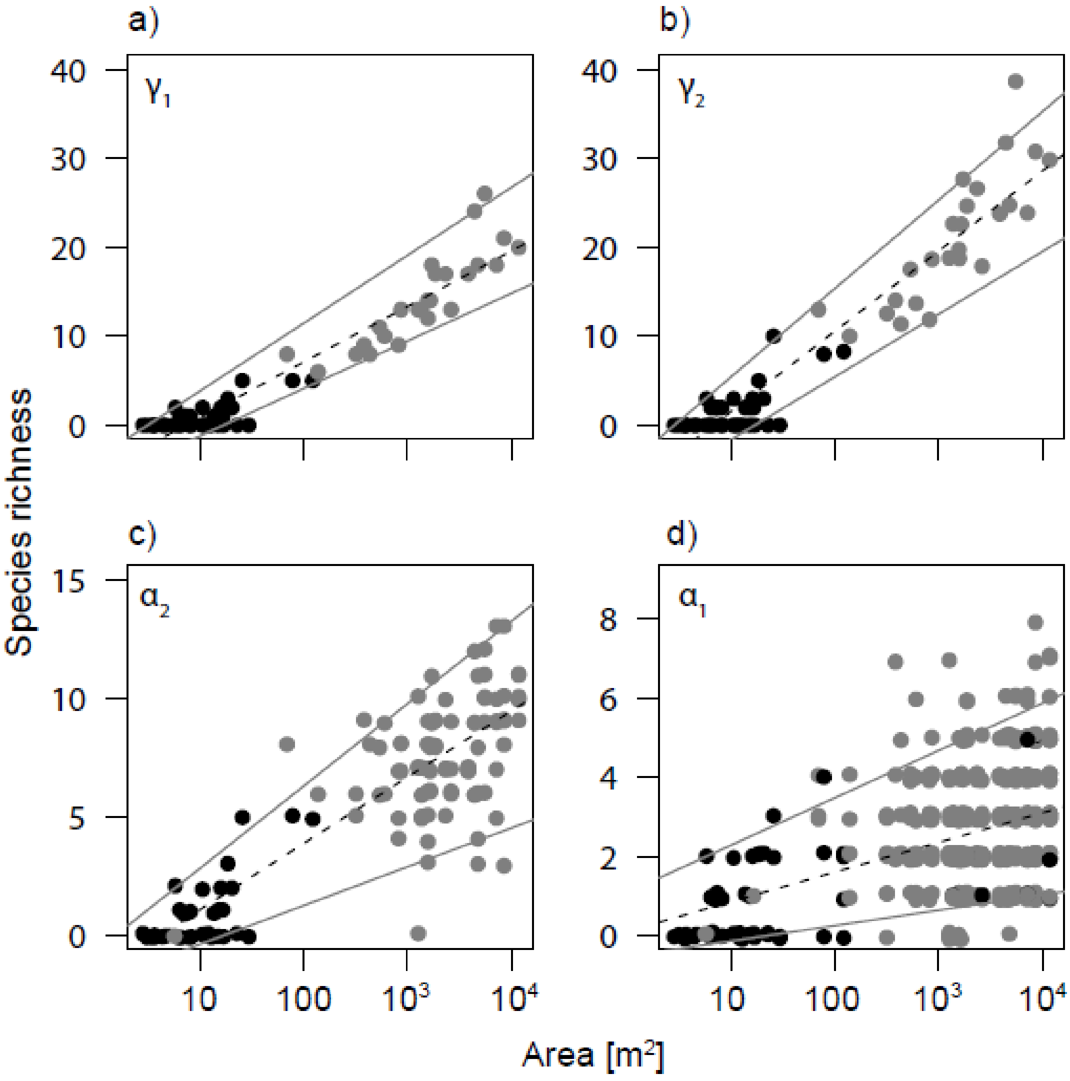

Figure 3.2 Species richness and island area at four different sampling scales (a - d) with normal regression line (dashed) and 0.95 and 0.05 quantiles (grey) shown. Sampling scale is divided into $\alpha_1$: size of a single subtransect, $\alpha_2$: size of a single transect, $\gamma_1$: observed species richness on a given island, and $\gamma_2$: estimated species richness (Jackknife 1) on a given island. Points in black indicate absence of soil at the sampling scale and points in grey indicate presence of soil.

We found strong support for a SIE at the island scale, but less so or not at all at the local scale. The two breakpoint models (left-horizontal function and continuous two-slope function) received stronger support at the island scale and for $\alpha_2$ than the one-slope (normal linear regression model). For $\alpha_1$, the one-slope model received higher support than the breakpoint models (for model support of all models at all sampling scales see Table B 6). However, the breakpoint and one-slope models always yielded the weakest support at all scales when all 11 models were considered (Figure 3.3 b-e). The sigmoidal Lomolino and Weibull models were best supported for $\gamma_1$ and $\gamma_2$ (Figure 3.3 b-e). The presence of the SIE was further supported by a null model that indicated that small islands have less species present than expected under random colonisations (Figure B 3; see also Schrader et al. 2019a). For $\alpha_2$, the Lomolino model performed best (note that five other models were similarly well supported with $\Delta$AICc < 2), but was less well supported than for $\gamma_1$ and $\gamma_2$ (Figure 3.3 d). The negative-exponential model performed best for $\alpha_1$ with two other models similarly well supported (with $\Delta$AICc < 2). SARs produced by the random subsampling of the plots on the four largest islands were best described by the Lomolino model in 59% of all cases. In 41% of all cases, the power model performed better.

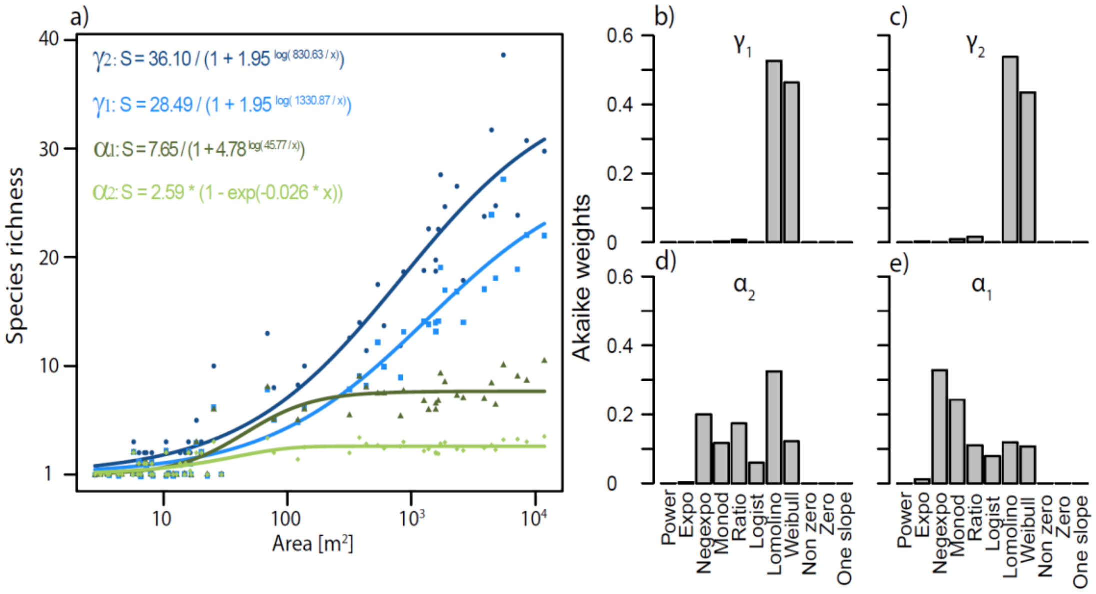

Figure 3.3 Best supported species-area relationships (SAR) and model support of 11 tested SAR at four different sampling scales. a) Best model explaining species richness on islands at four sampling scales. b-e) Akaike weights of 11 different models explaining species richness on islands at four different sampling scales. Sampling scale is divided into $\alpha1$ (dark green): size of a single transect, $\alpha2$ (light green): size of a single subtransect, $\gamma1$ (light blue): observed species richness on a given island, and $\gamma2$ (dark blue): estimated species richness (Jackknife 1) on a given island. Non zero model: continuous two-slope function, Zero: left-horizontal function, One slope: single linear regression model (see Table B 2 for model formulas), area was log-transformed for these three models.

At all grain sizes, island area was the most important predictor of species richness (Figure 3.4). At the local scale, soil depth also emerged as an important variable (RVI: 0.85 and 0.68 for $\alpha_2$ and $\alpha_1$, respectively). At all grain sizes, the shape index of islands had low RVI values ranging between 0.48 and 0.23. Similarly, the two isolation metrics had low RVI values, not exceeding 0.38 (for $\gamma_2$) for distance to Gam island and 0.43 for ($\gamma_2$) for surrounding landmass. Isolation was generally more important in explaining variation in species richness at island than at local scale (Figure 3.4; and Table B 6 for support of best five models).

Soil depth ranged from 0 cm (recorded on n = 35 islands) to 22.28 cm and was strongly and positively related to island area (Pearson correlation coefficient = 0.75). Islands had an average distance to Gam island of 284 m (SE = ±41 m; max = 1265 m) and had an average surrounding landmass within a 1000 m buffer circle of 0.68 km$^2$ (SE = ±0.51 km$^2$; max = 1.6 km$^2$). Shape index of islands ranged between 1.03 and 1.59 (SE = ±0.02).

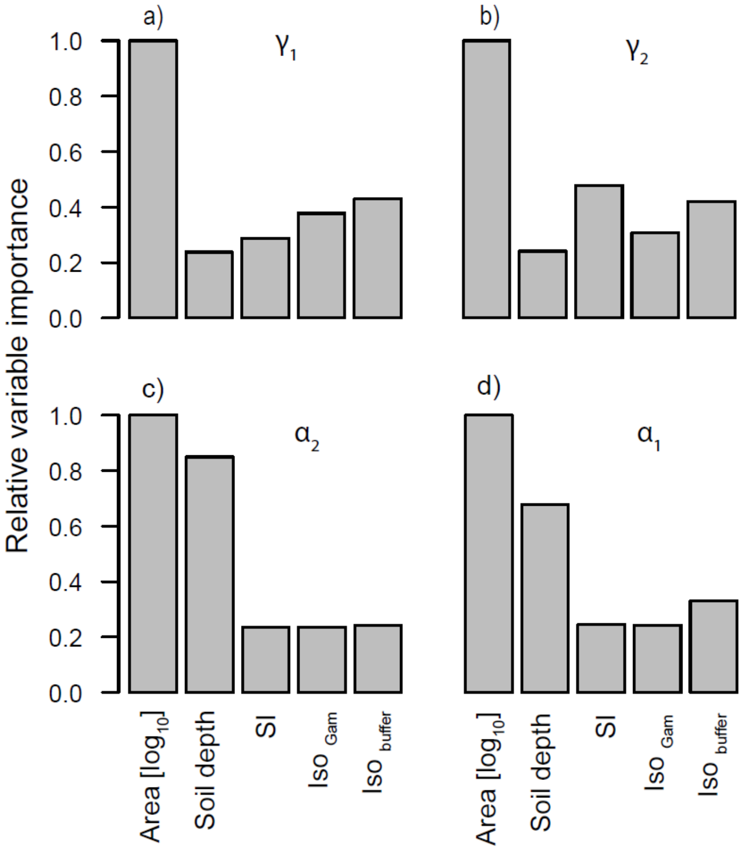

Figure 3.4 Relative importance of five explanatory variables explaining species richness on islands at four different sampling scales (a - d). Soil depth: mean soil depth recorded on each island; SI: shape index; iso$_{Gam}$: distance to Gam island; iso$_{buffer}$: surrounding landmass in 1000 m radius. Sampling scale is divided into $\alpha_1$: size of a single subtransect, $\alpha_2$: size of a single transect, $\gamma_1$: observed species richness on a given island, and $\gamma_2$: estimated species richness (Jackknife 1) on a given island.

## 3.5 Discussion

Our results demonstrate that SARs are strongly influenced by sampling scale. Species richness sampled at the local scale produced a different shape of the SAR compared to richness sampled at the island scale. Further, mean species richness at local scales showed high variation and reached an asymptote irrespective of island area. Area was the strongest predictor of species richness at all scales. Soil depth, reflecting habitat quality in our study system, significantly affected species richness at the local-scale. Exclusion of empty islands had no effect on the general pattern of the SAR at all sampling scales as well as the detection of the SIE.

Similar to many other studies (e.g. Lomolino & Weiser, 2001; Wang et al., 2016), we detected a SIE at island scale when comparing breakpoint models with a one-slope model. However, when comparing all 11 models, sigmoidal models (Lomolino and Weibull models) consistently received the highest support suggesting that sigmoidal models are useful to test for the presence of the SIE (Lomolino, 2000; Tjørve & Tjørve, 2011).

### Species-area relationship is dependent on sampling scale

Our spatially nested sampling design allowed us to investigate the effect of spatial scale on the SAR. Ideally, investigations of the island SAR should be based on observations or estimates of species richness for the entire island (e.g. $\gamma_2$; see also Hill et al. 1994, Scheiner 2003). However, many studies have used plot-based estimates in the absence of species inventories for the entire island (e.g. Keppel et al. 2010, Ibanez et al. 2018). In our study, species richness estimates derived from transect/plot sizes correlated with island area ($\gamma_1$) and produced a SAR similar in shape to that of the whole island species richness. However, this was not the case when sampling area was not correlated with island area ($\alpha_1$ and $\alpha_2$). Too small sampling areas therefore can lead to incorrect island SARs. Indeed, many previous studies have used transects or plots without any correction for undersampling (e.g. species richness standardised by area or individuals; Chase and Knight 2013) when estimating total species richness per island (e.g. Niering 1963, Kohn and Walsh 1994, Yu et al. 2012, Wang et al. 2015), and this may have led to biased SARs (see also Chase et al. 2019).

At the local scale, mean species richness increased with area before approaching an asymptote. This threshold may be interpreted as the *mean* species richness that can be sampled with a particular local grain size in the study system. This *mean* species richness increased with local grain size ($\alpha_1$ to $\alpha_2$; Figure 3.3 a) and saturated at an island area > c. 100 $m^2$. However, species richness at the local scale displayed a wide range of values with no strong relationship to island area (Figure 3.2 c-d). Here, quantile regression indicated that the upper and lower slopes differed more strongly at the local scale (e.g. $\alpha_1$ and $\alpha_2$) than at the island scale (e.g. $\gamma_1$ and $\gamma_2$), meaning that species richness varied more unequally at the local scale. Indeed, sampling units with no species occurred at the smallest local scale ($\alpha_1$) regardless of island area. Such high variation in species richness is often observed when relevé (transect/plot) grain size falls below a minimum area (Otýpková and Chytrý 2006). According to Chytrý and Otýpková (2003), the minimum sampling area in woody vegetation should not be smaller than 50 $m^2$ to 200 $m^2$, which is much larger than the local grain sizes used in this study (4 $m^2$ and 20 $m^2$).

While the transects alone obviously did not constitute a representative sample of the diversity of larger islands, they fell within the range of island areas included in studies of the SIE (Lomolino and Weiser 2001). Indeed, 50 % of islands in our study were ≤ 20 $m^2$, suggesting that at least part of the high variation in species richness with island area that characterises the SIE could be caused by sampling too small areas. We reproduced a pattern typical for the SIE in almost 60 % cases when sampling small grain sizes on our four largest islands. Therefore, sampling at very small grain sizes is likely to produce highly variable species richness estimates that vary independently of island area.

The high variability of species richness at local scales implies that the false detection (if by chance more islands with lower species richness are sampled), or non-detection (if more islands with higher richness are sampled) of the SIE could easily occur if only a few islands of small areas or few small areas in general are sampled. This may explain the great variety of relationships reported for and models fitted to the SIE (e.g. Lomolino & Weiser, 2001; Triantis et al., 2003; Dengler, 2010; Triantis & Sfenthourakis, 2012; Chisholm et al., 2016; Schrader et al. 2019a). Our results therefore highlight that great care needs to be taken when collecting and analysing data for studying the SAR in general and the SIE in particular.

## Effects of environmental heterogeneity and isolation

In our study, island area consistently emerged as the most important determinant of species richness at all grain sizes, supporting previous studies at various spatial extents (e.g. Kreft et al. 2008, Triantis et al. 2012). In addition, habitat quality emerged as strong predictor of species richness at local scales. Deeper soils may provide more nutrients and water for plants and offset partly the prevailing rather extreme environmental conditions (e.g. droughts), and may consequently support higher species richness (Niering 1963, Wardle and Zackrisson 2005, Michalet et al. 2014). Soil depth is important and facilitates the presence of some plant species in other study systems (do Carmo and Jacobi 2016, Keppel et al. 2017). In our study, soil depth varied greatly at local scales and this might contribute to the observed unequal variation in species richness. On the smallest islands, soil was normally absent, potentially contributing to the low overall species richness. At larger islands however, small-scale habitat quality may become averaged over the whole islands, explaining that here habitat quality was less important.

Isolation had no strong effect on species richness at any sampling scale. This is unsurprising considering that our study system is effectively not very isolated. All islands were located within the same bay and no island was more than 1265 m away from Gam Island, probably the main source pool of species colonisations. Most species on the islands appeared to be bird dispersed, as many plant species have fleshy and colourful fruits. Fruit eating birds like imperial pigeons (*Ducula myristicivora*), fruit doves (*Ptilinopus spp.*), friarbirds (*Philemon buceroides*), flowerpeckers (*Dicaeum pectorale*), and starlings (*Aplonis spp.*) were also abundant on all islands and often observed flying between them, further contributing to the low effective isolation (compare also with Burns, 2005).

## Conclusion

We found that patterns and drivers of species richness differed strongly between the local and island scale. Species richness inferred from local sampling scales produced SARs of different shapes, highlighting the importance of adequate sampling. The relative importance of determinants of species richness varied with scale, with area being the most important variable at all grain sizes and the single most important one at the island scale. However, habitat quality became increasingly more important at smaller grain sizes. Furthermore, scale and habitat quality may also influence local-regional richness relationships in other island-like systems, such as habitat fragments, and increase our understanding of the impact of incomplete sampling on the SAR. Therefore, our results highlight that great care needs to be taken when planning the sampling design for assessing the SAR for islands or island-like habitats. These insights are especially important in nature conservation, where erroneous assessment of and inference about the SAR based on incomplete sampling may lead to flawed management recommendations.

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# 4. Requirements of plant species are linked to area and determine species pool and richness on small islands

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## 4.1 Abstract

**Questions:** Small islands are ideal model systems to study community assembly. Due to harsher environmental conditions on smaller islands compared to larger ones, environmental filtering may preclude some species, potentially resulting in island size-dependent species pools. We tested whether the species pool size follows a similar species-area relationship as the observed richness. This can provide new insight into community assembly processes and the elusive small-island effect (SIE), which states that species richness on smaller islands is less dependent on area than on larger islands.

**Location:** Raja Ampat Archipelago, Indonesia.

**Methods:** We studied the woody vegetation on sixty small islands ranging from 3 $m^2$ to 11,806 $m^2$. For each recorded species, we estimated its area requirements and compared them against random colonization models. We developed a novel method to calculate probabilistic species pools for each island. We compared different species-area models for observed species richness and our index of species pool size to test whether the SIE results from differences in species pool size.

**Results:** We found that most species were restricted to islands significantly larger than expected from random colonization. The occurrence probability of all species increased with island size, indicating a lack of species that are specialized to the conditions on small islands. We found a SIE in observed species richness, but not in species pool size.

**Conclusion:** Woody plants in the studied island system have specific requirements that are linked to island area and determine island-specific species pools. Lower community completeness on smaller islands compared to larger ones indicated that the SIE is shaped by local limiting processes that have no impact on the species pool, but control how much of it is realized on an island. Together, these results clearly indicate non-random plant community assembly on small islands.

**Keywords:** Species pool, dark diversity, community completeness, species occurrence probability, small-island effect, species-area relationship, species richness, null model

## 4.2 Introduction

Species richness generally increases predictably with area, a pattern known as the species-area relationship (SAR; Arrhenius 1921; MacArthur & Wilson 1967). SARs were documented across different types of islands and also for fragmented and isolated mainland habitats, as well as for many different taxa (Connor and McCoy 1979, Rosenzweig 1995, Matthews et al. 2016). However, after a century of species-area research, the exact mechanisms underlying the SAR remain controversial (Warren et al. 2015).

Especially for islands, SARs have been studied extensively (Triantis et al. 2012). Island area *per se* can influence species richness directly via neutral processes (MacArthur and Wilson 1967, Coleman 1981, Hubbell 2001). Larger islands, for example, can support larger populations reducing the extinction probability due to stochastic events (Pimm et al. 1988). Additionally, larger islands have higher immigration rates than smaller islands (MacArthur and Wilson 1967, Lomolino 1990). Island area can also influence species richness indirectly as species are not equally well adapted to survive on all islands (Burns and Neufeld 2009, Sfenthourakis and Triantis 2009). Some species depend on specific habitats like forest interiors or cool and moist habitats at higher elevations, which are absent on small islands (Ricklefs and Lovette 1999, Keppel et al. 2016). However, indirect effects are often strongly related to area (Kohn and Walsh 1994, Triantis et al. 2006), making area usually the strongest predictor of species richness on islands (Kreft et al., 2008; Triantis et al., 2012).

Species may respond differently to the environmental conditions on islands, which could result in species-specific requirements that are strongly linked to island area (through either direct or indirect effects). Such species-area requirements can be influenced by population dynamics, habitat availability, body size, home range size, or trophic status (Shaffer 1981, Hanski et al. 1996, Holt et al. 1999, Pe'er et al. 2014). However, despite the fact that species-area requirements are well known, empirical estimates of area requirements are still missing for most species (Gurd et al. 2001).

Regardless of the ubiquitous SAR, an anomaly exists for small islands. The small-island effect (SIE) describes the observation that species richness on small islands may vary independently of island area (Niering 1963, Lomolino and Weiser 2001), or may increase at a different rate than on larger islands (Dengler 2010). The SIE and its underlying processes have been subject to an intensive debate (see Triantis et al. 2006). The SIE has been attributed to low habitat diversity (Heatwole and Levins 1973, Triantis et al. 2003), greater productivity on small islands due to nutrient influx from surrounding marine ecosystems (Anderson and Wait 2001), higher levels of disturbance (Whittaker 1995), and differential effects of isolation, topography, and geology (Triantis et al. 2006, Ackerman et al. 2007). Other authors have suggested that alternating effects of niche-related and neutral processes (Chisholm et al. 2016), high turnover rates (MacArthur and Wilson 1967, Heatwole and Levins 1973), species area requirements (Tjørve and Turner 2009), and species adapted to special conditions on small islands (Burns and Neufeld 2009, Sfenthourakis and Triantis 2009) explain the SIE. Moreover, mathematical constraints (rather than ecological effects) could cause the SIE, such as the log-transformation of island area or species numbers (Burns et al. 2009, Tjørve and Tjørve 2011). Overall, the SIE may be less common than previously supposed (Dengler 2010, Tjørve and Tjørve 2011), and it still remains unclear which effects ultimately shape and underlie the SIE.

Traditionally, the SIE has been studied for species numbers recorded within a certain, usually short, timespan. Morrison (2011, 2017), however, showed that some small islands without species are able to support life but have no species due to dispersal limitations and temporal variation in species richness. That suggests that potentially more species are able to survive on an island than are actually present and that species communities on islands assemble from a larger species pool (Figure 4.1 a; MacArthur & Wilson 1967). The species pool concept is tightly linked to environmental filtering, biotic interactions, and dispersal limitation (Diamond 1975, Gotelli and McCabe 2002, Zobel 2016) as it describes the combination of species present in a community and species absent from a community (dark diversity, Figure 4.1), but which can potentially inhabit a locality (Pärtel et al. 2011). Further, the difference between observed species richness and dark diversity can be used to assess community completeness, a valuable index for comparing how much of the potential biodiversity is realized locally (Pärtel et al. 2013, Pärtel 2014). Species pool concepts are especially useful to understand how communities assemble (MacArthur and

Wilson 1967, Ricklefs 1987, Cornell and Harrison 2014). Yet, species pools are rarely studied in island biogeography, despite the long history and great potential of islands as model systems and for studying community assembly processes, especially at local scales (Zobel 2016). Reasons why species pools on small islands are seldom studied may be challenges to define, which species are part of a specific species pool. The equilibrium theory of island biogeography describes that species richness on islands is determined by a dynamic equilibrium of random colonization and extinction events (MacArthur and Wilson 1963, 1967). Under random conditions, species should assemble from a common species pool (at least within an archipelago) with identical probabilities to establish on an island. However, previous studies have shown that species have different probabilities to establish on islands (Woodroffe 1986, Sfenthourakis and Triantis 2009, Morrison 2017). The differential establishment success of species questions random assembly of island communities (two possible scenarios of SARs of observed species richness and species pools under non-random community assembly are shown in Figure 4.1). These non-random patterns are mainly driven by differential dispersal limitations (Carlquist 1974, Arjona et al. 2018), environmental filtering (Kohn and Walsh 1994, Weigelt et al. 2015, Liu et al. 2018), biotic interactions (Si et al. 2017), and area requirements (Turner and Tjørve 2005). If species have specific habitat and area preferences, species pools should be different for each island, depending on the island area and environmental conditions (Figure 4.1).

Different approaches exist to estimate the species pool. For instance, the probabilistic species pool index is defined as the summed probability of species to occur at a focal site (Karger et al. 2016). That contrasts the binary species pool concept, which includes or excludes a species from the pool (Lewis et al. 2016). The binary species pool requires a defined occurrence threshold to determine when the survival of a species is assumed to be sufficient. Especially on small islands, many species are only temporarily present (Morrison 2011, Chiarucci et al. 2017), or considerably rare due to small population sizes (Triantis et al., 2006). This results in low overall occurrence probabilities making it difficult to define appropriate thresholds for including or excluding species in binary species pools. The probabilistic species pool, thus, seems to be particularly well suited to calculate species pools for small islands.

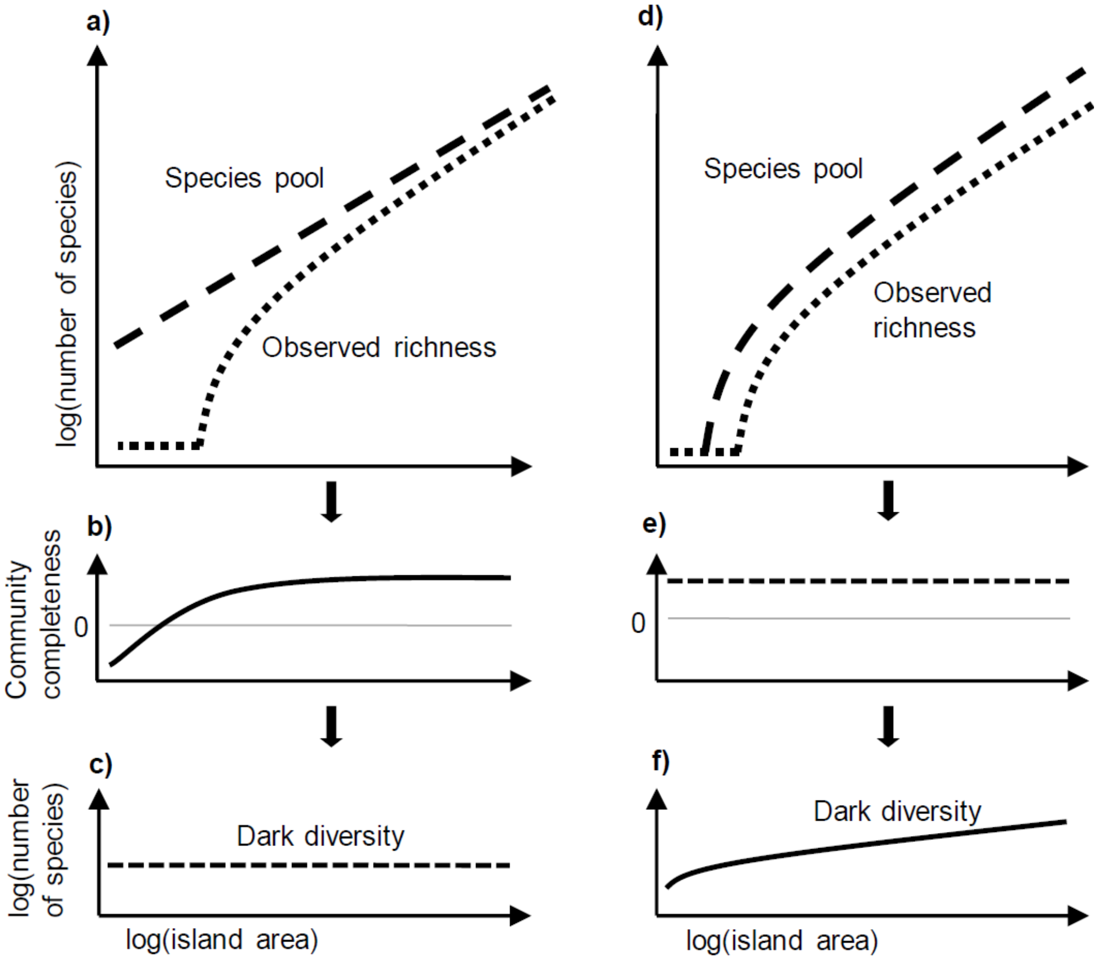

Figure 4.1 Schematic representation of the hypothesized relationships between island-specific species pools and observed species richness on small islands. In scenario (a-c) the species pool size follows a linear relationship with area (power function in arithmetic space), whereas the observed richness shows a species-area relationship typical for a small-island effect (SIE; sigmoidal form in arithmetic space). Community completeness increase with island area and can be negative for small islands when the observed richness falls below the dark diversity (number of absent species) (b) and dark diversity is equal on all islands (c). The SIE for observed richness can be derived from stochasticity and incomplete communities on small islands. In this scenario, filtering influencing the species pool (environmental filtering, dispersal filtering) would increase non-linearly with area, being stronger on smaller islands. In scenario (d-f) the species pool size shows a SIE and increases at the same rate as the observed richness (in log-log space). Community completeness is independent of area (e) and dark diversity increases with area (f). A SIE exists for both island-specific species pools and observed richness and can be derived from filtering processes acting on the species pool. Filtering on observed richness would follow a similar function with area as on species pool. Grey lines indicates zero community completeness and dashed lines in c) & e) indicate non-significant relationships.

Here, we studied woody plants on 60 small coralline islands in the Raja Ampat Archipelago (Indonesia). We modelled the area requirements of each species and applied a novel method to estimate the probabilistic species pool for each island. First, we tested whether observed species richness showed a SIE. Second, we tested whether the SIE originated already from the species pool and whether species communities on small islands assemble randomly by testing observed species occurrences against null models.

We hypothesized that environmental filtering affects species richness on small islands differently and that species within the archipelago have specific requirements linked to island area (H1). Empirical estimations of species-area requirements would allow calculating probabilistic island-specific species pools, which we hypothesized to show different relationships with area compared to the observed species richness (H2, Figure 4.1 a). We further hypothesized that species pools do not show a SIE (H2) as even the smallest islands can support some taxa but often appear empty due to barriers in colonization, high turnover, and harsh environmental conditions. When the SAR of the species pool and observed richness differed, we expected that small islands have lower community completeness compared to larger islands (Figure 4.1 a). Lower community completeness on small islands would indicate that local assembly processes control how much of the species pool is actually present on an island.

## 4.3 Material and methods

### Study region

We studied 60 coral islands in Gam Bay, a shallow bay on Gam Island in the Raja Ampat Archipelago, Indonesia (Figure 4.2 a). The size of the studied islands varied between 3 $m^2$ and 11,806 $m^2$ and thus covered the range at which the SIE for plants has been observed previously (Lomolino and Weiser 2001, Chisholm et al. 2016). The local climate is tropical, mostly calm, without the occurrence of strong storms, and lacking pronounced seasonality with mean annual temperature of 27.4°C and precipitation of around 2768 mm (at nearest weather station Sorong/Jefman; http://www.worldclimate.com 2017).

All studied islands consist of coralline karst, belong to the same limestone plateau, and are likely of similar age. The vegetation on all islands is dominated by woody species and in pristine condition without signs of anthropogenic use or disturbance. Islands that contained anthropogenically modified areas, such as gardens, clear-cuts, and buildings, were not sampled. This excluded all islands >12,000 $m^2$, as well as the large island of Gam (Figure 4.2 a). The surface of the islands is rugged with many crevices. Soil, when present, occurred only in the form of organic matter at various stages of decomposition.

## Sampling design and island area calculation

We conducted field work during six months between June 2016 and February 2018. On each island, we established transects of 2 x 10 m length, partitioned into five plots of 2 x 2 m (Figure 4.2 b). Transects were aligned along the largest diagonal extension of the island and increased in number with island size. When islands were < 10 m in diameter (length of one transect), we placed as many plots as possible along the islands longest axis. This was the case for the 30 smallest islands. On larger islands, two transects oriented towards the island centre were established on the opposite margins of the island. The island interior was then covered with a varying number from one to four interior transects of perpendicular orientation (Figure 4.2 b). The distance between transects on each island with multiple transects was held constant but was related to the longest extension of an island, and hence varied among islands. The sampled area per island was roughly proportional to island area. We inventoried all woody plants rooted within the transect and with a diameter at breast height ≥ 2 cm and recorded species identities. A diameter at breast high ≥ 2 cm is commonly used as threshold in tropical transects (e.g. Molino and Sabatier 2001, Brambach et al. 2017), and we expected species ≥ 2 cm to be well established in the community and to not reflect spontaneous shifts in species composition. We evaluated the potential effect of undersampling by estimating species richness using the *Chao 1* method implemented in the R package *iNEXT* (Hsieh et al 2016). The mean difference between observed richness and *Chao 1*-estimated species richness was 2.6 species and both were highly correlated (Pearson‘s r = 0.95). Moreover, the estimated and observed richness increased at a similar rate with island area, and both were best described by a sigmoidal SAR (Figure C 1). That led us to conclude that the observed richness was a good indicator for the expected total species richness on the islands.

We georeferenced all islands in Gam Bay (Figure 4.2) in ArcGIS (Version: 10.3), using satellite images (World Imagery, ESRI 2017). We then calculated island area (in m$^2$). For islands < 100 m$^2$, we additionally measured the dimensions in the field and matched them with the georeferenced shape. To assess the possible impact of isolation and edge effects on species richness, we calculated two alternative isolation metrics for each island: distance to the large island of Gam (Figure 4.1 a) and the surrounding landmass proportion within a 1000 m radius (following Weigelt & Kreft 2013). For each island, we calculated the shape index (Patton 1975), which quantifies the edge-to-interior-ratio and is a good proxy for possible edge effects (for detailed description on island isolation and shape see Table C 2).

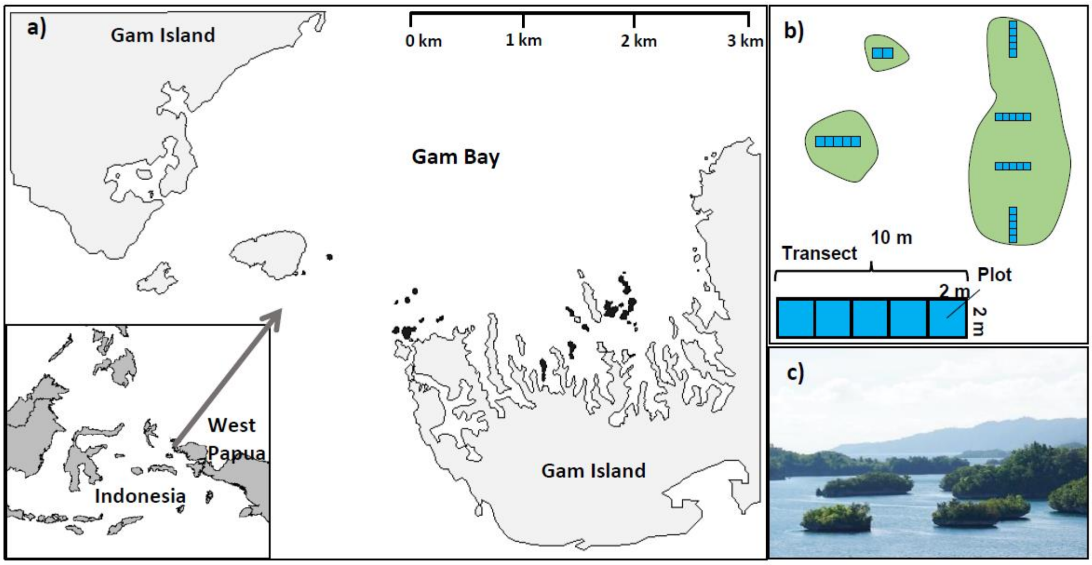

Figure 4.2 Study region and sampling design. a) Location of 60 islands studied (largest sampled islands highlighted in dark grey) in Gam Bay (Raja Ampat Archipelago, Indonesia). b) Species richness was recorded in plots (2 m x 2 m) placed along transects (10 m x 2 m). Number of transects placed on an island depended on island area, whereas larger islands received more transects. On islands smaller than the area of a single transect, we placed as many plots as possible on each island. c) Gam Bay with some of the islands studied (Photo credit: JS).

## Constructing the probabilistic species pool

We considered all species recorded on the sampled islands for the species pool analyses. Note that we did not sample larger islands, such as Gam Island (Figure 4.2 a), as larger islands featured other habitat types and may support different species communities compared to the environmentally homogenous small islands used for this study. Using the empirical presence/absence data of all observed species on the islands, we fitted binomial generalized linear models to estimate occurrence probability of each species as a function of island area. Area was the major axis of variation among islands in our study, since other environmental parameters – e.g. island shape, substrate, lack of deep mineralized soil and freshwater, or age – were very similar among islands. Further, island area emerged as by far the single most important variable in explaining species richness in contrast to environmental quality and heterogeneity, influence of edge effects, and isolation (Figure C 3 & Table C 2). The occurrence probability for each species was set to one when the species was actually recorded on a given island. We chose this approach as we regarded the actual occurrence of a species on an islands as proof that the given species is capable of establishing and surviving on that island. The sum of occurrence probabilities of all species per island is reflected by the probabilistic species pool size index (hereafter species pool size; compare Karger et al. 2016). We assumed that all species considered for the species pool estimates can potentially occur on all islands but with different probabilities (see also Karger et al. 2016).

Following Pärtel et al. (2011), we then calculated dark diversity for each island as the difference between the species pool size and the observed species richness. Community completeness was calculated as the log-ratio between observed richness and dark diversity. For 20 islands that had no species, we added a very small value of 0.1 to the observed species richness to calculate community completeness. This was justifiable as we noticed that some of the now empty islands had woody species present before and can potentially support plant life. Negative community completeness indicated that more species were absent from the species pool than actually present (i.e. dark diversity was higher than observed richness), and positive completeness values indicated that more species were present on an island from the pool than missing (i.e. dark diversity was lower than observed richness).

