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# Plants on small islands: using taxonomic and functional diversity to unravel community assembly processes and the small-island effect

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## Abstract

Islands are ideal research models to study ecological processes, as they vary in size, ecological conditions, and have clearly defined boundaries. Despite great advances in island research, comprehensive understanding of numerous aspects in island ecology is still lacking. Open questions include the effects of spatial scale on island biodiversity, community assembly processes, and the diversity of species forms and functions on islands. Here, I review recent studies investigating species assembly processes and resulting diversity patterns on small islands at local and global scales. I discuss how small-island communities are shaped by environmental, population-level, and species-level processes that differ in strength with island area. Functional trait-based approaches better explained these patterns than measures of species richness on small islands. Detailed ecological understanding of community assembly processes on islands is of paramount importance to conserve biodiversity in an increasingly fragmented natural world.

## Highlights

- The increase of species richness with island area (the species–area relation or SAR) can be decoupled for small islands, a phenomenon known as the small island effect (SIE).
- Based on two distinct datasets at regional (within one island system) and global (including 700 islands worldwide) scale, I review how plant communities assemble on small islands with special reference to the SAR and SIE.
- At the regional scale, island communities are shaped by a combination of non-random assembly processes that differ in strength with island area and which are better explained by functional trait approaches than total measures of species richness.
- At a global scale, species richness patterns dissected into growth forms (e.g., herbs, shrubs, and trees) varied in their response to island area and were differentially affected by environmental factors and isolation.
- Small-island communities are shaped by a combination of environmental, population level, and species-level processes that differ in their intensity with island area and which together may account for the SAR in general and the prevalence of the SIE in particular.

**Keywords:** Community assembly, functional diversity, functional traits, functional island biogeography, island ecology, species-area relationship, small-island effect

## Introduction

Islands constitute natural experiments to test ecological and evolutionary hypotheses in spatially discrete arenas (Whittaker and Fernández-Palacios 2007). Small islands are ideal models, as their distinct boundaries present a simplified landscape situation, making complex biodiversity patterns and ecological questions tractable

(Cody 2006, Morrison 1997, Burns 2016, Wang et al. 2010, Burns 2005).

Arguably the most influential work in island biogeography is the equilibrium theory (MacArthur and Wilson 1963, MacArthur and Wilson 1967), which provides 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 colonisation and extinction events, where larger and less isolated islands harbour more species than smaller and more isolated ones (MacArthur and Wilson 1967). According to the ETIB, species richness increases predictably with island area – also in form with increasing isolation – a pattern known as the species–area relationship (hereafter SAR). The SAR has been reported in a wealth of studies and many mathematical models have been developed to describe the relationship (e.g., Tjørve 2003, Williams et al. 2009, Dengler 2010, Triantis et al. 2012, Matthews et al. 2014). 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 not fully understood (Fattorini et al. 2017).

One of the few exceptions of the generality of the SAR is the small–island effect (hereafter SIE). The SIE states that on small islands, species richness displays high variation independently of island area (Lomolino and Weiser 2001, Niering 1963), or increases at a lesser rate than on larger islands (Dengler 2010). Numerous theories and concepts related to the SIE have been proposed (see Triantis et al. 2006 for review). Spatial scale affects the SIE, as small grain sizes inherently cause high species variability (Azovsky 2010). Other theories list environmental factors as drivers of the SIE, such as less habitat diversity on small islands (Heatwole and Levins 1973, Triantis et al. 2003, Chen et al. 2020), greater differences in productivity between islands (Anderson and Wait 2001, Barrett et al. 2003, but see Menegotto et al. 2020), high levels of disturbance (Whittaker 1995, Neufeld et al. 2017, Morrison 2014), 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 environmental conditions on small islands (Sfenthourakis and Triantis 2009), high turnover rates (Heatwole and Levins 1973, Morrison 2017), or greater stochasticity (Qie et al. 2011).

