RESEARCH ARTICLE

Disentangling direct and indirect effects of island area on plant functional trait distributions

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Abstract

Aim: Species diversity on islands generally increases with island area. This might arise either from direct effects of island area via neutral assembly processes or from indirect effects via habitat and structural differences between islands that scale positively with island area. Here, we tested whether community-weighted functional trait means of woody plants are directly or indirectly affected by island area to elucidate how functional traits mediate the assembly on differently sized islands.

Location: Twenty-eight tropical islands (25 m^2 – $12,000 \text{ m}^2$) in the Raja Ampat archipelago, Indonesia.

Taxon: Woody angiosperms.

Methods: Studied islands had a shared geological history but differed in terms of area, habitat quality expressed by soil depth, forest structure expressed by tree basal area and degree of isolation. Traits studied were seed and fruit mass, tree height, wood density, leaf mass per area, leaf nitrogen concentration and chlorophyll content (estimated from chlorophyll-meter units) and summarised as community-weighted means (CWM) for each island. Using liner regression, we tested whether CWMs were correlated to island area and basal area and structural equation models (SEMs) to test on direct and indirect effects of island area, basal area, soil depth and isolation on trait distributions.

Results: CWM of seed mass, tree height and chlorophyll content increased with both island area and basal area, whereas leaf nitrogen concentration decreased with increasing basal area. Fruit mass was not correlated to island area and basal area. SEMs revealed that the shifts in tree height, wood density, leaf nitrogen concentration and chlorophyll content were caused directly by basal area, which in turn was directly and positively affected by both island area and soil depth. Differences in seed mass among islands were explained by combined effects of basal area, island area and isolation, whereas fruit mass was only explained by isolation.

Main conclusions: Trait values shifted systematically across islands of different sizes. Being small and having light seeds are prevailing trait combinations for establishing on small islands with simple forest structure. For establishment on larger islands with

more complex forest structures, species are taller, have heavier seeds, higher chlorophyll content and lower leaf N concentrations. We conclude that mechanisms affecting CWM on islands directly link to ecological differences between islands like forest structure – and only indirectly to island area.

KEYWORDS
community-weighted means, dispersal strategy, forest structure, functional island biogeography, habitat quality, species competition

1 | INTRODUCTION

Island area is traditionally used to explain biodiversity patterns on and among islands and island-like habitats (Rosenzweig, 1995; Triantis et al., 2012). Early work assumed that island area directly determines the number of species that can inhabit an island, using neutral assembly processes as a mechanistic explanation (MacArthur & Wilson, 1967; Preston, 1960). Others suggested that habitat diversity is the main driver of species diversity, rendering island area to indirectly affect species diversity through the high correlation between island area and habitat diversity (Connor & McCoy, 1979; Kohn & Walsh, 1994; Ricklefs & Lovette, 1999). Long discussion followed on the dichotomy of direct and indirect effects of island area on biodiversity patterns (Hortal et al., 2009; Kallimanis et al., 2008) and the underlying processes are still not fully understood (Allouche et al., 2012).

Direct effects of island area on species diversity are attributed to the number of individuals sampled, populations sizes or immigration rates. Larger islands support more individuals, and this is generally coupled with higher species richness (Palmer & White, 1994; Wright, 1983). Species population sizes and immigration rates also increase with island area (Brown & Kodric-Brown, 1977), both leading to decreasing extinction risks and hence to higher species richness (Van Schmidt & Beissinger, 2020). Species diversity on islands is, thus, maintained by random immigration and extinction dynamics that change with area, with larger islands having higher species diversity than smaller ones (MacArthur & Wilson, 1967).

Indirect effects of island area on species diversity are predominantly attributed to close associations of species to specific habitats. For example, some species are associated with late-successional forests (Mueller-Dombois, 2006), certain levels of soil salinity (Buckley, 1985) and altitudes (Keppel et al., 2016), or require specific biotic interactions (Taylor et al., 2019). As larger islands support more habitats, they should also support more species (Hortal et al., 2009).

Most studies have used species richness recorded on islands to discern effects of island area and habitat heterogeneity (e.g., Hortal et al., 2009; Keppel et al., 2016; Kohn & Walsh, 1994; Kreft et al., 2008). However, species richness provides only limited inferential power to discern drivers of community assembly and its underlying ecological processes (Díaz & Cabido, 2001). Recent advances in island research have discussed the limitation of the classical species richness–based approach in island biogeography,

suggesting that a more functional perspective would make progress where classical approaches have not (Jacquet et al., 2017; Ottaviani et al., 2020; Schrader et al., 2021). Indeed, to identify mechanisms involved in structuring community composition on islands, functional traits are recently gaining increasing recognition and could provide comprehensive understanding of how species communities are structured and assemble and why they vary across islands (Ottaviani et al., 2020; Whittaker et al., 2014).

Plant functional traits characterise morphological, physiological or phenological features of a species that directly link to its ecological strategy and dispersal ability (Díaz & Cabido, 2001; Westoby et al., 2002). For example, leaf traits, such as size, mass per area and nutrient concentrations vary with climatic conditions (Firn et al., 2019; Wright et al., 2017) and help understand species investment into growth (Wright et al., 2004). Plant height positively scales with dispersal distance, competitive ability and carbon accumulation (Thomson et al., 2011; Westoby, 1998), wood density indexes tissue construction costs and the ability to withstand many abiotic and biotic stresses (Chave et al., 2009) and seed size correlates negatively to the level of disturbance and the number of recruits (Westoby, 1998). In addition, habitat characteristics have immediate effects on trait compositions within a community. For instance, forest successional stages, soil properties and species competition are important drivers of tree height, wood density and leaf traits (Kunstler et al., 2016; Lohbeck et al., 2014; Poorter et al., 2019), whereas habitat (or island) isolation affects seed and fruit mass and other reproductive traits (Biddick et al., 2019; Dupré & Ehrlén, 2002; Lindborg et al., 2012; Schrader et al., 2021). Knowing which traits will be favoured under which island conditions would enable predictions about community assembly processes on islands (Ottaviani et al., 2020). However, recent advances in functional island biogeography mainly focused on scaling relationships of functional diversity and island area (e.g., Schrader et al., 2021; Whittaker et al., 2014), and it is largely unknown whether and how single traits at the community level are affected by island area and/or habitat characteristics.

