OIKOS

Research article

Inferring community assembly processes from mangrove species–area relationships

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Oikos
2025: e11095
doi: 10.1002/oik.11095
Subject Editor: Dylan Craven
Editor-in-Chief: Pedro Peres-Neto
Accepted 24 February 2025

The increasing species–area relationship (SAR) is a nearly universal ecological law. But recent theory has predicted that in systems with low large-scale diversity the law should be violated and the SAR should be nearly flat at intermediate scales, with species richness roughly constant at some value typically greater than one. We tested this prediction using a global dataset of mangrove trees – a species-poor group. We used a published global dataset of mangrove tree distributions to construct an SAR spanning local to global scales. We found that over a large range of scales ($\approx 10^{-4}$ to 10^{6} km^2) the SAR was close to flat, in stark contrast to a classical power-law SAR, which would predict roughly a 300-fold change in species richness over these scales. Importantly, species richness was not simply equal to the minimum value of one or the maximum value of global mangrove richness over these scales, either of which possibilities would be reconcilable with the classical theory, but instead was maintained at an average value of between two and three species. Our theoretical interpretation of the results is that there are two to three stabilising niches (i.e. niches that would allow two to three species to stably coexist without substantial immigration) for mangrove trees in typical coastal settings and that immigrant propagule diversity is in most cases too low (because of low mangrove tree metacommunity diversity) for there to be more species than niches. Only at scales greater than $\approx 10^{6}$ km^2 is the diversity of immigrants typically sufficient to yield more species than niches. We speculate that in other systems, local niche diversity may be similarly low but that the nearly flat SAR phase is hidden by immigration from diverse source pools.

Keywords: community assembly, dispersal assembly, immigration, mangrove trees, niche assembly, species–area relationships

Introduction

Macroecology concerns the relationships between species diversity and other ecological variables on large spatial and temporal scales (Banks-Leite et al. 2022). Variables

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that influence species diversity include species traits, climate, landscape heterogeneity and landscape topography (Banks-Leite et al. 2022, Buckley and Puy 2022). However, the biggest driver of species diversity is area – a rule of thumb states that if one landscape has ten times the area of another, it will have roughly twice the number of species (Desmet and Cowling 2004). The increasing species–area relationship (SAR) has been touted as a general law in ecology (Lomolino 2000).

Here our focus is on nested SARs (Scheiner 2003), where the focal areas of various sizes are nested within one another. For a nested SAR, the observation that species richness increases with area is easily understood – it would be logically impossible for it to decrease. More remarkably, the functional form of the SAR varies across scales in repeatable and predictable ways. When viewed on log–log axes across scales ranging from a single individual to the whole world, the SAR, as traditionally understood, has three phases (Fig. 1a): a steep initial phase at local scales; a shallower power-law phase at regional scales (with an exponent of around 0.15–0.35 (Storch et al. 2012), whence the aforementioned rule of thumb); and another steep phase at continental to intercontinental scales (Hubbell 2001). The triphasic SAR was first observed by Preston (1960) in data for breeding birds and has since been explained using theoretical models (Durrett and Levin 1996, Grilli et al. 2012, O'Dwyer and Cornell 2018, Rosindell and Chisholm 2020).

The three phases of the classical SAR are referred to as the sampling phase, dispersal-structured phase, and speciation-structured phase (Chisholm and Fung 2021). The sampling phase occurs at small scales below the typical dispersal distance of the organisms concerned. At such scales, the community is nearly well-mixed, and sampling new individuals quickly reveals new species (Grilli et al. 2012, O'Dwyer and Cornell 2018). The second phase is referred to as the dispersal-structured phase because, in models, it appears only when dispersal limitation is present (Rosindell and Chisholm 2020, Chisholm and Fung 2021). The third phase is referred to as the speciation-structured phase because it begins at approximately the average species range size (Storch et al. 2012), which theoretical models suggest is inversely proportional to the per capita speciation rate (O'Dwyer and Cornell 2018).