### Simulation of species occurrence probability

To test whether the estimated species-specific occurrence probabilities differed from the null expectation of random colonization, we simulated species-specific occurrences by assigning random species communities to all islands as a function of area. To this end, we created 1000 random species incidence matrices that kept the total species abundance and species numbers fixed (Götzenberger et al. 2016). For every randomly created matrix, we estimated the species-specific occurrence probabilities as described above for the observed communities. For every species in each incidence matrix, we estimated the island area at which the species-specific occurrence probability equals 0.5. We further calculated mean island area and standard deviation from the 1000 randomizations. Next, we compared simulated and empirically estimated 0.5 species-specific occurrence probabilities based on the standardized effect size (Gotelli and McCabe 2002). If the standardized effect size differed more than ±1.96 ($\alpha = 0.05$), the difference between observed and simulated occurrence probabilities was assumed to be statistically significant (Nakagawa and Cuthill 2007). When observed species occurrence probability differed significantly, we assigned the area value for 0.5 occurrence probability as the species-specific minimum or maximum required area depending on whether the area value for observed species 0.5 occurrence probability was smaller (maximum required area) or larger (minimum required area) than for the simulated occurrence probabilities.

### Species-area relationships and detection of a SIE

To identify the most adequate SAR of observed species richness and species pool size with island area and to test for the presence of the SIE, we compared three species-area models with different shapes on untransformed data: The power model (convex shape), Linear model (linear shape), and Lomolino model (sigmoid shape). We considered the power and linear models because they are considered as the best fitting SAR for convex and linear shapes (Triantis et al. 2012, Matthews et al. 2016) and do not indicate a SIE. We included the Lomolino model as it can be interpreted as SIE model due the flat slope for small island sizes (Lomolino 2000), indicating varying species richness or lesser increase of species richness with area for small islands. The slope increases then rapidly for larger islands, which is typical for a diminishing SIE. Models were fitted using the package *mmSAR* (Guilhaumon et al. 2010) in the statistical software *R* (R Core Team 2017, version 3.4.1). We applied the second-order Akaike information criterion corrected for small sample size (AICc, Burnham & Anderson 2002) to test for the best supported model.

## 4.4 Results

We recorded a total 2253 individuals belonging to 57 woody plant species. Twenty of the 60 islands sampled had no species (on island areas ranging from 3 m$^2$ to 29 m$^2$), and the highest observed richness was 26 species (one island with size of 5527 m$^2$).

For 44 species (73%), observed species-specific area requirements differed significantly from the null assumption (standardized effect size <> ±1.96 or $p < 0.05$). For 18 species, area requirements were larger than expected by change, and 26 species were so rare that $P \geq 0.5$ (50% occurrence probability) was never reached. Simulations predicted these rare species only to occur on the largest islands (for results of species-area requirements see Table 4.1 and Table C 1). Small-island specialists, i.e. species with maximum area requirements, were not observed, but eight species showed decreasing occurrence probability with increasing area.

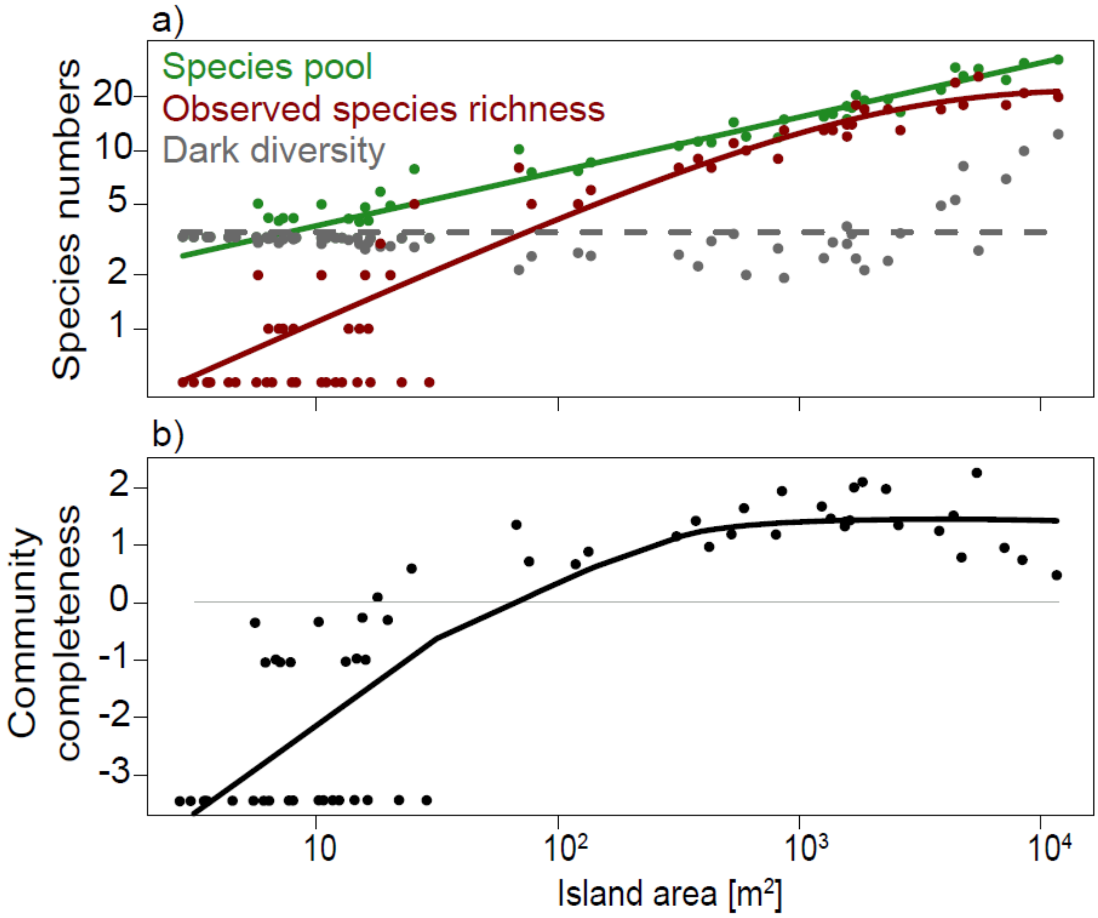

Figure 4.3 Observed species richness, island specific species pool, dark diversity (absent species), and community completeness on 60 small islands. a) Species-area relationship (SAR) in log-log space of species pool (green), observed species richness (red), and dark diversity (grey) on 60 islands. Best species-area model of species pool is a power model (linear shape in log-log space), which indicates no small-island effect (SIE) for the species pool size. Best model fitting SAR of observed richness is the Lomolino model indicating a pronounced SIE for small islands (sigmoidal form in arithmetic space). Dark diversity was not significant with island area (mean of dark diversity indicated as grey dashed line). Empty islands were assigned a richness value of 0.5 to be shown in log-log space. b) Community completeness of the same 60 islands. Community completeness is calculated as log-ratio between observed species richness and dark diversity and indicates how far a community is from its potential diversity. Negative values mean that dark diversity was higher than observed species richness and positive values show higher observed richness compared to dark diversity. Small islands have thus more incomplete communities than large islands. Black regression line is calculated by applying locally weighted scatterplot smoothing (LOWESS).

The SAR for the observed richness was best described by the sigmoidal Lomolino model (AICc weight: >0.99), indicating a SIE due to the shallow slope for small islands. In contrast to the observed richness, the SAR of the island-specific species pool size was best captured by the power model (AICc weight: 0.76) indicating that there was no SIE in the species-pool based SAR (see Figure 4.3 a and Table C 1 for results of model support). Our estimates of island-specific species pool size ranged from 3.2 to 32.3 species with a mean of 10 species (±8.4). Dark diversity varied between 1.93 and 12.34 with a mean of 3.5 (±1.75) absent species Figure 4.3 a; Table C 2 Island characteristics of 60 islands studied. Dark diversity (Dark div.) was calculated as the difference between species pool and actual richness and community completeness (Com. compl.) was calculated as log-ration of observed species richness (obs. rich.) and dark diversity. $\text{iso}_{\text{main}}$: distance to mainland; $\text{iso}_{\text{buffer}}$: surrounding landmass in 1000 m radius; SI: shape index, Soil mean: mean soil depth per island, Soil sd: standard deviation of soil depth recorded on each island. SE: Standard error of estimated species numbers.) and was not significantly related to area. The relationship between observed richness and dark diversity resulted in negative community completeness values on small islands (31 islands ranging from 3 m$^2$ to 29 m$^2$), which increased steadily with island area to a maximum completeness of 2.29 (Figure 4.3 b; Table C 2).

Table 4.1 Observed and simulated species-specific area requirements of 57 species on 60 islands for species occurrence probability p = 0.5 (50%). Occurrence probabilities of 26 species were below 50%, meaning that standardized effect size (SES) could not be calculated. Simulated occurrence probabilities are based on 1000 randomly created species incidence matrices. For each incidence matrix, species-specific occurrence probabilities as a function of island area were estimated for p = 0.5 using generalized-linear models with binomial distribution. Differences between simulated and observed species occurrence probabilities are expressed as SES and significant differences are highlighted in bold (see also Figure C 2 for visualization of area requirements for each species).

| **Species names** | **Observed (in m$^2$)** | **Simulated mean (in m$^2$)** | **Simulated SD (in m$^2$)** | **SES** |
|---|---:|---:|---:|---:|
| *Aglaia elaeagnoidea* | 4079.08 | 1467.52 | 646.45 | **4.04** |
| *Allophylus cobbe* | 10447.52 | 7640.09 | 2095.77 | 1.34 |
| *Antidesma bunius* | 9218.73 | 9749.8 | 1543.48 | -0.34 |
| *Bikkia gaudichaudiana* | - | 9454.48 | 1532.87 | - |
| *Buchanania arborescens* | 6572.11 | 7335.41 | 2053.8 | -0.37 |
| *Calophyllum inophyllum* | 3074.78 | 1033.38 | 479.52 | **4.26** |
| *Calophyllum vexans* | 3476.5 | 573.46 | 281.91 | **10.3** |
| *Canarium oleosum* | 7032.9 | 5979.96 | 2056.3 | 0.51 |
| *cf. Maytenus cupularis* | - | 6881.39 | 2179.71 | - |
| *Cupaniopsis sp.* | 8143.54 | 4630.94 | 1919.62 | 1.83 |
| *Decaspermum bracteatum* | 4847.07 | 2090.21 | 1044.84 | **2.64** |
| *Diospyros maritima* | 345.45 | 354.68 | 207.56 | -0.04 |
| *Eugenia reinwardtiana* | 711.72 | 35.83 | 15.55 | **43.46** |
| *Exocarpos latifolius* | 274.56 | 306.14 | 192.8 | -0.16 |
| *Ficus microcarpa* | 10258.48 | 1956.9 | 958.09 | **8.66** |
| *Ficus nervosa* | - | 10330.72 | 1203.44 | - |
| *Ficus pedunculosa* | - | 9650.46 | 1442.3 | - |
| *Ficus prasinicarpa* | - | 9713.85 | 1497.8 | - |
| *Ficus tinctoria* | 7044.72 | 3333.85 | 1486.92 | **2.5** |
| *Geijera sp.* | - | 9824.4 | 1444.22 | - |
| *Geniostoma rupestre* | - | 9284.58 | 1648.8 | - |
| *Glochidion castaneum* | - | 5700.56 | 2076.28 | - |
| *Gnetum gnemon* | 7647.3 | 3270.46 | 1504.14 | **2.91** |
| *Guettarda speciosa* | 2873.92 | 498.56 | 279.54 | **8.5** |
| *Intsia bijuga* | 4244.49 | 1490 | 688.89 | **4** |

Table 4.1 continued

| | | | | |
|---|---:|---:|---:|---:|
| *Ixora timorensis* | 5792.3 | 714.37 | 352.69 | **14.4** |
| *Lunasia amara* | - | 6823.14 | 2189.17 | - |
| *Macaranga dioica* | - | 10153.05 | 1260.06 | - |
| *Manilkara sp.* | - | 8103.9 | 1939.04 | - |
| *Micomelum minutum* | 10872.87 | 9801.35 | 1416.28 | 0.76 |
| *Mimusops elengi* | - | 9592.33 | 1555.83 | - |
| *Morinda citrifolia* | - | 9974.46 | 1388.84 | - |
| *Myrsine rawacensis* | 758.98 | 32.73 | 12.46 | **58.29** |
| *Pandanus sp.* | 7186.5 | 6867.94 | 2127.92 | 0.15 |
| *Pemphis acidula* | - | 9882.46 | 1399.48 | - |
| *Phyllanthus praelongipes* | 3665.55 | 1788.78 | 817.94 | **2.29** |
| *Pittosporum ferrugineum* | - | 10240.39 | 1268.43 | - |
| *Planchonella obovata* | 1373.38 | 655.09 | 334.75 | **2.15** |
| *Pleurostylia opposita* | - | 10248.85 | 1259.02 | - |
| *Podocarpus neriifolius* | 10423.89 | 6461.18 | 2126.39 | 1.86 |
| *Schefflera sp.* | - | 9816.69 | 1443.81 | - |
| *Severinia lauterbachii* | 3901.85 | 365.16 | 224.91 | **15.73** |
| *Spathiostemon javensis* | 9171.47 | 2977.14 | 1307.26 | **4.74** |
| *Syzygium nitidum* | - | 8399.82 | 1910.53 | - |
| *Tarenna sambucina* | 1314.3 | 488.02 | 258.04 | **3.2** |
| *Timonius sp. 1* | - | 1457.95 | 702.47 | - |
| *Timonius sp. 2* | 10388.44 | 8440.2 | 1899.33 | 1.03 |
| *Wikstroemia androsaemifolia* | 1479.72 | 1268.79 | 594.29 | 0.35 |
| Unidentified species 1 | - | 7358.45 | 2114.04 | - |
| Unidentified species 2 | - | 9983.16 | 1336.97 | - |
| Unidentified species 3 | - | 8076.26 | 2003.12 | - |
| Unidentified species 4 | - | 9267.74 | 1685.29 | - |
| Unidentified species 5 | - | 9750.16 | 1341.34 | - |
| Unidentified species 6 | 10081.25 | 5528.04 | 2111.17 | **2.16** |
| Unidentified species 7 | - | 9297.35 | 1660.18 | - |
| Unidentified species 8 | - | 9720.09 | 1478.02 | - |
| Unidentified species 9 | 9419.59 | 6496.76 | 2147.24 | 1.36 |

## 4.5 Discussion

Our results support the idea that species have specific requirements linked to island area, and that this shapes the island species pools. Most species in our study system showed minimum requirements on area, i.e. they were restricted to islands significantly larger than expected by a random colonization. Interestingly, we did not find evidence for small-island specialists. Species-area models showed that a SIE was only present for the observed species richness on islands, but not for the species pool size. This discrepancy was mirrored by differences in community completeness, which was lower on small islands than on larger ones. Low community completeness on small islands suggests that local processes act differently on species communities compared to larger islands. These local processes may cause species richness to vary independently with area, and could consequently generate the SIE.

## Species-area requirements and island-specific species pools

In order to establish on an island, species have to pass specific demographical, environmental, and dispersal filters (Weigelt et al. 2015, Carvajal-Endara et al. 2017, König et al. 2017), that are strongly associated to island area (Turner and Tjørve 2005). These filters may form species-specific area requirements, and explain the absence of some species on small islands and their presence on larger ones (Cole 1983, Burns and Neufeld 2009, Tjørve and Turner 2009). Indeed, we found that the occurrence of many species was strongly depended on island area, which confirmed our hypothesis H1. More species (c. 73%) were restricted to larger islands than predicted by random community assembly (Table 4.1). Due to their larger edge-to-interior ratio, the studied small islands are more strongly affected by disturbances such as sea spray, solar radiation, or storms (see also Niering 1963, Whittaker 1995, Morrison 2014). Moreover, we observed that certain habitat features, such as the presence of an organic soil layer, were mostly lacking on small islands (Table C 2). These effects may act as strong environmental filters, preventing successful colonization for many species. On large islands, edges led to similar environmental conditions, characterized by absence of soil and leaf litter, high solar radiation, and not being shaded from other trees. That may explain why species having a decreasing occurrence probability with area were rare with low overall occurrence probability. However, the impact of environmental factors, such as different habitat types and disturbance on islands, on specific species requirements should be tested more directly to allow precise conclusion why species respond differently to island area. Isolation had no effect on species richness in our study system (see Figure C 3), as all islands can be regarded as effectively non-isolated. All islands were located within the same bay and in close vicinity to other small islands (Figure 4.2). We thus assume that environmental filtering and species-area requirements likely had a higher impact on the community assembly compared to dispersal filtering (see also Burns 2005, Carvajal-Endara et al. 2017).

## Species pool and observed richness are differentially affected by area

The SAR for the observed species richness was best described by a sigmoidal SAR indicating the presence of a SIE, i.e. observed species richness on small islands increased at a lesser rate than on larger ones (for islands < 100 $m^2$). Following many previous studies, which studied SARs or the SIE (e.g. Niering 1963, Kohn & Walsh 1994, Yu et al. 2012, Wang et al. 2015), we used a transect design to sample plant species richness and abundance. By not sampling the whole island community, we might have missed some rare species, especially on the larger islands. That may have resulted in a slower increase of the SAR slope compared to species richness obtained through complete species inventories. However, estimated species richness per island was also best described by a sigmoidal SAR and the difference between estimated and observed species richness per island was on average only 2.6 species (Figure C 1). We thus could conclude that our sampling area was sufficiently large to obtain reliable results of the shape of the SAR and to be used to calculate species pools. In contrast to the observed species richness, the species pool size showed no support for a SIE and the SAR of the species pool size was best described by a power model - a predictably linear increase of species richness with island area in log-log space, which confirmed our hypothesis H2.

The difference between the SAR for observed richness and species pool size indicates that local processes – and not area – prevent species to establish on small islands. Otherwise, we would have expected that the SAR of the species pool size and observed richness were described by similar models (see also Figure 4.1). We relate the increasing slope of the SAR at larger island sizes to declining environmental processes preventing species establishment. A common feature of the observed species richness were islands without species (n = 20 islands). In contrast, the species pool size constantly predicted around 3.2 species - even for the smallest islands. Indeed, Morrison (2011, 2017) showed that some small empty islands are physically capable of sustaining some taxa in the long term, but often lack species due to low immigration rates and temporal variation in species richness (see also Chiarucci et al. 2017). Also in the studied system, some unsampled small rocks (< 2 $m^2$) occasionally harboured small trees or shrubs. Thus, the different relationships of the species pool size and observed richness with area indicated that the SIE is a phenomenon that only applies to observed species communities. A SIE likely appears when communities have greater constraints to overcome filtering processes on small islands, and not when species pools are formed through environmental filtering and area requirements of species.

## Community completeness on small islands

Community completeness provides information on how much of the species pool is realized locally (Pärtel et al. 2013). Local processes, like environmental filtering, high temporal turnover, negative biotic interactions, or simple stochastic variation, can prevent species to be present in a given community, and thus determine how incomplete a community is (Pärtel et al. 2013). We found negative values of community completeness for small islands below c. 30 m$^2$ in size but not for larger ones (Figure 4.3 b). This result was further supported by the dark diversity pattern, which, almost equal for all islands, was always higher than the observed richness for small islands. That implies for small islands that more species were absent from the island-specific species pool than actually present. We argue that the low community completeness of small islands is linked to the non-linear strength of environmental filtering along the area gradient. Environmental filtering may act more strongly on small islands compared to larger islands and species from the island-specific species pool may be less successful to establish on small islands. That may cause species numbers on small islands to increase at a different rate than on larger islands and could explain the presence of a SIE. Indeed, the range of the SIE for the observed species richness coincides with the relatively low community completeness on small islands (i.e. islands $< 100$ m$^2$). Long-term studies have shown that small islands often experience more extreme environmental conditions resulting in higher turnover rates compared to larger islands (Heatwole and Levins 1973, Wissel and Maier 1992, Morrison 2010, Chiarucci et al. 2017), which can be rapid enough so that extinction rates vary independently from area (MacArthur and Wilson 1967), or even outnumber colonization events (Burns and Neufeld 2009, Morrison 2017). Species turnover decreased from a certain island size onwards as larger islands support higher population densities, reducing the probability of stochastic extinction events (Ricklefs and Lovette 1999). Small islands may also have earlier or different successional states compared to larger islands, initiated by high disturbance (Huston 1979, Whittaker 1995), or higher levels of negative biotic interaction (Cole 1983, Mittelbach and Schemske 2015).

## Conclusion

We demonstrated that plants on small islands have specific area requirements that determine island-specific species pools. Species area requirements are likely caused by environmental processes that differ in strength between islands of different area, suggesting that more species depend on larger islands for successful establishment than predicted by random community assembly. We further found that the SIE did not originate from species pools but that it was rather linked to community completeness and local processes acting differently on smaller islands. From our study, there was clear evidence that island communities did not assemble randomly. Non-random community composition and completeness hinted at environmental filtering and at island area affecting species requirements indirectly through habitat availability.

Our findings are relevant for understanding ecological processes in small and isolated habitat islands, and are thus of high relevance for nature conservation in an increasingly fragmented world, where many species have area requirements larger than the remaining habitat fragments. Probabilistic species pools have a great potential to study these insular systems as they allow to estimate how many species establish locally, indicate probabilities for single species to occur at a focal site, and contain information about species requirements.

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# 5. Life-history dimensions explain filtering in tropical island tree communities

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## 5.1 Abstract

Classic neutral island biogeography theory provides a conceptual framework to quantitatively examine diversity patterns across islands. However, one of its key assumptions - that species are functionally equivalent - has not been rigorously tested using a trait-based framework, despite its potential to provide insights into interspecific variation in ecological strategies and the underlying assembly processes.

Here, we developed a trait-based framework with null models to test for filtering processes and apply it to woody plant communities on 40 tropical islands. We measured 11 plant functional traits that represent major dimensions and variation in plant form and function. We grouped the traits into four different life-history dimensions related to dispersal and niche partitioning of the fast-slow economic dimension and light and nutrients acquisition, to test for non-random assembly processes on the islands.

The investigation of different life-history dimensions revealed a strong role for non-random dispersal and environmental filters shaping island communities. These filters operate simultaneously, but with different strengths, suggesting that multiple niche-based mechanisms act simultaneously. Shifts in filtering strength with island area increased the diversity of dispersal and acquisition strategies in island communities. Our null models reveal that these patterns could not be captured by absolute measures of functional diversity.

*Synthesis*. Recent advances in functional island biogeography were largely descriptive and offered limited insights to the mechanisms underlying the scaling of functional diversity with area. Our framework revealed the prevalence of non-random assembly processes that change with island area thereby offering fresh perspectives to classical island biogeography theory.

**Keywords:** Biogeography and macroecology, Community assembly, Dispersal filtering, Environmental filtering, Functional dispersion, Functional island biogeography, Functional traits, Neutral model, Niche theory

## 5.2 Introduction

Islands constitute natural laboratories to test ecological and evolutionary hypotheses in spatially discrete arenas and provide a continuing source of inspiration for scientists (Losos and Ricklefs 2009). The study of islands has yielded many influential theories on the maintenance of species diversity in isolated fragmented habitats (Warren et al. 2015, Whittaker et al. 2017), first and foremost the equilibrium theory of island biogeography (ETIB; MacArthur & Wilson 1963, 1967). The ETIB posits that the species richness on islands results from a dynamic equilibrium of random colonisation and extinction events, where larger and less isolated islands support more species than smaller and more isolated ones (MacArthur and Wilson 1963, 1967).

The ETIB is based on the neutral assumption that species are functionally equivalent in terms of their ability to disperse to and colonise islands (MacArthur and Wilson 1967), but does not make specific predictions about assembly processes. However, the geographic and ecological factors on islands, such as colonisation barriers and island isolation (Carlquist 1965, Gillespie et al. 2012), niche shifts (Diamond 1970, 1975), and biotic interactions (Carlquist 1974, Taylor et al. 2019), suggest that island floras are a non-random subset of species. Consequently, biodiversity patterns on islands likely have been shaped by non-random community assembly processes (Simberloff 1974, Whittaker and Fernández-Palacios 2007, Emerson and Gillespie 2008), limiting the application of the ETIB to community assembly on islands. Indeed, there is a growing consensus that a functional trait-based approach to island biogeography will yield novel insights to mechanisms underlying biodiversity patterns (Jacquet et al. 2017, Patiño et al. 2017).

Functional traits characterise morphological, physiological, or phenological features (Violle et al. 2007) that can be directly linked to species' dispersal abilities and niche requirements (Díaz and Cabido 2001, Arjona et al. 2018). The value and range of species traits allows for the quantification of functional diversity (FD) (Díaz and Cabido 2001), while also capturing aspects of community structure, e.g. functional commonness and rarity of species, that is often neglected in island studies. So far, only a few studies have investigated island assemblages using a trait-based approach. For islands, there is evidence that FD increases with area, showing a similar relationship with area as species richness (Ding et al. 2013, Whittaker et al. 2014, Si et al. 2016). However, FD-area relationships should be interpreted with caution as FD can be positively affected by both species richness and habitat diversity (Tilman et al. 1997, Petchey and Gaston 2002, Schleuter et al. 2010). This suggests that absolute measures of FD may not provide new insights into insular diversity patterns and the underlying assembly processes, as an increase in species richness, habitat diversity, or area could increase FD (Figure 5.1 a-c). Alternatively, FD may vary independently of area or habitat diversity due to ecological processes such as abiotic and biotic requirements (Violle and Jiang 2009), competition (Kraft et al. 2008), predator-prey interactions and herbivory (Cadotte and Tucker 2017), or dispersal constraints (Burns 2005). To assess the underlying mechanisms behind FD-area relations, it is paramount to make accurate predictions about community assembly on islands. Previous studies examining insular FD-area relationships, however, have not identified the underlying mechanism(s) (Ding et al. 2013; Whittaker et al. 2014; Si et al. 2016; but see Si et al. 2017), and it is still unclear to which degree island area, species richness, or other factors determine this pattern.

Colonising an island imposes two main challenges for species: crossing the water and reaching the island (dispersal filtering) and finding suitable abiotic and biotic conditions (environmental filtering) (Gillespie et al. 2012; Cadotte & Tucker 2017; but see Kraft et al. 2015). Thus, multiple filters operate on the structure and composition of island communities. To test for filtering, FD is commonly compared to random subsamples of traits from the regional species pool (Mason et al. 2013, Cadotte and Tucker 2017) and can be either more similar (underdispersed) or dissimilar (overdispersed) than expected by chance (Figure 5.1 e,f; Ackerly & Cornwell 2007; Craven et al. 2018). For instance, Burns & Neufeld (2009) reported that plant species on small islands have more similar dispersal-related traits than plants on larger islands, as they are predominantly bird dispersed. Plants on atolls are often widely dispersed and well-adapted to tropical and coastal conditions (Stoddart 1992), likely leading to an underdispersion of dispersal syndromes and traits associated with tolerating environmental conditions on atolls. Overdispersion on islands can occur when high competition for limited resources among species leads to niche differentiation (MacArthur and Levins 1967, Astor et al. 2014), or due to the absence of predation or herbivory (Schoener and Toft 1983), allowing many functionally different species to coexist (Cadotte and Tucker 2017). Testing for filtering, therefore, has the potential to reveal new insights into island community assembly and into the mechanisms underlying FD-area relationships. To date, no common framework exists that incorporates FD, non-random community compositions, and filtering with island biogeography theories.

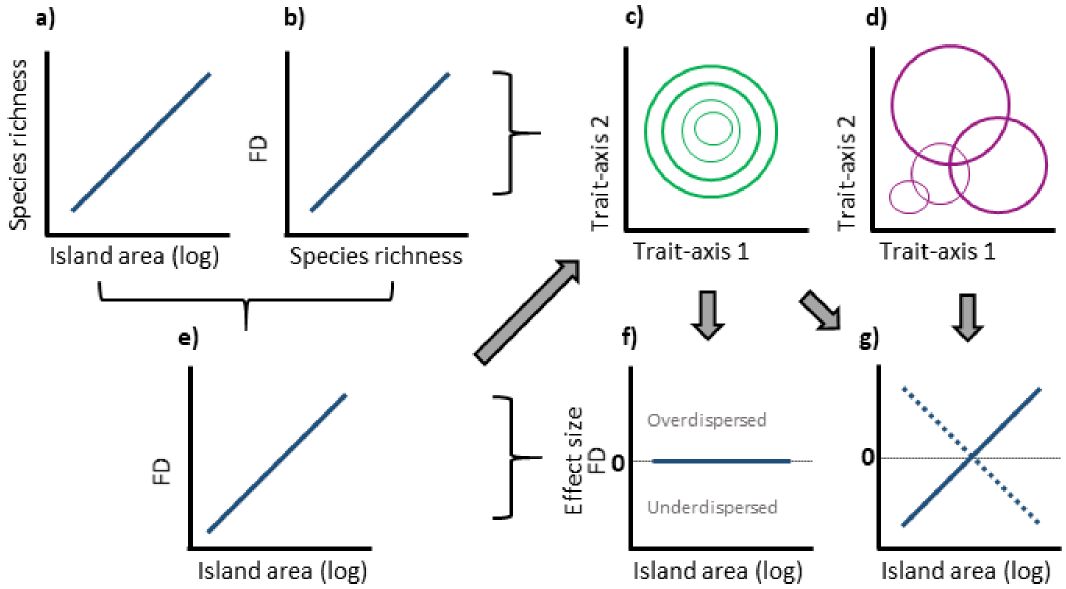

Figure 5.1 Conceptual framework to integrate functional diversity (FD) into classical island biogeography theory and test for non-random assembly and filtering processes along gradients in island area. (a) The equilibrium theory of island biogeography (ETIB) predicts that species richness increase with island area. (b) FD normally increases with species richness, as both are strongly correlated. (e) Consequently, FD can be expected to increase with island area. An increase in FD with island area alone, however, is uninformative about community assembly and filtering processes on islands. This pattern may arise either by (c) a trait space of smaller islands located within the trait space of larger islands or (d) by separate trait spaces of each island (which can overlap to varying degrees). Using a null model approach to account for species richness effects on FD, the extent to which island area influences FD patterns can be examined. When the effect size is not correlated with island area (f), communities can be regarded as a random subsample of a larger species pool without filtering processes shaping these communities. (g) When the effect sizes increase (solid line) or decrease (dashed line) with island area, FD is either under- or overdispersed for certain communities. That would be a strong signal of filtering (dispersal and/or environmental filters) and non-random community assembly processes.

Here, we develop a trait-based functional island biogeography framework to examine the assembly of island communities and apply it to a novel dataset of woody plants on 40 tropical islands that vary in size by three orders of magnitude. Using a null model approach, we first investigate how species richness and abundances affect FD on islands directly. We then focus on different life-history dimensions related to dispersal and niche partitioning of the fast-slow economic dimension and light and nutrients acquisition, to test for non-random assembly processes. We expect that FD (also when grouped into life-history dimensions) will increase with island area, as more functionally different species may co-occur on larger than on smaller islands. Further, we hypothesise that community assembly of island communities will be independent of island area and will be shaped by dispersal and environmental filters operating on different life-history dimensions.

## 5.3 Material and Methods

We studied 40 islands ranging in size from 6 $m^2$ to 11,806 $m^2$. All islands were located in a bay of Gam Island in the Raja Ampat Archipelago, Indonesia (Figure D 1). Climate in the region is wet tropical and lacks a pronounced seasonality with mean annual precipitation of around 2,768 mm and a mean annual temperature of 27.4°C (nearest weather station Sorong / Jefman, ca. 50 km apart; http://www.worldclimate.com, 2019). All islands consist of coralline substrate, belong to the same limestone plateau, and are of approximately similar age. Therefore, differences in elevation and topographic heterogeneity across islands were very small, ranging for elevation between ca. one to eight m.a.s.l. Woody vegetation dominates on all islands (Takeuchi 2003). Mineral soil was absent and the only soil present consists of organic matter. We calculated island area ($m^2$) by georeferencing island shapes from satellite images (World Imagery, ESRI 2017) in ArcGIS (Version: 10.3). We only included islands that contained similar habitat types and had not been subjected to recent anthropogenic disturbances, limiting the maximum island size to ca. 12,000 $m^2$. Moreover, the studied islands can be regarded as effectively non-isolated and isolation had no effect on species richness patterns (Schrader et al. 2019b). All islands share a common origin, ontogeny, and have very similar ecological conditions and habitats allowing us to focus exclusively on island area in our analyses (Schrader et al. 2019a).

Botanical field surveys and trait measurements were performed between June 2016 and February 2018. We used a transect design where sampling area was roughly proportional to island area, covering island edges as well as the interior (Schrader et al. 2019b). We identified all woody plants with a diameter at breast height of $\geq$ 2 cm that were rooted within transects and recorded species identity, height, and stem numbers. Soil depth was recorded in all transects at five spots with equal distance to each other (33 cm) and spaced along the central axis of the transect (for detailed description of sampling design see Figure D 1).

We studied 11 plant functional traits that represent major dimensions and variation in plant form and function (Westoby et al. 2002, Reich 2014, Díaz et al. 2016). We measured traits following standardised trait protocols (Pérez-Harguindeguy et al. 2013). These traits included leaf area, leaf mass per area (LMA), chlorophyll content, leaf N, C:N, C:P, and N:P, wood density, plant maximum height, and fruit and seed mass. The number of individuals sampled ranged from one to ten individuals, depending on the rarity of a species. All measurements were aggregated into species' mean trait values (Table 5.1, Table D 2).

We measured leaf traits on ten mature and sun-exposed leaves from several individuals when available. We calculated leaf mass per area (LMA; g $cm^{-2}$) by calculating leaf area ($cm^2$) using Leaf-IT (Schrader et al. 2017) and by using a digital balance (± 0.001) for measuring dry leaf mass. Leaves were oven-dried at 80°C for 48 h. We measured leaf chlorophyll content using a chlorophyll-meter (Konica Minolta, SPAD – 502DI Plus), and converted the SPAD measurements to chlorophyll concentrations (µm $cm^{-2}$) using the correlation $Chl = 117.1 * SPAD/148.84 - SPAD$ (Coste et al. 2010).

We determined leaf nitrogen and carbon concentration (mg $g^{-1}$) by automated dry combustion (Elementar, Vario EL Cube). We measured leaf phosphorus concentration (mg $g^{-1}$) using inductively coupled plasma-atomic emission spectrometer (iCAP 6300 Duo VIEW ICP Spectrometer, Thermo Fischer Scientific GmbH, Dreieich, Germany).

We measured wood density (g $cm^{-3}$) as the volume (using the water displacement method) of the main stem without branches (green parts and bark were removed) divided by its oven-dry weight and dried samples at 100°C for 48 h. We used two mature individuals per species for measuring wood density as more extensive sampling was impossible due to many rare species.

We calculated maximum tree height (m) as the mean height of the three tallest individuals of each species (following King et al. 2006).

We collected and measured the dry fruit and seed mass (g) of 44 and 38 species, respectively, aiming for at least ten fruits per species, which was difficult for some species when fruiting was scarce (number of fruits sampled per species ranged from 1 to 40; mean = 11.6). Fruit and seeds were oven-dried at 80°C for 72 h. For the 13 species for which we were unable to collect data in the field, we used seed mass data from the KEW seed database (http://data.kew.org/sid; accessed: July 2018). For eight species not present in the KEW database or not identified to species level, we used genus-level means from the KEW database.

As trait data were missing for 32 of the 627 species-trait combinations (one trait value missing for LMA, leaf area, Leaf N, Leaf C:N, C:P, N:P; three for wood density; four for chlorophyll; six for seed mass; 13 for fruit mass), we applied trait imputation to estimate missing trait data by using multivariate imputation using chained equations in the R-package mice 3.4.0 (Buuren and Groothuis-Oudshoorn 2011). Multivariate imputation is a commonly applied imputation method and yields robust results, especially when missing data represents less than 30% of gaps (Penone et al. 2014, Taugourdeau et al. 2014), as in our dataset (5% gaps). We log-transformed leaf area and seed and fruit mass to account for their highly skewed distributions.

We grouped the 11 traits into four life-history dimensions (Westoby 1998, Lavorel and Garnier 2002, Adler et al. 2014) that capture important plant strategies for colonisation and establishment on islands (Table 5.1). Grouping of traits into life-history dimensions allows for in-depth analyses of community assembly processes (Kohli et al. 2018), which can vary non-uniformly along a gradient that may not be captured by total measures of FD (Spasojevic and Suding 2012). The four life-history dimensions, each represented by three traits (note that tree height was used in two life-history dimensions), were:

- Dispersal ability: island colonisation greatly depends on species' dispersal abilities (Carlquist 1974). Seed and fruit mass determine long distance dispersal, as lighter and smaller seeds are more easily dispersed over longer distances and fruits are often transported by birds between islands (Burns 2005, Gillespie et al. 2012, Arjona et al. 2018). Additionally, tree height increases dispersal distance, especially for shorter distances (Thomson et al. 2011).

- Fast-slow economic dimension: plant economic strategies depend on environmental conditions and differ greatly between species. Plant height, LMA, and wood density represent the fast-slow life-history dimension (Wright et al. 2004, Reich 2014, Díaz et al. 2016).

- Light acquisition: light availability can differ greatly with island size, with plants on smaller islands being more exposed to light than plants on larger islands where denser forest canopies and lower edge-to-core ratios may decrease light availability. Chlorophyll content, leaf N, and leaf area respond strongly to light availability

(Valladares et al. 2000, Wright et al. 2004, Díaz et al. 2016), and were used to represent the light acquisition dimension.

- Nutrient availability: smaller islands may have fewer nutrients available for plants due to less developed soil and frequent disturbances caused mainly by waves (Whittaker 1995). Nutrients and soils on larger islands in turn can accumulate more easily as they are less disturbed. Thus, we used leaf C:N, C:P, and N:P to represent the nutrient availability dimension (Wassen et al. 2005, Pérez-Harguindeguy et al. 2013).