Here, we address woody plant community properties described via community-weighted means of functional traits linked to species dispersal, competition and light acquisition strategies. We compared small tropical coralline islands in the Raja Ampat archipelago, Indonesia. A related study (Schrader et al., 2021) showed that the diversity of community traits in this island system was affected by non-random assembly processes caused by environmental and

dispersal filtering that changed in strength with island area. In this study, our aim is to elucidate how differently sized islands affect community functional trait values (not their diversity) and how this helps to understand how island communities are structured. To this end, we investigate whether and how community trait values differ along island area and whether island area affects trait distributions directly or indirectly via other environmental factors.

The islands in the Raja Ampat archipelago are well suited to answer these questions as they share a common geological history, are of similar age and elevation, were likely connected in the past, consist of coralline limestone and mainly differ in area, soil depth and tree basal area (hereafter basal area). Soil depth varies considerably on these islands; it is an important predictor of species richness in this system and thought to provide water and nutrients and offset stressful environmental conditions like drought in this karstic environment (Schrader et al., 2021; Schrader et al., 2019; see also, e.g., Niering, 1963). Basal area is a proxy for forest structure and successional stage and indicates the level of species competition and resource availability (Craven et al., 2015; Lohbeck et al., 2014; Pinho et al., 2018). Both soil properties and basal area are known to have strong effects on species trait combinations in mainland plant communities (Lebrija-Trejos et al., 2010), but their relative importance in structuring traits of island communities is poorly understood. Resource competition among plants drives communities on larger islands, whereas limited niche space and ocean-borne disturbances structure plant communities on smaller islands (Schrader et al., 2021; Schrader et al., 2019; see also Whitehead & Jones, 1969).

Fruit-eating birds of different body size are the main animal seed dispersers in this island system (Schrader, Parsch, et al., 2020). Large birds are able to consume larger seeds and fruits (expressed by their mass; Herrera, 1987; Wheelwright, 1985). They also prefer larger islands with higher basal area for roosting and perching because disturbance there tends to be relatively low. Consequently, we might expect that this favours an increase of seed and fruit mass with island area.

Based on the natural history of the island system and these previous studies, our working hypotheses were as follows:

1. Community-weighted means (CWM) of seed and fruit mass increase with island area, through both direct and indirect species effects. Direct effects entail the preference of larger birds to fly to larger islands. Indirect effects are mediated by forest structure via basal area that – increasing with island area – attracts larger birds for roosting and foraging. Furthermore, we expect seed mass to increase with basal area through seed establishment strategies. On islands with larger basal area and late-successional forests, seeds need more resources for germination compared with seeds establishing on islands with less basal area and early-successional forests (Moles & Westoby, 2004; Westoby, 1998).

2. CWM of tree height, wood density, leaf mass per area (LMA), leaf nitrogen concentration (leaf N; expressed per unit dry mass) and leaf chlorophyll content (expressed per unit leaf area) all increase with island area. However, our working hypothesis is that island area does not affect these traits directly but that their prevalence in the community can be understood as mediated by basal area and soil depth. These traits all indicate species competition and light acquisition strategies (Díaz et al., 2016; Kunstler et al., 2016; Reich, 2014; Wright et al., 2004). Species competition for nutrients, water and light is higher on islands with high basal area, facilitating taller species with higher wood density, LMA, chlorophyll content and less leaf N. Deeper soils provide more water and nutrients for plants thereby offsetting stressful environmental conditions, leading to an increase in tree height and leaf N (Bernard-Verdier et al., 2012).

2 | MATERIAL AND METHODS

2.1 | Study region

We studied the woody vegetation on 28 small islands located in the Raja Ampat archipelago in Indonesia (Figure 1a). The Raja Ampat archipelago is tropical and without pronounced seasonality. Mean annual precipitation is around 2,768 mm, being lowest in November (154 mm) and highest in June (366 mm). Mean annual temperature is 27.4°C (weather station Sorong/Jefman; www.worldclimate.com). All studied islands are located in Gam Bay, a bay sheltered from the open ocean (coordinates: 130°34′E, 0°31′S; Figure 1a; for island coordinates, see Table S2). Islands studied ranged in area from 25 m² to 11,809 m² and consist of limestone karst and are of approximately similar age and elevation (one to eight m. a.s.l.). Due to the close proximity to the much larger island of Gam (200 km²), which acts as mainland to the studied islands, and the shallow sea floor between the islands and Gam (approx. 10–20 m), it is likely that all studied islands were once connected to each other and formed subsequent to the last glacial maximum. Vegetation on all islands was dominated by woody species. Soil, when present, comprised of organic matter at various stages of decomposition. Due to the rugged surface of the islands, soil depth was highly variable, ranging from 0 to >1 m. Birds are the only potential animal–plant dispersers in this island system as other larger animals (including herbivores) were absent.

2.2 | Sampling design

We only sampled islands that had at least five plant species present, to exclude islands with very simplified forest structure and very few individuals present and to calculate robust community-weighted mean trait values. Furthermore, we excluded islands that were affected by human-caused disturbances such as clear-cuts, gardens or settlements. That excluded all islands >12,000 m² as well as the large island of Gam (Figure 1a). These strict criteria produced a subset of islands that were environmentally very similar to each other. The only major notable differences between islands were area, availability and depth of soil, basal area and degree of isolation (Schrader, König, et al., 2019; Schrader, Moeljono, et al., 2019).