In addition to these theoretical explanations, analytical and methodological problems in the detection of the SIE have been identified (Burns et al. 2009, Dengler 2010, Tjørve and Tjørve 2011). Recent studies have demonstrated that, as argued a long while ago, the inclusion or exclusion of islands lacking any species affects the detectability of the SIE (Williams 1996, Dengler 2010, Wang et al. 2016). Furthermore, using different mathematical models can produce an adequate fit for small-island data sets that did not conform to the SAR when alternative models were used (Lomolino and Weiser 2001, Dengler 2010, Chisholm et al. 2016). Despite such analytical and methodological issues, the SIE appears to be a very common feature (Lomolino and Weiser 2001). However, no consensus has been reached yet on its underlying mechanisms and why and how species occurrences vary independently with area on small islands.

In my doctoral thesis (Schrader 2019), I used the flora of small islands to test and advance existing

theories in island biogeography. I put special emphasis on exploring processes that shape the SAR in general and the SIE in particular. To achieve that, I combined taxonomic richness and functional diversity of plants on small islands using two distinct datasets. First, I compiled a dataset at a regional scale in the Raja Ampat Archipelago (Indonesia; all data to this dataset can be found in Schrader et al. 2020a). I collected taxonomic and functional accounts of 57 tree species. I sampled the species in standardised transects using a hierarchically nested sampling design on 60 small islands that vary in size from a few square meters to more than one hectare. The nested sampling design allowed to investigate species richness patterns at different spatial scales ranging from the plot/transect scale to the island scale (Schrader et al. 2019a, Schrader et al. 2019b). For leaf trait analyses in the remote Raja Ampat Archipelago, I developed the smartphone application *Leaf-IT* for measuring leaf area (Schrader et al. 2017). For the second dataset, I collected species occurrence data for more than 700 small islands worldwide and collated information on species growth forms (Schrader et al. 2020b).

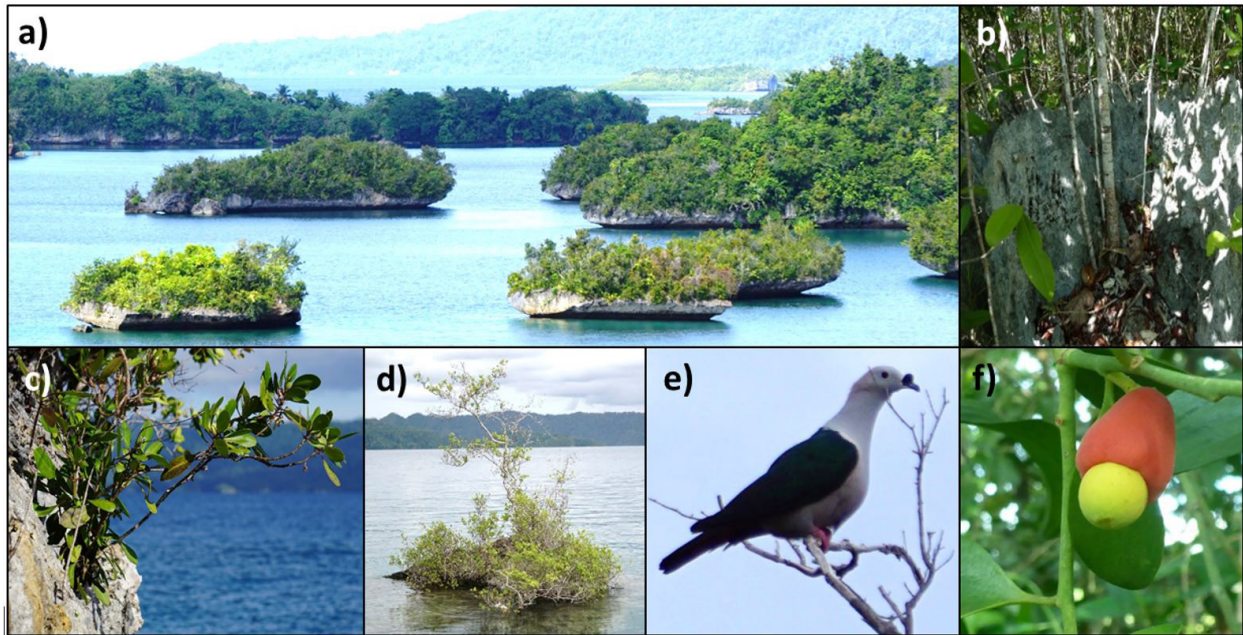
## Community assembly on small islands: The Raja Ampat Archipelago as a model system

The results of my thesis showed that multiple geo-environmental factors act simultaneously on island communities (Fig. 1 & Fig. 2a,b) and differ in strength between the spatial scales considered. These scale-dependent and multilevel assembly processes became especially clear when examining the species diversity patterns found in the island system in the Raja Ampat Archipelago.