Table 5.1 Traits, ranges of trait values, number of species for which trait values were sampled, and classification into four life-history dimensions. LMA: leaf mass per area. Note that maximal tree height was used for both dispersal and the fast-slow dimension. For definitions of the studied traits, see Methods, for species-trait matrix see Table D 2.

| **Trait and unit** | **Range** | **No of species** | **Life-history dimension** | **References to life-history dimensions** |
|---|---:|---:|---|---|
| Fruit mass (g) | 0.01-20.03 | 44 | Dispersal | Ordano *et al.* 2017 |
| Seed mass (g) | 0.00004-5.07 | 51* | Dispersal | Westoby *et al.* 1996; Moles & Westoby 2006 |
| Height (m) | 1.5-15.8 | 57 | Dispersal<br>Fast-slow dimension | Westoby 1998; Thomson *et al.* 2011 |
| Wood density (g cm$^{-3}$) | 0.29-0.99 | 53 | Fast-slow dimension | Chave *et al.* 2009; Adler *et al.* 2014; Reich 2014 |
| LMA (g cm$^{-2}$) | 0.52-2.6 | 56 | Fast-slow dimension | Reich *et al.* 1999; Wright *et al.* 2004 |
| Leaf area (cm$^{2}$) | 1.78-126.66 | 56 | Light acquisition | Wright *et al.* 2004, 2017 |
| Chlorophyll (µm cm$^{-2}$) | 19.45-114.55 | 52 | Light acquisition | Valladares *et al.* 2000; Walker *et al.* 2014 |
| Leaf N (%) | 0.63-2.79 | 56 | Light acquisition | Reich *et al.* 1997; Wright *et al.* 2004 |
| Leaf C:N (ratio) | 18.10-86.46 | 56 | Nutrient acquisition | Pérez-Harguindeguy *et al.* 2013; Buzzard *et al.* 2016 |
| Leaf C:P (ratio) | 43.52-421.27 | 56 | Nutrient acquisition | Pérez-Harguindeguy *et al.* 2013 |
| Leaf N:P (ratio) | 0.98-13.41 | 56 | Nutrient acquisition | Reich & Oleksyn 2004; Wassen *et al.* 2005 |

* Seed mass data for 13 species were obtained from the KEW Seed Information Database (http://data.kew.org/sid/).

## Data analysis

To visualise the trait space occupied by all species, for different island size classes, and by the four life-history dimensions, we performed Principal Component Analysis (PCA) using the R function *prcomp*. We divided the 40 islands into four classes based on island area (class 1: islands < 10 $m^2$; class 2: islands > 10 $m^2$ and < 100 $m^2$; class 3: islands >100 $m^2$ and < 1000 $m^2$; class 4: islands > 1000 $m^2$) and calculated the convex hull for each class for visualisation of the trait space occupied (Figure 5.2). All statistical analyses were performed using R version 3.4.4 (R Core Team, 2018).

For each island, we calculated FD as functional dispersion (FDis), which is the species' mean distance from the community centroid, using all traits and the four life-history dimensions separately in the R package FD 1.0-12 (Laliberté and Legendre 2010). FDis accounts for relative abundances and is less affected by differences in species richness compared to other FD indices (Schleuter et al. 2010). We calculated FDis in its incidence ($FDis_{inc}$) and abundance ($FDis_{abun}$) version to compare the effects of common and rare species on FD. We used the number of individuals recorded in all plots on an island to calculate species abundance. We calculated the partial residuals of a linear model with FDis as a response variable and island area (log-transformed) and basal area per ha ($m^2$ $ha^{-1}$) as predictor variables to account for varying forest structure among islands (Dobbertin 2005). Basal area was weakly positively correlated with island area (Pearson correlation = 0.45, $P<0.05$). The recorded number of individuals differed between islands, which may affect FDis in the same way as it affects species richness (Gotelli and Colwell 2001). Individual-based rarefaction has been used to disentangle effects of island area and habitat diversity on species richness patterns (Chase et al. 2019). For these reasons, we also used a rarefaction approach to calculate FDis (Ricotta et al. 2012) and rarefied FDis to 20 individuals per island on the 23 islands with at least this number of individuals, which we calculated (as described above) as the mean across 1000 random samples (without replacement).

We constructed null models to test whether observed FDis varied from the neutral expectation that island area had no direct effect on FDis. To this end, we randomly assigned trait values to each island while keeping species richness constant (Götzenberger et al. 2016). This was done in the R package picante 1.7 (Kembel et al. 2010) and repeated to create 1000 random communities. We then calculated FDis including all traits and for each life-history dimension separately for both incidence and abundance data. Next, we calculated the effect size to test for differences between the observed community and the null communities. The effect size of FDis for both incidence and abundance data for all traits and each life-history dimension was calculated by using probit-transformed P-values (Lhotsky et al. 2016), because FDis of the random communities was not normally distributed (see Figure D 2).

We did not assume a specific relationship between FDis and island area, and thus fitted generalised additive models (GAM) with a Gaussian distribution using the package mgcv 1.8-28 (Wood 2001). To make our results comparable to the large body of literature on species-area relationships (e.g. Rosenzweig 1995) and FD-area relationships (e.g. Ding et al. 2013; Whittaker et al. 2014), we fitted a power model (Arrhenius 1921), which is the most commonly used species-area model and normally provides the best fit to island species-area relationships (Matthews et al. 2016). We calculated and fitted functional richness (Laliberté and Legendre 2010) to island area using a GAM model. Functional richness was commonly used by other studies to describe FD-area relationships (e.g. Ding et al. 2013; Whittaker et al. 2014) (see Figure D 5 for power model fit and FD-area relationship constructed using functional richness).

## 5.4 Results

We recorded a total of 2215 individuals (range = 1 to 188; mean = 55) and 57 species (range = 1 to 27; mean = 6.5) from the 40 sampled islands. The species found on smaller islands occupied less trait space than those on larger islands. Moreover, trait space on smaller islands was nested within that of larger islands, for all traits and for each life-history dimension (Figure 5.2).

Species richness increased linearly with island area in the GAM and in the power model in log-log space (GAM: adj. $R^2=0.92$; power model: adj. $R^2=0.90$; Figure 5.3 a). Stem numbers also increased linearly with island area in log-log space (Figure 5.3 b). $FDis_{inc}$ and $FDis_{abun}$ were strongly correlated ($r=0.94$) and exhibited similar relationships with area as species richness, both increasing significantly with island area (Figure 5.3 c-d). Rarefied functional dispersion was correlated with $FDis_{inc}$ and $FDis_{abun}$ and also exhibited a similar relationship with island area (Figure D 6). In contrast, effect sizes of $FDis_{inc}$ and $FDis_{abun}$ did not vary with island area, indicating that FDis was similar among islands once controlling for species richness (Figure 5.3 e-f).

FDis of each life-history dimension increased significantly with island area and peaked on larger islands (Figure 5.4). Effect sizes of FDis for each life-history dimension yielded contrasting results. The effect size of $\mathrm{FDis}_{\mathrm{inc}}$ for dispersal increased significantly with area and shifted from underdispersed to overdispersed (Figure 5.5 a). However, the effect size of $\mathrm{FDis}_{\mathrm{abun}}$ for dispersal did not vary significantly with island area (Figure 5.5 b). We also observed a similar pattern for the fast-slow dimension (Figure 5.5 c-d). $\mathrm{FDis}_{\mathrm{inc}}$ of the light acquisition dimension showed overdispersion for smaller islands, shifting to randomly dispersed communities with increasing island area (Figure 5.5 e), whereas the effect size of $\mathrm{FDis}_{\mathrm{abun}}$ was not influenced by island area (Figure 5.5 f). In contrast, the effect size for $\mathrm{FDis}_{\mathrm{inc}}$ for nutrient acquisition was not significantly related to island area, but the effect size for $\mathrm{FDis}_{\mathrm{abun}}$ increased with island area from underdispersed to moderately overdispersed (Figure 5.5 g-h).

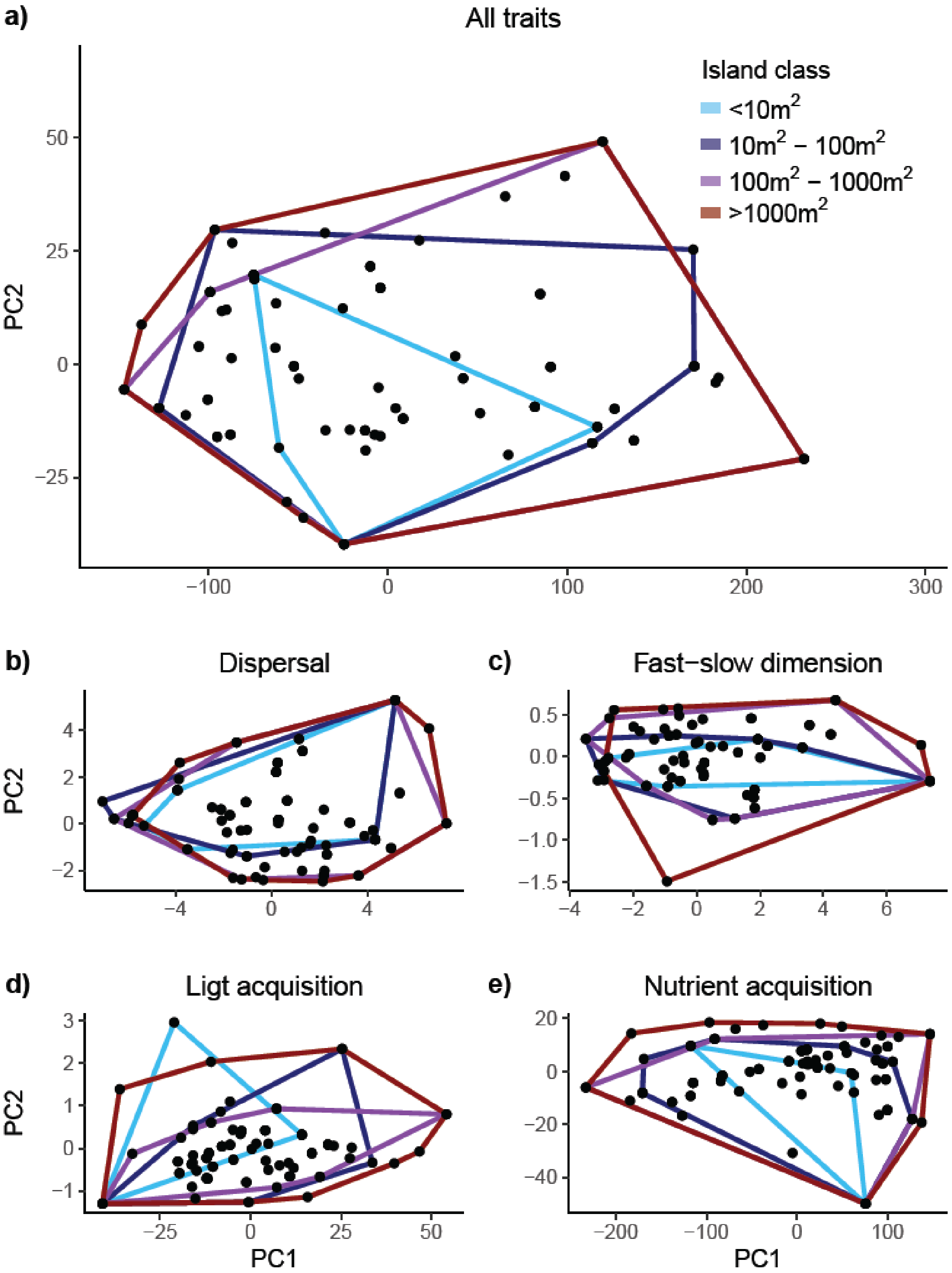

Figure 5.2 Trait space of tree assemblages on islands using 11 traits (a) and four life-history dimensions (b-e). Trait space is visualised as convex hulls of four island area classes that were calculated using principal component analyses. Only the first two principal component axes are shown (PC1 & PC2). Grouping of traits into life-history dimensions are shown in Table 5.1.

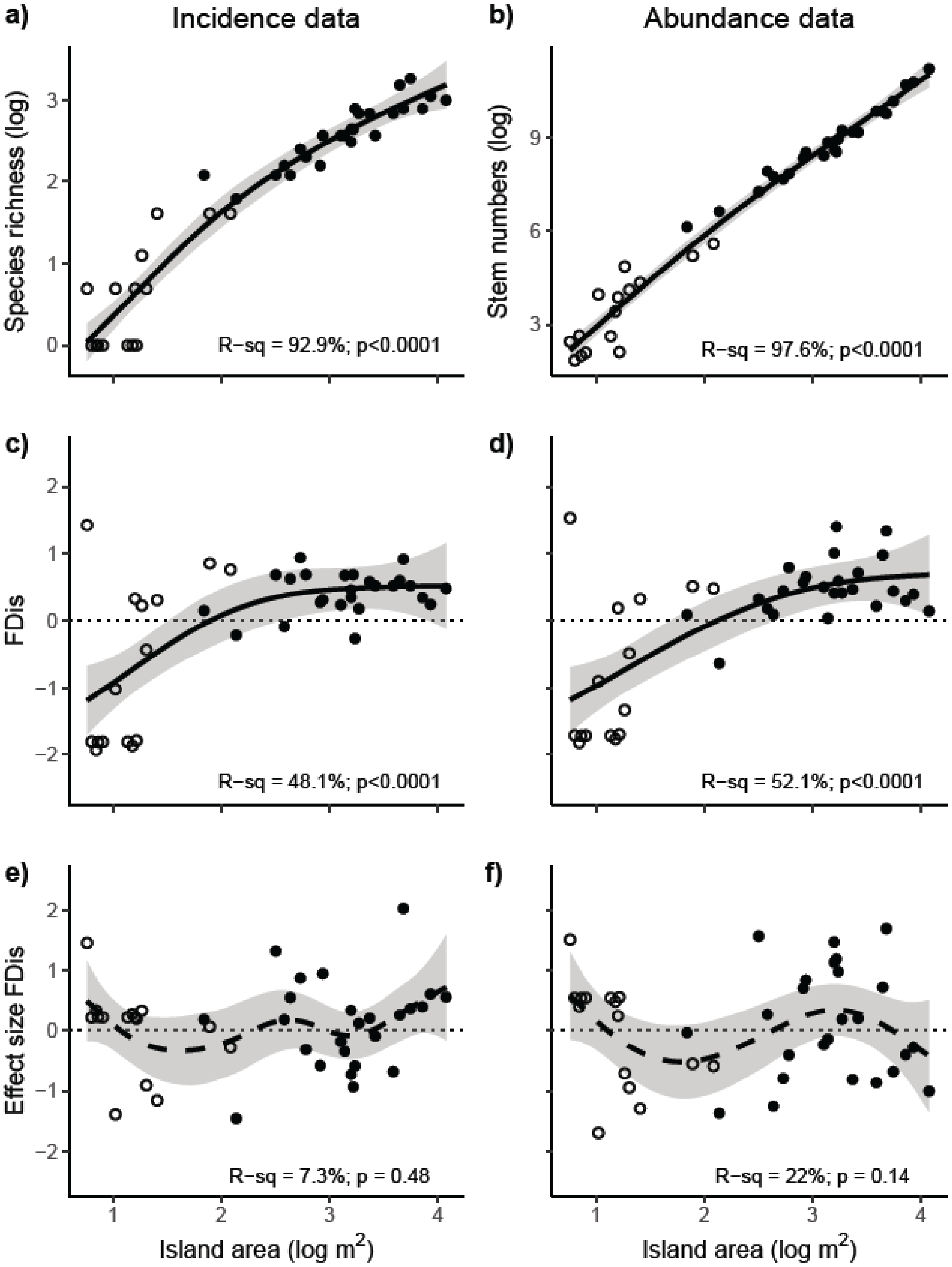

Figure 5.3 Spatial scaling of species richness, abundance, and functional dispersion (FDis) of trees on islands. a) Species richness and stem numbers increase both linearly with island area (as predicted by the equilibrium theory of island biogeography). c & d) FDis increased with area for both incidence and abundance data. e & f) Effect size of FDis between observed and randomly created communities using incidence and abundance data. Regression lines indicate partial fits of island area after accounting for tree basal area. Empty points indicate islands where soil was absent, and solid points where soil was present. 95% confidence intervals are displayed by grey bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p<0.05$) are indicated by solid black lines and non-significant smoothed fixed effects are indicated by dashed lines.

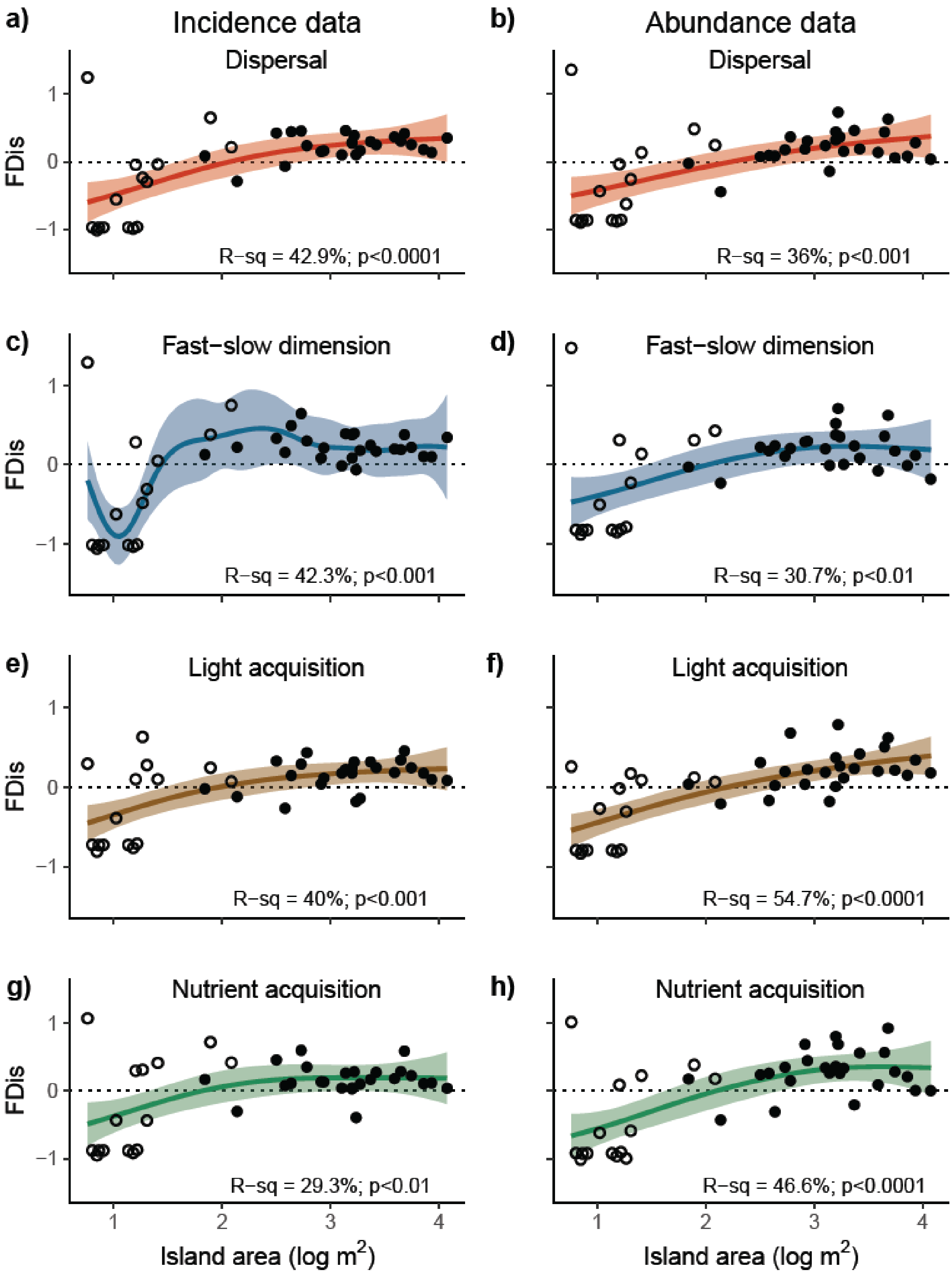

Figure 5.4 Spatial scaling of functional dispersion (FDis) divided into four life-history dimensions for incidence (left panels) and abundance (right panels) data of insular tree communities. FDis increases for all life-history dimensions with island area. Regression lines indicate partial fits of island area after accounting for tree basal area. Circled points indicate islands where soil was absent, and solid points where soil was present. 95% confidence intervals are indicated by coloured bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p<0.05$) are indicated by solid black lines. Grouping of traits into life-history dimensions are shown in Table 5.1.

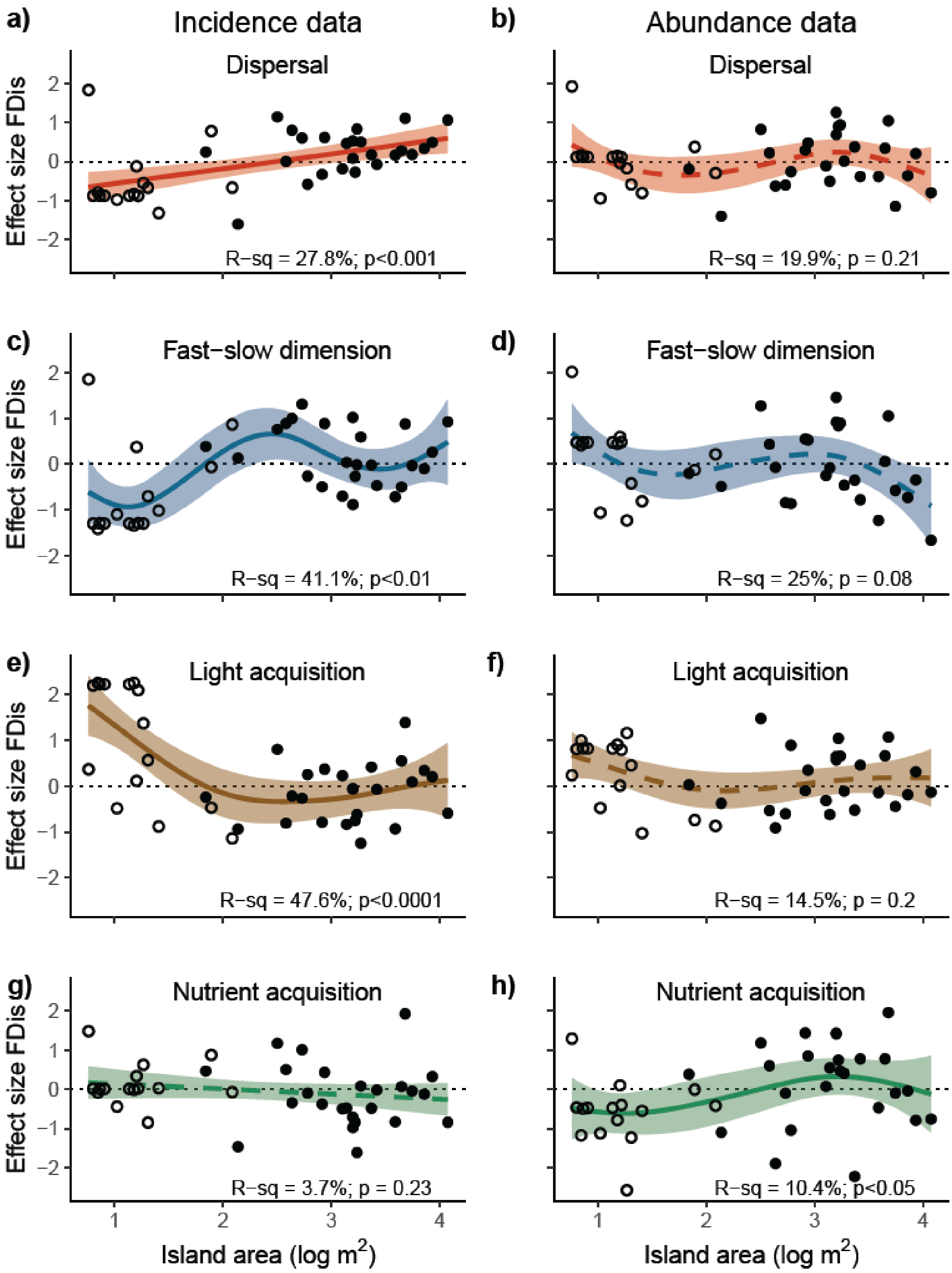

Figure 5.5 Spatial scaling of the effect size of functional dispersion (FDis) calculated between observed and randomly created communities of four life-history dimensions based on species incidences (left panels) and abundances (right panels) of insular tree communities. Positive effect sizes indicate that the observed FDis on the island was greater than expected and negative effect size indicate that the observed FDis was lower than expected. Regression fits indicate partial fits of island area after accounting for tree basal area. Open points indicate islands where soil was absent, and solid points where soil was present. 95% confidence intervals are indicated by coloured bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p<0.05$) are indicated by solid black lines and non-significant smoothed fixed effects are indicated by dashed lines. Grouping of traits into life-history dimensions are shown in Table 5.1.

## 5.5 Discussion

Our results provide evidence that tree communities in our island system are shaped by non-random dispersal and environmental filters. Different trait dispersion patterns of life-history dimensions with island area suggest that several niche-based mechanisms act simultaneously but with different strengths on assembly processes. Our null models reveal that these patterns could not be captured by absolute measures of FD. We relate the shift in the strength of dispersal and environmental filtering with island area to increases in the diversity of dispersal and acquisition strategies. Smaller islands may impose greater dispersal barriers and may provide fewer available niches than larger islands, resulting in underdispersed communities. On larger islands, stochasticity and higher competition lead to functionally overdispersed communities. Our results thus indicate that island communities are shaped by non-random assembly processes that change with island area, and thereby add a novel perspective to island biogeography theory.

### Functional diversity scales with island area

Similar to previous island studies (Ding et al. 2013, Whittaker et al. 2014, Si et al. 2016), we observed a positive FD-area relationship, which exhibited a similar form as that of the species (richness)-area relationship (Figure 5.3 a-b). The shape of the FD-area relationship did not differ between incidence and abundance data, suggesting that rare and common species have unique trait combinations and both contribute to increasing trait space. An increase in FD with island area was also apparent for each of the four life-history dimensions, although the FD-area relationship seemed to saturate for islands larger than 100 to 1000 m$^2$. Two mechanisms likely underpin positive FD-area relationships. First, FD was correlated with species richness (Figure D 5; see also Petchey & Gaston 2002, 2006), suggesting that additional species add novel trait combinations to communities (Boersma et al. 2016). Therefore, increasing FD with area likely is a consequence of increasing species richness with area, which could occur under neutral assembly processes on islands (Figure 5.3 e,f; Si *et al.* 2017). Second, increasing FD with island area can be attributed to greater niche diversity on larger islands (Hortal et al. 2009, Chisholm et al. 2016). Traits are good predictors of species' niche requirements (Kraft et al. 2008, Cadotte et al. 2011), suggesting that larger trait space reflects higher niche diversity (Sterck et al. 2011). Indeed, we found that the functional trait space of smaller islands was nested within that of larger islands (Figure 5.2), which supports the idea that niche diversity increases with area (Losos and Ricklefs 2009, Chisholm et al. 2016) and that larger islands share similar niches with smaller islands (Schrader et al. 2019a). However, the saturation of the FD-area relationship could indicate that the niche diversity is finite on larger islands.

## Filtering processes shape island tree communities

We found evidence that island communities are shaped by an interplay of dispersal and environmental filters that act simultaneously, but that the strength of these filters varies with island area. In general, communities on small islands were underdispersed (except for the light acquisition dimension), whereas larger islands had randomly or overdispersed communities. This result coincides with those reported by Astor *et al.* (2014) and Si *et al.* (2017) for snail and plant communities on land-bridge islands, respectively. The smallest islands in our island system had very uniform habitats, lacked soil (i.e. organic matter), and were regularly exposed to waves and salt water (Schrader et al. 2019b). In particular, the degree of soil development on these islands strongly shapes community composition, as the islands are otherwise similar in terms of precipitation, elevation, shape, and substrate (Schrader et al. 2019b). Deeper soil can offset stressful environmental conditions like droughts, provide more nutrients, enable facultative interactions with soil biota (e.g. mycorrhiza), and increase fine-scale environmental heterogeneity, enabling higher FD (Weiher et al. 1998, Ackerly and Cornwell 2007, Cornwell et al. 2008). Islands with poorly developed soil may filter many species from the regional pool (Schrader et al. 2019a), resulting in a subset of co-occurring species that share similar habitat requirements (Niering 1963, Morrison 2011) and nutrient acquisition strategies (Weiher et al. 1998, Cornwell et al. 2006). Indeed, the transition from underdispersed (or for light acquisition, overdispersed) communities to randomly or overdispersed communities usually occurred on islands that had more developed soil (Figure 5.5, Table D 1). Further, smaller islands are less likely to be colonised by species with wind-dispersed seeds (target effect; Brown & Kodric-Brown 1977) and may be less frequented by birds, the dominant seed dispersers of woody plants in our island system (personal observation; see also Burns 2005). Mean canopy height was lower on smaller islands than on larger ones (Table D 1), suggesting that here light availability was not limiting for most species. The higher solar radiation on small islands may rather support a greater than expected diversity of leaf adaptations (Givnish 1988, Wright et al. 2004). For example, *Guettarda speciosa* L. has large leaves with low chlorophyll content, *Pemphis acidula* J.R. Forst. & G. Forst. tiny leaves, and *Bikkia gaudichaudiana* Brongn. very high chlorophyll contents (Table D 2), indicating that species with contrasting strategies to cope with high solar radiation can co-occur on small islands, increase FD, and lead to overdispersed communities.

We found that filtering differentially affected both rare and common species (Figure 5.5). The effect size of $\text{FDis}_{\text{inc}}$ for dispersal, the fast-slow dimension, and light acquisition increased significantly with island area, whereas $\text{FDis}_{\text{abun}}$ for the same life-history dimensions did not vary with island area. This result suggests that rare species increase the trait space of the community and occur more frequently than expected on larger islands, once accounting for species richness. Indeed, it has been shown that rare species often add novel traits to a community and contribute disproportionately to ecosystem functioning (Mouillot et al. 2013, Umaña et al. 2017), which may be lacking on smaller islands (Wardle et al. 1997). Common species increased trait diversity of nutrient acquisition with increasing area, possible due to better developed soils on larger islands. This supports the idea that common species partition niche space along gradients in belowground resources (Laliberté et al. 2012, van Breugel et al. 2019) to a greater extent on larger islands.

In conclusion, we show that the assembly processes structuring plant communities on islands are largely deterministic and jointly shaped by environmental and dispersal filtering. Recent advances in functional island biogeography were largely descriptive and offered limited to the mechanisms underlying the scaling of FD with area. However, we see a bright future for functional approaches to island biogeography, and our trait-based framework can be used to test for filtering processes that shape community assembly on islands.

## Acknowledgements

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# 6. Species-area relationships on small islands worldwide differ among growth forms

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## 6.1 Abstract

**Aim:** We tested whether species-area relationships on small islands worldwide differ among growth forms and whether this influences the prevalence of the small-island effect (SIE). The SIE states that species richness on smaller islands is independent or less dependent on area than on larger islands. In addition, we investigated whether island isolation affects the limits of the SIE and which environmental factors drive species richness on small islands.

**Location:** 700 small islands (<100 km²) worldwide belonging to 17 archipelagos.

**Major taxa studied:** Angiosperms.

**Methods:** We applied linear and breakpoint species-area models for total angiosperm species richness and for herb, shrub, and tree species richness per archipelago separately, to test for the existence of SIEs. For archipelagos featuring the SIE, we calculated the breakpoint area that indicates the upper limit of the SIE and used linear models to test whether breakpoint areas vary with isolation. We used linear mixed effect models to discern the effects of seven environmental variables related to island area, isolation, and other environmental factors on species richness of each growth form for islands smaller than the breakpoint area.

**Results:** For 71% of all archipelagos, we found evidence for the SIE for total and herb species richness and in 59% and 53% for shrub and tree richness. Shrub and tree richness showed larger breakpoint areas than total and herb richness. The breakpoint area was significantly affected by isolation for total and shrub richness. Species richness on islands within the range of the SIE was differentially affected by environmental factors across growth forms.

**Main conclusion:** Plant functional types, such as growth forms, affect the SIE and provide new insights into this long-standing pattern. Species richness on small islands was differentially affected by environmental factors, possibly driven by similar environmental requirements of species having the same growth form.

**Keywords**: Breakpoint, Environmental factors, Functional island biogeography, Growth form, Isolation, Plant functional types, Small-island effect, Species-area relationship

## 6.2 Introduction

The *small island effect* (hereafter SIE) describes an 'anomalous' feature of species richness on smaller islands compared with larger ones (Triantis and Sfenthourakis 2012). Usually, it is identified as the independent variation of species richness with island area on small islands, representing one of the few exceptions to the species-area relationship (SAR; Heatwole & Levins, 1973; Lomolino & Weiser, 2001). Since its first description by Niering (1963), a wealth of studies reported on the existence of the SIE and put forward several hypotheses to explain it (Lomolino & Weiser, 2001; Triantis *et al.*, 2006 for review). MacArthur & Wilson (1967) hypothesised that the SIE occurs when species extinctions outnumber colonisation events. According to their equilibrium theory of island biogeography, extinction rates are higher on small and isolated islands while larger and less isolated islands have higher immigration rates (MacArthur and Wilson 1963, 1967, Brown and Kodric-Brown 1977, Lomolino 1990). Hence, colonisation and extinction dynamics should determine the upper limit of the SIE and the SIE should be more pronounced on more isolated islands. Alternative, but not mutually exclusive explanations for understanding the SIE stress the importance of limited habitat availability (Triantis et al. 2003, Sfenthourakis and Triantis 2009), species-area requirements (Schrader et al. 2019a), greater influence of disturbances on smaller islands (Whittaker 1995), alternating effects of niche-based and neutral processes (Chisholm et al. 2016), or differential effects of isolation, topography, and geology (Triantis et al. 2006, Ackerman et al. 2007).

In addition to ecological explanations for the SIE, the importance of analytical and methodological factors has been stressed (Gentile and Argano 2005, Burns et al. 2009, Dengler 2010, Tjørve and Tjørve 2011, Triantis and Sfenthourakis 2012). For example, the inclusion or exclusion of empty islands (Dengler 2010, Morrison 2011, Wang et al. 2015, 2016) or the choice of the mathematical model may affect the detection rate of the SIEs considerably (Lomolino 2000, Lomolino and Weiser 2001, Gentile and Argano 2005, Dengler 2010, Matthews et al. 2014, Chisholm et al. 2016). Overall, the SIE appears to be a common feature of small-island systems worldwide (Chisholm et al. 2016, Wang et al. 2016). However, the quantity of theories and analytical considerations behind the SIE indicate that no consensus exists about its underlying processes.

The breakpoint area (i.e. the upper area-limit) of the SIE differs greatly among taxa. Small or sessile organisms, such as invertebrates or plants, show smaller breakpoint areas than larger or more mobile taxa (Lomolino and Weiser 2001, Chisholm et al. 2016). Differences between taxa have been attributed to variation in species dispersal abilities, environmental requirements, diet, or habitat preferences (Sfenthourakis and Triantis 2009, Chisholm et al. 2016). However, even within taxonomic groups, dispersal ability and environmental requirements may vary considerably among species (Duckworth et al. 2000, Moles et al. 2005), questioning whether taxonomic groups are useful units to explain differences in the prevalence and breakpoint of the SIE. In fact, species functional traits may be better predictors of assembly processes on islands (Si et al. 2017), and such a functional island biogeography perspective may provide novel and mechanistic insights into processes shaping the SAR in general (Franzén et al. 2012, Whittaker et al. 2014, Si et al. 2017) and the SIE in particular.

For plants, functional types such as growth forms (herbs, shrubs, and trees) are simple but powerful proxies for differences in life-history strategies, dispersal abilities, ecological adaptations, and habitat requirements (Moles et al. 2005, Knapp et al. 2008, Wullschleger et al. 2014) with potential consequences for community assembly on islands. Perennial woody species (shrubs and trees), for example, might underlie stronger climatic filtering than annual herbs, due to different strategies to cope with unfavourable conditions (Šímová et al. 2018), such as often occurring on small islands (Whittaker 1995, Schrader et al. 2019b). Herbs often exhibit more diverse ecological adaptations (Pierce et al. 2017) and are on average better dispersers than shrubs or trees (Moles et al. 2005, Thomson et al. 2010), suggesting that herbs may reach and establish more frequently on small islands (Abbott and Black 1980, Panitsa et al. 2008). Moreover, herbaceous species can build up larger populations on small islands due to their small body size (Greuter and Höner 1988) and may face lower extinction risks compared to larger species. In addition, the distance decay of similarity is considerably shallower for herb assemblages on islands than for shrub or tree assemblages, likely due to the higher dispersal abilities of herbaceous plants (König et al. 2017). Also, species turnover is higher on small islands (Morrison 2011, Chiarucci et al. 2017), potentially resulting in communities with high proportion of species adapted to rapid colonisation processes, such as herbs (Grime 1977). Trees and shrubs often follow life-history strategies connected to longevity, demographic stability, resource acquisition, and dispersal (Westoby 1998, Poorter et al. 2008, Díaz et al. 2016). Trees can dominate on larger islands where other factors like competition and biotic interactions become prevalent factors shaping community assembly (Chiarucci et al. 2017, Si et al. 2017).

The contrasting strategies of herbs, shrubs, and trees in combination with the different environmental conditions on small and large islands may have confounding effects on the shape of the SAR (Panitsa et al. 2006) and possibly the breakpoint area of the SIE. SARs constructed for herbs show steeper slopes compared to SARs constructed for shrubs or trees, which show flatter slopes (Whitehead and Jones 1969, Woodroffe 1986). Island isolation might also affect the shape of the SAR differently for different growth forms (Negoita et al. 2016). Moreover, different extinction probabilities may affect the breakpoint area for different growth forms. Larger organisms need larger areas to form stable populations and their extinction risk increases with decreasing area. Hence, larger organisms may extend the breakpoint area of the SIE to the point where their extinction rates equal colonisation events (MacArthur and Wilson 1967). In their seminal paper on the SIE, Lomolino & Weiser (2001) showed that the shape of the SAR and the breakpoint area of the SIE differ between taxonomic groups. Using species richness data from an isolated atoll, Lomolino & Weiser (2001) detected different SIEs for herbs, shrubs, and trees, while total species richness did not show a SIE. Moreover, Lomolino & Weiser (2001) found the breakpoint area of the SIE to be larger for more isolated islands compared to less isolated ones. However, they provided no specific explanations why the breakpoint area differed between herbs, shrubs, and trees and, to the best of our knowledge, no study dissected species richness patterns into different growth forms to test for differential patterns in the shape of the SAR and the prevalence of the SIE for a globally representative dataset.

Here, we contrast SARs for different growth forms and test for the existence of SIEs based on a comprehensive dataset of 17 archipelagos worldwide featuring 700 small islands and 5101 plant species. We tested whether the shape of the SAR and the breakpoint area of the SIE differed between herbs, shrubs, and trees. We further test whether additional environmental and physical geographic variables like island isolation, elevation, climate, and environmental heterogeneity may explain the variation in species richness across small islands and whether their effect differs among growth forms.