We based all analyses on species communities recorded at the island scale (for further information on community composition and
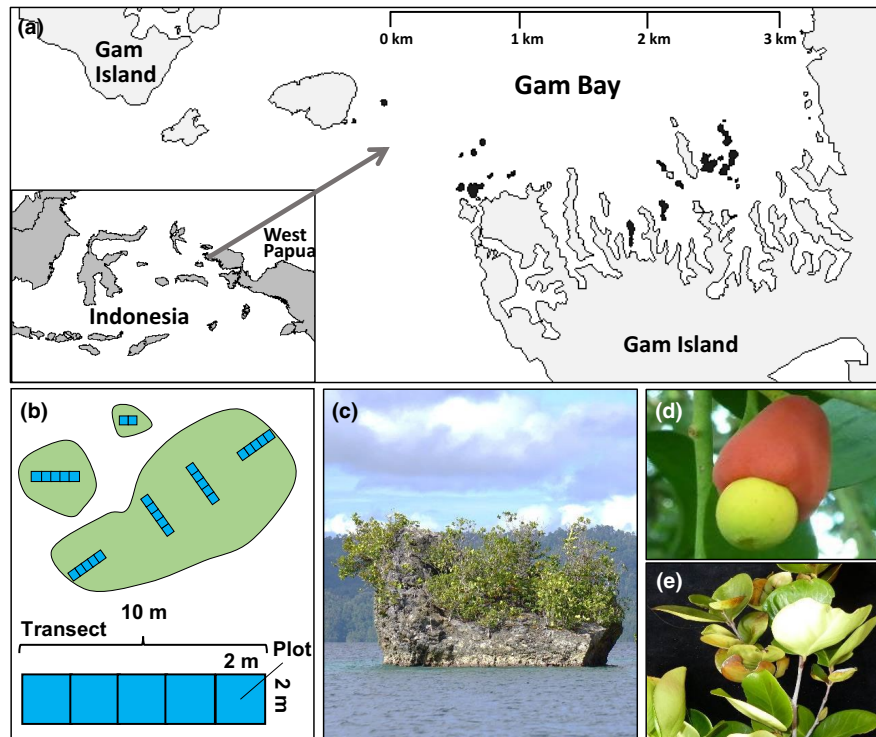
FIGURE 1 Study region in Gam Bay in the Raja Ampat archipelago, Indonesia (a), study design (b) and woody plant species on the small islands (c-e). Sampled islands are highlighted in black (a). (b) Transects were aligned at the longest extension of the island, from one edge to the other edge. The number of transects on the islands were roughly proportional to island area. (c) Small-island communities were dominated by small species with light seeds. (d) *Exocarpus latifolius* (Santalaceae) is a common species on medium sized to large islands, and its colourful seeds and fruits are dispersed by birds. (e) *Eugenia reinwardtiana* (Myrtaceae) is a tall species with high wood density and chlorophyll content and low leaf nitrogen concentration and is very common on larger islands. Its relatively large seeds are dispersed by bird.

species richness pattern in this island system, see Schrader, König, et al., 2019; Schrader, Moeljono, et al., 2019; Schrader et al., 2020). We sampled all woody vegetation on the islands using a transect design and pooled all species recorded in the transect for each island (Figure 1b). Transects were 2 × 10 m in size and subdivided into five plots of 2 × 2 m. The number of transects on an island depended on island area and sampling area was roughly proportional to island area. Transects were aligned along the largest diagonal extension of the island. On the three islands that had a diameter <10 m, we placed as many plots as possible. On the larger islands, two transects were oriented towards the island centre. The island interior was covered with one to four transects equally spaced depending on the island area (for number of plots and transects sampled per islands, see Table S2). Species richness was adequately sampled using the transects as only a few, possibly rare species may have not been recorded that, however, did not affect the overall species richness patterns on and among the islands (Schrader, Moeljono, et al., 2019). We sampled all woody plants rooted within the plots and with a diameter at breast height (by convention, 1.3 m) ≥2 cm and recorded the diameter of each individual. Additionally, in each plot, we measured soil depth at five spots with equal distance to each other (33 cm) and spaced along the transects central axis. We measured soil depth to a maximum of 35 cm. The rugged surface of the islands made

measurements beyond that unfeasible. On 23 islands, soil depth was >35 cm on at least one spot.

We georeferenced all islands in Gam Bay in ArcGIS (v. 10.3), using satellite images (World Imagery, ESRI 2017). Proportions of islands <100 m² were also measured in the field and later matched with georeferenced shape. To test whether isolation affected seed and fruit mass, we included four isolation metrics that represent different aspects of island connectivity: the closest distance to the largest neighbouring landmass, which was the island of Gam (area = 200 km²; Figure 1a) and the surrounding landmass proportion within three alternative buffer radii of 100 m, 1,000 m and 10,000 m around each focal island (following Weigelt & Kreft, 2013). We used the inverse of the surrounding landmass proportion, so higher values indicated more isolation. The distance to the large island of Gam indicated whether species dispersal occurred mostly from Gam island, whereas the buffer areas also included the network connectivity of neighbouring smaller islands (Carter et al., 2020; Weigelt & Kreft, 2013). Gam island is more than five orders of magnitude larger than the largest islands studied, making it effectively the mainland in this island system (Figure 1a). The surrounding landmass proportion within a buffer of 1,000 m had highest predictive power in our models and was, therefore, included in the main text (results for the other isolation metrics can be found in Figure S3).

Based on the diameter of each stem and the number of stems within the transects, we calculated the basal area for each island (m^2 ha^{-1}). Basal area scales with light availability and environmental conditions and is a good surrogate of forest structure and successional stage and reflects competition among species (Craven et al., 2015; Lohbeck et al., 2014; Paquette & Messier, 2011; for island characteristics, see Table S2).

2.3 | Plant functional traits

We encountered a total of 55 species for which we measured six plant functional traits linked to species dispersal, competition and resource acquisition strategies (Chave et al., 2009; Díaz et al., 2016; Westoby et al., 2002; Wright et al., 2004). We aimed at sampling traits for all species recorded on the studied islands. These traits were seed mass, fruit mass, maximum tree height, wood density, leaf mass per area (LMA), leaf nitrogen concentration (leaf N) and chlorophyll content. We then aggregated trait measurements into species´ mean trait values.

Seed mass (g) was sampled for 38 species in the field from at least five individuals per species. Seeds were oven-dried at 80°C for 72 h. For the remaining 17 species for which we could not collect seeds, we tried to extract seed mass data from the KEW Seed Information Database (http://data.kew.org/sid; accessed June 2018). For six species, we extracted the species-level information from the Kew database. For additional five species that were not present in the Kew database or not identified to species level, we used genus-level means from the Kew database (see Supplementary Discussion S4 for possible bias in seed mass data acquired from the KEW database). For six species, we could not obtain seed mass data. Seed mass is represented as the average mass of 1,000 seeds.