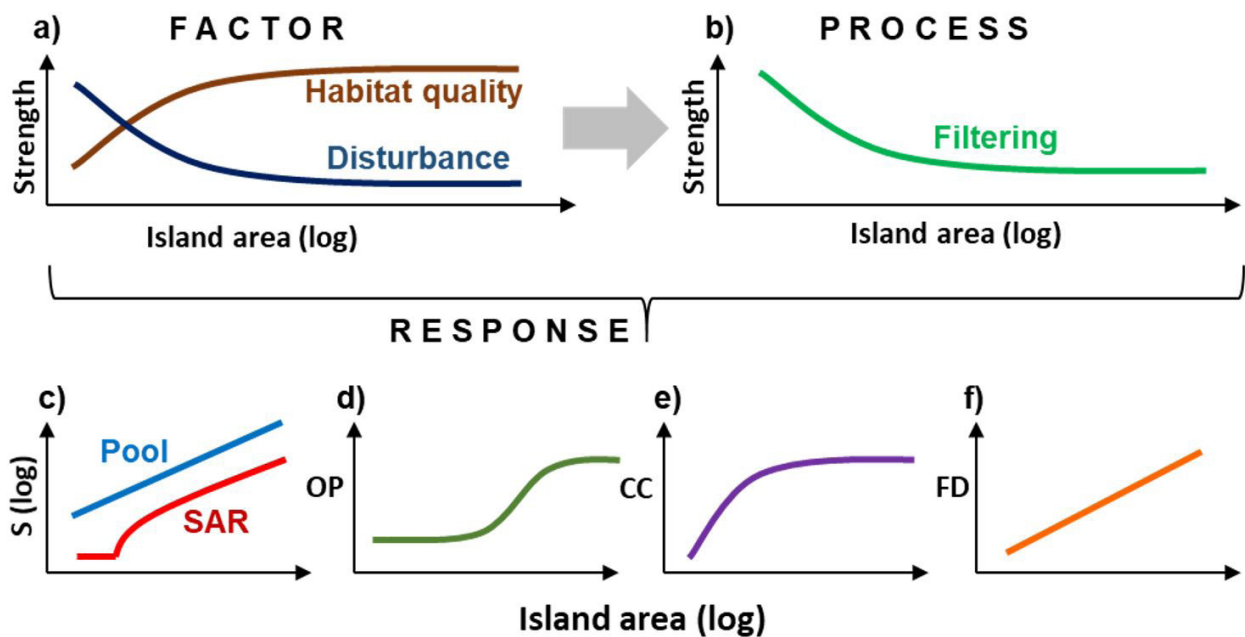
The 60 studied tropical islands in the Raja Ampat Archipelago shared a common origin and featured very similar ecological conditions. Island isolation had no significant effect on species richness, possibly because all islands were clustered within the same bay and were close together (Schrader et al. 2019a). Differences between islands could be attributed to island area and the number of high-quality habitats expressed by soil depth (Schrader et al. 2019a).

Species richness on these islands was best described by a sigmoidal SAR (Fig. 2c), indicating the presence of the SIE (Lomolino 2000). The SIE prevailed on islands with an area <130 m<sup>2</sup>, where species richness varied independently of island area (Schrader et al. 2019a). I tested which environmental factors determine species richness sampled at small spatial scales on the Raja Ampat islands, whether SARs constructed from species richness sampled at different spatial scales differ in shape and function and whether species richness sampled at small spatial scales inherently causes high species variability independent of island area, thereby mirroring a SIE-like pattern (Schrader et al. 2019a).