## 6.3 Material and Methods

### Data acquisition

We extracted environmental island data and angiosperm species richness deconstructed into growth forms (herb, shrub and tree) from the GIFT database (Weigelt et al. 2019). The GIFT database collates species occurrences and functional traits from regional plant checklists and floras and features species composition data for more than 1500 islands worldwide (see Weigelt *et al.* (2019) for details on data processing and extended Table E 3 for resources). We extracted growth form data per species and information on island area (km$^2$), island perimeter (km), annual precipitation (mm year$^{-1}$), annual mean temperature (°C; CHELSA climate layers; Karger *et al.*, 2017), and two isolation metrics for all islands for all 953 islands with information on angiosperm species composition belonging to 72 archipelagos worldwide. The two isolation metrics were the distance to the nearest mainland ($ISO_{dist}$; km) and the proportion of area of surrounding landmass (following Weigelt & Kreft, 2013). The latter metric considers the spatial arrangement and neighbouring islands, and was calculated as the area proportion within a buffer of 100 km ($ISO_{100}$) and 1,000 km ($ISO_{1000}$) respectively around each focal island. To account for the complexity of island coastlines, we calculated a shape index as *shape index* $= P / [2 * (\pi * A)^{0.5}]$, where P is the perimeter and A is island area (Patton 1975). We obtained elevation data at a resolution of one arc-second from the Shuttle Radar Topography Mission (https://earthdata.nasa.gov) and extracted the mean and maximum elevation and calculated the terrain ruggedness index (Wilson et al. 2007) for each island to account for the islands topographic heterogeneity using the R package *raster* (Hijmans and van Etten 2014).

### Island selection

To increase the statistical power for detecting the SIE, we used the following criteria to subset the data: First, as fine scale elevation data was only available for landmasses between 60°N and 60°S, we excluded all islands located beyond those limits. Second, we only included islands for which we had growth form data for at least 75% of all species present. We used a threshold of 75% coverage as values of at least 70% (Penone et al. 2014) to 80% (Pakeman and Quested 2007, Májeková et al. 2016) are recommended for unbiased analyses and higher thresholds would have led to omitting many islands from the dataset. Third, we only included islands <100 km$^2$. This threshold is much larger than the SIE breakpoint area commonly reported for plants (mean 0.016 km$^2$, 95% CI: 0.001 km$^2$, 0.3 km$^2$; Chisholm *et al.*, 2016), but small enough to exclude islands with high probability of in-situ speciation (Kisel and Barraclough 2010) and where in-situ speciation likely influences the shape of the SAR (Lomolino 2000). Fourth, since we analysed the shape of the SAR at the level of single archipelagos, we only included archipelagos containing at least ten islands. In total, 700 islands from 17 archipelagos met our criteria and were included in all subsequent analyses. This subset of islands also included empty islands as they are important for the correct detection of the SIE (Dengler 2010, Wang et al. 2016).

## Species-area relationships and statistical analyses

To test for the presence of the SIE, we used the approach proposed by Dengler (2010), which is based on comparisons of alternative species-area models using the Akaike Information Criterion (AIC; Burnham & Anderson, 2002). We calculated two breakpoint models and one linear model for total species richness and for richness of herbs, shrubs, and trees respectively (hereafter referred to as growth forms) as response variable and log$_{10}$-transformed island area as explanatory variable for all archipelagos separately. The first breakpoint model has a zero slope before the breakpoint describing a SIE where species richness varies independently of island area (Lomolino 2000). The second breakpoint model allowed for two different slopes where species richness with area increase at a different rate for smaller islands (Dengler 2010, Matthews et al. 2014). Breakpoint models were calculated using the R package *segmented* (Muggeo 2008). The model with the lowest AIC was identified as the best fitting model and was used for all subsequent analyses. If a breakpoint model received more support than the linear model, we assumed the existence of an SIE. We used the position of the breakpoint (island area in km$^2$) to define the maximum island area up to which the SIE extends for the respective archipelago.

To test whether the breakpoint areas differ between growth forms, we applied paired t-tests on the breakpoint area values between all growth form combinations. To test whether the breakpoint area varies with isolation, we applied linear models of the breakpoint areas ($log_{10}$-transformed) as response and the isolation metrics ($ISO_{dist}$ (log-transformed), $ISO_{100}$, $ISO_{1000}$) as predictor variables.

We selected all islands that were within the range of the SIE for each archipelago to test, which factors determine species richness on small islands. We applied linear mixed effect models with Gaussian distribution using the package *lme4* (Bates et al. 2013). Mixed effect models constitute an effective tool to test for patterns in island biogeography when groups of data points vary idiosyncratically (Bunnefeld and Phillimore 2012), as in our dataset at the level of archipelagos, which we included as random effect in all models. We log-transformed species richness (value of one added) to attain normal distribution in the response variables. As fixed effects, we included seven explanatory variables in each model. To avoid issues arising from multi-collinearity of explanatory variables (Figure E 3), we only included variables that were not strongly correlated using a coefficient of correlation threshold of $|r| < 0.7$ (Dormann et al. 2013). Non-collinear variables included island area (log-transformed), the shape index, annual precipitation, and mean annual temperature. When variables were collinear, we only included the variable we expected to be most important for plant species richness on islands. Of the three isolation metrics, we selected the $ISO_{100}$, as for small islands smaller buffers are better predictors of colonisation events than larger ones (Diver 2008). From the variables describing island topography, we opted to use maximum elevation as it has been shown to influence plant species richness on islands (Ackerman et al. 2007, Keppel et al. 2016), and the mean terrain ruggedness index to quantify topographic heterogeneity (Riley et al. 1999). Next, we standardised all variables to a mean of zero and a variance of one and calculated standardised parameter estimates and their confidence intervals for all variables from the full model using the package *broom* (Robinson and Hayes 2018). All analyses were implemented in the statistical software *R* (v.3.5.2; R Core Team, 2019).

## 6.4 Results

Species richness on the islands ranged from zero species (observed on 28 islands) to 817 species (island of Aegina, Greece). In general, herb richness was higher than shrub or tree richness (Figure E 4, Figure 6.1 & Figure 6.2). 58% of all species were classified as herbs, 11.9% as shrubs, and 13.4% as trees. For 16.7% of the species, we could not obtain growth form data.

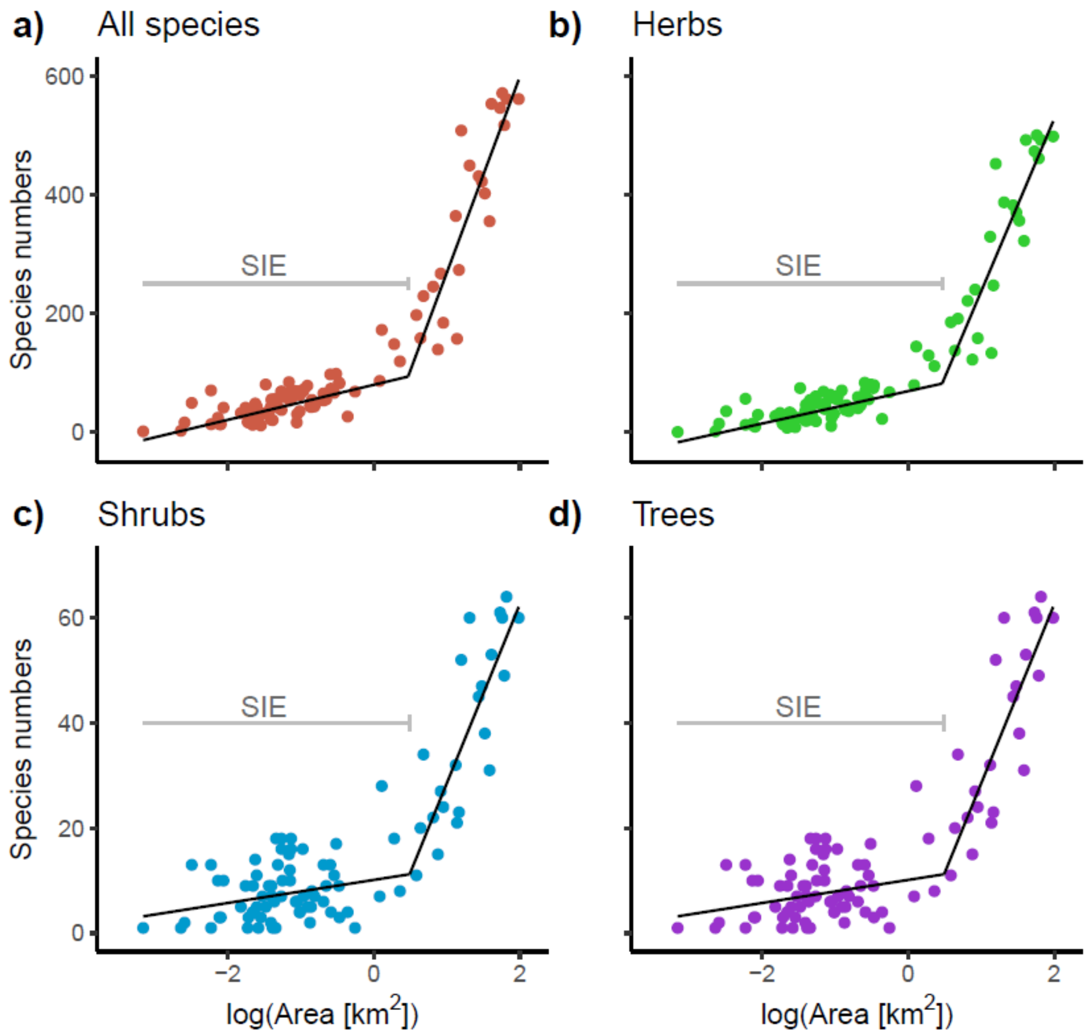

Figure 6.1 Best supported species-area relationships (SAR) for total species richness and species richness of herbs, shrubs, and trees from islands in the east Aegean Sea. In this exemplary case, the best fitting SAR model was a breakpoint model allowing for two distinct slopes indicating the presence of a small-island effect (SIE).

For total species richness, we found evidence for an SIE for 70.6% of the archipelagos. When dissecting total species richness per island into herbs, shrubs, and trees 70.6%, 58.8%, and 52.9% of all archipelagos respectively showed an SIE (Figure 6.2). Both SIE models were equally common for all species, herbs and shrubs. For trees, however, the SIE describing no relationship between species richness and island was more common (66%, Figure 6.2; Table E 1; the form of the SIE for one exemplary archipelago is shown in Figure 6.1).

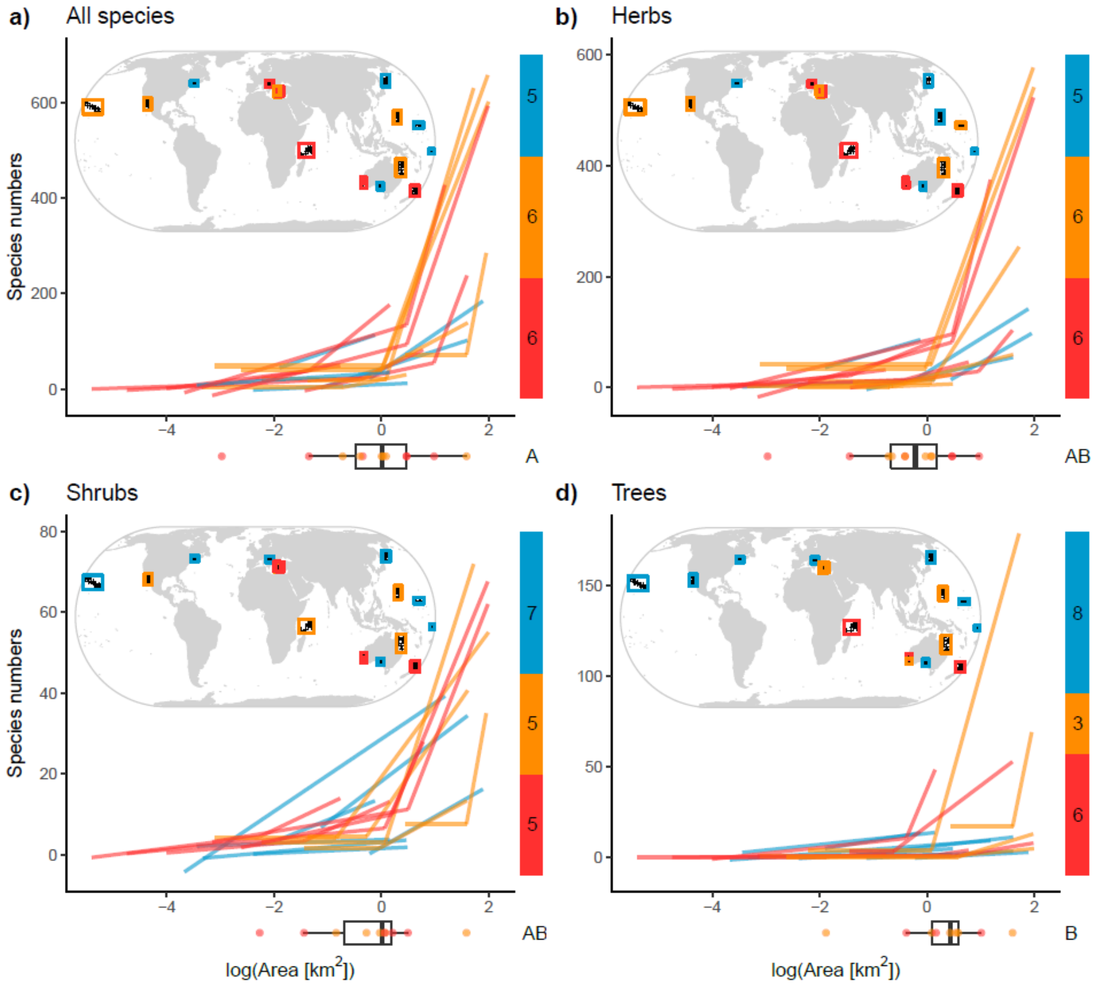

Figure 6.2 Species-area relationships (SARs) for a) total species richness and b) herb, c) shrub, and d) tree species richness for 17 archipelagos worldwide. Best fitting SARs for each archipelago are shown. SARs were fitted in semi-log space and model selection was based on lowest AIC. Candidate SARs consisted of one linear model (blue) and two breakpoint models that indicate the presence of the small-island effect (orange: zero slope before the breakpoint; red: breakpoint model allowing for two distinct slopes). Maps show the location of the archipelagos (rectangles). Colours of rectangles correspond to colours of best fitting SARs. Note that two archipelagos in western Australia and three archipelagos in the Aegean Sea partly overlap in the map. Model prevalence is indicated by numbers and coloured bars. Boxplots indicate the location of the breakpoint of the two breakpoint models and capital letters indicate significant differences between groups calculated using paired t-tests at the level of archipelagos (see also Table E 2).

For those archipelagos exhibiting an SIE, the breakpoint area was larger for shrub and tree than for total and herb species richness. Total (mean breakpoint area 3.7 km$^2$, SE ±3.2 km$^2$) and herb species richness (mean breakpoint area 0.7 km$^2$, SE ±0.2 km$^2$) showed the lowest breakpoint area. Shrub (mean breakpoint area 4.5 km$^2$, SE ±3.8 km$^2$) and tree species richness (mean breakpoint area 5.7 km$^2$, SE ±4.2 km$^2$) had greater breakpoint areas Figure 6.2), with the breakpoint area of tree species richness being significantly larger than that of total species richness ($p<0.05$).

We found contrasting effects of the isolation mectrics on the breakpoint areas for the growth forms. In general, more isolated archipelagos had higher breakpoint areas in their SARs. Although, only $ISO_{100}$ indicated significant patterns on the breakpoint area, which increased significantly with island isolation for total ($p<0.05$; adj $R^2 = 0.33$) and for shrub species richness ($p<0.05$; adj $R^2 = 0.36$). The location of the breakpoint area slightly increased with isolation for tree species richness ($p=0.28$; adj $R^2 = 0.05$), but not for herb species richness ($p=0.53$; adj $R^2 = -0.05$) (Figure 6.3). $ISO_{dist}$ and $ISO_{1000}$ did not explain variation in the breakpoint areas between archipleagos (Figure E 1 & Figure E 2).

Total species richness and species richness of the different growth forms on islands within the area range of the SIE were differently affected by environmental factors. Total species richness was positively influenced by terrain ruggedness (estimate = 0.21; SE ±0.09). Herb richness increased with island area (est. = 1.62; SE ±0.55) and terrain ruggedness (est. = 0.41; SE ±0.17) but decreased with mean annual temperature (est. = -0.82; SE ±0.40). Shrub richness increased with isolation (est. = 0.32; SE ±0.11). Tree richness responded strongly to annual precipitation (est. = 0.41; SE ±0.10) and peaked on wet islands. The islands shape complexity and maximum elevation had little or no effect on species richness on small islands (Figure 6.4).

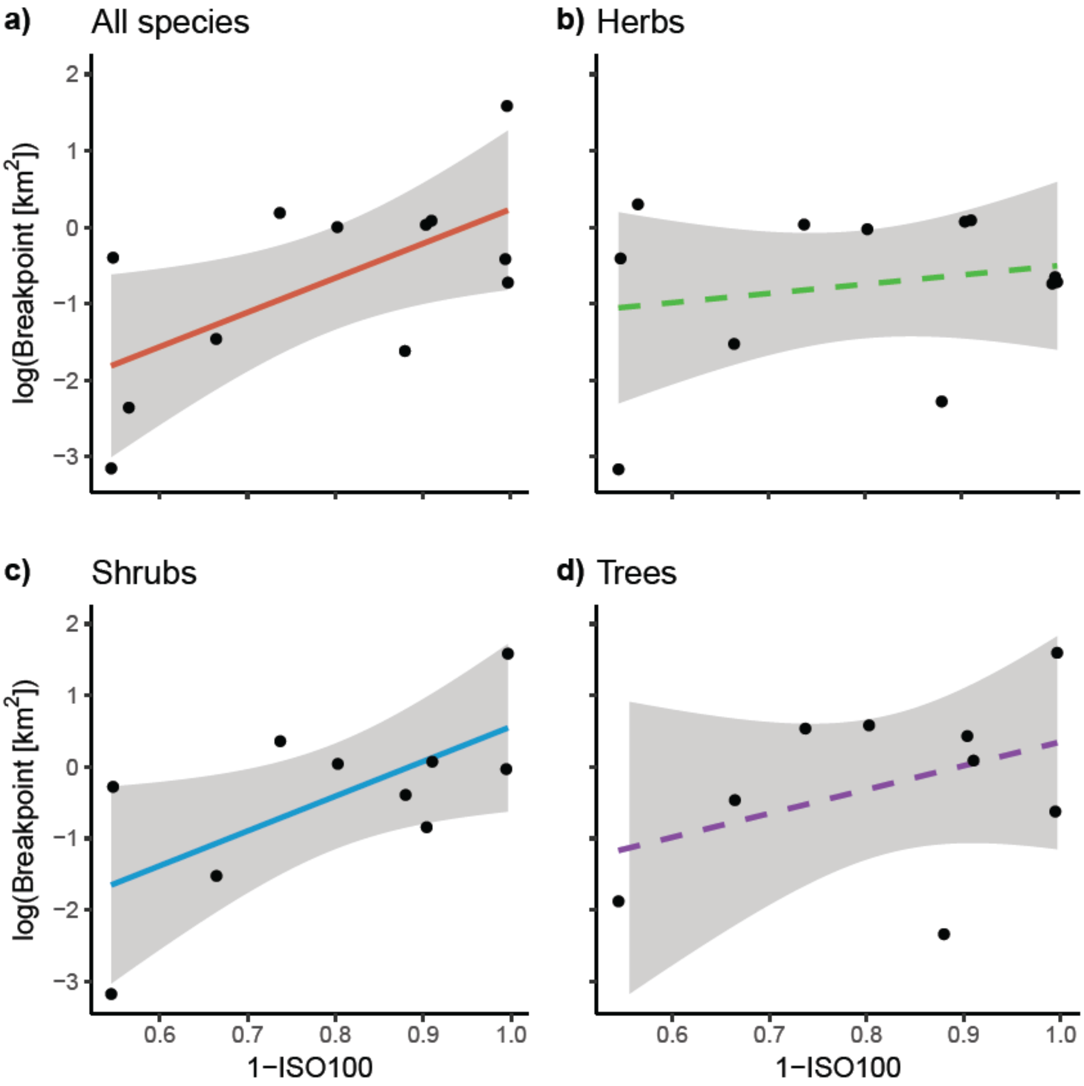

Figure 6.3 Relationship between archipelago isolation and breakpoint area of the small-island effect (SIE) for a) total species richness, and species richness of b) herbs, c) shrubs, d) and trees. Only archipelagos that featured a SIE were considered. The breakpoint area was determined by fitting breakpoint models. 1-ISO100: Isolation, represented by one minus the mean landmass area within a buffer of 100 km per island and refers to the proportion of ocean around all islands within an archipelago. Larger values indicate more isolated archipelagos.

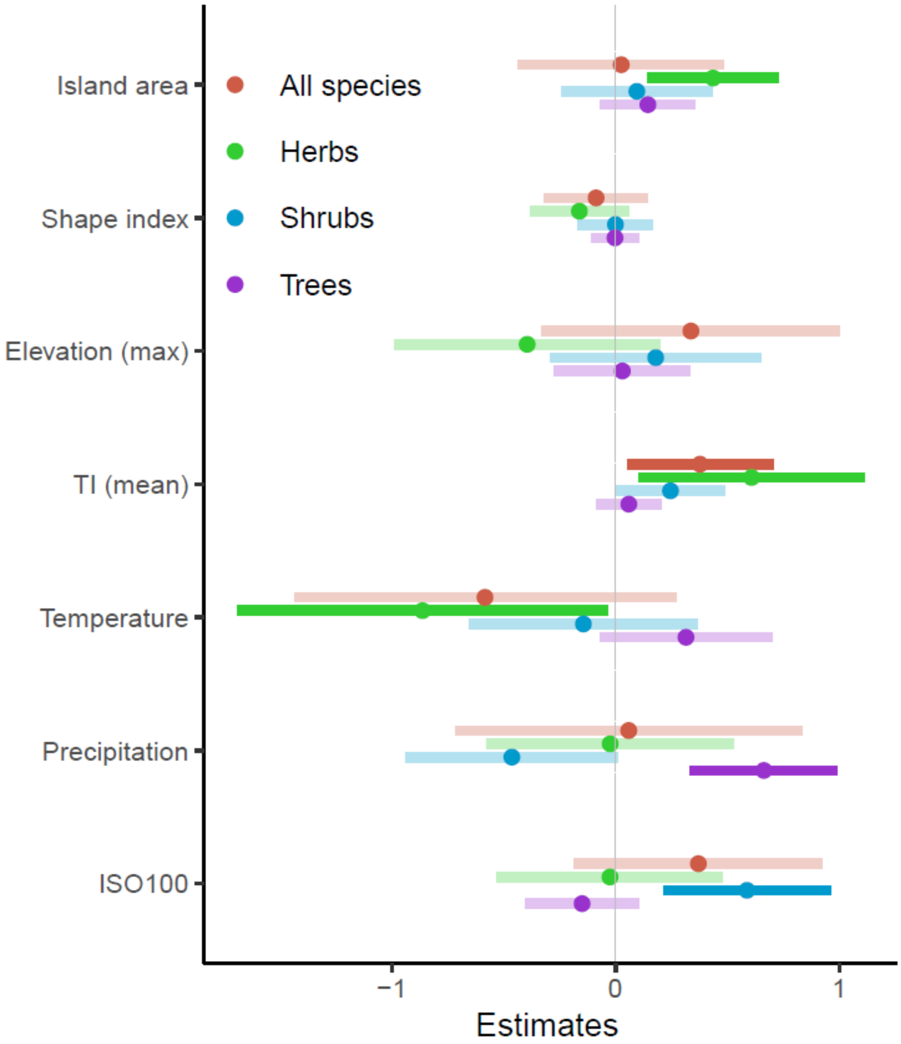

Figure 6.4 Standardised parameter estimates (dots) and confidence intervals (whiskers) for seven predictor variables of total species richness, and richness of herbs, shrubs, and trees on islands within the area range of the small-island effect. Positive estimates indicate that the respective variable led to an increase in species richness, negative estimates to a decrease. Linear mixed effect models with all seven variables as predictors were used to calculate the estimates. Archipelago type (not shown) was included as random factor. Island area was log-transformed. Shape index represents the islands edge-to-area ratio. TI: terrain ruggedness index. Temperature indicates the islands annual mean values and precipitation the islands annual value. ISO100: Isolation, represented by one minus the buffer area ratio within 100 km around each island.

## 6.5 Discussion

The majority of archipelagos in our study featured the SIE and the breakpoint area was affected by growth form and island isolation. We found evidence that the shape of the SAR and the prevalence of the SIE and its breakpoint area differed between total species richness and richness of herbs, shrubs, and trees. Species richness on islands within the range of the SIE was differentially affected by environmental factors, possibly driven by similar environmental requirements of species having the same growth form. Overall, our results indicate that biogeographical patterns differ between functional groups. We attribute these patterns to different dispersal strategies and environmental requirements that become evident at the level of growth forms but are disguised for total measures of species richness.

## Growth form influences the shape of the SAR

Most archipelagos featured the SIE for total species richness and for the three growth forms. However, the SIE was less common for shrub and tree species richness than for total and herb species richness. Differences in the SIE prevalence between growth forms were small and only occurred in a few archipelagos with low overall species richness, especially regarding shrub and tree species richness. Possibly, the low overall species richness of shrubs and trees in some archipelagos caused shallow SARs, which prevented a biphasic SAR critical to detect the SIE. Furthermore, the islands of some archipelagos could still be within the area range of the SIE for shrub and tree richness, causing a linear model to best predict species richness, even though a SIE may actually be present.

The prevalence of the SIE detected in our study (Figure 6.2) was comparable to previous studies (Lomolino and Weiser 2001, Wang et al. 2016) reported the SIE in 73-89% and 49% respectively for all studied archipelagos. Our results therefore support the notion that the SIE is a widespread feature of archipelagos worldwide. Previous studies indicated sensitivity of the SAR towards taxonomic groups (Patiño et al. 2014, Lenzner et al. 2017) and for functional traits (Franzén et al. 2012, 2019). Here, we provide evidence that the shape of the SAR is also sensitive to plant functional types. Meaningful species groupings can therefore lead to new insights to biogeographical patterns of island communities.

## Range of the SIE is sensitive to growth forms and degree of isolation

The location of the breakpoint area of the SIE differed considerably according to plant growth form and was increased by the degree of isolation, especially for total and shrub species richness (Figure 6.1). This finding is in line with the Equilibrium Theory of Island Biogeography, which considers island species richness as a dynamic equilibrium of colonisation and extinction events, i.e. smaller and more isolated islands support less species than larger or less isolated ones (MacArthur and Wilson 1963). MacArthur & Wilson (1967) hypothesised that the SIE occurs when extinction events outnumber colonisation events, reducing the strength of the SAR towards low richness values. Thus, species groups with high dispersal abilities and low extinction probabilities should show smaller breakpoint areas, as only on very small islands extinction rates may be greater than colonisation events. In contrast, weak dispersers and species groups with high extinction probabilities should indicate a larger breakpoint. Possibly, herbs are, on average, better dispersers than shrubs or trees, and may form higher population densities within limited areas due to their smaller size, thus decreasing extinction probability on small islands (Pimm et al. 1988). Consequently, herbs may reach small islands more easily and may form less extinction-prone populations on small islands (see also Negoita *et al.*, 2016), which decreases the breakpoint area of the SIE. Shrubs and trees may have lower immigration rates and require larger islands to establish persisting populations and consequently exhibit larger breakpoint areas. These patterns are further enhanced by the degree of isolation (Negoita et al. 2016), with more isolated archipelagos having fewer immigration events causing larger breakpoints (Lomolino and Weiser 2001, Ackerman et al. 2007). However, whether island immigration rates and inter-island dispersal abilities differ between growth forms remains speculative and should be more rigorously investigated in the future.

Interestingly, the SIE breakpoint area was only significantly affected by the isolation metric that considers small-scale variation in the proportion of neighbouring landmasses, i.e. within 100 km buffer distances ($ISO_{100}$), whereas larger buffer distances ($ISO_{1000}$) and distance to nearest mainland ($ISO_{dist}$) had no effect on the breakpoint area (Figure 6.3; Figure E 1 & Figure E 2). Small islands generally support less stable populations with high temporal species turnover (Heatwole and Levins 1973, Chiarucci et al. 2017). Turnover could be considerably affected by the degree of isolation. Constant immigration from neighbouring islands or mainlands can counteract high extinction rates by promoting complex metapopulation systems (Hanski and Gilpin 1991, Leibold et al. 2004, Burns and Neufeld 2009) and source and sink dynamics (*rescue effect*; Brown & Kodric-Brown, 1977; Pulliam, 1988). Small-island metapopulations may only extend over certain distances and are therefore best captured by isolation metrics that consider the spatial arrangement of nearby landmasses (Diver 2008). This could explain why we did not find the larger buffer distance ($ISO_{1000}$) and the distance to the nearest mainland ($ISO_{dist}$) to capture these dynamics resulting in insignificant patterns. Some of our analysed archipelagos were in close vicinity to large islands like New Zealand, likely acting as sufficient source pool for small-island communities. That de-emphasises the importance of the next mainland as source pools for small islands, which in our example for New Zealand would be Australia. Our results therefore highlight the scale-dependent influence of isolation and that considering small-scale spatial arrangements of neighbouring landmasses is important in explaining species richness on small islands (see also Weigelt & Kreft, 2013).

## Contrasting effects of environmental factors on species richness

The SIE posits that species richness on small islands is less dependent on area than on large islands (Lomolino and Weiser 2001, Dengler 2010). However, which factors affect species richness on small islands is still debated (Triantis et al. 2006, Dengler 2010, Triantis and Sfenthourakis 2012, Schrader et al. 2019a). Therefore, we tested for effects of different environmental, climatic, and geographical variables on growth form species richness and found heterogeneous results (Figure 6.4). Topographic heterogeneity, a surrogate of habitat diversity, was the only important factor influencing total species richness (see also Kohn & Walsh, 1994; Triantis *et al.*, 2003). Species richness of herbs, shrubs, and trees, however, was affected by climatic variables (for herb and tree richness) and isolation (for shrub richness). Indeed, the strong influence of climatic variables on our results mirrors global trends in growth form composition (Hawkins et al. 2011, Keil and Chase 2019, König et al. 2019). The positive relationship of shrub richness with isolation is possibly due to the fact that many of the most isolated islands in our dataset were atolls, which are characterised by shrubby vegetation. Some shrubs are specialised to stressful environmental conditions on atolls (Stoddart 1992) possibly making shrubs more competitive on isolated islands compared to herbs or trees.

The contrasting results of environmental factors highlight that herbs, shrubs, and trees have different environmental requirements (Echeverría-Londoño et al. 2018, Šímová et al. 2018). These requirements influence group specific species richness patterns and are not captured by drivers of overall species richness. Possibly, habitat diversity may be a good surrogate of differences in general but may not be the ultimate driver of species richness on small islands.

## Conclusion

We show that dissecting overall plant species richness on small islands into growth forms reveals differences in its relationship with island area and other environmental predictors and hence increases our understanding of a central pattern in island biogeography. The shape of the SAR and the prevalence and breakpoint area of the SIE differed between growth forms and the breakpoint area was further affected by the spatial arrangement of landmasses surrounding the small islands in our data set and by their degree of isolation. Environmental factors differently acted on growth form species richness, indicating ecological processes that were not discernible when using total measures of species richness. Our results therefore highlight the potential of functional island biogeography for answering long standing island biogeographic questions.

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# 7. Synopsis

Islands constitute natural laboratories to test a wide array of ecological and evolutionary hypotheses in spatially discrete arenas (Losos and Ricklefs 2009). Especially small islands are ideal model systems, as species diversity patterns can be attributed to a limited number of assembly processes that are relatively easy to observe (Morrison 1997, Burns 2005, Cody 2006). Indeed, how island communities assemble constitutes one of the most important questions in the field of ecological island research (Patiño et al. 2017), which however, is still poorly understood.

Community assembly processes on islands often strongly correlate with island area, making island area the strongest predictor of species richness (Kreft et al. 2008, Triantis et al. 2012). Consequently, island area is the central part of island biogeography theory, principally the equilibrium theory (ETIB; MacArthur and Wilson 1963, 1967). According to the ETIB, island area directly influences the number of species that exist on an island via neutral community assembly processes (MacArthur and Wilson 1963, Hubbell 2001). Larger islands support bigger populations than smaller islands, thus reducing the extinction probability due to stochastic events (Pimm et al. 1988). Additionally, larger islands tend to have higher immigration rates than smaller islands (MacArthur and Wilson 1967, Lomolino 1990). However, the prevalence of neutral community assembly processes in island biogeography has been increasingly questioned (Emerson and Gillespie 2008, Jacquet et al. 2017, Si et al. 2017), drawing the attention towards factors besides island area that influence species richness. Examples for such alternative factors are habitat and niche diversity (Kohn and Walsh 1994, Hortal et al. 2009, Chisholm et al. 2016), topographic complexity (Ackerman et al. 2007, Keppel et al. 2016), competition (Astor et al. 2014, Si et al. 2017), and dispersal and environmental filtering (Gillespie et al. 2012, Si et al. 2017, Arjona et al. 2018). Especially for small islands, island area is a poor predictor of species richness (i.e. as described by the small-island effect), inspiring scientists to search for new hypotheses (Whittaker 1995, Anderson and Wait 2001, Triantis et al. 2006, Chisholm et al. 2016). However, to date, no consensus has been reached about the underlying causes and mechanisms behind species richness patterns and community assembly processes on small islands.

The central aim of my thesis was to single out the underlying factors of species diversity patterns and assembly processes on small islands. In the 14chapter, I presented a new method to measure leaf area, which was crucial for analysing the plant traits in chapter 5. In chapters 3-5, I analysed a dataset of tree occurrences on 60 small islands in the Raja Ampat Archipelago to gain detailed ecological knowledge of local patterns and processes of species diversity. In chapter 6, I investigated the prevalence of the small-island effect (hereafter SIE) at the global scale for species richness dissected into plant functional types. The main results and conclusions of my thesis were:

**Chapter 2**: I introduced a new method to calculate leaf area using smartphones as a platform (Schrader et al. 2017). I designed an application called *Leaf-IT*, which is free, works reliably under remote field conditions, and can be used and expanded by all interested users. Developing new methods is particularly important to generate accurate and precise results in the rapidly expanding research field of functional ecology.

**Chapter 3**: Here, I investigated whether the shape of the SIE differs with sampling scale. Further, I tested which environmental factors influence species richness at different spatial scales (Schrader et al. 2019b). I found clear evidence that the SAR is scale-dependent and differs in shape depending on the sampling scale used (e.g. size of the plots/transects). When sampling scale increased proportionally with island area, the SAR displayed a sigmoidal form and indicated the presence of the SIE. However, when the sampling scale remained constant irrespective of island area, species richness followed a different relationship with area, and the SIE was not detectable. Moreover, sampling small grain sizes inherently caused high species variability exhibiting a SIE-like pattern. Hence, the SIE is not restricted to small islands but could rather be an artefact of small sample sizes. Environmental factors that determined species richness greatly differed between scales. Island area was the principal variable, but with decreasing sampling scale habitat quality, expressed by soil availability and soil depth, it became increasingly deterministic of species richness.

**Chapter 4**: In this part of my thesis, I investigated the relationship between environmental requirements of species and island area. Species requirements caused species pools to be unique for each island (Schrader et al. 2019a). The SIE, detected for observed richness, was not mirrored by the species pool sizes. Species communities on small islands were less complete than communities on larger ones. I related differences in community completeness between islands to local limiting processes, which act more strongly on small islands, thus preventing many species from the pool to establish. Local limiting processes could be the main drivers of low species richness on small islands and could consequently cause the SIE.

**Chapter 5:** Here, I identified the local limiting processes that caused island-specific species pools and incomplete communities, which were highlighted in chapter 4 to be of special importance for the SIE. Small-island communities were shaped by a combination of non-random dispersal and environmental filters that operate simultaneously, but with different intensity, on island communities. Communities on larger islands were formed by greater niche differentiation. This trait-based framework can be used to test for filtering processes on other island or island-like systems.

**Chapter 6**: Here, I collated a global dataset of small islands to test whether the shape of the SAR and the prevalence of the SIE differed between species richness of herbs, shrubs, and trees. Species richness of herbs had a smaller breakpoint of the SIE (i.e. the island area to which the SIE occurs) and the breakpoint was not affected by the degree of isolation. Shrub and tree species richness displayed larger breakpoints and, particularly for shrub species richness, the SIE increased with the degree of isolation. These patterns were possibly caused by different dispersal strategies and population level dynamics between herbs, shrubs, and trees. On islands within the range of the SIE, environmental factors acted differently on growth form species richness, indicating ecological processes that were not discernible when using total measures of species richness.

In the following sections, I discuss the main results of my thesis, elaborate synergies between chapters, and point towards challenges and new directions for island research.

## 7.1 Community assembly on small islands: The Raja Ampat Archipelago as a model system

The results of my thesis show that multiple factors act simultaneously on island communities (Figure 7.1). The multilevel assembly processes become especially clear when examining the species diversity patterns found in the island system in the Raja Ampat Archipelago.

The islands in the Raja Ampat Archipelago share a common origin (ontogeny), are effectively non-isolated, and feature very similar ecological conditions. Differences between islands can be attributed to island area and the number of high-quality habitats expressed by soil availability and soil depth (chapters 3 & 4). Deeper soils may provide more nutrients and water availability for plants and partly offset the prevailing harsh environmental conditions. Species richness on these islands was best described by a sigmoidal SAR (Figure 7.1 c), indicating the presence of the SIE (Lomolino 2000). The SIE prevailed on islands with an area <130 m$^2$, where species richness varied independently of island area (chapters 3 & 4).

Sampling at different grain sizes on the islands revealed that island area was the strongest predictor of species richness. However, with decreasing sampling size, habitat quality became increasingly important. Higher habitat quality allowed more species to co-exist in small grain sizes irrespective of the islands' spatial extent. Soil was widely absent on islands within the range of the SIE, possibly causing the low observed species richness on the respective islands (chapter 3).

Species occurring on these islands had specific requirements related to island area (chapter 4). Species requirements were likely caused by environmental processes, which differed in strength between islands (e.g. availability of soil or soil depth). Most species preferred islands larger than expected under neutral assembly processes, and no species seemed specifically adapted to small island life (Figure 7.1 d). Smaller islands were more strongly affected by disturbances such as sea spray, solar radiation, or storms (Figure 7.1 a; see also Niering 1963, Whittaker 1995, Morrison 2014). Moreover, the lack of certain habitat types on small islands may explain the strong local limiting processes for species assembly. These processes possibly prevented successful colonisation of many species, limiting their occurrences to larger islands. On larger islands, edges exhibited environmental conditions similar to smaller islands, characterised by an absence of soil and leaf litter, high solar radiation, and missing shade effects from other trees. The shared habitat types of smaller and larger islands may explain why small island specialists did not occur in the Raja Ampat Archipelago.