We measured the fruit mass (g) of 42 species from at least five individuals. Fruits were oven-dried for 72 h.

Maximum tree height (m) for each species represents the mean height of the three tallest individuals in our survey (following King et al., 2006), except for four species that only occurred once (here, height of the single individual represents tree height) and 12 species that occurred twice (here, tree height was calculated as the mean of the two individuals of these species, respectively) in the transects. Species frequencies used to calculate tree height can be found in Table S1.

We measured wood density (g cm^{-3}) as the volume of the main trunk (bark, green parts and branches were removed) of two individuals per species divided by its oven-dry weight. The main trunk was cut in cylinders of 2 cm length, which were used for wood density measurements. Wood samples were oven-dried at 100°C for 48 h.

We measured all leaf traits on ten mature and sun-exposed leaves from 5–10 individuals, depending on the species rarity. For LMA (g cm^{-2}), we divided the oven-dry leaf mass (dried at 80°C for 48 h) by leaf area (cm^2). We calculated leaf area using the *Leaf-IT* application run on a mobile device (Schrader et al., 2017). Leaf N (%) was measured by automated dry combustion (Elementar, Vario EL

Cube). For chlorophyll content, we used a chlorophyll-meter (Konica Minolta, SPAD – 502DI Plus) and converted the *SPAD* units to chlorophyll contents (μm cm^{-2}) using the empirical formula *CHL = 117.1 * SPAD / 148.8 - SPAD* from Coste et al., (2010). Further information and data on sampling design and trait analyses can be found in Schrader, Moeljono, et al., (2020).

2.4 | Statistical analyses

Trait data were missing for 28 (7.3%) of the 385 species–trait combinations (one trait value missing for LMA, one for leaf N; three for wood density; four for chlorophyll content; six for seed mass; 13 for fruit mass). We estimated these missing trait data by using multivariate imputation, using chained equations in the R-package *mice v.3.4.0* (Van Buuren & Groothuis-Oudshoorn, 2011). We log-transformed seed and fruit mass to reduce skew. Next, using the R-package *FD* (Laliberté & Legendre, 2010), we calculated the CWM of all six traits for each island, based on the species and their respective abundance recorded in the transects. CWM capture important aspects of community trait structure, link to ecosystem processes and are useful to reveal changes in trait composition along geo-environmental gradients, such as island area, basal area or soil properties (Craven et al., 2015; Laliberté & Legendre, 2010).

To test whether trait values systemically differed between rare and abundant species and influence CWM, we created violin plots for all traits for all species combined and for the 25% rarest and most abundant species respectively. Violin plots indicated no systemic bias in trait values between rare and abundant species suggesting that trait values were relatively evenly spread among rare and abundant species (Figure S5; see also Schrader et al., 2021).

To apply linear models to fit the scaling-relationship between the CWM trait values and island area and basal area, we log-transformed island area and basal area to reduce skew.

We applied piecewise structural equation models (SEMs) to estimate direct and indirect effects of island area and direct effects of island isolation, soil depth and basal area on CWM data for each trait. This analysis used the R-package *piecewiseSEM* (Lefcheck, 2016) and fitted linear models with Gaussian error distributions. SEMs were chosen based on our *a priori* working hypotheses about the study system, as outlined in the Introduction. SEMs included island area (log-transformed), mean soil depth per island, basal area (log-transformed), island isolation (only included in the model with CWM seed mass and fruit mass) and the respective CWM trait value. The first model tested for effects of island area on soil depth, expected on the basis that larger islands support deeper soil through less disturbance by wind and waves (model formula: soil depth ~ island area; Schrader, Moeljono, et al., 2019). For the second model, we assumed that island area and soil depth affect basal area because (i) larger islands are less disturbed and therefore support higher basal area and (ii) soil depth provides more nutrients and water, thereby increasing basal area (basal area ~ island area + soil depth). Thereby, the first two models tested for the links between the three predictor

variables of the CWM traits values, which were the response variables in the overall model. The third model included island area, basal area and soil depth as predictor variables and the respective CWM trait values as response variable (CWM trait value ~ island area + soil depth + basal area). Isolation indicates the effective magnitude of dispersal barriers to species (Weigelt & Kreft, 2013) and is known to affect seed and fruit mass (as surrogate for species dispersal potential; Thomson et al., 2011) and was included only in the third models including seed and fruits mass (CWM seed/fruit mass ~ island area + soil depth + basal area + island isolation). We did not have *a priori* assumptions for the other trait values than seed and fruit mass how and why they should be affected by island isolation and to avoid pseudo correlations we excluded isolation from those models. For all models, we calculated the independent contribution (R^2) of each single predictor variable (using the R-package *hier.part*; Mac Nally & Walsh, 2004), the significance level (*p*-value), the total contribution of all variables combined (R^2) for each response variable and the overall P-value (associated to χ^2 statistics) of the model as indicator of model fit (overall *p*-values <0.05 indicate poor model fit). All analyses were implemented in the statistical software *R* (v.3.6.0; R Core Team, 2020).

3 | RESULTS

We recorded a total of 55 species on the islands. Species numbers ranged from five species on three islands to 26 on one island (mean 13.3). Mean soil depth ranged from 0 cm on three islands to 22 cm (mean 9 cm) and varied largely independently of island area. Basal area on the islands ranged from 3.4 to 30.7 m^2 ha^{-1} (mean 16.9) and increased significantly with both island area and soil depth (Figure 2).

CWM values of seed mass, tree height and chlorophyll content increased significantly with both island area and basal area (Figures 3 & 4). Basal area was correlated positively with wood density and negatively with leaf N. Wood density, LMA and leaf N showed no significant relationship with island area (Figure 3), and fruit mass was not correlated with either island area or basal area (Figures 3 & 4).

SEMs showed that 35% of variation in basal area was explained by island area and soil depth together. Seed mass was directly, significantly and positively affected by island area (independent contribution: R^2 = 0.29), basal area (R^2 = 0.35) and island isolation (R^2 = 0.14), which together explained 81% of the total variation of seed mass (Figure 5a). Fruit mass was only significantly and positively related to island isolation (R^2 = 0.22), whereas all predicator variables combined explained 33% of variation in fruit mass (Figure 5b).