Island area emerged as the strongest predictor of species richness across all spatial scales considered (i.e., plot/transect scale and island scale). However, with decreasing sampling size, habitat quality – expressed



**Figure 1:** 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 such as exposure to salt water or high solar radiation, 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 by the author, from the Raja Ampat Archipelago, Indonesia).



**Figure 2:** 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 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)] and island area shown.

by soil depth – 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 (ca. <math>130\text{ m}^2</math>), possibly causing the low observed species richness on the respective islands. Deeper soil may offset stressful environmental conditions like droughts, provides more nutrients, enables interactions with soil biota, and increases fine-scale environmental heterogeneity, possibly allowing more species to co-exist.

Further, I showed that the shape and function of the SAR greatly depended on the spatial sampling scale considered. Species richness sampled at the plot/transect scale resulted in an exponential shape of the SAR that did not indicate the presence of the SIE. Sampling at the island scale produced a sigmoidal SAR, indicating the presence of the SIE. This is an important finding, as many studies have used species richness sampled at small scales (such as in plots or transects) to construct the SAR for whole island assemblages and to test for the prevalence of the SIE (e.g., Niering 1963, Kohn and Walsh 1994, Yu et al. 2012). However, sampling at small scales may inherently lead to flawed predictions of the SAR for whole islands. Species richness sampled at local scales to produce SARs for whole islands may also explain, at least to some degree, the high numbers of different SARs fitted to small island data (e.g., Lomolino 2000, Lomolino and Weiser 2001, Triantis et al. 2003, Dengler 2010, Chisholm et al. 2016). Further, species richness sampled at small scales within islands showed high variation irrespective of the island spatial extent mirroring the decoupling of species richness and island area typical for the SIE (see also Kohn and Walsh 1994, Azovsky 2010). These results indicate that sampling scales can greatly affect the shape of the SAR in general and the detection of the SIE in particular.

Next, I introduced a novel approach to calculate species area requirements and to estimate probabilistic species pools for small islands (i.e., the number of species that could potentially inhabit an island; Schrader et al. 2019b). Species often have specific environmental requirements, such as to nutrients or water availability, or habitat associations (Phillips et al. 2003, Keppel et al. 2016, Tews et al. 2004). These environmental requirements can be linked to island area as some habitats or environmental conditions are not generally available across all islands. Small islands in particular often lack soil, water resources, or specific habitat types (Niering 1963, Sfenthourakis and Triantis 2009).

Comparing the observed species occurrences against random expectations, most species preferred islands larger than expected by chance, and no species seemed specifically adapted to small island life (Fig. 2d; Schrader et al. 2019b). These species requirements were likely caused by local limiting processes, which differed in strength between islands. Smaller islands were more strongly affected by disturbances such as sea spray, solar radiation, or storms (Fig. 2a; see also Niering 1963, Whittaker 1995,

Morrison 2014, Neufeld et al. 2017). The lack of certain habitat types on small islands may explain the strong local limiting processes for species assembly possibly preventing successful colonisation of many species, limiting their occurrences to larger islands (see also Sfenthourakis and Triantis 2009, Chen et al. 2020). On larger islands, island edges (i.e., the first outward meters of an island) exhibited environmental conditions similar to those on smaller islands, characterised by an absence of soil and leaf litter, high solar radiation, and missing shade from other trees. The shared habitat types of smaller and larger islands may explain why no species only occurred on small islands.

Next, I constructed probabilistic species pools for each island by adding up the estimated species occurrence probabilities. This resulted in a unique species pool size for each island (Fig. 2c; see also Karger et al. 2016), which can be used to fit SARs in the same way as for species richness on islands. The SAR constructed from the island species pool sizes indicated no prevalence of the SIE in contrast to the observed species richness. This suggested that the SIE did not originate from species pool constraints. Rather, the SIE was likely driven by the same local limiting processes that also caused species area requirements. These local limiting processes acted more strongly on smaller islands, caused lower community completeness (Fig. 2e) and prevented fewer species from the pool persisting on small islands compared to larger ones (Schrader et al. 2019b, Pärtel et al. 2013).