The strong area requirements of most species led to unique species pools for each island (Figure 7.1 c). The SAR constructed from island species pool sizes indicated no SIE in contrast to the observed species richness. The SIE was likely linked to the same local limiting processes that also caused species area requirements. These processes acted more strongly on smaller islands, caused lower community completeness (Figure 7.1 e), and prevented fewer species from the pool to be present on small islands compared to larger ones (chapter 4).

Functional diversity of the island communities showed that the local limiting processes can be attributed to dispersal and environmental filtering (Figure 7.1 b). Small island communities were functionally underdispersed, meaning that only species with specific life-history dimensions occurred here. With increasing island area, filtering strength decreased, indicated by functionally even or overdispersed communities. This evidence shows that the SIE is caused by strong dispersal and environmental filters, preventing many species of the species pool from successful establishment. The SIE disappeared with decreasing filtering strength.

In summary, the species distributions in the Raja Ampat Archipelago are shaped by a combination of environmental (e.g. niche diversity), population level (e.g. biotic interactions), and species level (e.g. area requirements) dynamics. These results provide clear evidence for a non-random assembly of island communities.

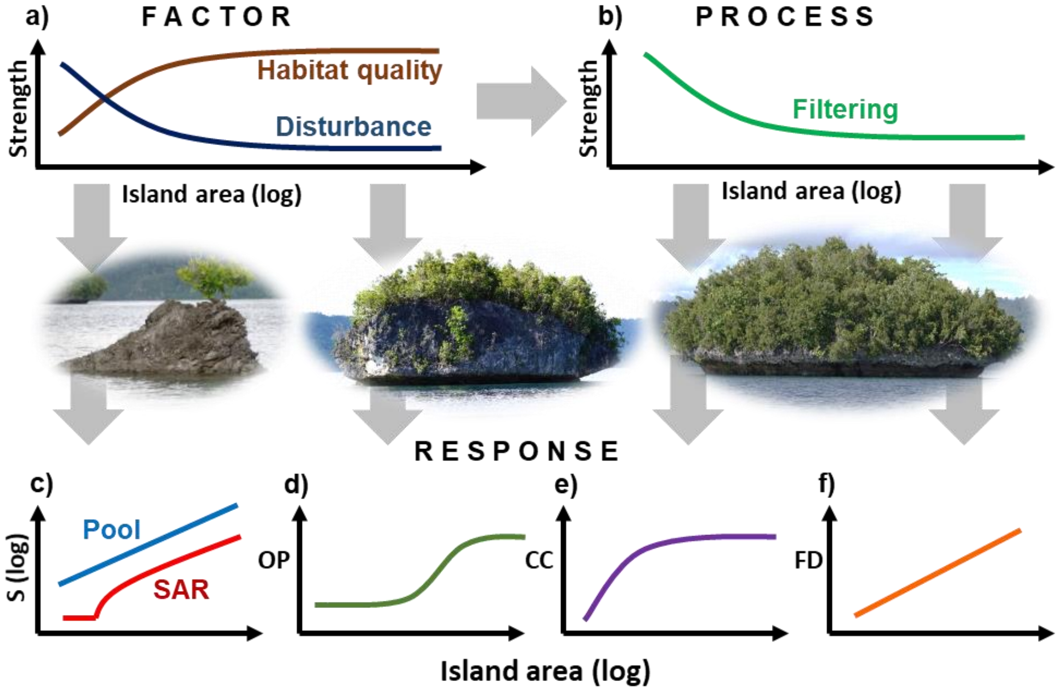

Figure 7.1 Schematic figure showing the factors and processes acting on island communities and their effect on species occurrences and community assembly in the Raja Ampat Archipelago. a) Habitat quality increased with island area while disturbance decreased. b) The scaling of these factors had profound effects on the filtering strength along island area, which was strongest for small islands and gradually decreased with increasing island area. c) The small-island effect present for observed species richness (species-area relationship: SAR) was not reflected in the species pool-area relationship (Pool). Species pool size directly depended on d) species occurrence probabilities (OP), which increased with island area for most species. e) Greater differences between species pool size and species observed species richness on smaller islands caused small-island communities to be less complete (community completeness: CC) than those on larger islands. f) Functional diversity (FD) increased with island area, driven by increasing habitat and niche diversity. c) Scaling for log-transformed species richness [S (log)] shown.

The field study in the Raja Ampat Archipelago revealed that species ecological strategies play a key role in community assembly. These novel insights into assembly processes were based on my detailed understanding of the local flora, including species taxonomic identities, functional traits, and island properties. However, whether the same drivers singled out in the Raja Ampat Archipelago also shape island communities globally remains to be tested.

## 7.2 Small island communities at the global scale

In chapter 6, I went beyond the study of a single archipelago and zoomed out to the global scale. I therefore compiled a novel dataset of 5101 plant species occurring on 700 small islands worldwide in the framework of the GIFT database (Weigelt et al. 2019) to analyse the effects of plant growth forms on the SAR and the prevalence of the SIE. Growth forms capture major variation in plant form and function (Westoby 1998, Reich 2014, Díaz et al. 2016), and are good indicators for ecological strategies and requirements of species at macroecological scales (Šímová et al. 2018, Keil and Chase 2019, König et al. 2019).

The main results indicated the shape of the SAR and the breakpoint of the SIE to depend on the growth form under consideration. The observed patterns implied different strength of dispersal and environmental filtering to affected herb, shrub, and tree species richness. Moreover, the impact of isolation on species richness only became evident when considering the spatial arrangement of islands within a relatively small buffer area (in chapter 6: 100 km). Small buffer areas may indicate the forming of metacommunities composed of many small islands (Hanski and Gilpin 1991, Leibold et al. 2004). Less isolated islands may have more frequent immigration events that offset extinction rates, which results in smaller breakpoints. More isolated islands, in turn, have fewer immigration events but higher extinction rates, thereby exhibiting larger breakpoints (MacArthur and Wilson 1967). Larger buffer distances or spatial distance to the nearest mainland did not capture these metacommunity dynamics. The results from chapter 6 highlight the importance of small scale isolation metrics in explaining species richness patterns on small islands (Diver 2008, Weigelt and Kreft 2013).

Only datasets containing multiple archipelagos over large spatial scales are capable of revealing the multilevel assembly processes of island communities these patterns. Species assembly rules derived from field studies can be validated at larger spatial scales. Vice versa, testing global scale patterns in more thorough field studies can help to understand the exact mechanisms behind certain phenomena that often remain concealed at macroecological scales (Beck et al. 2012).

## 7.3 Revisiting the small-island effect

Despite the long-standing debate about the causes behind the SIE, no consensus has been found on its underlying mechanisms (Burns et al. 2009, Dengler 2010, Triantis and Sfenthourakis 2012). Manifold theories were proposed to explain the SIE (see *Introduction* and Triantis et al. 2006 for review), and some authors have even suggested to abandon the SIE theory altogether (Tjørve and Tjørve 2011). The controversy about the SIE calls for a rigorous revision of facts and artefacts, and a unifying framework is needed in order to determine the origin of the SIE.

I showed that the SIE occurs in the Raja Ampat Archipelago (chapters 3 & 4) as well as in 53 - 71 percent of global archipelagos (see also Chisholm et al. 2016, Wang et al. 2016, 2018), depending on the plant growth form considered (chapter 6). The field studies in the Raja Ampat Archipelago showed that the SIE is likely caused by dispersal and environmental filtering. Indeed, these filtering processes have been suspected to be the underlying causes of the SIE (e.g. Kohn and Walsh 1994, Whittaker 1995, Triantis et al. 2003), but mechanistic-based evidence for filtering is largely lacking. The species pool method (chapter 4) and the trait-based framework (chapter 5) can be used to identify further mechanisms behind the SIE.

However, the SIE may not exclusively be caused by filtering processes. In chapter 3, I presented a SIE-like pattern by sampling species richness in small grain sizes on the largest islands. High variation in species richness may inherently occur in small grain sizes, indicating that stochastic processes also contribute to the SIE (MacArthur and Wilson 1967, Azovsky 2010).

In addition to the ecological theories behind the SIE, some authors have pointed out methodological flaws to incorrect detections of the SIE (Burns et al. 2009, Dengler 2010, Tjørve and Tjørve 2011). Most studies used breakpoint models to test for the presence of the SIE (e.g. Niering 1963, Morrison 2014, Wang et al. 2016). Breakpoint models suggest a sharp transition between islands featuring the SIE and islands beyond its limits.

However, smooth transitions often provide more realistic representations of natural phenomena than sharp transitions (Toms and Lesperance 2013), such as the SIE (see also Chisholm et al. 2016). Lomolino (2000) suggested that the usage of sigmoidal models is more suitable, as these models test for the presence of the SIE while allowing a smooth transition between the SIE and the linear phase of SAR. Indeed, sigmoidal models were better supported as breakpoint models for the dataset in the Raja Ampat Archipelago (chapter 2). I recommend using sigmodal models to test for the presence of the SIE and only draw on breakpoint models when estimates for the breakpoint are needed (analogous to the analysis I described in chapter 6).

I conclude that the SIE is a real biogeographical phenomenon, driven by dispersal and environmental filtering, species area requirements, and stochastic processes. These various factors differ in strength with island area and possibly caused the manifold explanations for the SIE. Rigorous ecological understanding and application of mechanistic-based frameworks are needed to identify the drivers behind the SIE. To gain deeper knowledge of the SIE and its causes, functional traits and community composition should be coherently tested. Moreover, investigations focusing on the SIE may also be extended to other island-like habitats and isolated areas. After all, the SIE debate has made valuable contribution to understanding community assembly on small islands and isolated habitats.

## 7.4 Challenges and future perspectives in island research

Islands form important geographical entities in ecological research, and their significance for our understanding of the natural world remains unabated. Throughout the course of my thesis, I identified two research fields related to island conservation and island community assembly, of which we still know surprisingly little. Developing new strategies in island conservation and detailed ecological understanding of the assembly of island biota should therefore be of paramount importance in future island research.

Global biodiversity is declining at unprecedented rates (Barnosky et al. 2011, Ceballos et al. 2015). Island species are especially vulnerable to suffer extinction as they are often less competitive than invasive species (Caujapé-Castells et al. 2010, Moser et al. 2018, Dyer et al. 2019), often adapted to unique habitats only present on particular islands (Keppel et al. 2014, Heinen et al. 2018), and exhibit small population sizes (Hanski 1986, Cody and

Overton 1996). Detailed knowledge of ecological adaptations of island communities is essential to develop conservation strategies in order to address species loss (Caujapé-Castells et al. 2010). Especially small island communities are often overlooked in conservation measures, even though they can feature rare and unique biodiversity (Greuter and Höner 1988, Morley and Winder 2013). Pressing questions related to island conservation that I identified throughout the course of my thesis include:

- How resilient are small island communities against external disturbances and invasive species?
- Why are some species rare on islands, what are the functions of rare species in island communities, and do rare species perform unique ecosystem functions on islands?
- How common are small-island specialists globally, how threatened are they, and how can they be conserved?

To understand ecological processes on islands and fragmented habitats, (small-) island model systems are needed. Such small-island models have proven to be valuable (e.g. Morrison 1997, Cody 2006, Wang et al. 2009) and findings from small island models have successfully been transferred to the mainland, as well as to fragmented and isolated habitats (e.g. Ding et al. 2013, Si et al. 2017, MacDonald et al. 2018). However, island studies could also implement methods and concepts developed on mainland communities. In my thesis, I used three methods mostly developed and tested on mainland systems, which I adapted and fitted to serve my research in small island systems (e.g. effects of sampling scales on species richness, estimation of probabilistic species pools, and the trait-based framework to test for filtering). I see great potential to further interlink knowledge gained from island and mainland systems and to test for consistent ecological patterns among these geographical realms.

Thus far, island research has mainly been focused on species richness patterns, while species ecological adaptations and requirements have been widely neglected. Functional traits have proved to be useful surrogates to describe species ecology and ecosystem functioning (Díaz and Cabido 2001, Violle et al. 2007). Indeed, there is growing consensus on integrating functional traits into island biogeography (e.g. Ding et al. 2013, Whittaker et al. 2014, Karadimou et al. 2016), but coherent frameworks and theories are still largely lacking. Future challenges in functional island biogeography entail to achieve satisfactory data coverage of important functional traits and integration of trait-based approaches to island biogeography theory. The lack of data coverage can be addressed by developing new tools for trait measurements that are able to perform under challenging field conditions (e.g. Schrader et al. 2017) or by integrating trait and island databases (e.g. Kattge et al. 2011, König et al. 2019, Weigelt et al. 2019). In chapter 5, I presented how a trait-based approach can be incorporated into island biogeography theory and in chapter 6, I provided an example of how plant species richness of functional types identified new biogeographical patterns. Therefore, I see great opportunities for functional approaches to island biogeography that will likely foster our understanding of community assembly on islands. Important questions that arise from these functional approaches to island biogeography include:

- How does functional diversity assemble at different spatial scales?
- Does the functional diversity of island communities differ from those on the mainland?
- Which species functional traits are predominately filtered out from island communities?

## 7.5 Conclusion

In my thesis, I provided new insights into the assembly of small island communities and disclosed underlying mechanisms behind the long-standing debate about the SIE. Island systems, such as the Raja Ampat Archipelago, provide ideal ecological laboratories to test theories, to formulate new concepts, and to develop new frameworks. Global databases that cover species occurrences and functional traits can help to validate ecological theories at larger scales. In particular, the rapidly developing field of functional ecology can foster new frameworks and theories to understand community assembly of island biota.

Despite the long tradition of islands to serve as model systems in ecology, biogeography, and evolution, we are still scratching the surface with our understanding of community assembly processes on islands and island-like habitats. Detailed ecological knowledge of community assembly processes will be of paramount importance to understand how biodiversity responds to an increasingly fragmented natural world.

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# 9. Appendix

# Appendix A – Supporting information to chapter 2

## Leaf-IT: An Android application for measuring leaf area

Julian Schrader, Giso Pillar, & Holger Kreft

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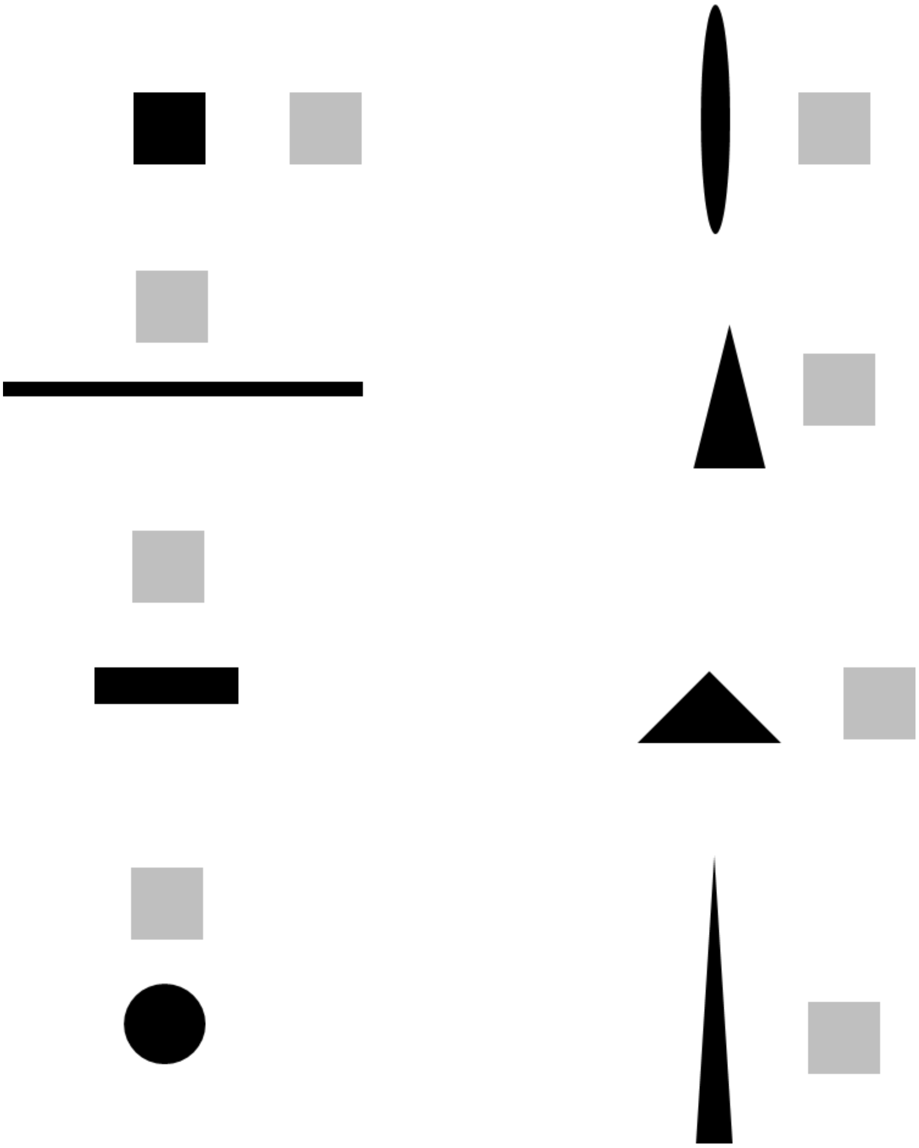

Figure A 1 Eight different shapes (black) and reference object (grey) used for testing accuracy and precision of Leaf-IT. Different shapes were created with the software Microsoft PowerPoint Version 10 and printed out using a high-resolution printer (Xerox Colour 550, 2.400 dpi x 2.400 dpi) on 160 g/m$^2$ paper. Area of shapes and reference objects shown here is 1 cm$^2$. For testing accuracy and precision for different area classes, the same shapes were also printed in 10 cm$^2$ 100 cm$^2$ respectively.

Table A 1 Species list of 25 leaves with measured area by Leaf-IT and WinFOLIA. The difference indicates the area value measured by WinFOLIA minus the value measured by Leaf-IT. The accordance shows the similarity in % of the area values measured by both methods (area value of WinFOLIA equals 100%). All numbers are rounded by two decimal figures. Nomenclature follows: The Plant List, Version 1.1; accessed: August 2016.

| **Species** | **Leaf-IT ($cm^2$)** | **WinFOLIA ($cm^2$)** | **Difference ($cm^2$)** | **Accordance (%)** | **Mean Leaf-IT & WinFOLIA ($cm^2$)** |
|---|---|---|---|---|---|
| *Veronica hederifolia* | 1.88 | 1.86 | -0.02 | 99 | 1.87 |
| *Lonicera xylostemon* | 2.26 | 2.29 | 0.03 | 102 | 2.27 |
| *Symphoricarpus albus* | 4.55 | 4.53 | -0.02 | 100 | 4.54 |
| *Populus nigra* | 5.61 | 5.41 | -0.20 | 96 | 5.51 |
| *Lonicera xylostemon* | 7.18 | 7.11 | -0.07 | 99 | 7.15 |
| *Crataegus monogyna* | 11.47 | 11.43 | -0.04 | 100 | 11.45 |
| *Populus nigra* | 14.68 | 14.75 | 0.07 | 100 | 14.71 |
| *Sambucus nigra*$^L$ | 17.47 | 17.42 | -0.05 | 100 | 17.44 |
| *Acer campestre* | 17.96 | 18.18 | 0.21 | 101 | 18.07 |
| *Prunus padus* | 24.12 | 24.23 | 0.11 | 100 | 24.18 |
| *Hedera helix* | 24.13 | 24.39 | 0.26 | 101 | 24.26 |
| *Malus domesticus* | 26.11 | 26.05 | -0.06 | 100 | 26.08 |
| *Plantago lanceolata* | 29.62 | 29.73 | 0.11 | 100 | 29.67 |
| *Tilia cordata* | 35.83 | 36.19 | 0.36 | 101 | 36.01 |
| *Malus domesticus* | 36.46 | 36.53 | 0.07 | 100 | 36.50 |
| *Prunus padus* | 36.85 | 36.72 | -0.13 | 100 | 36.78 |
| *Ribes rubrum* | 38.92 | 39.26 | 0.35 | 101 | 39.09 |
| *Allearia petiolata* | 54.12 | 54.20 | 0.08 | 100 | 54.16 |
| *Acer campestre* | 58.59 | 59.04 | 0.45 | 101 | 58.82 |
| *Carpinus betulus* | 64.33 | 64.28 | -0.05 | 100 | 64.31 |
| *Syringa vulgaris* | 76.53 | 76.99 | 0.46 | 101 | 76.76 |
| *Hedera helix* | 100.83 | 100.41 | -0.42 | 100 | 100.62 |
| *Acer campestre* | 101.68 | 102.16 | 0.47 | 100 | 101.92 |
| *Aesculus hippocastanum*$^L$ | 104.35 | 105.00 | 0.65 | 101 | 104.68 |
| *Arctium sp.* | 114.93 | 115.57 | 0.64 | 101 | 115.25 |

**L - leaflet**

Table A 2 Precision of Leaf-IT. For each area class the same object was measured 10 times respectively (with *reference object* method in Leaf-IT). The values estimated by Leaf-IT are shown with mean and confidence intervals (CI). All numbers are rounded by two decimal figures.

| | **Area class** | | |
|---:|---:|---:|---:|
| **run** | **1 cm$^2$** | **10 cm$^2$** | **100 cm$^2$** |
| 1 | 0.99 | 10.07 | 100.58 |
| 2 | 1.01 | 10.08 | 100.37 |
| 3 | 1.00 | 10.12 | 100.07 |
| 4 | 1.02 | 10.10 | 100.78 |
| 5 | 1.00 | 9.96 | 99.26 |
| 6 | 0.99 | 10.02 | 100.98 |
| 7 | 0.99 | 10.01 | 101.23 |
| 8 | 1.00 | 10.07 | 100.70 |
| 9 | 1.02 | 9.97 | 99.10 |
| 10 | 0.98 | 10.07 | 101.00 |
| mean | 1.00 | 10.05 | 100.41 |
| CI lower | 0.99 | 10.01 | 99.90 |
| CI upper | 1.01 | 10.09 | 100.90 |

Table A 3 Estimated area by Leaf-IT on 22 standardised object. The *true area* indicates the standardised area of the objects. *Form*, *length* and *width* show the properties of the objects. All objects were measured with the *set size* and *reference object* method in Leaf-IT under optimized conditions (level) and under field conditions (free). All numbers are rounded by two decimal figures.

| true area (cm²) | form | length (cm) | width (cm) | set size (level) (cm²) | set size (free) (cm²) | reference object (level) (cm²) | reference object (free) (cm²) |
|---|---|---|---|---|---|---|---|
| 1 | square | 1.00 | 1.00 | 1.01 | 1.01 | 0.99 | 1.00 |
| 1 | rectangle | 0.50 | 2.00 | 1.01 | 1.00 | 0.99 | 0.99 |
| 1 | rectangle | 0.20 | 5.00 | 0.98 | 0.98 | 0.99 | 0.98 |
| 1 | circle | 1.13 | 1.13 | 1.01 | 0.99 | 1.00 | 1.01 |
| 1 | ellipse | 0.40 | 3.18 | 1.01 | 1.00 | 1.00 | 1.02 |
| 1 | triangle | 1.00 | 2.00 | 0.98 | 1.02 | 0.98 | 1.00 |
| 1 | triangle | 2.00 | 1.00 | 1.00 | 1.01 | 1.01 | 0.98 |
| 1 | triangle | 0.50 | 4.00 | 1.00 | 1.00 | 1.01 | 1.01 |
| 10 | square | 3.16 | 3.16 | 10.13 | 9.97 | 9.87 | 9.87 |
| 10 | rectangle | 1.58 | 6.32 | 9.92 | 9.93 | 9.79 | 10.03 |
| 10 | rectangle | 0.63 | 15.81 | 9.92 | 9.90 | 9.72 | 9.83 |
| 10 | circle | 3.57 | 3.57 | 10.19 | 10.16 | 9.79 | 10.18 |
| 10 | ellipse | 1.26 | 10.07 | 9.94 | 9.90 | 10.00 | 10.05 |
| 10 | triangle | 3.16 | 6.32 | 9.93 | 10.07 | 9.88 | 10.03 |
| 10 | triangle | 6.32 | 3.16 | 9.95 | 10.09 | 9.98 | 10.13 |
| 10 | triangle | 1.58 | 12.65 | 9.99 | 10.07 | 9.83 | 10.26 |
| 100 | square | 10.00 | 10.00 | 100.22 | 100.35 | 100.25 | 100.22 |
| 100 | rectangle | 5.00 | 20.00 | 100.20 | 100.49 | 99.28 | 101.05 |
| 100 | circle | 11.28 | 11.28 | 100.79 | 100.82 | 97.77 | 97.33 |
| 100 | ellipse | 4.00 | 31.83 | 99.53 | 99.08 | 100.17 | 100.54 |
| 100 | triangle | 10.00 | 20.00 | 100.84 | 99.52 | 97.89 | 99.09 |
| 100 | triangle | 20.00 | 10.00 | 99.36 | 101.03 | 98.13 | 97.39 |

# Appendix B – Supporting information to chapter 3

## Plants on small islands revisited: the effects of spatial scale and habitat quality on the species-area relationship

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Table B 1 Species richness for four different spatial scales and island parameter for the 60 islands studied. $\mathrm{iso}_{\mathrm{Gam}}$: distance to Gam island; $\mathrm{iso}_{\mathrm{buffer}}$: surrounding landmass in 1000 m radius. SE: Standard error of estimated species richness.

| **Island** | **Island coordinates** | **$\gamma_1$** | **$\gamma_2$ (±SE)** | **$\alpha_1$** | **$\alpha_2$** | **Area ($m^2$)** | **$\mathrm{Iso}_{\mathrm{Gam}}$ (m)** | **$\mathrm{iso}_{\mathrm{buffer}}$ (ha)** | **Shape index** | **Soil depth mean (cm)** |
|---|---|---|---|---|---|---|---|---|---|---|
| GB1 | 130°34'52.115"E<br>0°31'14.524"S | 18 | 24.8 (±2.7) | 7.25 | 2.25 | 4774.04 | 59.30 | 146.90 | 0.70 | 11.40 |
| GB2 | 130°34'30.544"E<br>0°31'2.808"S | 1 | 2 (±0) | 1.00 | 1.00 | 7.29 | 56.65 | 71.06 | 0.60 | 0.00 |
| GB3 | 130°34'6.453"E<br>0°31'3.816"S | 17 | 26.6 (±3.5) | 7.25 | 2.35 | 2329.91 | 172.07 | 45.80 | 0.61 | 3.72 |
| GB4 | 130°34'6.641"E<br>0°31'4.363"S | 1 | 2 (±0) | 1.00 | 1.00 | 8.06 | 191.69 | 44.91 | 0.64 | 0.00 |
| GB5 | 130°34'10.814"E<br>0°31'2.308"S | 2 | 3 (±0) | 2.00 | 2.00 | 20.27 | 136.06 | 47.01 | 0.59 | 0.00 |
| GB6 | 130°34'7.001"E<br>0°30'55.021"S | 8 | 12.6 (±1.8) | 4.67 | 2.09 | 316.83 | 381.77 | 33.60 | 0.76 | 3.94 |
| GB7 | 130°34'10.684"E<br>0°30'54.074"S | 13 | 18.7 (±2.5) | 6.50 | 1.95 | 1575.25 | 344.67 | 36.22 | 0.60 | 9.77 |
| GB8 | 130°34'20.533"E<br>0°30'59.87"S | 14 | 18.8 (±1.9) | 6.75 | 2.15 | 1263.62 | 106.69 | 53.70 | 0.78 | 12.74 |
| GB9 | 130°34'12.378"E<br>0°30'52.021"S | 19 | 27.6 (±3) | 9.25 | 2.85 | 1716.25 | 400.15 | 33.95 | 0.58 | 0.73 |
| GB10 | 130°34'19.367"E<br>0°31'0.326"S | 5 | 8.3 (±1.3) | 5.00 | 1.40 | 121.47 | 115.03 | 52.69 | 0.67 | 0.00 |
| GB11 | 130°34'14.995"E<br>0°31'0.318"S | 9 | 11.9 (±1.3) | 5.33 | 2.60 | 817.06 | 148.18 | 49.87 | 0.67 | 8.16 |
| GB12 | 130°33'47.023"E<br>0°30'41.63"S | 14 | 22.6 (±3) | 6.75 | 1.90 | 1649.94 | 1091.20 | 21.38 | 0.60 | 2.63 |
| GB13 | 130°33'39.392"E<br>0°30'46.509"S | 10 | 13.7 (±1.6) | 7.50 | 2.40 | 601.88 | 1198.45 | 20.51 | 0.58 | 7.66 |
| GB14 | 130°35'16.783"E<br>0°31'0.992"S | 12 | 17.5 (±2) | 7.50 | 2.70 | 535.20 | 270.27 | 78.52 | 0.62 | 19.66 |
| GB15 | 130°35'18.591"E<br>0°31'1.654"S | 9 | 14 (±3.6) | 9.00 | 3.40 | 380.60 | 226.00 | 87.76 | 0.63 | 22.28 |
| GB16 | 130°35'38.096"E<br>0°30'45.256"S | 6 | 10 (±1.9) | 6.00 | 2.50 | 137.07 | 63.37 | 150.20 | 0.59 | 15.50 |
| GB17 | 130°35'37.496"E<br>0°30'33.986"S | 3 | 5 (±0.7) | 3.00 | 2.00 | 18.43 | 5.40 | 133.54 | 0.67 | 0.00 |

**Table B 1 continued**

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| GB18 | 130°35'35.864"E<br>0°30'22.88"S | 8 | 11.4 (±1.4) | 8.00 | 2.80 | 432.77 | 15.69 | 106.46 | 0.59 | 11.44 |
| GB19 | 130°35'38.468"E<br>0°30'20.568"S | 1 | 2 (±0) | 1.00 | 1.00 | 15.10 | 8.52 | 111.52 | 0.64 | 0.00 |
| GB20 | 130°35'14.153"E<br>0°30'55.705"S | 13 | 18.7 (±2.1) | 7.67 | 3.00 | 864.00 | 414.66 | 54.45 | 0.61 | 15.37 |
| GB21 | 130°34'28.442"E<br>0°31'2.992"S | 2 | 3 (±0) | 2.00 | 2.00 | 10.51 | 1.63 | 68.47 | 0.60 | 0.00 |
| GB22 | 130°34'51.27"E<br>0°31'17.771"S | 14 | 19.7 (±2.1) | 6.00 | 2.05 | 1571.48 | 39.82 | 156.79 | 0.67 | 8.59 |
| GB23 | 130°34'59.55"E<br>0°31'11.114"S | 14 | 22.6 (±3) | 6.00 | 2.35 | 1375.63 | 62.99 | 120.73 | 0.66 | 6.08 |
| GB24 | 130°35'4.149"E<br>0°31'2.038"S | 17 | 24.7 (±2.5) | 8.50 | 2.95 | 1862.75 | 257.00 | 76.22 | 0.68 | 11.19 |
| GB25 | 130°35'15.603"E<br>0°30'46.099"S | 8 | 13 (±2.6) | 8.00 | 3.33 | 69.14 | 665.68 | 38.40 | 0.81 | 4.87 |
| GB26 | 130°34'59.574"E<br>0°31'8.023"S | 17 | 23.8 (±2.4) | 7.00 | 2.44 | 3865.84 | 82.44 | 109.18 | 0.69 | 17.14 |
| GB27 | 130°35'11.779"E<br>0°30'56.904"S | 22 | 29.8 (±2.6) | 10.50 | 3.50 | 11806.28 | 314.32 | 64.45 | 0.81 | 7.19 |
| GB28 | 130°35'15.345"E<br>0°30'58.95"S | 24 | 31.7 (±2.9) | 8.40 | 2.72 | 4429.05 | 301.33 | 74.54 | 0.64 | 17.24 |
| GB29 | 130°35'17.546"E<br>0°30'54.676"S | 27 | 38.6 (±3.5) | 10.00 | 3.20 | 5526.65 | 351.65 | 74.66 | 0.70 | 13.19 |
| GB30 | 130°34'9.677"E<br>0°31'3.813"S | 22 | 30.7 (±3.1) | 8.67 | 3.00 | 8520.55 | 63.21 | 51.24 | 0.71 | 8.19 |
| GB31 | 130°35'16.863"E<br>0°30'50.919"S | 19 | 23.9 (±2.4) | 9.00 | 3.27 | 7181.16 | 510.54 | 56.03 | 0.90 | 9.99 |
| GB32 | 130°34'6.863"E<br>0°30'54.819"S | 1 | 2 (±0) | 1.00 | 1.00 | 13.63 | 397.35 | 32.24 | 0.78 | 0.00 |
| GB33 | 130°34'6.66"E<br>0°30'55.563"S | 0 | 0 (±0) | 0.00 | 0.00 | 12.78 | 382.15 | 33.40 | 0.60 | 0.00 |
| GB34 | 130°34'6.787"E<br>0°30'55.537"S | 0 | 0 (±0) | 0.00 | 0.00 | 12.01 | 381.02 | 33.51 | 0.59 | 0.00 |
| GB35 | 130°34'7.41"E<br>0°30'54.959"S | 0 | 0 (±0) | 0.00 | 0.00 | 29.39 | 386.14 | 32.97 | 0.62 | 0.00 |
| GB36 | 130°33'34.803"E<br>0°30'47.294"S | 1 | 2 (±0) | 1.00 | 0.50 | 16.46 | 1246.85 | 20.40 | 0.72 | 0.00 |
| GB37 | 130°33'28.821"E<br>0°30'47.557"S | 2 | 3 (±0) | 2.00 | 2.00 | 15.94 | 1123.65 | 21.64 | 0.61 | 0.00 |
| GB38 | 130°34'7.208"E<br>0°31'6.28"S | 0 | 0 (±0) | 0.00 | 0.00 | 3.64 | 148.07 | 47.92 | 0.61 | 0.00 |
| GB39 | 130°34'7.093"E<br>0°31'6.345"S | 0 | 0 (±0) | 0.00 | 0.00 | 6.22 | 149.39 | 47.80 | 0.59 | 0.00 |
| GB40 | 130°34'6.966"E<br>0°31'6.537"S | 0 | 0 (±0) | 0.00 | 0.00 | 10.52 | 151.70 | 47.49 | 0.64 | 0.00 |
| GB41 | 130°34'7.252"E<br>0°31'4.431"S | 0 | 0 (±0) | 0.00 | 0.00 | 6.57 | 173.71 | 45.72 | 0.60 | 0.00 |
| GB42 | 130°34'7.829"E<br>0°31'4.02"S | 1 | 2 (±0) | 1.00 | 1.00 | 7.00 | 169.31 | 46.05 | 0.61 | 0.00 |
| GB43 | 130°34'10.58"E<br>0°31'6.067"S | 0 | 0 (±0) | 0.00 | 0.00 | 4.63 | 58.87 | 50.82 | 0.60 | 0.00 |
| GB44 | 130°33'36.627"E<br>0°30'46.95"S | 0 | 0 (±0) | 0.00 | 0.00 | 22.60 | 1265.85 | 20.44 | 0.71 | 0.00 |
| GB45 | 130°35'15.361"E<br>0°30'45.971"S | 0 | 0 (±0) | 0.00 | 0.00 | 5.66 | 674.75 | 37.33 | 0.64 | 0.00 |
| GB46 | 130°34'20.991"E<br>0°31'0.022"S | 5 | 8 (±2) | 5.00 | 2.00 | 77.94 | 137.26 | 53.35 | 0.65 | 0.00 |
| GB47 | 130°34'20.828"E<br>0°31'0.302"S | 0 | 0 (±0) | 0.00 | 0.00 | 8.24 | 137.89 | 53.38 | 0.62 | 0.00 |
| GB48 | 130°34'28.425"E<br>0°31'2.795"S | 0 | 0 (±0) | 0.00 | 0.00 | 4.34 | 7.30 | 67.70 | 0.60 | 0.00 |
| GB49 | 130°34'28.094"E<br>0°31'2.949"S | 0 | 0 (±0) | 0.00 | 0.00 | 7.93 | 2.00 | 67.90 | 0.67 | 0.00 |
| GB50 | 130°34'45.708"E<br>0°31'7.12"S | 0 | 0 (±0) | 0.00 | 0.00 | 11.01 | 171.78 | 102.53 | 0.63 | 0.00 |

**Table B1 continued**

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| GB51 | 130°34'45.413"E<br>0°31'9.299"S | 0 | 0 (±0) | 0.00 | 0.00 | 2.81 | 123.18 | 113.99 | 0.59 | 0.00 |
| GB52 | 130°34'51.319"E<br>0°31'19.832"S | 2 | 3 (±0) | 2.00 | 2.00 | 5.75 | 2.41 | 160.87 | 0.60 | 0.00 |
| GB53 | 130°34'51.217"E<br>0°31'19.918"S | 0 | 0 (±0) | 0.00 | 0.00 | 3.58 | 1.43 | 161.70 | 0.58 | 0.00 |
| GB54 | 130°34'51.404"E<br>0°31'19.849"S | 0 | 0 (±0) | 0.00 | 0.00 | 3.53 | 0.65 | 161.44 | 0.58 | 0.00 |
| GB55 | 130°35'4.526"E<br>0°31'3.507"S | 6 | 10 (±2.9) | 6.00 | 3.00 | 25.49 | 257.43 | 74.51 | 0.65 | 0.00 |
| GB56 | 130°35'3.783"E<br>0°31'3.081"S | 1 | 2 (±0) | 1.00 | 1.00 | 6.34 | 286.96 | 72.30 | 0.61 | 0.00 |
| GB57 | 130°35'2.06"E<br>0°30'59.367"S | 0 | 0 (±0) | 0.00 | 0.00 | 14.81 | 362.61 | 55.63 | 0.64 | 0.00 |
| GB58 | 130°35'2.336"E<br>0°30'59.581"S | 0 | 0 (±0) | 0.00 | 0.00 | 16.77 | 360.80 | 56.48 | 0.65 | 0.00 |
| GB59 | 130°34'59.79"E<br>0°30'58.346"S | 14 | 17.9 (±1.7) | 7.00 | 2.20 | 2620.30 | 328.73 | 54.83 | 0.79 | 7.23 |
| GB60 | 130°34'11.493"E<br>0°31'2.615"S | 0 | 0 (±0) | 0.00 | 0.00 | 3.11 | 116.35 | 47.89 | 0.62 | 0.00 |

Table B 2 Eleven different species-area relationships used for comparison of best model at four different spatial scales according to Guilhaumon et al. (2010). S = species richness; A = island area; c, z, d, and f = fitted parameter, T = breakpoint. Area was log-transformed for the two breakpoint models and the linear model prior to model calculation.

| **Model** | **Formula** | **Space & Shape** | **Source** |
|---|---|---|---|
| Power | $S = c * A^{z}$ | Arithmetic convex | Guilhaumon et al., 2010 |
| Exponential | $S = c + z * \log A$ | Arithmetic convex | Guilhaumon et al., 2010 |
| Negative exponential | $S = d/(1 - \exp(-z * A))$ | Arithmetic convex | Guilhaumon et al., 2010 |
| Monod | $S = d/(1 + c * A^{-1})$ | Arithmetic convex | Guilhaumon et al., 2010 |
| Rational function | $S = (c + z * A)/(1 + d * A)$ | Arithmetic convex | Guilhaumon et al., 2010 |
| Logistic | $S = d/(1 + \exp(-z * A + f))$ | Arithmetic sigmoid | Guilhaumon et al., 2010 |
| Lomolino | $S = \frac{d}{1} + (z^{\log(\frac{f}{A})})$ | Arithmetic sigmoid | Guilhaumon et al., 2010 |
| Cumulative Weibull | $S = d(1 - \exp(-z * A^{f}))$ | Arithmetic sigmoid | Guilhaumon et al., 2010 |
| Left-horizontal function | $S = c + z * ((\mathrm{A} - T) * (A \geq T))$ | Semi-log breakpoint | Lomolino & Weiser, 2001 |
| Continuous two-slope | $S = c + (\mathrm{A} \leq T) * z_1 * A + (\mathrm{A} > T) * [z_1 \log T + z_2(\mathrm{A} - T)]$ | Semi-log breakpoint | Dengler, 2010 |
| Single linear regression model | $S = c + z * A$ | Semi-log linear | Dengler, 2010 |

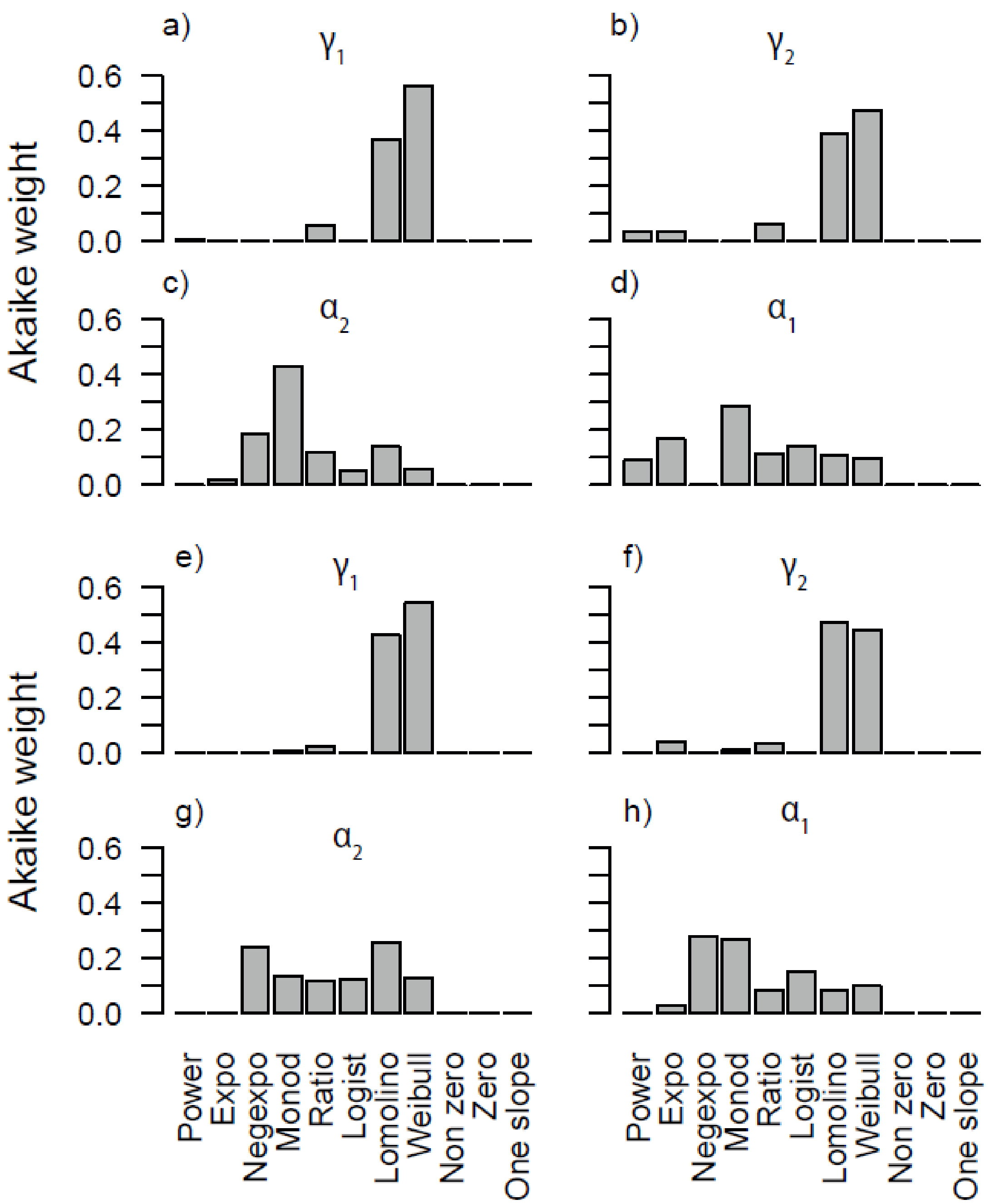

Figure B 1 Akaike weights of 11 different models explaining species richness on islands at four different spatial scales when all empty islands are excluded from the dataset (a – d) and when only empty islands are included that are larger than the smallest inhabited island (e – h). Spatial scale is divided into $\alpha_1$ (d & h): size of a single subtransect, $\alpha_2$ (c & g): size of a single transect, $\gamma_1$ (a & e): observed species richness on a given island, and $\gamma_2$ (b & f): estimated species richness (Jackknife 1) on a given island. Non zero model: continuous two-slope function, Zero: left-horizontal function, One slope: single linear regression model (see Table B 2 for model formulas).