Island area, basal area and soil depth combined explained 47% of total variation of tree height (Figure 5c), 24% of wood density (Figure 5d), 10% of LMA (Figure 5e), 36% of leaf N (Figure 5f) and 38% of chlorophyll content (Figure 5g). Tree height (independent contribution: R^2 = 0.37), wood density (R^2 = 0.18) and chlorophyll content (R^2 = 0.26) were only directly significantly affected by basal area. Leaf N decreased with increasing basal area (R^2 = 0.24) and increased with island area (R^2 = 0.07). LMA was not significantly affected by any variable. Soil depth had no direct, significant effect on any of the CWM trait values.

4 | DISCUSSION

Our results show that the community weighted means of seed mass, tree height and chlorophyll content scale positively with island area. However, these traits as well as wood density and leaf N were also correlated with basal area, raising questions about the causative mechanisms of island area and/or basal area on trait distributions. SEMs supported our expectation that basal area increased with increasing island area and soil depth and suggested that the shift of seed mass, tree height, wood density and leaf N were directly caused by basal area. Island area had only a strong direct effect on seed mass and a weak direct effect on leaf N. Seed and fruit mass further increased with island isolation. Soil depth had no direct link to any of the trait values.

We relate the observed trends in seed and fruit mass to plant–bird interactions that affect dispersal strategies, and the trends in seed mass, tree height, wood density, leaf nitrogen concentration and chlorophyll content to differences in forest structure between
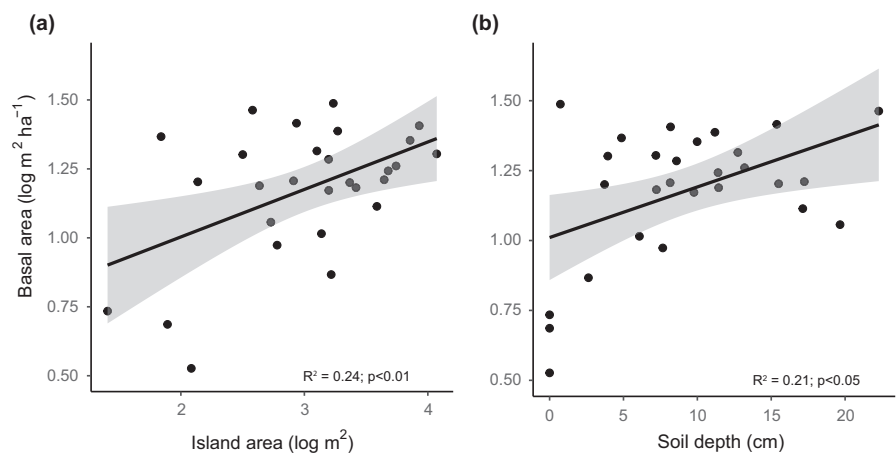
FIGURE 2 Basal area of woody plant communities in relation to island area (a) and mean soil depth (b) on 28 islands in the Raja Ampat archipelago, Indonesia. Regression lines are calculated by applying linear models. Grey bands indicate 95% confidence intervals. Basal area and island area are log$_{normal}$-transformed.
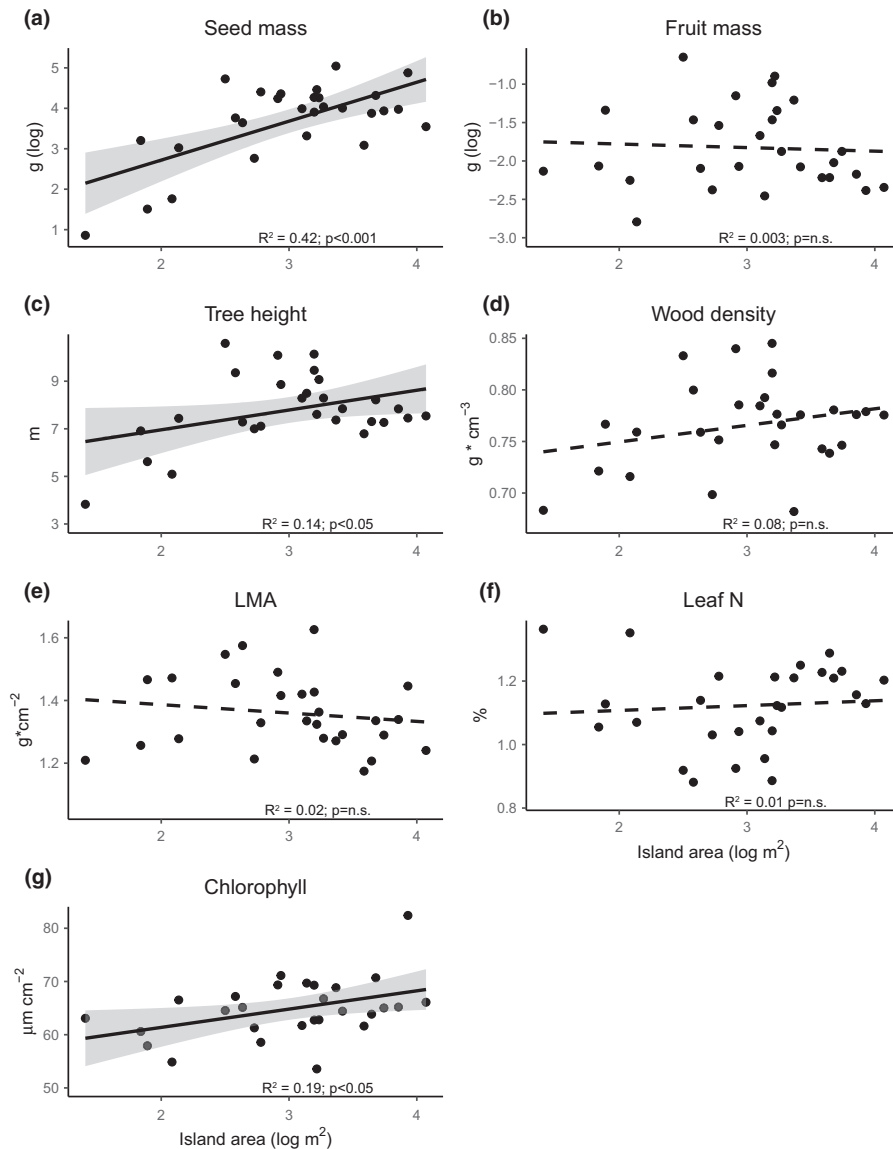
FIGURE 3 Community-weighted means (CWM) of seven traits in relation to island area ($\log_{normal}$-transformed) of woody plant communities on small islands in the Raja Ampat archipelago, Indonesia. (a) CWM seed mass; (b) CWM fruit mass; (c) CWM maximum tree height; (d) CWM wood density; (e) CWM leaf mass per area (LMA); (f) CWM leaf nitrogen content (Leaf N) and (g) CWM chlorophyll content. Regression lines are calculated by applying linear models. Solid lines indicate significant change of CWM trait values with island area; dashed lines are not significant. Grey bands indicate 95% confidence intervals.