To disentangle the nature of these local limiting processes, I sampled 11 plant functional traits connected to species dispersal and resource acquisition strategies for all species recorded on the Raja Ampat islands. Functional traits indicate species physiological, morphological, or phenological features and can be linked to species ecological strategy (Díaz and Cabido 2001). The value and range of species traits allows for the quantification of functional diversity (Laliberté and Legendre 2010), which can indicate ecological filtering processes. Filters describe barriers to species colonisation and establishment success, and are categorised into dispersal and environmental (e.g., abiotic and biotic) filters (Cadotte and Tucker 2017, Gillespie et al. 2012, but see Kraft et al. 2015). To colonise an island, plants first have to cross water (dispersal filters) and, second, have to find suitable abiotic and biotic conditions for establishment (environmental filters). Using functional diversity, filtering processes are commonly inferred from over- or under-dispersion of functional diversity on a focal site, such as an island, compared to the null expectation of neutral species assembly (Cadotte and Tucker 2017). Non-random distribution of functional diversity linked to dispersal-related traits (e.g., functional diversity of seed and fruit size or tree height) can then be associated with dispersal filters (Burns 2005, Thomson et al. 2011). Non-random distribution of functional diversity calculated from, e.g., leaf traits or wood density can identify abiotic or biotic filters where the environment selects against certain traits (Cornwell and Ackerly 2009, Craven et al. 2018).

Applying the functional diversity-based filtering framework to the Raja Ampat island communities showed that local limiting processes of species assembly can be linked to dispersal and environmental filtering (Fig. 2b). Small island communities were functionally under-dispersed, i.e., functional diversity was smaller than expected by chance (see also Si et al. 2017, Liu et al. 2019). With increasing island area filtering strength decreased, indicated by communities having a functional diversity equal or higher than expected by chance (Schrader 2019). The strongest filtering processes acted on species communities within the area range of the SIE. These filters likely prevented many species of the species pool from successful establishment, causing the SIE. Filtering strength decreased on larger islands that were beyond the range of the SIE (i.e., functional diversity was equal to or large than expected by chance). Species competition or neutral assembly processes likely shaped species communities on larger islands.

### Small island communities at the global scale

To test whether the prevalence of the SIE was related to plant growth forms (e.g., herbs, shrubs, and trees), I compiled a novel dataset of 5101 plant species occurring on 700 small islands worldwide within the framework of the GIFT database (Weigelt et al. 2020, Schrader et al. 2020b). Growth forms capture major variation in plant form and function (Reich 2014, Díaz et al. 2016), and are good indicators for ecological strategies and requirements of species at macroecological scales (König et al. 2019, Šímová et al. 2018, Keil and Chase 2019).

The main results from this study indicated that the shape of the SAR and the breakpoint of the SIE depend on the species growth form. The SIE was observed in 71% of all studied archipelagos for total and herb species richness and in 59% and 53% for tree and shrub species richness. The breakpoint area was smaller for total and herb species richness than for the species richness of shrubs and trees (Schrader et al. 2020b). Environmental factors affected differently species richness on islands with the range of the SIE. Habitat heterogeneity was the most important driver of total and herb species richness, the degree of isolation had the strongest effect on shrub species richness, and tree species richness was most affected by precipitation. The observed patterns suggested 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 (e.g., 100 km). Small buffer areas may indicate the forming of metacommunities composed of many small islands (Hanski & Gilpin, 1991). Less isolated islands may have more frequent immigration events that offset extinction rates, which results in smaller area ranges of the SIE. More isolated islands, in turn, may have fewer immigration events but higher extinction

rates, thereby exhibiting larger area ranges of the SIE (MacArthur and Wilson 1967). Larger buffer areas or spatial distance to the nearest mainland did not capture these metacommunity dynamics. The results highlight the importance of small-scale isolation metrics in explaining species richness patterns on small islands.

Only datasets containing multiple archipelagos over large spatial scales are capable of revealing the multilevel assembly processes of island communities (see also Chisholm et al. 2016, Wang et al. 2018, Menegotto et al. 2020). Species assembly rules derived from field studies can be validated at larger spatial scales. Conversely, testing global scale patterns in more thorough field studies can help us understand the exact mechanisms behind certain phenomena that often remain concealed at macroecological scales (Beck et al. 2012).