Table B 3 Pearson correlation matrix of five explanatory variables used for model selection and relative variable importance. Island area was log-transformed. SI: shape index; $iso_{Gam}$: distance to Gam island; $iso_{buffer}$: surrounding landmass in 1000 m radius; soil mean: mean soil depth recorded on each island.

| | **Area $_{[log10]}$** | **$Iso_{buffer}$** | **$Iso_{Gam}$** | **SI** |
|---|---|---|---|---|
| $Iso_{buffer}$ | 0.01 | | | |
| $Iso_{Gam}$ | 0.10 | -0.59 | | |
| SI | 0.46 | -0.14 | 0.19 | |
| Soil mean | 0.75 | 0.22 | -0.05 | 0.24 |

Table B 4 Spatial autocorrelation (Moran´s I) of six variables used for model selection and relative variable importance. All variables, except the buffer surrounding landmass in 1000 m radius, were not spatially autocorrelated. Moran´s I was calculated using the function *moran.test* in the R-package *spdep* (Bivand, R. & Piras, G. 2015. Comparing implementations of estimation methods for spatial econometrics. J. Stat. Softw., 63.). Island area was log-transformed. SI: shape index; $iso_{Gam}$: distance to Gam island; $iso_{buffer}$: surrounding landmass in 1000 m radius; soil depth: mean soil depth recorded on each island.

| | **Moran´s I values** | | | |
|---|---|---|---|---|
| **Variable** | Observed | Expected | Standard deviation | P-value |
| Species richness | 0.2 | -0.02 | 1.38 | 0.08 |
| Area | 0.19 | -0.02 | 1.33 | 0.09 |
| $Iso_{buffer}$ | 0.57 | -0.02 | 3.75 | <0.01 |
| $Iso_{Gam}$ | 0.17 | -0.02 | 1.22 | 0.11 |
| SI | -0.15 | -0.02 | -0.89 | 0.81 |
| Soil depth | -0.01 | -0.02 | 0.35 | 0.49 |

Table B 5 Intercept and slope of linear quantile regression (lower 0.05 and upper 0.95 quantile) and regular single slope linear regression of species richness and island area ($log_{10}$ transformed). p-value indicates significance level between the coefficients of the slopes of the lower and upper quantile for each spatial scale. Lower adjusted $R^2$ indicated greater difference between the slopes. Spatial scale is divided into $\alpha_1$: size of a single subtransect, $\alpha_2$: size of a single transect, $\gamma_1$: observed species richness on a given island, and $\gamma_2$: estimated species richness (Jackknife 1) on a given island.

| **Spatial scale** | **Model** | **Intercept** | **Slope** | **p-value** | **Adjusted $R^2$** |
|---|---|---|---|---|---|
| $\gamma_1$ | Quantile 0.05 | -8.61 | 7.03 | 0.0143 | 0.91 |
| | Quantile 0.95 | -4.44 | 9.92 | | |
| | Regular | -7.41 | 8.99 | | |
| $\gamma_2$ | Quantile 0.05 | -6.53 | 5.33 | 0.0104 | 0.91 |
| | Quantile 0.95 | -3.75 | 7.61 | | |
| | Regular | -5.56 | 6.45 | | |
| $\alpha_2$ | Quantile 0.05 | -0.54 | 0.4 | 0.0015 | 0.71 |
| | Quantile 0.95 | 1.09 | 1.19 | | |
| | Regular | 0.08 | 0.76 | | |
| $\alpha_1$ | Quantile 0.05 | -2.00 | 1.63 | 0.0045 | 0.16 |
| | Quantile 0.95 | -0.7 | 3.55 | | |
| | Regular | -1.62 | 2.75 | | |

Table B 6 Model support of 11 different species-area relationship models at four spatial scales. Spatial scale is divided into $\alpha_1$: size of a single subtransect, $\alpha_2$: size of a single transect, $\gamma_1$: observed species richness on a given island, and $\gamma_2$: estimated species richness (Jackknife 1) on a given island. For model formulas and description see Table B 2.

| Spatial scale | Model | AICc | AICc weights |
|---|---|---|---|
| $\gamma_2$ | Power | 160.82 | 0.00 |
| | Expo | 146.74 | 0.01 |
| | Negexpo | 156.76 | 0.00 |
| | Monod | 145.30 | 0.02 |
| | Ratio | 144.60 | 0.02 |
| | Logist | 171.94 | 0.00 |
| | Lomolino | 138.35 | 0.48 |
| | Weibull | 138.40 | 0.47 |
| | Non zero | 310.61 | 0.00 |
| | Zero | 308.60 | 0.00 |
| | One slope | 317.01 | 0.00 |
| $\gamma_1$ | Power | 104.27 | 0.00 |
| | Expo | 99.84 | 0.00 |
| | Negexpo | 99.20 | 0.00 |
| | Monod | 85.87 | 0.01 |
| | Ratio | 84.64 | 0.01 |
| | Logist | 123.81 | 0.00 |
| | Lomolino | 77.00 | 0.46 |
| | Weibull | 76.71 | 0.53 |
| | Non zero | 251.13 | 0.00 |
| | Zero | 252.48 | 0.00 |
| | One slope | 270.11 | 0.00 |
| $\alpha_2$ | Power | 70.85 | 0.00 |
| | Expo | 40.65 | 0.00 |
| | Negexpo | 30.77 | 0.19 |
| | Monod | 32.38 | 0.08 |
| | Ratio | 31.41 | 0.14 |
| | Logist | 32.13 | 0.10 |
| | Lomolino | 29.53 | 0.35 |
| | Weibull | 31.29 | 0.15 |
| | Non zero | 207.31 | 0.00 |
| | Zero | 212.93 | 0.00 |
| | One slope | 210.92 | 0.00 |
| $\alpha_1$ | Power | -24.81 | 0.00 |
| | Expo | -36.20 | 0.01 |
| | Negexpo | -42.91 | 0.34 |
| | Monod | -42.30 | 0.25 |
| | Ratio | -40.60 | 0.11 |
| | Logist | -40.03 | 0.08 |
| | Lomolino | -40.74 | 0.11 |
| | Weibull | -40.62 | 0.11 |
| | Non zero | 131.44 | 0.00 |
| | Zero | 136.38 | 0.00 |
| | One slope | 134.08 | 0.00 |

Table B 7 Best models explaining species richness at four different spatial scales. Shown are all models with ΔAICc < 2, but at least the best five models. Generalised linear models were used with Gaussian distribution. We used Gaussian distribution as Poisson (only integers) or Gamma (no zero richness values allowed) distribution were not applicable to our dataset. Scales are divided into $\alpha_1$: size of a single subtransect, $\alpha_2$: size of a single transect, $\gamma_1$: observed species richness on a given island, and $\gamma_2$: estimated species richness (Jackknife 1) on a given island. SI: shape index; $Iso_{Gam}$: distance to Gam island; $Iso_{buffer}$: surrounding landmass in 1000 m radius; soil mean: mean soil depth recorded on each island. df: degrees of freedom; AICc: second-order information criterion for small sample size; Weight: weighted AICc values.

| Scale | Model | df | AICc | Weight |
|---|---|---|---|---|
| $\gamma_1$ | Area $_{[log10]}$ + SI | 4 | 316.74 | 0.15 |
| | Area $_{[log10]}$ + $Iso_{buffer}$ | 4 | 316.99 | 0.13 |
| | Area $_{[log10]}$ | 3 | 317.01 | 0.13 |
| | Area $_{[log10]}$ + SI + $Iso_{buffer}$ | 5 | 317.45 | 0.11 |
| | Area $_{[log10]}$ + $Iso_{Gam}$ | 4 | 317.89 | 0.09 |
| | Area $_{[log10]}$ + SI + $Iso_{Gam}$ | 5 | 318.19 | 0.07 |
| $\gamma_2$ | Area $_{[log10]}$ + $Iso_{buffer}$ | 4 | 269.88 | 0.17 |
| | Area $_{[log10]}$ | 3 | 270.11 | 0.16 |
| | Area $_{[log10]}$ + $Iso_{Gam}$ | 4 | 270.25 | 0.14 |
| | Area $_{[log10]}$ + SI | 4 | 271.57 | 0.07 |
| | Area $_{[log10]}$ + SI + $Iso_{buffer}$ | 5 | 271.81 | 0.07 |
| | Area $_{[log10]}$ + $Iso_{Gam}$ + $Iso_{buffer}$ | 5 | 271.82 | 0.07 |
| $\alpha_2$ | Area $_{[log10]}$ + soil mean | 4 | 207.13 | 0.38 |
| | Area $_{[log10]}$ + soil mean + $Iso_{Gam}$ | 5 | 209.47 | 0.12 |
| | Area $_{[log10]}$ + soil mean + SI | 5 | 209.50 | 0.12 |
| | Area $_{[log10]}$ + soil mean + $Iso_{buffer}$ | 5 | 209.50 | 0.12 |
| | Area $_{[log10]}$ | 3 | 210.92 | 0.06 |
| $\alpha_1$ | Area $_{[log10]}$ + soil mean | 4 | 132.05 | 0.28 |
| | Area $_{[log10]}$ + soil mean + $Iso_{buffer}$ | 5 | 133.87 | 0.11 |
| | Area $_{[log10]}$ | 3 | 134.08 | 0.10 |
| | Area $_{[log10]}$ + SI + soil mean | 5 | 134.26 | 0.09 |
| | Area $_{[log10]}$ + soil mean + $Iso_{Gam}$ | 5 | 134.35 | 0.09 |

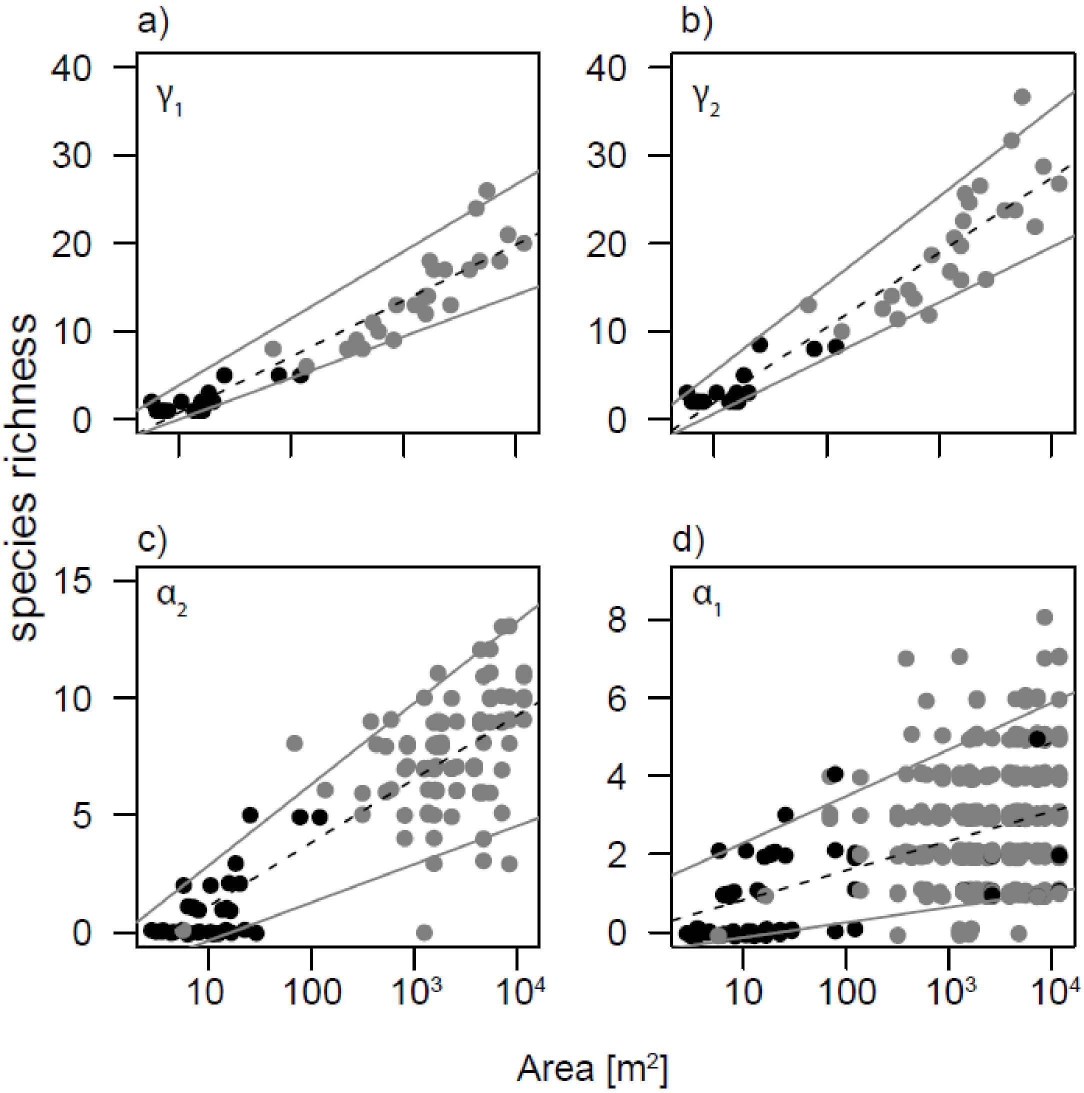

Figure B 2 Species richness and island area (empty islands excluded, compare with Figure 3.2 in main document) at four different sampling scales (a - d) with normal regression line (dashed) and 0.95 and 0.05 quantiles (grey) shown. Sampling scale is divided into $\alpha_1$: size of a single subtransect, $\alpha_2$: size of a single transect, $\gamma_1$: observed species richness on a given island, and $\gamma_2$: estimated species richness (Jackknife 1) on a given island. Points in black indicate absence of soil at the sampling scale and points in grey indicate presence of soil.

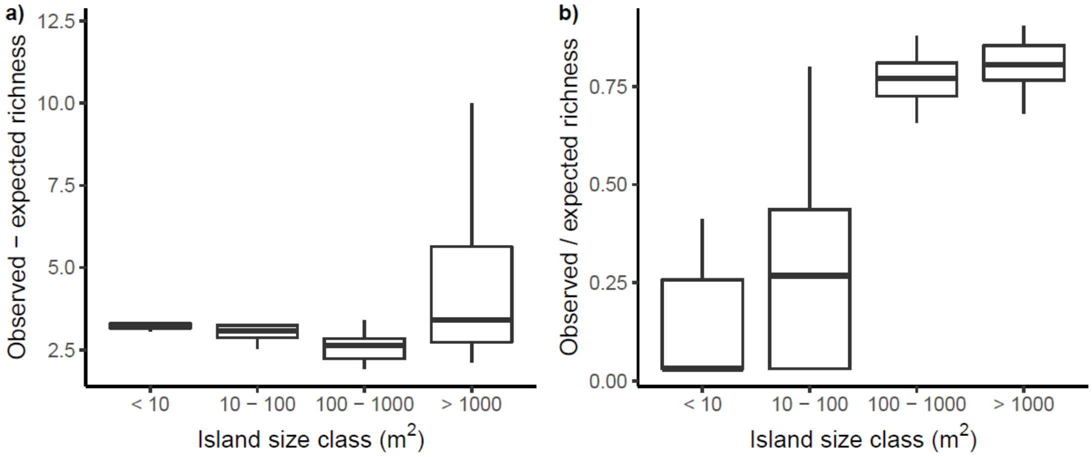

Figure B 3 Absolute (a) and proportional (b) difference between observed species richness and expected species richness for four island classes. Expected species richness was generated by applying a null model based on incidence data (according to Burns et al. 2009). a) Absolute differences between observed and expected richness are higher on very small islands than on intermediate islands and raise again for the very largest islands. The higher differences for small islands compared to intermediate island sizes hint towards the presence of the small-island effect. b) The presence of the small-island effect in the dataset becomes particularly obvious when comparing the proportional differences between the island classes. Small islands support proportionally less species than the lager island classes. The change between large differences and small differences in the proportions occurs at around 100 m$^2$, which correspond to the area range of the small-island effect identified by fitting sigmoidal species-area relationships to the dataset (Figure 3.3 a in main document).

The applied null model can be used to test for the unambiguous presence of the small-island effect irrespective of artefacts possibly arising by axis-transformation. To construct the null model, we fitted sigmoidal models using the incidences of all species on the islands. We used the generated species occurrence probabilities for each island to assign the species randomly to the islands and extracted the resulting species richness values. This procedure was repeated 1000 times and the mean species richness for each island calculated. We then grouped islands into four island size classes (class 1: islands < 10 m$^2$; class 2: islands > 10 m$^2$ and < 100 m$^2$; class 3: islands >100 m$^2$ and < 1000 m$^2$; class 4: islands > 1000 m$^2$) and tested whether the mean species richness values of the random communities differed from the observed values within the island size classes (Burns et al. 2009).

# Appendix C – Supporting information to chapter 4

## Requirements of plant species are linked to area and determine species pool and richness on small islands

Julian Schrader, Christian König, Soetjipto Moeljono, Meelis Pärtel, & Holger Kreft

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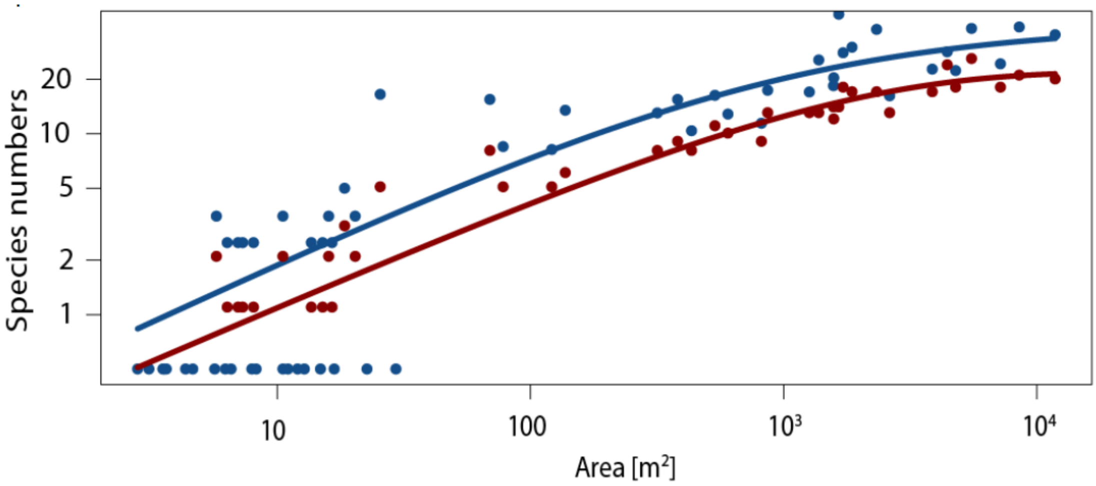

Figure C 1 Species-area relationships of observed (red) and estimated species numbers (blue) of woody plants on 60 small islands in Raja Ampat (Indonesia). Lines indicate best supported species-area relationships out of three tested models (see Table C 1 for tested model formula). Best supported species-area relationship for observed and estimated species richness was a sigmoidal model (Lomolino Model). Species numbers were estimated using the *Chao 1* estimator in the package *iNEXT* in R (Hsieh et al. 2016). Observed and estimated species numbers are strongly related to each other (Pearson correlation coefficient: r = 0.95). The mean difference between estimated and observed species richness was 2.6 species, indicating that the sampling design was sufficiently large to assess plant species richness on the studied islands.

Figure C 2 Presence/absence, logistic regression, and simulated and empirical species occurrence probability of 57 species on 60 islands. Dark blue line indicates 50 % probability for a species to occur on an island under simulated condition (random species placement) with light blues lines showing 95% confidence interval. Red line indicates actual species probability to occur on an island (50%) with black curve showing the logistic regression for each species. When red line was outside the light blue lines, species area requirements differed significantly from random species placement. Presence / absence is indicated by black dots. Island area ranges from 3 m² to 11,806 m².

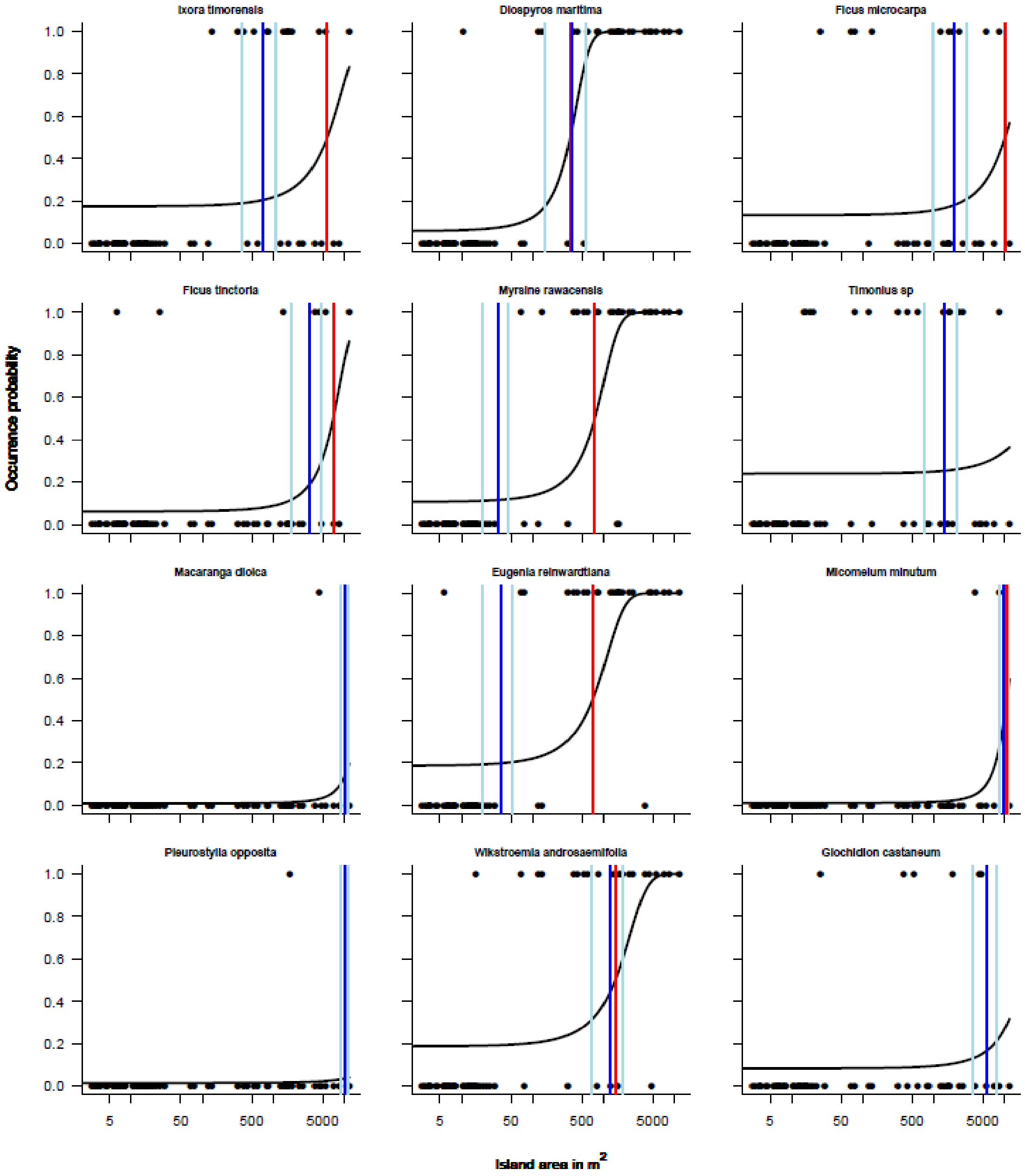

Figure C 2 continued

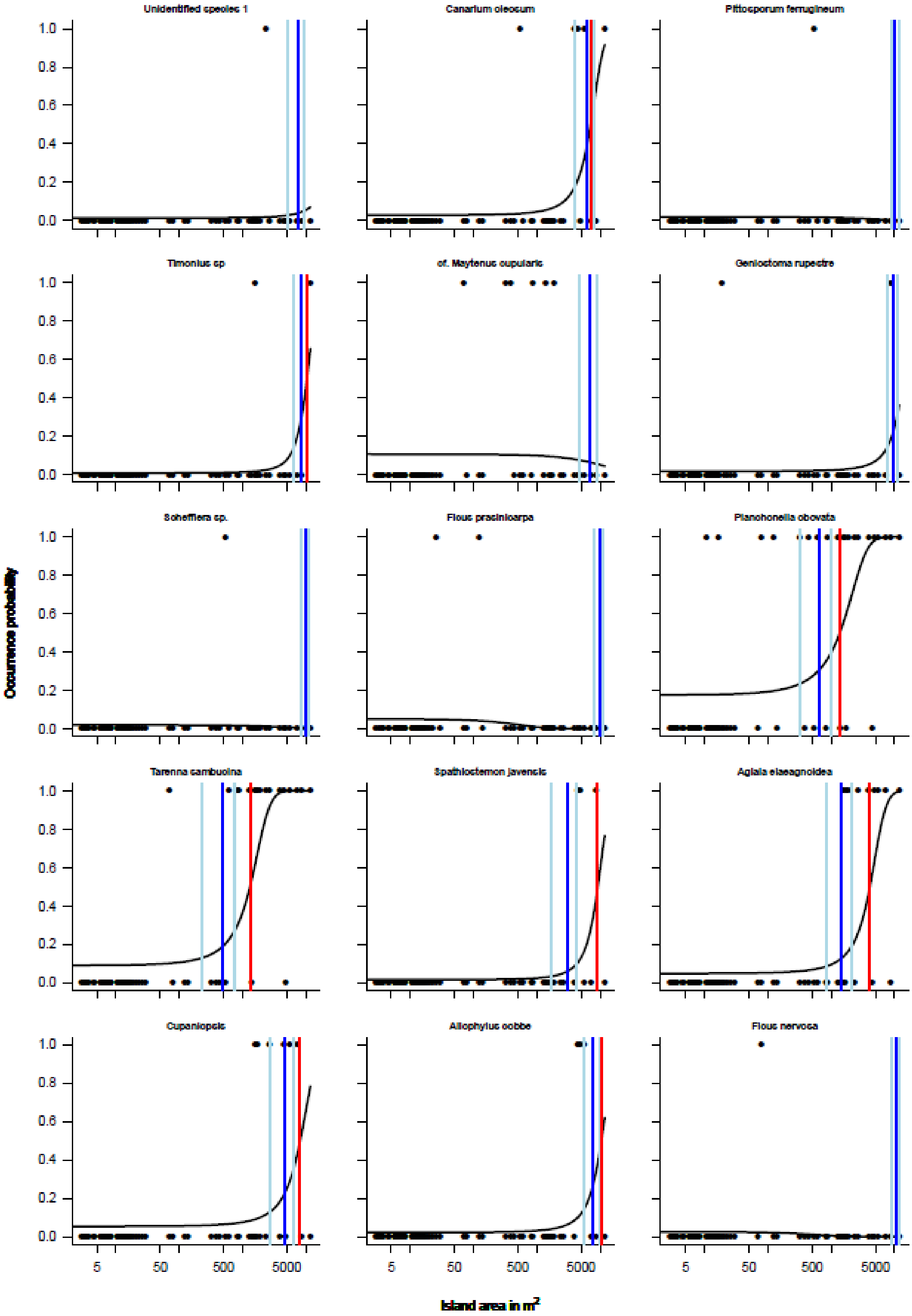

Figure C 2 continued

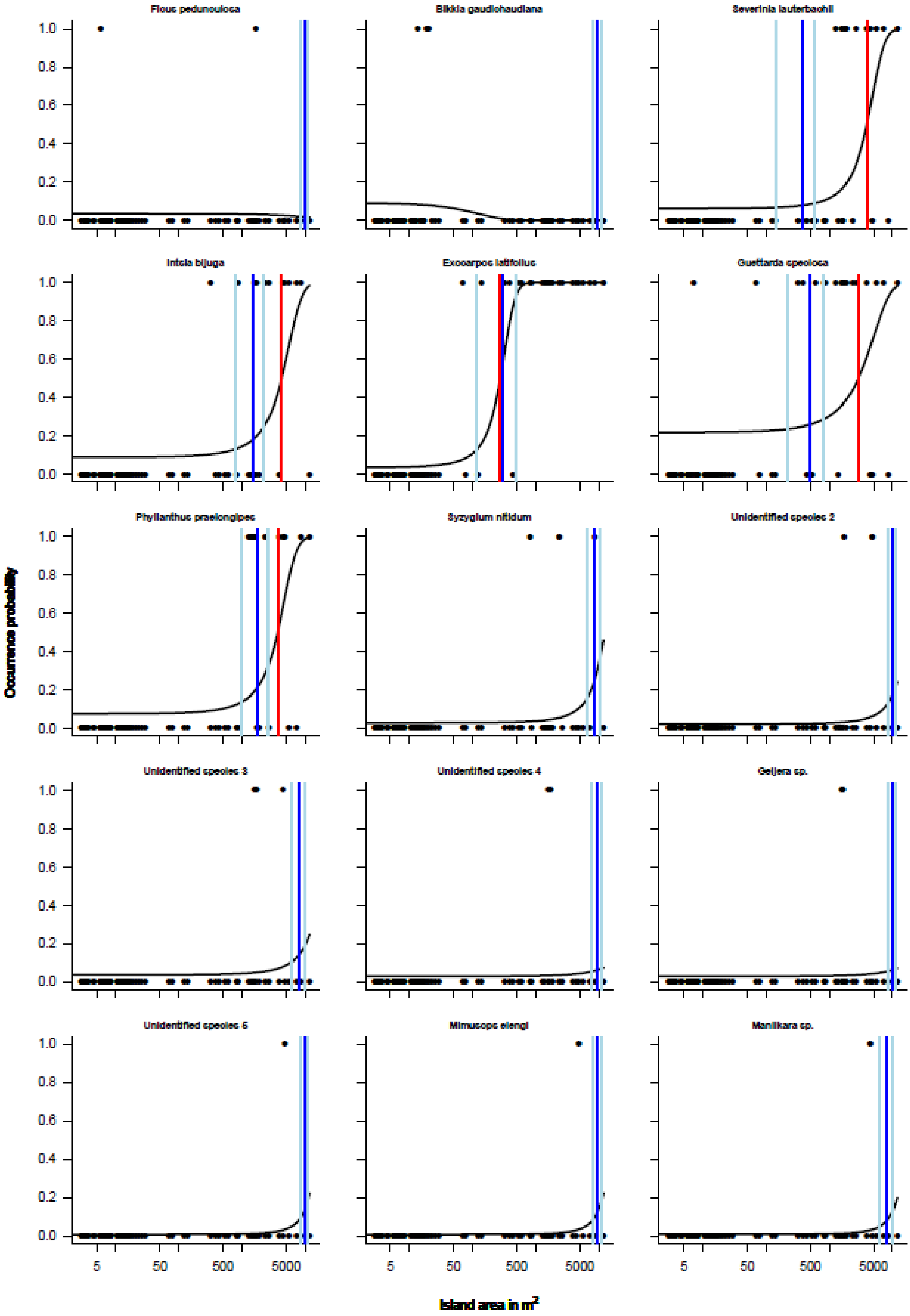

Figure C 2 continued

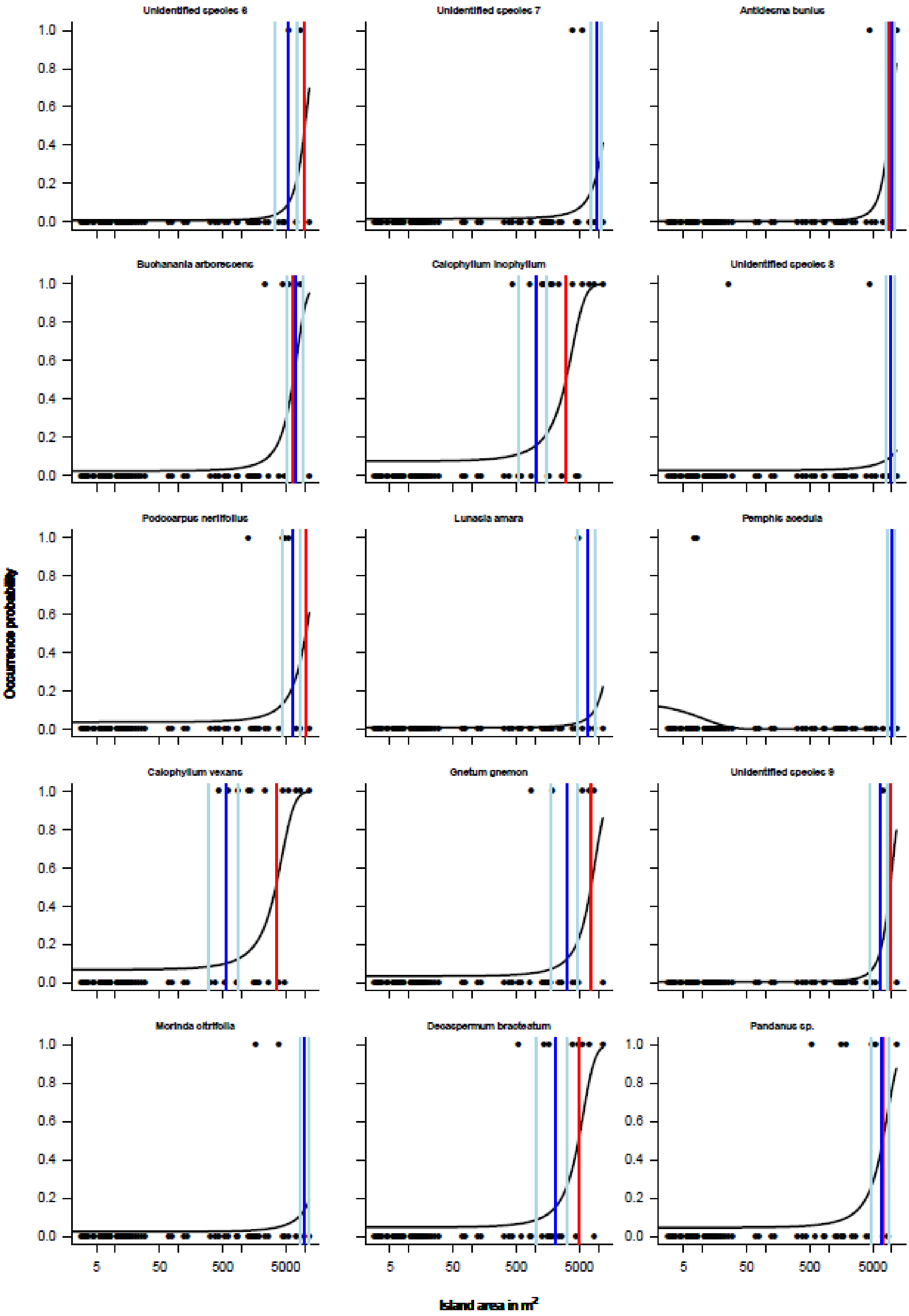

Table C 1 Model support for three species-area relationship (SAR) models. Models were fitted to data from 60 islands for estimated species pool and observed species richness. Convex and sigmoidal models were calculated using *mmSAR*-package (Guilhaumon et al. 2010). AICc and their weights were rounded after two decimal figures.