islands. Overall, island area *per se* seems to be only of minor importance in structuring trait distributions of island communities.

## 4.1 | Island area, basal area and isolation explain dispersal strategies

In our island system, seed and fruit mass were directly affected by island isolation. The links of seed and fruit mass to island isolation indicate that (at least some) plant species follow specific dispersal strategies in this island system (see also Schrader et al., 2021). Most plant species on the islands had fleshy, colourful fruits that were likely bird dispersed, leading us to conclude that dispersal for most species was tightly connected to bird behaviour (see also Burns, 2005; Liu et al., 2019). Only six species (11%) had tiny woody and/or winged diaspores that seemed to be either water or wind dispersed. These only occurred on the smallest islands or the island edges that were most exposed to waves and winds. However, we cannot clearly deduce that all fleshy fruits are only

dispersed by birds. Some fleshy fruits were buoyant and known to disperse by water (e.g., *Calophyllum inophyllum, Pandanus sp.*, *Guettarda speciosa*; Nakanishi, 1988) and may be, thus, less affected by island isolation than the animal dispersed species. An alternative outcome could be that the size of buoyant fruits influence immersion time tolerated in salt water, thereby increasing dispersal distance by water of larger-fruited species. However, other means of fruit dispersal may also be important as only relatively small variation (22%) in fruit mass was explained by island isolation and scaling relationships of fruit size and island isolation should be further investigated.

In our island system, we observed that bird species partitioned islands according to their size with larger birds preferring larger islands for foraging and perching than smaller birds that were also frequently observed on smaller islands (see also Boyer & Jetz, 2010). As larger fruits can only be consumed by larger birds, dispersal of larger fruits might be restricted to larger islands, whereas smaller fruits – mainly consumed by smaller birds – could also reach smaller islands. Furthermore, larger birds were often observed flying over

FIGURE 4 Community-weighted means (CWM) of seven traits in relation to basal area (log$_{normal}$-transformed) of woody plant communities on small islands in the Raja Ampat archipelago, Indonesia. (a) CWM seed mass; (b) CWM fruit mass; (c) CWM maximum tree height; (d) CWM wood density; (e) CWM leaf mass per area (LMA); (f) CWM leaf nitrogen content (Leaf N) and (g) CWM chlorophyll content. Regression lines are calculated by applying linear models. Solid lines indicate significant change of CWM trait values with basal area; dashed lines are not significant. Grey bands indicate 95% confidence intervals.
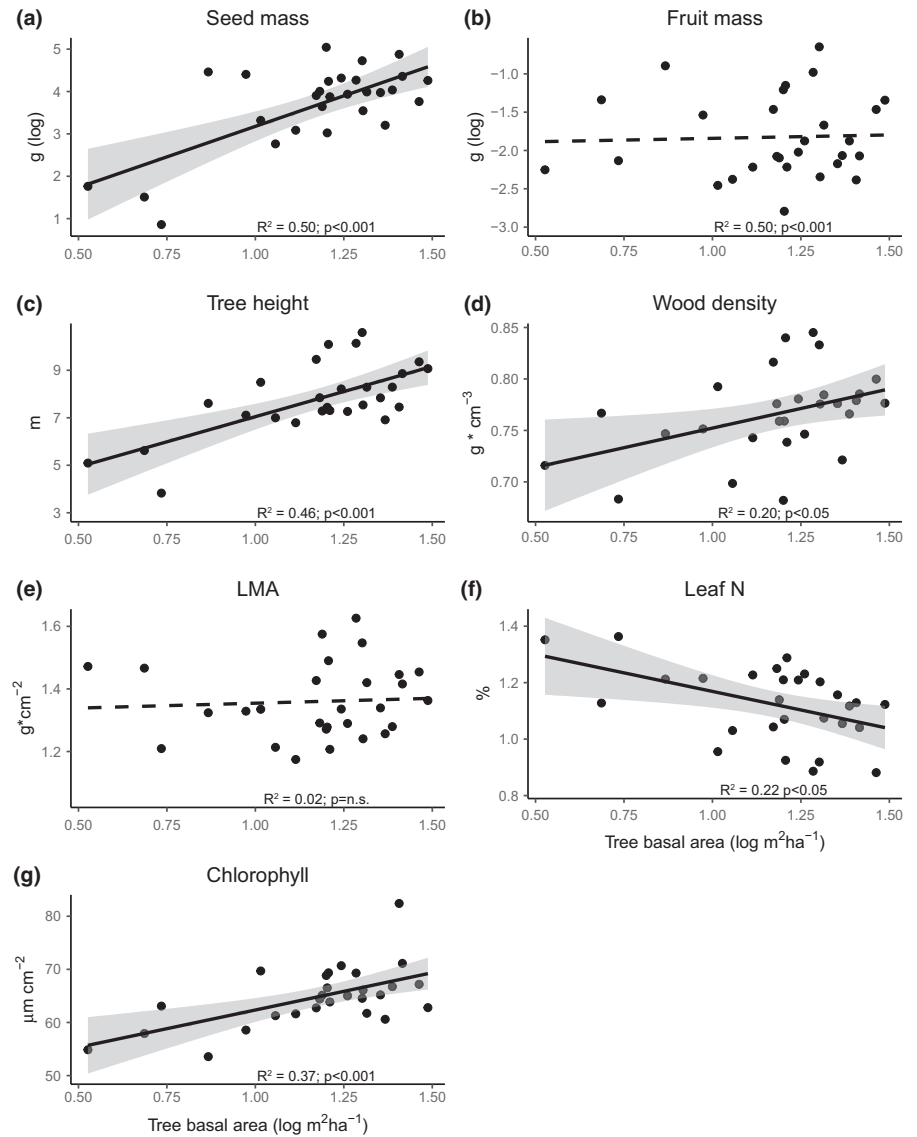
open water to more isolated islands (Schrader, Parsch, et al., 2020), thereby possibly dispersing larger fruited species better to these islands. For seed mass, however, a possible link between bird dispersal and island characteristic remains more speculative and should be the subject of future studies. One plausible explanation why seed mass increased with isolation could entail the positive correlation between seed mass and fruit size (Figure S6; Herrera, 1987), linking increasing seed mass with isolation to the same process as for fruit mass described above.