### Revisiting the small-island effect

Despite the long-standing debate about the causes of the SIE, no consensus has been reached on its underlying mechanisms (Triantis and Sfenthourakis 2012, Dengler 2010, Burns et al. 2009, 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 its origin.

I showed that the SIE occurred in the Raja Ampat Archipelago as well as in 53 to 71 percent of global archipelagos included in my dataset, depending on the plant growth form considered (Schrader et al. 2019a, Schrader et al. 2020b). 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 before to be the underlying driver for community assembly on small islands (e.g., Whittaker 1995, Triantis et al. 2003, Burns 2005, Si et al. 2017). However, filtering processes are inherently difficult to disentangle and should be interpreted with caution (Kraft et al. 2015, Cadotte and Tucker 2017). More evidence is needed to conclusively attribute the SIE to these processes. Integration of species functional traits to island biogeography may help to unravel assembly processes on (small) islands. However, the SIE may not exclusively be caused by filtering processes. Also, a SIE-like pattern can occur by sampling species richness in small grain sizes (Schrader et al. 2019a). High variation in species richness may inherently occur in small grain sizes, indicating that random processes could also contribute to the SIE (see also MacArthur and Wilson 1967, Kohn and Walsh 1994, Azovsky 2010, Sfenthourakis and Panitsa 2012).

In addition to the ecological theories of the SIE, some authors have pointed out methodological flaws in SIE methods (e.g., Burns et al. 2009, Dengler 2010, Tjørve and Tjørve 2011). However, most studies used SARs featuring breakpoints to test for the presence of the SIE (e.g., Lomolino and Weiser 2001, Morrison 2014, Wang et al. 2016). Breakpoint models suggest a sharp transition between islands within the range of 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. 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 the SAR. Indeed, sigmoidal models were better supported as breakpoint models for the dataset in the Raja Ampat Archipelago. I recommend using sigmoidal models to test for the presence of the SIE and only draw on breakpoint models when estimates for the breakpoint area are needed (such as in Schrader et al. 2019a, 2020b).

Based on the results of my thesis, I conclude that the SIE is a real biogeographical phenomenon driven by stochastic processes, local limiting processes including dispersal and environmental filtering, and species area requirements. Stochastic processes result in high variation of species richness at small spatial scales, such as small islands or small sampling units (see also Kohn and Walsh 1994, Azovsky 2010, Sfenthourakis and Panitsa 2012), thereby contributing to the SIE (see also Qie et al. 2011). Local limiting processes shape community composition on small islands. Such processes can be linked to high disturbances (Neufeld et al. 2017, Morrison 2014), absence of specific habitat types (Sfenthourakis and Triantis 2009, Chen et al. 2020, Wang et al. 2010), or dispersal constraints (Burns 2005, Gao and Perry 2016), and result in strong dispersal and environmental filtering (Liu et al. 2019, Si et al. 2017, Burns 2005). These filters prevent many species from the pool from successfully colonising small islands and explain why most species had requirements linked to area and were restricted to islands larger than expected by chance (Schrader et al. 2019b).

These various factors differ in strength with island area and possibly caused the manifold explanations for the SIE (Triantis et al. 2006) and may even have led some authors to argue that it is not a real pattern (Tjørve and Tjørve 2011). Rigorous ecological understanding and application of mechanistic-based frameworks are needed to identify the drivers behind the SIE. Using sigmoidal or mechanistic based SAR models (e.g., Lomolino 2000, Chisholm et al. 2016, Schrader et al. 2019a), together with alternative approaches, such as use of null models (Burns et al. 2009), can provide supporting evidence for the existence of the SIE. To gain deeper knowledge of the SIE and its causes, functional traits, community composition, species pools, and species environmental requirements 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 contributions to our understanding of community assembly on small islands and isolated habitats.

## Conclusion

Here, I discussed new insights into the assembly of small island communities and revealed potential mechanisms underpinning the SIE. Island systems, such as the Raja Ampat Archipelago, provide good ecological settings to test theories and formulate

new concepts. 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 the community assembly of island biota.

Despite the long tradition of islands serving 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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