| | | | Species pool | | Observed richness | |
|---|---|---|---|---|---|---|
| **SAR-model** | **Space & Shape** | **Formula** | **AICc** | **AICc weight** | **AICc** | **AICc weight** |
| Power | Arithmetic convex | $S = c * A^z$ | 55.76 | 0.76 | 104.27 | 0.00 |
| Linear | Arithmetic linear | $S = c + z * A$ | 344.51 | 0.00 | 361.96 | 0.00 |
| Lomolino | Arithmetic sigmoid | $S = \frac{d}{1} + (z^{\log\left(\frac{f}{A}\right)})$ | 58.06 | 0.24 | 77.00 | 1.00 |

Table C 2 Island characteristics of 60 islands studied. Dark diversity (Dark div.) was calculated as the difference between species pool and actual richness and community completeness (Com. compl.) was calculated as log-ration of observed species richness (obs. rich.) and dark diversity. iso$_{main}$: distance to mainland; iso$_{buffer}$: surrounding landmass in 1000 m radius; SI: shape index, Soil mean: mean soil depth per island, Soil sd: standard deviation of soil depth recorded on each island. SE: Standard error of estimated species numbers.

| Island Area (m$^2$) | Island coordinates | Species pool | Obs. rich. | Dark div. | Com compl. | Iso$_{main}$ (m) | Iso$_{buffer}$ (ha) | SI | Soil mean (cm) | Soil sd (cm) |
|---|---|---|---|---|---|---|---|---|---|---|
| 2.8 | 130°34'45.413"E<br>0°31'9.299"S | 3.28 | 0 | 3.28 | -3.45 | 123.2 | 114.0 | 1.0 | 0.0 | 0.0 |
| 3.1 | 130°34'11.493"E<br>0°31'2.615"S | 3.28 | 0 | 3.28 | -3.45 | 116.3 | 47.9 | 1.1 | 0.0 | 0.0 |
| 3.5 | 130°34'51.404"E<br>0°31'19.849"S | 3.27 | 0 | 3.27 | -3.45 | 0.7 | 161.4 | 1.0 | 0.0 | 0.0 |
| 3.6 | 130°34'51.217"E<br>0°31'19.918"S | 3.27 | 0 | 3.27 | -3.45 | 1.4 | 161.7 | 1.0 | 0.0 | 0.0 |
| 3.6 | 130°34'7.208"E<br>0°31'6.28"S | 3.27 | 0 | 3.27 | -3.45 | 148.1 | 47.9 | 1.1 | 0.0 | 0.0 |
| 4.3 | 130°34'28.425"E<br>0°31'2.795"S | 3.27 | 0 | 3.27 | -3.45 | 7.3 | 67.7 | 1.1 | 0.0 | 0.0 |
| 4.6 | 130°34'10.58"E<br>0°31'6.067"S | 3.27 | 0 | 3.27 | -3.45 | 58.9 | 50.8 | 1.1 | 0.0 | 0.0 |
| 5.7 | 130°35'15.361"E<br>0°30'45.971"S | 3.26 | 0 | 3.26 | -3.45 | 674.8 | 37.3 | 1.1 | 0.0 | 0.0 |
| 5.7 | 130°34'51.319"E<br>0°31'19.832"S | 5.03 | 2 | 3.03 | -0.42 | 2.4 | 160.9 | 1.1 | 0.0 | 0.0 |
| 6.2 | 130°34'7.093"E<br>0°31'6.345"S | 3.26 | 0 | 3.26 | -3.45 | 149.4 | 47.8 | 1.0 | 0.0 | 0.0 |
| 6.3 | 130°35'3.783"E<br>0°31'3.081"S | 4.19 | 1 | 3.19 | -1.16 | 287.0 | 72.3 | 1.1 | 0.0 | 0.0 |
| 6.6 | 130°34'7.252"E<br>0°31'4.431"S | 3.25 | 0 | 3.25 | -3.45 | 173.7 | 45.7 | 1.1 | 0.0 | 0.0 |
| 7.0 | 130°34'7.829"E<br>0°31'4.02"S | 4.03 | 1 | 3.03 | -1.11 | 169.3 | 46.0 | 1.1 | 0.0 | 0.0 |
| 7.3 | 130°34'30.544"E<br>0°31'2.808"S | 4.18 | 1 | 3.18 | -1.16 | 56.6 | 71.1 | 1.1 | 0.0 | 0.0 |
| 7.9 | 130°34'28.094"E<br>0°31'2.949"S | 3.25 | 0 | 3.25 | -3.45 | 2.0 | 67.9 | 1.2 | 0.0 | 0.0 |
| 8.1 | 130°34'6.641"E<br>0°31'4.363"S | 4.18 | 1 | 3.18 | -1.16 | 191.7 | 44.9 | 1.1 | 0.0 | 0.0 |
| 8.2 | 130°34'20.828"E<br>0°31'0.302"S | 3.24 | 0 | 3.24 | -3.45 | 137.9 | 53.4 | 1.1 | 0.0 | 0.0 |
| 10.5 | 130°34'28.442"E<br>0°31'2.992"S | 4.99 | 2 | 2.99 | -0.40 | 1.6 | 68.5 | 1.1 | 0.0 | 0.0 |
| 10.5 | 130°34'6.966"E<br>0°31'6.537"S | 3.24 | 0 | 3.24 | -3.45 | 151.7 | 47.5 | 1.1 | 0.0 | 0.0 |
| 11.0 | 130°34'45.708"E<br>0°31'7.12"S | 3.23 | 0 | 3.23 | -3.45 | 171.8 | 102.5 | 1.1 | 0.0 | 0.0 |

**Table C 2 continued**

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 12.0 | 130°34'6.787"E<br>0°30'55.537"S | 3.23 | 0 | 3.23 | -3.45 | 381.0 | 33.5 | 1.1 | 0.0 | 0.0 |
| 12.8 | 130°34'6.66"E<br>0°30'55.563"S | 3.23 | 0 | 3.23 | -3.45 | 382.2 | 33.4 | 1.1 | 0.0 | 0.0 |
| 13.6 | 130°34'6.863"E<br>0°30'54.819"S | 4.14 | 1 | 3.14 | -1.15 | 397.3 | 32.2 | 1.4 | 0.0 | 0.0 |
| 14.8 | 130°35'2.06"E<br>0°30'59.367"S | 3.23 | 0 | 3.23 | -3.45 | 362.6 | 55.6 | 1.1 | 0.0 | 0.0 |
| 15.1 | 130°35'38.468"E<br>0°30'20.568"S | 3.99 | 1 | 2.99 | -1.09 | 8.5 | 111.5 | 1.1 | 0.0 | 0.0 |
| 15.9 | 130°33'28.821"E<br>0°30'47.557"S | 4.79 | 2 | 2.79 | -0.33 | 1123.7 | 21.6 | 1.1 | 0.0 | 0.0 |
| 16.5 | 130°33'34.803"E<br>0°30'47.294"S | 4.04 | 1 | 3.04 | -1.11 | 1246.9 | 20.4 | 1.3 | 0.0 | 0.0 |
| 16.8 | 130°35'2.336"E<br>0°30'59.581"S | 3.22 | 0 | 3.22 | -3.45 | 360.8 | 56.5 | 1.2 | 0.0 | 0.0 |
| 18.4 | 130°35'37.496"E<br>0°30'33.986"S | 5.88 | 3 | 2.88 | 0.04 | 5.4 | 133.5 | 1.2 | 0.0 | 0.0 |
| 20.3 | 130°34'10.814"E<br>0°31'2.308"S | 4.90 | 2 | 2.90 | -0.37 | 136.1 | 47.0 | 1.0 | 0.0 | 0.0 |
| 22.6 | 130°33'36.627"E<br>0°30'46.95"S | 3.22 | 0 | 3.22 | -3.45 | 1265.8 | 20.4 | 1.3 | 0.0 | 0.0 |
| 25.5 | 130°35'4.526"E<br>0°31'3.507"S | 7.87 | 5 | 2.87 | 0.56 | 257.4 | 74.5 | 1.2 | 0.0 | 0.0 |
| 29.4 | 130°34'7.41"E<br>0°30'54.959"S | 3.23 | 0 | 3.23 | -3.45 | 386.1 | 33.0 | 1.1 | 0.0 | 0.0 |
| 69.1 | 130°35'15.603"E<br>0°30'46.099"S | 10.14 | 8 | 2.14 | 1.32 | 665.7 | 38.4 | 1.4 | 4.9 | 6.7 |
| 77.9 | 130°34'20.991"E<br>0°31'0.022"S | 7.55 | 5 | 2.55 | 0.67 | 137.3 | 53.4 | 1.2 | 0.0 | 0.0 |
| 121.5 | 130°34'19.367"E<br>0°31'0.326"S | 7.67 | 5 | 2.67 | 0.63 | 115.0 | 52.7 | 1.2 | 0.0 | 0.0 |
| 137.1 | 130°35'38.096"E<br>0°30'45.256"S | 8.56 | 6 | 2.56 | 0.85 | 63.4 | 150.2 | 1.0 | 15.5 | 14.3 |
| 316.8 | 130°34'7.001"E<br>0°30'55.021"S | 10.60 | 8 | 2.60 | 1.12 | 381.8 | 33.6 | 1.3 | 3.9 | 7.5 |
| 380.6 | 130°35'18.591"E<br>0°31'1.654"S | 11.24 | 9 | 2.24 | 1.39 | 226.0 | 87.8 | 1.1 | 22.3 | 15.5 |
| 432.8 | 130°35'35.864"E<br>0°30'22.88"S | 11.11 | 8 | 3.11 | 0.95 | 15.7 | 106.5 | 1.0 | 11.4 | 14.7 |
| 535.2 | 130°35'16.783"E<br>0°31'0.992"S | 14.40 | 11 | 3.40 | 1.17 | 270.3 | 78.5 | 1.1 | 19.7 | 16.4 |
| 601.9 | 130°33'39.392"E<br>0°30'46.509"S | 12.00 | 10 | 2.00 | 1.61 | 1198.4 | 20.5 | 1.0 | 7.7 | 12.5 |
| 817.1 | 130°34'14.995"E<br>0°31'0.318"S | 11.82 | 9 | 2.82 | 1.16 | 148.2 | 49.9 | 1.2 | 8.2 | 13.3 |
| 864.0 | 130°35'14.153"E<br>0°30'55.705"S | 14.93 | 13 | 1.93 | 1.91 | 414.7 | 54.5 | 1.1 | 15.4 | 15.1 |
| 1263.6 | 130°34'20.533"E<br>0°30'59.87"S | 15.49 | 13 | 2.49 | 1.65 | 106.7 | 53.7 | 1.4 | 12.7 | 15.4 |
| 1375.6 | 130°34'59.55"E<br>0°31'11.114"S | 16.06 | 13 | 3.06 | 1.45 | 63.0 | 120.7 | 1.2 | 6.1 | 9.4 |
| 1571.5 | 130°34'51.27"E<br>0°31'17.771"S | 17.75 | 14 | 3.75 | 1.32 | 39.8 | 156.8 | 1.2 | 8.6 | 11.2 |
| 1575.2 | 130°34'10.684"E<br>0°30'54.074"S | 14.99 | 12 | 2.99 | 1.39 | 344.7 | 36.2 | 1.1 | 9.8 | 14.6 |
| 1649.9 | 130°33'47.023"E<br>0°30'41.63"S | 17.39 | 14 | 3.39 | 1.42 | 1091.2 | 21.4 | 1.1 | 2.6 | 7.2 |
| 1716.2 | 130°34'12.378"E<br>0°30'52.021"S | 20.48 | 18 | 2.48 | 1.98 | 400.2 | 33.9 | 1.0 | 0.7 | 4.2 |
| 1862.7 | 130°35'4.149"E<br>0°31'2.038"S | 19.14 | 17 | 2.14 | 2.07 | 257.0 | 76.2 | 1.2 | 11.2 | 12.8 |
| 2329.9 | 130°34'6.453"E<br>0°31'3.816"S | 19.41 | 17 | 2.41 | 1.96 | 172.1 | 45.8 | 1.1 | 3.7 | 9.5 |
| 2620.3 | 130°34'59.79"E<br>0°30'58.346"S | 16.43 | 13 | 3.43 | 1.33 | 328.7 | 54.8 | 1.4 | 7.2 | 11.7 |
| 3865.8 | 130°34'59.574"E<br>0°31'8.023"S | 21.90 | 17 | 4.90 | 1.24 | 82.4 | 109.2 | 1.2 | 17.1 | 14.2 |
| 4429.1 | 130°35'15.345"E<br>0°30'58.95"S | 29.27 | 24 | 5.27 | 1.52 | 301.3 | 74.5 | 1.1 | 17.2 | 13.3 |

**Table C 2 continued**

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 4774.0 | 130°34'52.115"E<br>0°31'14.524"S | 26.18 | 18 | 8.18 | 0.79 | 59.3 | 146.9 | 1.2 | 11.4 | 13.7 |
| 5526.6 | 130°35'17.546"E<br>0°30'54.676"S | 28.75 | 26 | 2.75 | 2.25 | 351.6 | 74.7 | 1.2 | 13.2 | 14.0 |
| 7181.2 | 130°35'16.863"E<br>0°30'50.919"S | 24.91 | 18 | 6.91 | 0.96 | 510.5 | 56.0 | 1.6 | 10.0 | 13.2 |
| 8520.5 | 130°34'9.677"E<br>0°31'3.813"S | 30.95 | 21 | 9.95 | 0.75 | 63.2 | 51.2 | 1.3 | 8.2 | 9.2 |
| 11806.3 | 130°35'11.779"E<br>0°30'56.904"S | 32.34 | 20 | 12.34 | 0.48 | 314.3 | 64.4 | 1.4 | 7.2 | 11.5 |

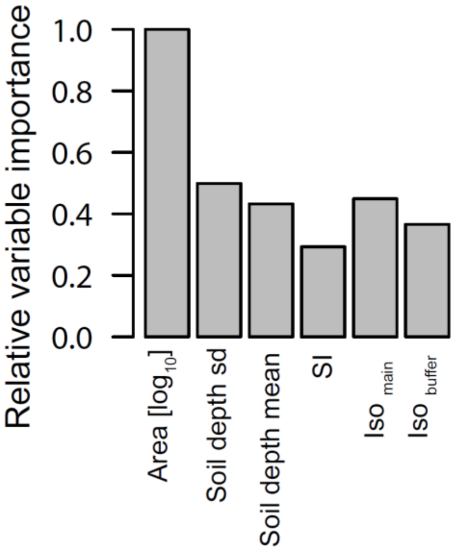

Figure C 3 Relative importance of six explanatory variables explaining observed species richness on the studied islands. Island area emerged as by far the most important variable explaining species richness. Other variables attributable to environmental heterogeneity (soil depth sd) and quality (soil depth mean), edge effects (SI), or isolation ($\text{Iso}_{\text{main}}$ and $\text{Iso}_{\text{buffer}}$) were only of marginal importance. Soil depth mean: mean soil depth recorded on each island; soil depth sd: standard variation of soil depth recorded on each island; SI: shape index – surrogate for the proportion of edge habitat on the islands (calculated as: shape index = $P / [2 * (\pi * A)^{0.5}]$ (Patton 1975); $\text{iso}_{\text{main}}$: distance to the nearest mainland; $\text{iso}_{\text{buffer}}$: surrounding landmass in 1000 m radius of the island (see S4 for data used). Relative variable importance was calculated based on generalized linear models with Gaussian distribution. All above mentioned variables were used in the model and the entire set of possible candidate models were evaluated. The relative variable importance indicated the importance of each variable in explaining species numbers and was calculated using the package MuMIn (Bartoń 2018).

# Appendix D – Supporting information to chapter 5

## Life-history dimensions explain filtering in tropical island tree communities

Julian Schrader, Dylan Craven, Cornelia Sattler, Rodrigo Cámara Leret, Soetjipto Moeljono, & Holger Kreft

In review in *Journal of Ecology*

### Sampling design:

We established transects of 2 x 10 m comprised of five 2 x 2 m plots. The number of transects on an island was roughly proportional to the island area and ranged from one to six transects. For islands < 10 $m^2$ we placed as many plots as possible on the island at the longest extension. This was the case for the ten smallest islands. Larger islands had two transects oriented towards the island centre on the opposite of the island. The interior was covered with a varying number of transects (depending on the island size) of perpendicular orientation ranging from one to four transects. Distance between transects on each island with multiple transects was held constant but was related to the longest extension of an island, and hence varied among islands. Following this method, we ensured to sample the island edge as well as the interior. Soil depth was recorded in all plots at five spots with equal distance to each other (33 cm) and spaced along the central axis of the transect.

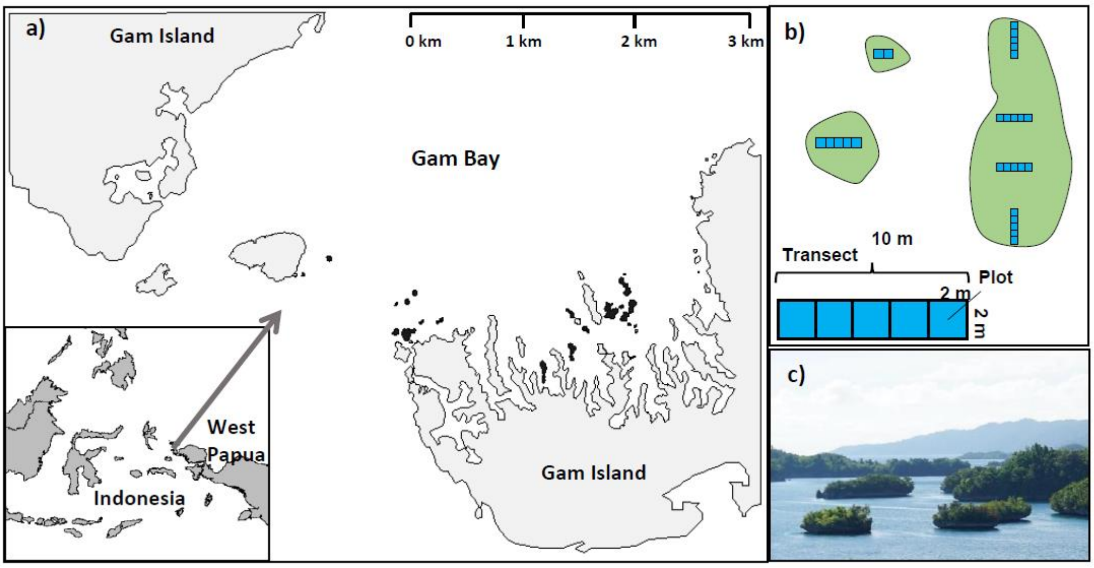

Figure D 1 Study region and study design. a) Location of 40 islands studied (largest sampled islands highlighted in dark grey) in Gam Bay (Raja Ampat Archipelago, Indonesia). b) Species richness and stem numbers were recorded in plots (2 m x 2 m) and transects (10 m x 2 m). Number of transects placed on an island depended on island area, whereas larger islands received more transects. On islands smaller than the area of a single transect, we placed as many plots as possible on each island. c) Gam Bay with some of the islands studied (Photo credit: JS).

Table D 1 Island properties of the 40 islands studied. Stem numbers were extrapolated to the whole island from the stem numbers recorded in the transects. FDis: functional dispersion, calculated from eleven traits using the R-package *FD* (Laliberté and Legendre 2010). FDis$_{inc}$: FDis calculated based on incidence data. FDis$_{abun}$: FDis calculated based on abundance data. Soil depth sd: standard deviation of soil depth recorded in plots on each island.

| **Area (m$^2$)** | **Island coordinates** | **Species richness** | **Extra-polated stem numbers** | **Basal area (m$^2$ ha$^{-1}$)** | **FDis$_{inc}$** | **FDis$_{abun}$** | **Soil depth sd (cm)** | **Mean canopy height (m)** |
|---|---|---|---|---|---|---|---|---|
| 4774.04 | 130°34'52.115"E<br>0°31'14.524"S | 18 | 17568 | 17.49 | 3.44 | 3.67 | 13.67 | 8.22 |
| 7.29 | 130°34'30.544"E<br>0°31'2.808"S | 1 | 7 | 0.95 | 0 | 0 | 0.00 | 1.80 |
| 2329.91 | 130°34'6.453"E<br>0°31'3.816"S | 17 | 9786 | 15.86 | 3.04 | 2.74 | 9.55 | 7.37 |
| 8.06 | 130°34'6.641"E<br>0°31'4.363"S | 1 | 8 | 0.87 | 0 | 0 | 0.00 | 1.80 |
| 20.27 | 130°34'10.814"E<br>0°31'2.308"S | 2 | 61 | 6.65 | 1.62 | 1.44 | 0.00 | 3.54 |
| 316.83 | 130°34'7.001"E<br>0°30'55.021"S | 8 | 1426 | 20.04 | 3.32 | 2.75 | 7.55 | 10.59 |
| 1575.25 | 130°34'10.684"E<br>0°30'54.074"S | 13 | 5513 | 14.86 | 2.76 | 3.24 | 14.58 | 9.46 |
| 1263.62 | 130°34'20.533"E<br>0°30'59.87"S | 14 | 4549 | 20.65 | 2.90 | 2.95 | 15.38 | 8.29 |
| 1716.25 | 130°34'12.378"E<br>0°30'52.021"S | 19 | 7809 | 30.74 | 2.83 | 3.42 | 4.19 | 9.07 |
| 121.47 | 130°34'19.367"E<br>0°31'0.326"S | 5 | 267 | 3.36 | 2.68 | 2.29 | 0.00 | 5.09 |
| 817.06 | 130°34'14.995"E<br>0°31'0.318"S | 9 | 4194 | 16.09 | 2.74 | 2.85 | 13.32 | 10.09 |
| 1649.94 | 130°33'47.023"E<br>0°30'41.63"S | 14 | 5115 | 7.36 | 2.77 | 3.36 | 7.21 | 7.61 |
| 601.88 | 130°33'39.392"E<br>0°30'46.509"S | 10 | 2528 | 9.41 | 2.86 | 2.82 | 12.51 | 7.11 |
| 535.20 | 130°35'16.783"E<br>0°31'0.992"S | 12 | 2141 | 11.40 | 3.20 | 2.55 | 16.40 | 7.00 |
| 380.60 | 130°35'18.591"E<br>0°31'1.654"S | 9 | 2740 | 29.03 | 2.93 | 2.94 | 15.45 | 9.36 |
| 137.07 | 130°35'38.096"E<br>0°30'45.256"S | 6 | 754 | 15.96 | 2.24 | 1.64 | 14.32 | 7.44 |
| 18.43 | 130°35'37.496"E<br>0°30'33.986"S | 3 | 129 | 16.39 | 2.70 | 0.96 | 0.00 | 4.05 |
| 432.77 | 130°35'35.864"E<br>0°30'22.88"S | 8 | 2337 | 15.45 | 3.06 | 2.35 | 14.74 | 7.28 |
| 15.10 | 130°35'38.468"E<br>0°30'20.568"S | 1 | 30 | 2.22 | 0 | 0 | 0.00 | 3.54 |
| 864 | 130°35'14.153"E<br>0°30'55.705"S | 13 | 5011 | 26.04 | 3.20 | 3.30 | 15.14 | 8.86 |
| 10.51 | 130°34'28.442"E<br>0°31'2.992"S | 2 | 53 | 14.47 | 1.37 | 1.32 | 0.00 | 6.34 |
| 1571.48 | 130°34'51.27"E<br>0°31'17.771"S | 14 | 7072 | 19.26 | 3.06 | 2.81 | 11.19 | 10.14 |
| 1375.63 | 130°34'59.55"E<br>0°31'11.114"S | 14 | 7016 | 10.35 | 2.89 | 2.11 | 9.39 | 8.49 |
| 1862.75 | 130°35'4.149"E<br>0°31'2.038"S | 17 | 10245 | 24.39 | 3 | 3 | 12.77 | 8.29 |
| 69.14 | 130°35'15.603"E<br>0°30'46.099"S | 8 | 461 | 23.28 | 2.92 | 2.64 | 6.73 | 6.91 |
| 3865.84 | 130°34'59.574"E<br>0°31'8.023"S | 17 | 18865 | 13 | 2.86 | 2.38 | 14.24 | 6.79 |
| 11806.28 | 130°35'11.779"E<br>0°30'56.904"S | 22 | 73986 | 20.15 | 3.12 | 2.57 | 11.55 | 7.54 |

**Table D 1 continued**

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 4429.05 | 130°35'15.345"E<br>0°30'58.95"S | 24 | 18779 | 16.24 | 3.07 | 3.27 | 13.34 | 7.30 |
| 5526.65 | 130°35'17.546"E<br>0°30'54.676"S | 27 | 26159 | 18.22 | 3.08 | 2.80 | 14.01 | 7.27 |
| 8520.55 | 130°34'9.677"E<br>0°31'3.813"S | 22 | 48283 | 25.50 | 3.11 | 3.02 | 9.16 | 7.45 |
| 7181.16 | 130°35'16.863"E<br>0°30'50.919"S | 19 | 44044 | 22.57 | 3.09 | 2.82 | 13.20 | 7.84 |
| 13.63 | 130°34'6.863"E<br>0°30'54.819"S | 1 | 14 | 0.87 | 0 | 0 | 0.00 | 1.83 |
| 16.46 | 130°33'34.803"E<br>0°30'47.294"S | 1 | 8 | 0.39 | 0 | 0 | 0.00 | 1.83 |
| 15.94 | 130°33'28.821"E<br>0°30'47.557"S | 2 | 48 | 4.25 | 2.28 | 2.03 | 0.00 | 1.89 |
| 7 | 130°34'7.829"E<br>0°31'4.02"S | 1 | 14 | 3.70 | 0 | 0 | 0.00 | 4.91 |
| 77.94 | 130°34'20.991"E<br>0°31'0.022"S | 5 | 182 | 4.86 | 2.83 | 2.38 | 0.00 | 4.28 |
| 5.75 | 130°34'51.319"E<br>0°31'19.832"S | 2 | 11 | 2.92 | 3.32 | 3.32 | 0.00 | 4.23 |
| 25.49 | 130°35'4.526"E<br>0°31'3.507"S | 6 | 76 | 5.42 | 2.31 | 2.21 | 0.00 | 1.83 |
| 6.34 | 130°35'3.783"E<br>0°31'3.081"S | 1 | 6 | 0.79 | 0 | 0 | 0.00 | 4.40 |
| 2620.30 | 130°34'59.79"E<br>0°30'58.346"S | 14 | 9695 | 15.20 | 2.95 | 2.96 | 11.68 | 6.87 |

Table D 2 Species-trait matrix of 57 species sampled on 40 islands in the study area. Seed mass refers to the dry mass of an average seed. Height indicated the maximal tree height for each species sampled. LMA: leaf mass per area; Chlorophyll values from Chlorophyll-meter (Konica Minolta, SPAD – 502DI Plus) were transformed using the equation from Coste et al. (2010). WD: wood density. LA: Leaf area. Ch: Chlorophyll.

| **Species** | **Fruit mass (g)** | **Seed mass (g)** | **Height (m)** | **WD (g $cm^{-3}$)** | **LMA (g $cm^{-2}$)** | **LA ($cm^2$)** | **Ch. (µm $cm^{-2}$)** | **Leaf N (%)** | **Leaf C:N** | **Leaf C:P** | **Leaf N:P** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aglaia elaeagnoidea* (A.Juss.) Benth. | 0.01 | 0.4546* | 6.23 | 0.84 | 1.14 | 32.68 | 83.37 | 1.93 | 27.56 | 101.72 | 3.72 |
| *Allophylus cobbe* (L.) Raeusch. | 1.46 | 0.0522 | 4.37 | 0.74 | 0.55 | 47.74 | 68.44 | 2.24 | 21.91 | 96.94 | 4.43 |
| *Antidesma bunius* (L.) Spreng. | 0.05 | 0.0233 | 2.95 | 0.78 | 0.71 | 48.61 | 44.45 | 1.41 | 33.08 | 155.44 | 4.69 |
| *Bikkia gaudichaudiana* Brongn. | 0.43 | 0.0001 | 1.83 | 0.82 | 1.12 | 57.63 | 94.06 | 1.01 | 46.54 | 358.02 | 7.68 |
| *Buchanania arborescens* (Blume) Blume | 0.35 | 0.3297 | 5.37 | 0.52 | 1.07 | 60.23 | 100.11 | 0.92 | 52.41 | 252.30 | 4.79 |
| *Calophyllum inophyllum L.* | 9.07 | 5.0717 | 9.17 | 0.48 | 1.07 | 77.52 | 79.53 | 1.07 | 49.65 | 272.95 | 5.48 |
| *Calophyllum vexans* P.F.Stevens | 0.04 | 2.6556* | 6.73 | 0.81 | 1.83 | 19.05 | 114.55 | 1 | 57.26 | 305.75 | 5.32 |
| *Canarium oleosum* (Lam.) Engl. | 0.24 | 4.3642* | 6.67 | 0.63 | 0.77 | 60.06 | 40.72 | 1.56 | 31.56 | 102.44 | 3.25 |
| *cf. Maytenus cupularis* Ding Hou | 1.04 | 0.0164 | 3.33 | 0.57 | 1.45 | 54.13 | 44.15 | 0.93 | 51.36 | 61.24 | 1.19 |
| *Cupaniopsis sp.* | 0.40 | 0.1678* | 5.07 | 0.74 | 1.30 | 21.62 | 44.52 | 1.47 | 37.67 | 182.75 | 4.84 |
| *Decaspermum bracteatum (*Roxb.) A.J.Scott | 0.04 | 0.0020 | 6.93 | 0.67 | 1.25 | 20.48 | 49.52 | 0.86 | 60.86 | 325.99 | 5.43 |
| *Diospyros maritima* Blume | 0.22 | 0.0304 | 6.10 | 0.74 | 1.94 | 34.35 | 54.72 | 1.04 | 47.61 | 271.15 | 5.69 |
| *Eugenia reinwardtiana* (Blume) A.Cunn. ex DC. | 0.59 | 0.0886 | 12.27 | 0.89 | 1.72 | 30.15 | 74.56 | 0.63 | 86.46 | 110.70 | 1.28 |
| *Exocarpos latifolius* R.Br. | 0.38 | 0.4330 | 6.73 | 0.88 | 1.61 | 32.68 | 81.77 | 1.72 | 32.24 | 178.74 | 5.54 |
| *Ficus microcarpa* L.f. | 0.14 | 0.0415 | 5.17 | 0.75 | 1.23 | 41.42 | 77.34 | 1.46 | 33.11 | 184.55 | 5.58 |
| *Ficus nervosa B.*Heyne ex Roth | 0.24 | 0.0001 | 2 | 0.74 | 1.32 | 21.10 | 44.52 | 1.12 | 42.84 | 185.61 | 4.34 |
| *Ficus pedunculosa* Miq. | 0.32 | 0.0024 | 2.15 | 0.80 | 1.05 | 60.39 | 45.42 | 1.23 | 37.71 | 177.30 | 4.72 |
| *Ficus prasinicarpa* Elmer | 0.05 | 0.0002 | 1.45 | 0.44 | 0.83 | 45.93 | 40.29 | 1.51 | 32.35 | 95.09 | 2.93 |
| *Ficus tinctoria* G.Forst. | 0.13 | 0.0005 | 4 | 0.77 | 1.47 | 34.46 | 52.46 | 1.22 | 38.54 | 306.72 | 7.98 |
| *Geijera sp.* | **0.38** | 0.0347* | 2.80 | **0.7**0 | 1.03 | 36.47 | **44.15** | 2.10 | 21.25 | 78 | 3.67 |
| *Geniostoma rupestre* | 0.04 | 0.0003 | 2 | 0.65 | 1.22 | 3.66 | 85.71 | 1.21 | 38.10 | 91.27 | 2.40 |

|  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
| J.R.Forst. & G.Forst. |  |  |  |  |  |  |  |  |  |  |  |
| *Glochidion castaneum* Airy Shaw | 0.21 | 0.0071 | 5.13 | 0.66 | 1.40 | 75.15 | 71.24 | 1.06 | 49.61 | 88.69 | 1.79 |
| *Gnetum gnemon* L. | 0.77 | 0.4966 | 4.30 | 0.68 | 0.87 | 65.20 | **44.15** | 1.93 | 25.64 | 89.76 | 3.50 |
| *Guettarda speciosa* L. | 2.47 | 0.8814* | 6.87 | 0.67 | 1.03 | 122.73 | 19.45 | 1.34 | 38.22 | 166.58 | 4.35 |
| *Intsia bijuga* (Colebr.) Kuntze | 20.03 | 0.3242 | 9.33 | 0.53 | 0.67 | 57.66 | 48.51 | 2.79 | 18.10 | 43.52 | 2.40 |
| *Ixora timorensis* Decne. | 0.07 | 0.0144 | 8.50 | 0.79 | 0.91 | 82.50 | 59.24 | 1.18 | 42.70 | 231.20 | 5.40 |
| *Lunasia amara* Blanco | 0.14 | 0.0138 | 3.93 | 0.82 | 0.77 | 110.58 | 76.15 | 1.82 | 25.64 | 114.64 | 4.46 |
| *Macaranga dioica* (G.Forst.) Müll.Arg. | 0.01 | 0.0060 | 3.90 | 0.50 | 0.56 | 114.29 | 45.12 | 1.38 | 35.57 | 168.90 | 4.74 |
| *Manilkara sp.* | **0.43** | 0.4448* | 4.13 | 0.76 | 1.37 | 33.80 | 61.95 | 1.08 | 51.97 | 50.65 | 0.98 |
| *Micromelum minutum* Wight & Arn | 0.20 | 0.0745 | 3.15 | 0.64 | 0.79 | 50.37 | 72.27 | 2.35 | 21.72 | 164.47 | 7.57 |
| *Mimusops elengi* L. | **0.35** | 0.6030* | 4.40 | 0.78 | 0.63 | 19.48 | 55.48 | 2.38 | 21.31 | 140.65 | 6.60 |
| *Morinda citrifolia* L. | 3.18 | 0.0117 | 2.35 | 0.44 | 0.52 | 83.28 | 44.22 | 1.63 | 29.32 | 257.88 | 8.77 |
| *Myrsine rawacensis* A. DC. | **2.47** | 0.0147 | 8.27 | 0.78 | 1.17 | 15.23 | 67.55 | 0.92 | 59.35 | 358.98 | 6.04 |
| *Pandanus sp.* | **9.07** | 0.5758* | 5.40 | 0.29 | 1.97 | 51.15 | 55.65 | 0.78 | 65.27 | 314.65 | 4.84 |
| *Pemphis acedula* J.R. Forst. & G. Forst. | 0.03 | 0.0006 | 1.80 | 0.99 | 1.29 | 1.78 | 39.30 | 1.15 | 38.02 | 129.41 | 3.40 |
| *Phyllanthus praelongipes* Airy Shaw & G.L.Webster | **0.52** | 0.0003 | 5 | 0.72 | 0.98 | 15.46 | 52.13 | 1.05 | 44.28 | 240.95 | 5.44 |
| *Pittosporum ferrugineum* W.T.Aiton | 0.21 | 0.0076 | 3.60 | 0.52 | 0.91 | 35.96 | 27.73 | 1.72 | 30.71 | 134.81 | 4.40 |
| *Planchonella obovata* (R.Br.) Pierre | 0.03 | 0.0190 | 6.70 | 0.88 | 1.70 | 22.68 | 64.44 | 1.63 | 34.43 | 280.39 | 8.17 |
| *Pleurostylia opposita* (Wall.) Alston | **0.43** | **0.0003** | 4.20 | 0.73 | 1.17 | 12.35 | **94.06** | 1.01 | 49.33 | 183.60 | 3.74 |
| *Podocarpus neriifolius* D.Don | **0.11** | 1.2990* | 6.50 | 0.60 | 1.69 | 4.97 | 49.46 | 0.68 | 72.11 | 192.09 | 2.66 |
| *Schefflera sp.* | **0.13** | 0.0434* | 2.20 | 0.51 | 0.60 | 98.58 | 67.65 | 0.96 | 51.95 | 97.84 | 1.89 |
| *Severinia lauterbachii* Swingle | 0.52 | 0.1176 | 5.77 | 0.77 | 1.06 | 45.58 | 64.57 | 1.80 | 26.09 | 227.47 | 8.71 |
| *Spathiostemon javensis* Blume | 0.02 | **0.0190** | 4.90 | 0.70 | 0.99 | 40.35 | 107.10 | 1.79 | 28.69 | 286.66 | 9.98 |
| *Syzygium nitidum* Benth. | 0.76 | 0.3260 | 5.13 | 0.67 | 1.37 | 58.25 | 49.94 | 0.89 | 60.98 | 421.27 | 6.92 |
| *Tarenna sambucina* (G.Forst.) | 0.07 | 0.0119 | 7.17 | 0.76 | 1.11 | 39.56 | 48.91 | 1.31 | 37.75 | 198.36 | 5.23 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| T.Durand ex Drake | | | | | | | | | | | |
| *Timonius sp. 1* | 0.51 | 0.0025* | 4.40 | 0.70 | 1.43 | 46.24 | 48.20 | 1.02 | 52.26 | 303.44 | 5.80 |
| *Timonius sp. 2* | 0.24 | 0.0044 | 3.93 | 0.82 | 2.60 | 8.36 | 24.21 | 1.15 | 43.77 | 143.43 | 3.27 |
| *Wikstroemia androsaemifolia* Decne. | 0.02 | 0.0114 | 4.07 | 0.38 | 0.90 | 22.39 | 57.91 | 1.72 | 28.49 | 137.40 | 4.83 |
| Unidentified species 1 | **0.02** | **0.0025** | 4.80 | **0.76** | **1.25** | **58.25** | **44.22** | **0.92** | **51.36** | **140.65** | **2.40** |
| Unidentified species 2 | 0.33 | 0.2656 | 3.90 | 0.56 | 1.28 | 39.02 | 88.34 | 1.12 | 46.51 | 205.11 | 4.43 |
| Unidentified species 3 | **0.52** | **0.0323** | 4.50 | 0.83 | 1.12 | 26.48 | 41.15 | 1.42 | 36.60 | 177.85 | 4.86 |
| Unidentified species 4 | 0.30 | 0.0836 | 2.70 | 0.74 | 1.08 | 48.20 | 87.85 | 1.38 | 37.70 | 152.86 | 4.06 |
| Unidentified species 5 | **0.77** | **0.0147** | 12 | 0.72 | 1.29 | 35.40 | 65.33 | 0.85 | 63.11 | 372.49 | 5.93 |
| Unidentified species 6 | 0.37 | 0.0323 | 5.13 | 0.63 | 0.71 | 51.55 | 70.94 | 1.43 | 38.67 | 126.19 | 3.27 |
| Unidentified species 7 | 0.06 | 0.0220 | 2.80 | 0.77 | 1.04 | 26.32 | 57.59 | 1.16 | 38.93 | 101.87 | 2.62 |
| Unidentified species 8 | 0.11 | 0.0002 | 2.05 | 0.73 | 1.09 | 126.66 | 59.83 | 1.47 | 30.99 | 83.96 | 2.72 |
| Unidentified species 9 | **0.04** | **0.0347** | 4.53 | 0.51 | 1.23 | 38.13 | 60.77 | 1.08 | 45.17 | 125.85 | 2.80 |

* Seed data from Royal Botanic Gardens Kew. (2018) Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/ (August 2018)

Trait values in bold were derived from trait imputation using R-package ‘mice’ (Buuren and Groothuis-Oudshoorn 2011).