This particular pattern of larger fruits and seeds on larger and more isolated islands is not necessarily general; it seems to depend on the context of dispersal agents and island configuration (Carlquist, 1966; Gillespie et al., 2012). For instance, Liu et al., (2019) found seed mass of woody plants on islands in an artificial lake in China to decrease with island area (opposite to our result), due to birds becoming more important relative to mammals and dispersing smaller seeds. Burns (2005) found birds to be the main disperser of woody plants leading to an underrepresentation of non-bird-dispersed plants on small islands in British Columbia (Canada).

Another plausible explanation why seed mass increases with basal area may entail strategies of seedling establishment in early- versus late-successional forest communities. Under closed forest canopies with high basal area, larger seeds provide seedlings with more resources to grow tall and to establish (Moles & Westoby, 2004; Westoby et al., 2002). On islands with lower basal area and consequently open conditions and reduced competition, seeds can directly germinate without facing high initial competition for light. The link between seed mass and forest successional stage is well supported for mainland communities, but whether similar mechanisms also explain the observed seed mass patterns on islands should be further investigated.

4.2 | Forest structure explains species competition and light acquisition strategies on islands

We observed a positive effect of island area on tree height and chlorophyll content but not on wood density, LMA or leaf N. SEMs
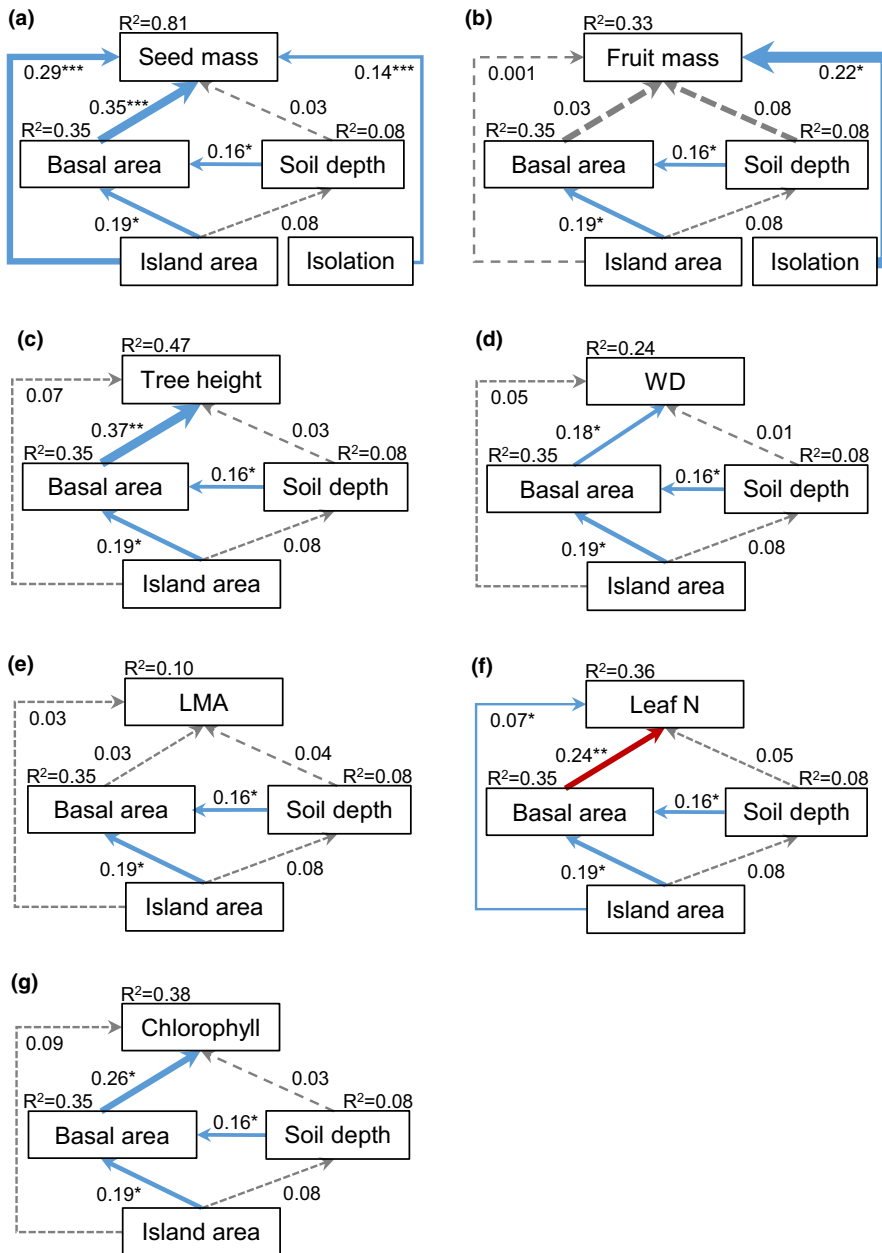
FIGURE 5 Direct and indirect effects of four different factors on functional trait distributions of woody plant communities on small islands in the Raja Ampat archipelago, Indonesia. SEMs show the effects of island area (log_{normal}-transformed), mean soil depth, basal area (log_{normal}-transformed) and island isolation (calculated as the inverse of surrounding landmass in 1000 m radius: positive value indicate increasing trait value with increasing isolation) on community weighted mean trait values on small islands: (a) seed mass; (b) fruit mass: (c) maximum tree height; (d) wood density; (e) leaf mass per area; (f) leaf nitrogen concentration (Leaf N); (g) chlorophyll content. Both overall models fitted the data well as indicated by overall p-values >0.05. Solid lines indicate significant relationships with p-values: *0.05 > p > 0.01; **0.01 > p > 0.001; ***0.001 > p; dashed lines indicate non-significant relationships. Blue arrows indicate positive correlations and red negative correlations. Arrow width is proportional to independent contribution of each predictor variable on the response variable. Independent contribution (R^2) is shown by number along lines. Total contribution of all predictor variables (R^2) for each response variable is shown above corresponding boxes. Indirect effects are paths involving sequences of two or more arrows, and their strength is measured by multiplying the R^2 on the arrows.