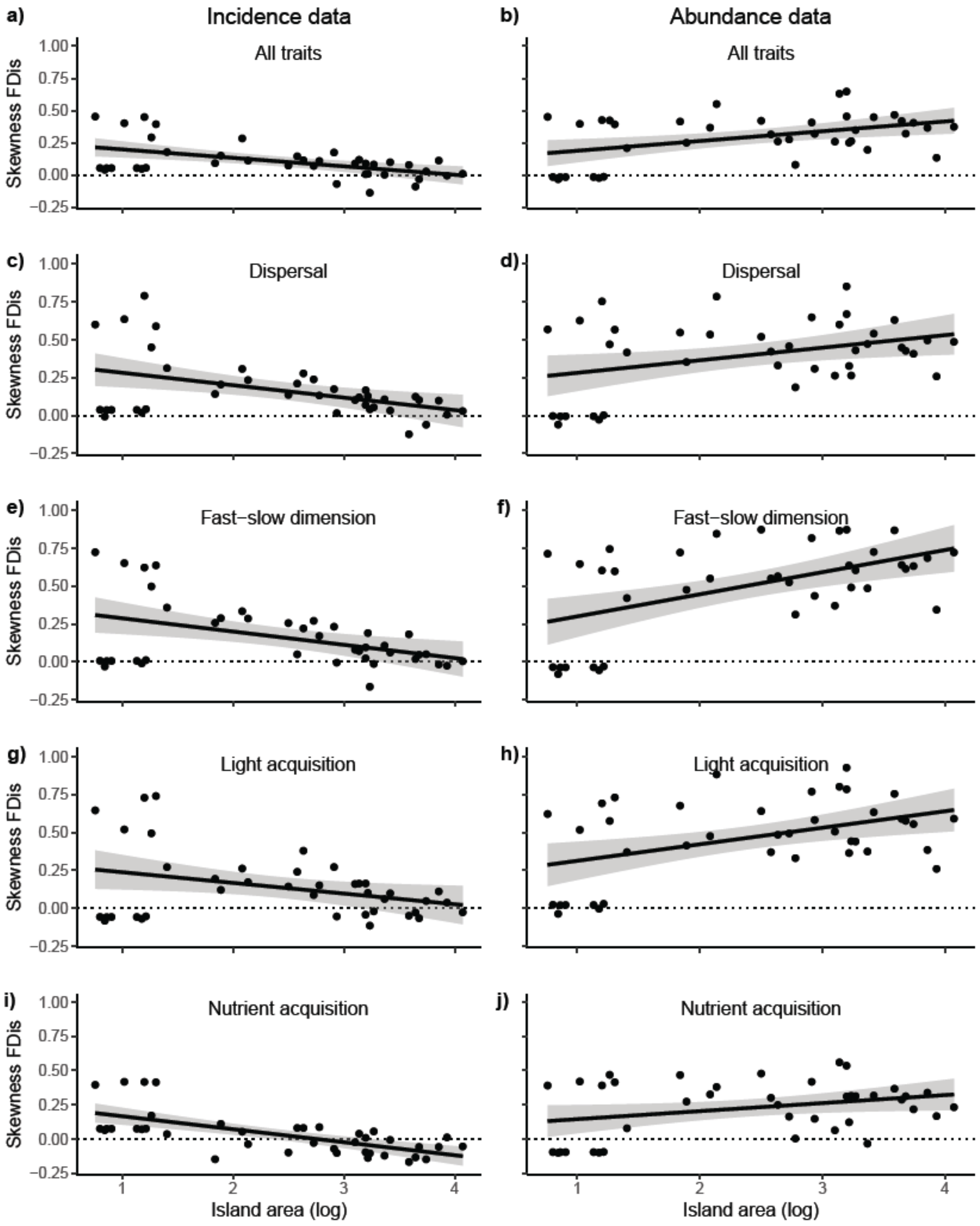

Figure D 2 Skewness values of functional dispersion (FDis) for incidence and abundance data for all traits and trait syndromes with island area of the 1,000 randomisations (null models were used that maintained sampled species richness). Linear regression indicate that data was left-skewed (positive values) and differed significantly with island area. 95% confidence intervals are indicated by grey bands. Significant responses ($p < 0.05$) are indicated by solid black lines.

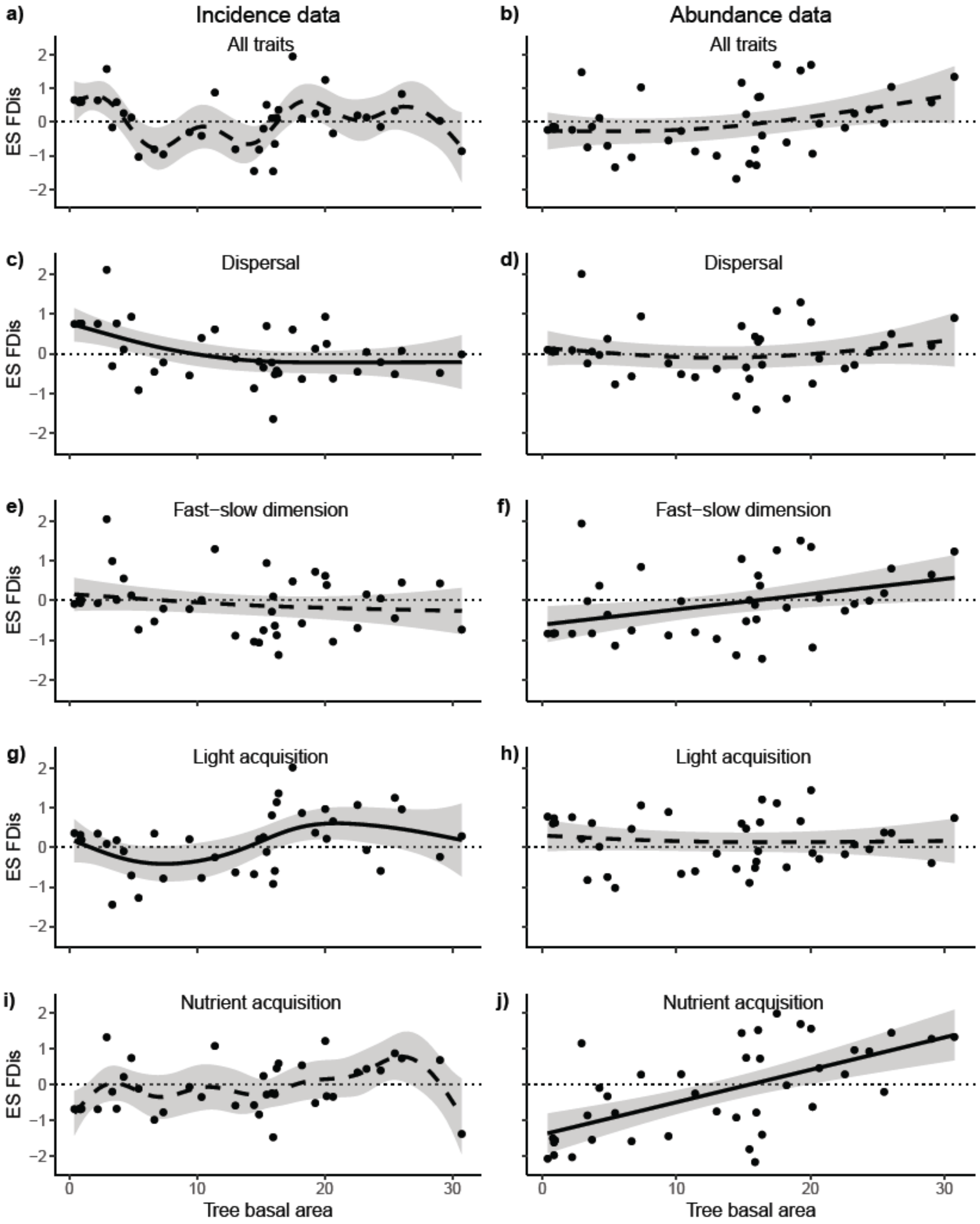

Figure D 3 Scaling of the effect size (ES) of functional dispersion (FDis) of observed communities and randomly created communities of all traits and four trait syndromes with tree basal area for incidence (left panels) and abundance (right panels) data of trees on islands. Positive ES indicate that the observed functional dispersion on the island is greater than expected and negative ES indicate that the observed FDis is lower than expected. FDis was calculated as partial residuals of tree basal area corrected for island area. 95% confidence intervals are indicated by grey bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p < 0.05$) are indicated by solid black lines and not significant smoothed fixed effects are indicated by dashed lines. Grouping of traits into life history dimensions are shown in Table 5.1 in the main document.

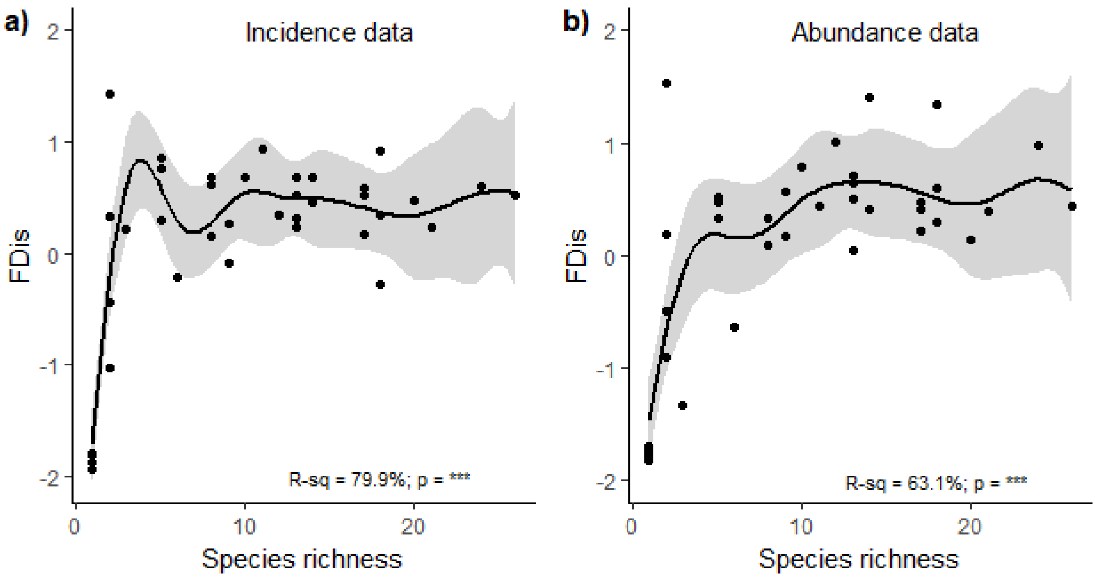

Figure D 4 Scaling of functional dispersion (FDis) and species richness for incidence (left panels) and abundance (right panels) data of trees on islands. 95% confidence intervals are indicated by grey bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p < 0.05$) are indicated by solid black lines.

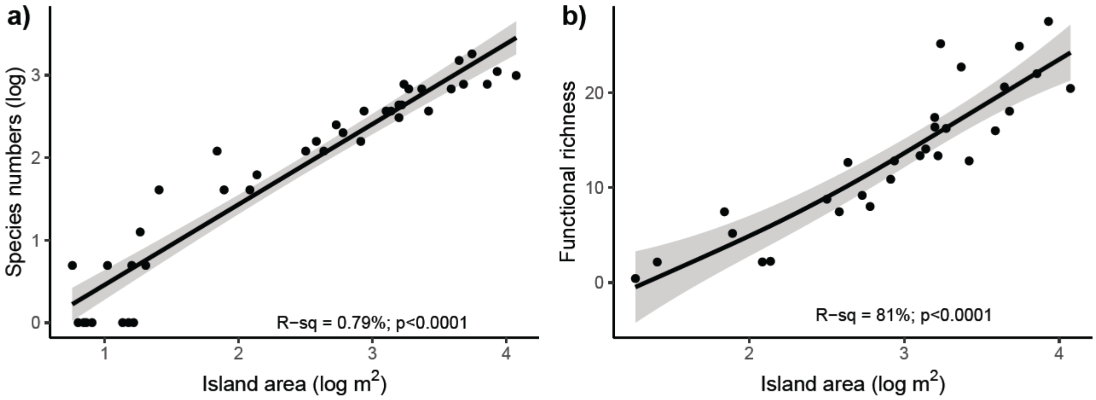

Figure D 5 Scaling of species richness and functional richness with island area in log-log space. a) The Power model is used to fit the relationship of species richness and island area. The Power model is most the most commonly used species-area model and normally provides the best fit to island species-area relationships (Matthews et al. 2016). b) Functional richness is a commonly used measure to describe functional diversity on islands (e.g. Ding et al. 2013; Whittaker et al. 2014) and we provide the fit of functional richness with island area to make our results comparable to other literature on functional diversity-area relationships. Regression line for the functional richness-area relationship was calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p < 0.05$) are indicated by solid black lines.

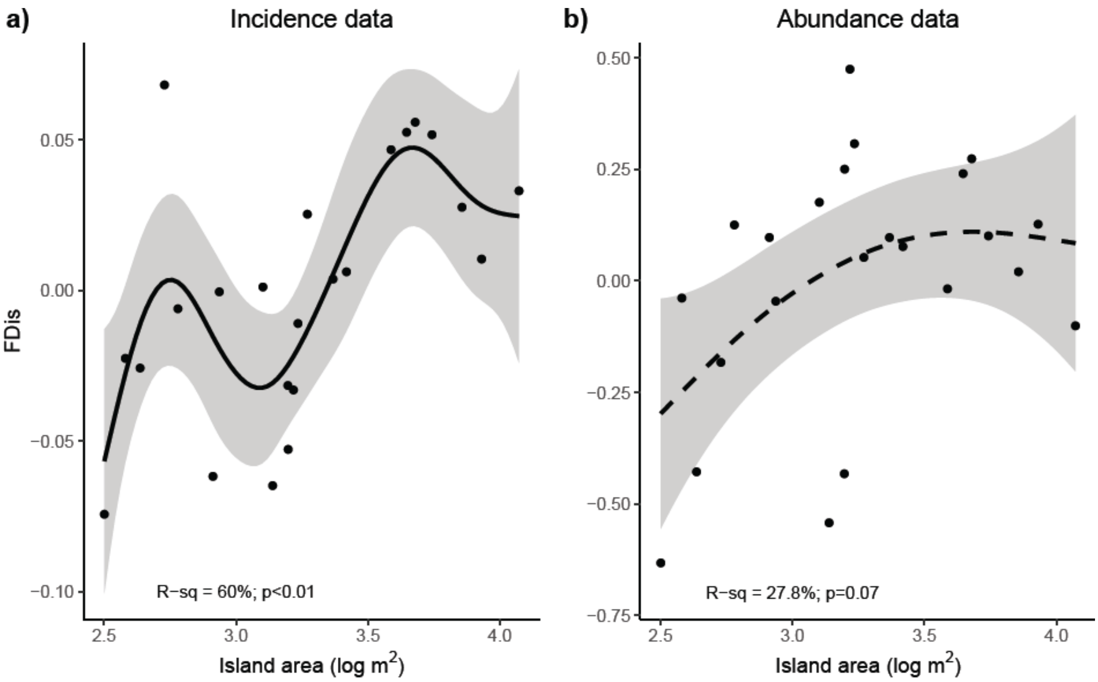

Figure D 6 Spatial scaling of rarefied functional dispersion (FDis) in its a) incidence and b) abundance form of trees on islands. Rarefied FDis increased for both incidence and abundance data indicating that other effects but area, such as habitat and niche diversity, lead to an increase in FDis with island area. Rarefied functional diversity was calculated from the mean FDis of 20 randomly drawn individuals repeated 1000 times for each island. Note that only on 23 islands more than 20 individuals were sampled, which was the threshold for islands being included in this analyses. Regression lines indicate partial fits of island area after accounting for tree basal area. 95% confidence intervals are displayed by grey bands. Regression lines are calculated by applying generalised additive mixed effects models. Significant smoothed fixed effects ($p<0.05$) are indicated by solid black lines and non-significant smoothed fixed effects are indicated by dashed lines.

Table D 3 Pearson correlation between effect size of functional dispersion (for all traits and four trait syndromes) of observed communities and communities derived from 1,000 randomisations of two different null models for incidence and abundance data. Null models were calculated within the R-package *picante* (Kembel et al. 2010) using the command *randomizeMatrix*. One null model maintained sampled species richness for each island (*richness*) and one null model maintaining species occurrence frequency and sampled species richness (*independentswap*).

| **Data type** | **All traits** | **Dispersal** | **Fast-slow dimension** | **Light acquisition** | **Nutrient acquisition** |
|---|---|---|---|---|---|
| Incidence | 0.99 | 0.98 | 0.98 | 0.98 | 0.94 |
| Abundance | 0.66 | 0.70 | 0.80 | 0.46 | 0.65 |

# Appendix E – Supporting information to chapter 6

## Species-area relationships on small islands worldwide differ among growth forms

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Table E 1 Best supported species-area relationship (SAR) and breakpoint area for 17 archipelagos and species richness for all plant species and herb, shrub, and tree species richness. Best SAR was calculated based on lowest AIC.

| **Archipelago** | **Growth form** | **Best SAR** | **Breakpoint (in km$^2$)** |
|---|---|---|---|
| Kuril Islands | all | linear | NA |
| Kuril Islands | herb | linear | NA |
| Kuril Islands | shrub | linear | NA |
| Kuril Islands | tree | linear | NA |
| Mariana Islands | all | zero_slope | 38.52 |
| Mariana Islands | herb | linear | NA |
| Mariana Islands | shrub | zero_slope | 38.38 |
| Mariana Islands | tree | zero_slope | 39.44 |
| Central Pacific Islands | all | linear | NA |
| Central Pacific Islands | herb | zero_slope | 0.19 |
| Central Pacific Islands | shrub | linear | NA |
| Central Pacific Islands | tree | linear | NA |
| New Zealand Islands | all | two_slope | 0.03 |
| New Zealand Islands | herb | two_slope | 0.03 |
| New Zealand Islands | shrub | two_slope | 0.03 |
| New Zealand Islands | tree | two_slope | 0.34 |
| Great Barrier Reef Islands | all | zero_slope | 1.22 |
| Great Barrier Reef Islands | herb | zero_slope | 1.23 |
| Great Barrier Reef Islands | shrub | zero_slope | 1.18 |
| Great Barrier Reef Islands | tree | zero_slope | 1.22 |
| Mascarene Islands | all | two_slope | 0.38 |
| Mascarene Islands | herb | two_slope | 0.18 |
| Mascarene Islands | shrub | zero_slope | 0.93 |
| Mascarene Islands | tree | two_slope | 0.24 |

**Table E 1 continued**

| | | | |
|---|---|---|---|
| Houtman Abrolhos Islands | all | two_slope | 0.02 |
| Houtman Abrolhos Islands | herb | two_slope | 0.01 |
| Houtman Abrolhos Islands | shrub | two_slope | 0.41 |
| Houtman Abrolhos Islands | tree | two_slope | 0 |
| West Hawaii Islands and Midway Atoll | all | zero_slope | 0.19 |
| West Hawaii Islands and Midway Atoll | herb | zero_slope | 0.22 |
| West Hawaii Islands and Midway Atoll | shrub | linear | NA |
| West Hawaii Islands and Midway Atoll | tree | linear | NA |
| Sea of Cortez Islands | all | zero_slope | 0.4 |
| Sea of Cortez Islands | herb | zero_slope | 0.39 |
| Sea of Cortez Islands | shrub | zero_slope | 0.53 |
| Sea of Cortez Islands | tree | linear | NA |
| Maine Islands | all | linear | NA |
| Maine Islands | herb | linear | NA |
| Maine Islands | shrub | linear | NA |
| Maine Islands | tree | linear | NA |
| Nuyts Archipelago (South Australia) | all | linear | NA |
| Nuyts Archipelago (South Australia) | herb | linear | NA |
| Nuyts Archipelago (South Australia) | shrub | linear | NA |
| Nuyts Archipelago (South Australia) | tree | linear | NA |
| Islands near Perth | all | two_slope | 0 |
| Islands near Perth | herb | two_slope | 0 |
| Islands near Perth | shrub | two_slope | 0 |
| Islands near Perth | tree | zero_slope | 0.01 |
| Nui Atoll | all | linear | NA |
| Nui Atoll | herb | linear | NA |
| Nui Atoll | shrub | linear | NA |
| Nui Atoll | tree | linear | NA |
| Adria | all | two_slope | 0 |
| Adria | herb | two_slope | 2 |
| Adria | shrub | linear | NA |
| Adria | tree | linear | NA |
| West Aegean Islands | all | zero_slope | 1.08 |
| West Aegean Islands | herb | zero_slope | 1.19 |
| West Aegean Islands | shrub | zero_slope | 0.14 |
| West Aegean Islands | tree | zero_slope | 2.7 |
| East Aegean Islands | all | two_slope | 1.54 |
| East Aegean Islands | herb | two_slope | 1.09 |
| East Aegean Islands | shrub | two_slope | 2.29 |
| East Aegean Islands | tree | zero_slope | 3.44 |
| South Aegean Islands | all | zero_slope | 1.01 |
| South Aegean Islands | herb | zero_slope | 0.94 |
| South Aegean Islands | shrub | two_slope | 1.1 |
| South Aegean Islands | tree | zero_slope | 3.82 |

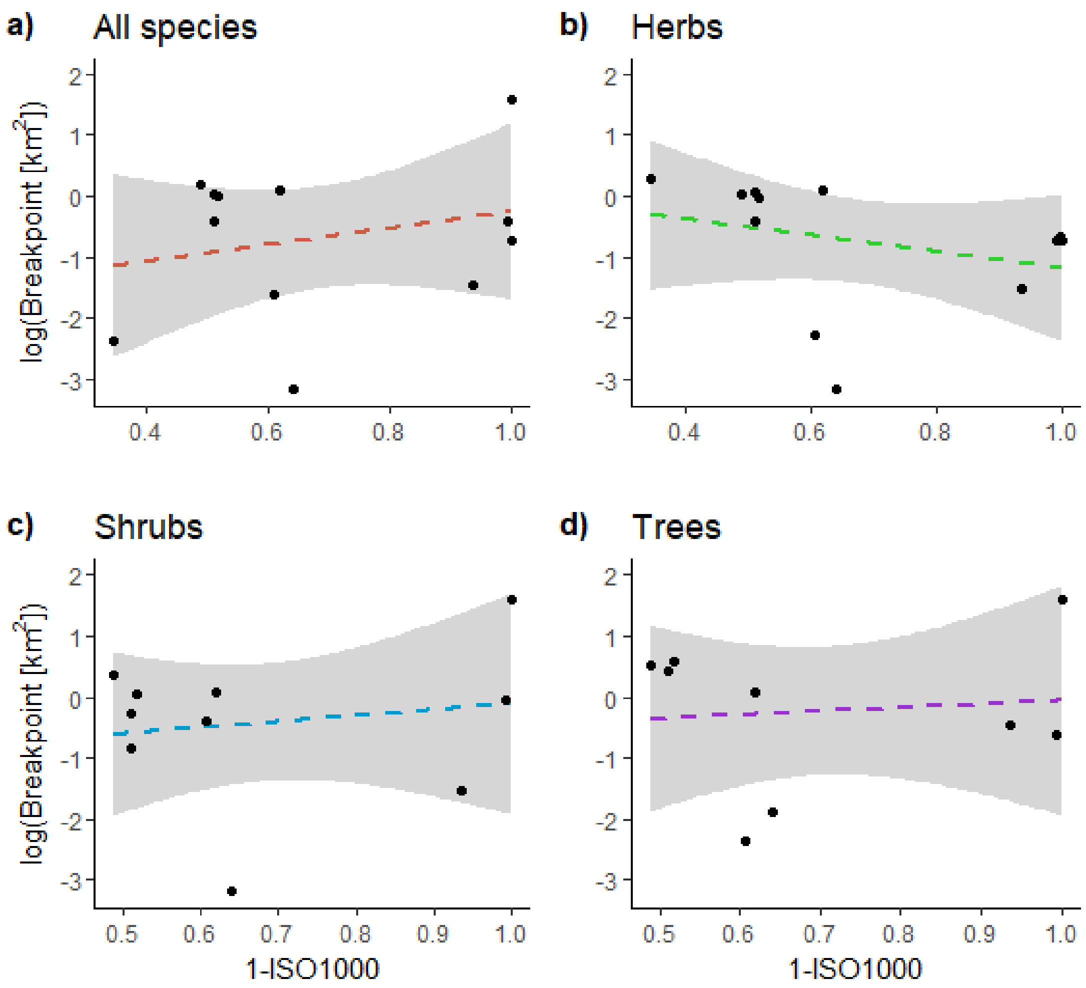

Figure E 1 Relationship between archipelago isolation and range of the small-island effect (SIE) for species richness data for a) total species richness, and species richness of b) herbs, c) shrubs, d) and trees. Only archipelagos were considered that indicated the presence of a SIE. The range of the SIE was determined by using the breakpoint of fitted breakpoint models. Isolation is represented by one minus the mean buffer area (1000 km) and refers to the proportion of ocean around all islands within an archipelago.

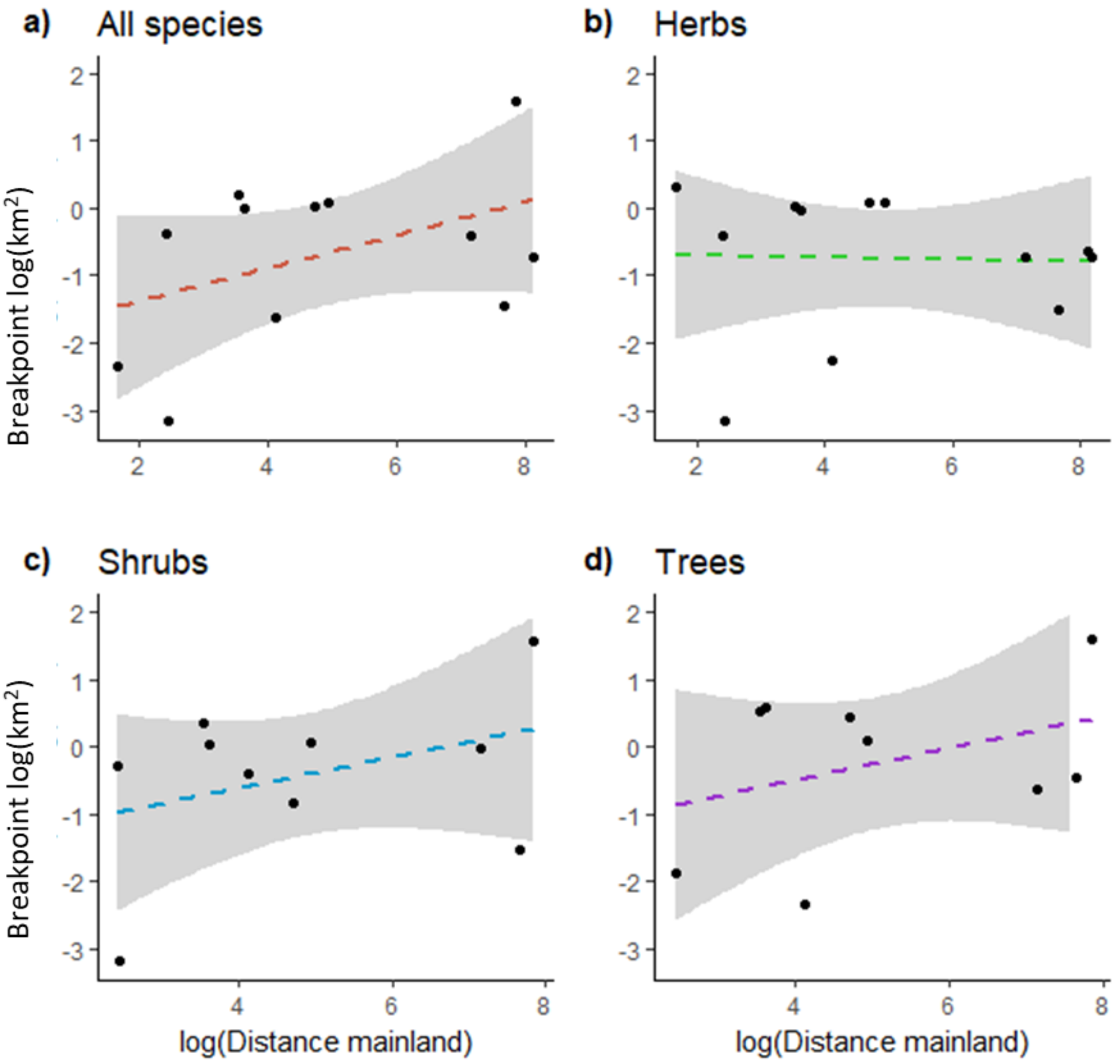

Figure E 2 Relationship between archipelago isolation and range of the small-island effect (SIE) for species richness data for all species, and all herbs, shrubs, and trees. Only archipelagos were considered that indicated the presence of a SIE. The range of the SIE was determined by using the breakpoint of fitted breakpoint models. Isolation is represented as the distance to the nearest mainland (ISOdist; km).

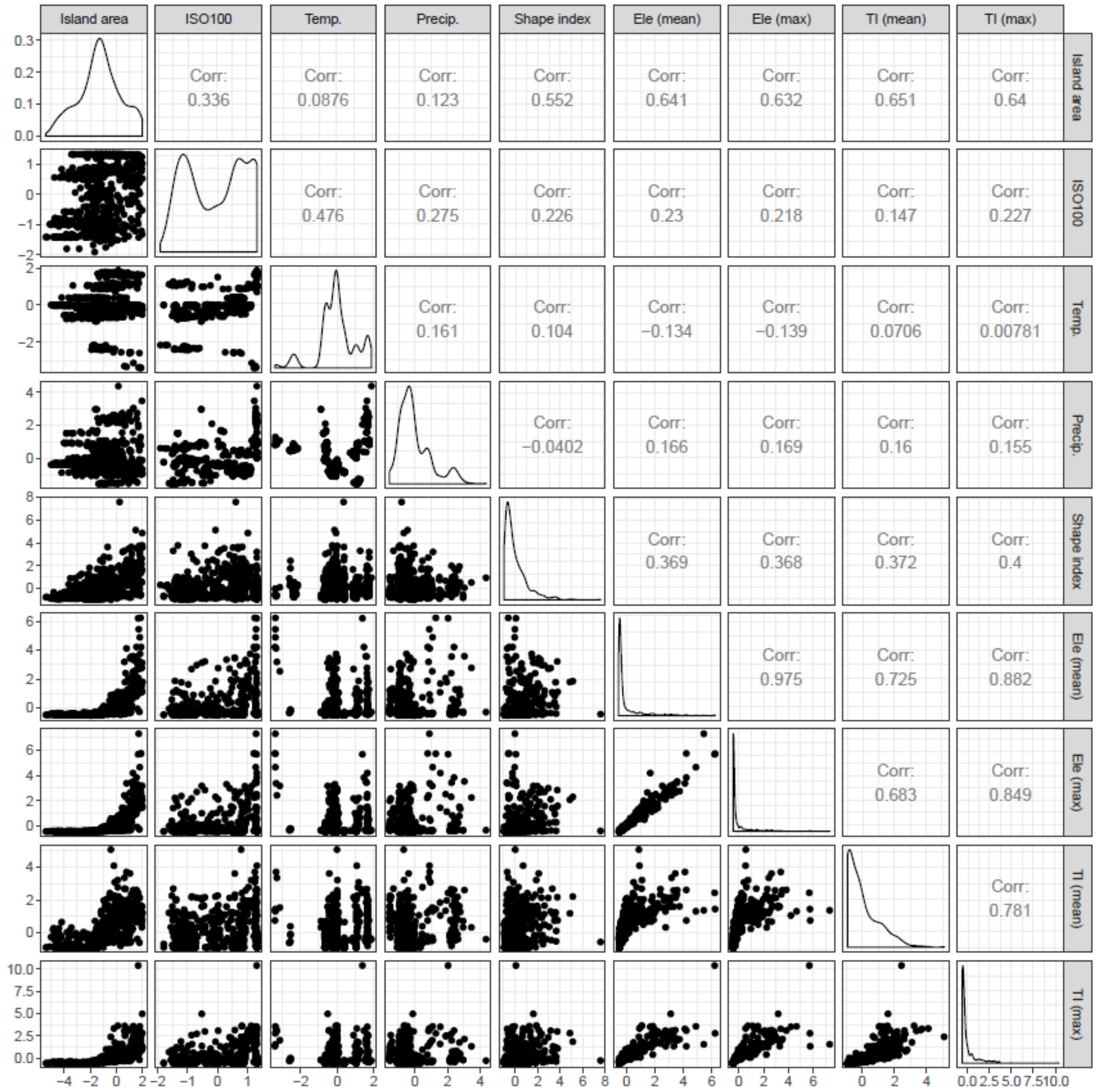

Figure E 3 Pearson´s correlation of nine environmental variables. Island area was log-transformed (in km²); 1-ISO100: Isolation metric representing by one minus the mean buffer area (100 km) and refers to the proportion of ocean around all islands; Temp: mean annual temperature of each island (in °C); Precip: annual precipitation (in mm); Shape index: refers to the edge-to-area ratio of each island; Ele (mean) and Ele (max): mean and maximum island elevation of each island (in m); TI (mean) and TI (max): mean and maximum terrain ruggedness index of each island.

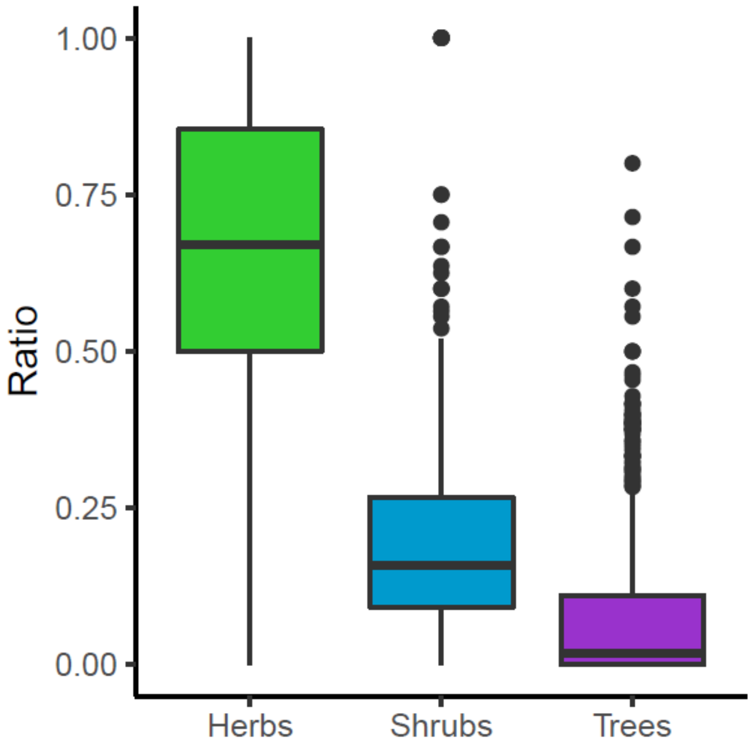

Figure E 4 Relative proportion of herb, shrub, and tree species richness on 645 small islands (empty islands excluded). All groups are significantly different from each other.

Table E 2 Paired t-test results to test for significant differences in the range of the small-island effect between growth forms. df: degree of freedom; CI: confidence interval.

| **Growth form comparison** | **p-value** | **t-value** | **df** | **CI** |
|---|---|---|---|---|
| Total richness - herbs | 0.52 | -0.66 | 10 | -0.56 – 0.30 |
| Total richness –shrubs | 0.60 | -0.54 | 9 | -0.40 – 0.25 |
| Total richness – trees | **<0.05** | -2.33 | 8 | -1.64 – -0.01 |
| Herbs – shrubs | 0.43 | -0.84 | 8 | -0.64 – 0.30 |
| Herbs – trees | 0.07 | -2.12 | 7 | -1.88 – 0.10 |
| Shrubs - trees | 0.10 | -1.84 | 8 | -1.69 – 0.19 |

Table E 3 Data sources for microanalyses presented in chapter 6.

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