revealed that island area could be interpreted as not affecting these traits directly (except a weak positive effect on leaf N) but through indirect effects via basal area. SEMs further indicated the close relationships between island area, soil depth and basal area.

First, contrary to our expectation, soil depth varied independently from island area. The distribution of soils showed substantial within-island variability (Table S2). The surface of the islands is highly rugged, including many crevices and holes. Soil mostly accumulated in these crevices and holes meaning that most islands, regardless of their area, had spots with soil and others without. Second, larger islands supported higher basal area possibly as they were less disturbed by wind and waves that allowed for larger trees with larger diameters to develop on the islands (see also Schrader, Moeljono, et al., 2019). Third, basal area was also positively affected by soil depth. Deeper soils provide more water and nutrients allowing for

higher basal area (Meyer et al., 2007). Higher basal area in turn could also increase soil depth through accumulating litter and holding soil against erosion. That hints towards synergistic effects between soil depth and basal area that may be difficult to separate. However, the variation of basal area was also higher on both smaller islands compared with larger islands and shallower soil compared with deeper soil (Figure S7). This suggest that basal area may also be affected by stochastic processes possibly linked to higher disturbance on smaller islands or availability of soil (Schrader, Moeljono, et al., 2019).

Basal area then scaled positively with tree height, wood density and chlorophyll content and negatively with leaf N. These patterns may be driven by shifts in competition and light acquisition strategies among communities of low and high basal area, respectively (Craven et al., 2015; Lohbeck et al., 2014; Pinho et al., 2018). In fact, the observed basal area–trait relationships mirror those described

from different forest successional stages. Early-successional forests with low basal area feature smaller species with small diameters that are adapted to fast growth and resource acquisition expressed by low tree height, low wood density (in wet tropical forests) and chlorophyll content. Competition among species and resource conservatism strategies – expressed by being tall and by high wood density and chlorophyll content and low leaf N – drive communities in late-successional forests with high basal area (Craven et al., 2015; Lohbeck et al., 2014; Poorter et al., 2019).

However, it is questionable whether differences in CWM of tree height, wood density, leaf N and chlorophyll content on islands can be attributed to forest successional dynamics only. In fact, we cannot clearly discern whether lower basal area on small islands is either due to succession in the sense that these islands were actually cleared more recently by disturbance events or rather due to continuing edge effects, strong winds and salinity that may limit water availability and soil development and hence basal area on small islands. Thus, forest successional stage on small islands could be in a state of equilibrium maintained by opposing trends of disturbance and progressive succession.

LMA, a trait associated with resource acquisition and leaf lifetime (Wright et al., 2004), was not affected by any of our explanatory variables. Perhaps, other factors such as protection against physical damage may affect LMA more strongly in our study system, overriding patterns associated with resource acquisition strategy (Coley, 1988; Cunningham et al., 1999).

The intricate ecological relationships between island area, habitat quality and forest structure observed in this small island system caution against making generalisations about environmental–trait relationships across archipelagos. For instance, the Raja Ampat archipelago is dominated by woody species communities that are shaped by forest structural dynamics that differ in strength with island area. Island systems more exposed to wind and wave disturbance could foster plant communities with high turnover rates that show trait values connected to high seed production and annual life forms (Kuiters et al., 2009). Rising sea levels as a consequence of global change could increase salinity on low-lying islands leading to prevalence of succulent and/or wind dispersed plant species (Díaz et al., 1998; Mahdavi & Bergmeier, 2016).

5 | CONCLUSION

Here, we offer a fresh perspective on the long-standing debate on direct versus indirect effects of island area on species community composition through the lens of plant functional traits. Our results show that being small and having light seeds are good trait combinations for establishing on small islands in this island group. In contrast, to establish on larger islands species tend to have trait combinations oriented towards competitive ability and resource acquisition. This is expressed by many tall species in a community that have heavy seeds and leaves with high chlorophyll content and low N concentrations. Thereby, our results provide evidence

that plant communities on islands are not a random selection of species but are subject to filtering processes resulting in communities with distinct traits (see also, e.g., Burns, 2005; Hamann, 1979; Schrader et al., 2021).

These shifts in trait values – especially in traits connected to competition and light acquisition strategies – can be parsimoniously understood as being driven by forest structure, as measured by basal area. It is not necessary to invoke island area as having a direct effect on traits, except for seed mass. Basal area in turn is influenced by island area. These are correlative data and do not decisively demonstrate pathways of causation. Nevertheless, our results suggest that most of the influences of island area on traits operate via influence on forest structure, rather than directly.

DATA AVAILABILITY STATEMENT
All data used in this contribution are available in the Supplementary Information (Table S1 for taxonomic and species-level trait data and Table S2 for island data and community-weighted mean trait data). The original data including the species-island matrix are available in the Supplementary Material in Schrader, Moeljono, et al., (2020).

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BIOSKETCH

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Authors contribution: JS, MW, IJW and HK conceived the research ideas; JS assembled and analysed the data and led the writing with major contribution from all co-authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.