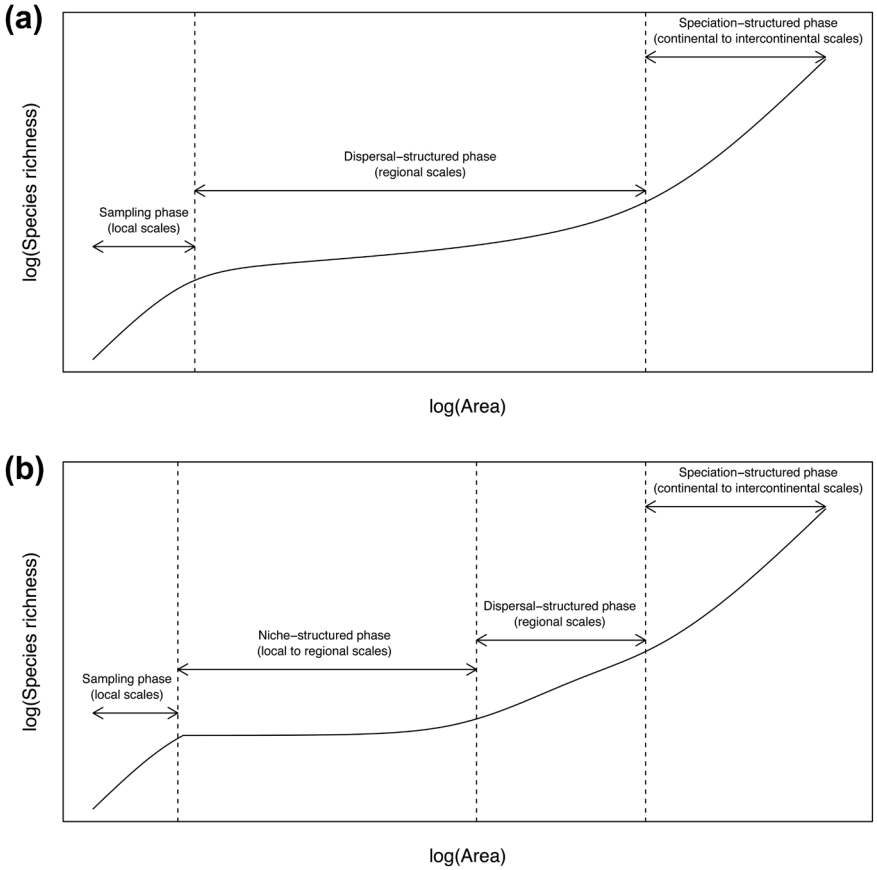

Figure 1. Qualitative shapes of theoretical SARs. (a) The classical triphasic SAR exhibits a steep sampling phase at local scales, a shallower power-law phase at regional scales, and a steep speciation-structured phase at continental to intercontinental scales (Preston 1960, Hubbell 2001, O'Dwyer and Cornell 2018). (b) The tetraphasic SAR exhibits, in addition to the three phases of the classical SAR, a niche-structured phase at local to regional scales (Chisholm and Fung 2021). The niche-structured phase is typically not observed in empirical data because immigration of novel species to focal areas is usually sufficiently high for the sampling phase to transition directly into the dispersal-structured phase; it is predicted to be observed only in systems where dispersal is very low or metacommunity diversity is very low or both.

This phase occurs at scales large enough that small increases in log(area) can lead to the inclusion of the entire ranges of new species, which, in nature, may correspond to new biogeographic realms.

Recent theoretical work has suggested that, more generally, the SAR should be tetraphasic (i.e. consist of four phases), with a typically unobserved phase occurring between the sampling and dispersal-structured phases (Fig. 1b) (Chisholm and Fung 2021). This phase has been dubbed the niche-structured phase because theory indicates that, within it, the number of species in a given area simply reflects the number of stabilising niches available for the guild under consideration (Chisholm and Fung 2021). The term "stabilising niches" means that competition within species is stronger than competition between species to a sufficient extent that multiple species can coexist indefinitely in a community with negligible immigration and negligible stochasticity. At equilibrium, the number of species is equal to the number of stabilising niches. Such stable, niche-based coexistence occurs in a range of niche models, from Lotka–Volterra competition models to resource–consumer models to models of natural enemy effects (Broekman et al. 2019). Theory predicts that the niche-structured SAR phase should, furthermore, be nearly flat – or at least much shallower than the other phases – because niche diversity does not increase very rapidly with area (Chisholm and Fung 2021). A diagnostic feature of the niche-structured phase is that species richness does not approach one as area decreases, as would be predicted by a model with negligible immigration and no stabilising niches, in which some combination of drift and competitive exclusion would drive all but one species locally extinct. Instead, the stabilising niches maintain species richness at some larger value. The niche-structured phase has been proposed as an explanation for the small-island effect in island biogeography (Chisholm et al. 2016): a phenomenon whereby species richness varies little with area among small islands, violating the classical increasing island SAR (Niering 1963, MacArthur and Wilson 1967, Lomolino and Weiser 2001). However, the niche-structured phase has not yet been observed in mainland SARs.

Observation of the niche-structured phase in a mainland SAR would be an important validation of our understanding of the processes that structure ecological communities. Theory suggests that the reason the niche-structured phase has not been observed in mainland communities is that (unlike on small islands) usually the diversity of immigrant propagules to local patches is sufficiently high as to make the dispersal-structured phase manifest at fairly small areas, roughly coinciding with where the sampling phase ends (Chisholm and Fung 2021). Therefore, in theory, the niche-structured phase should be revealed in situations where the diversity of immigrant propagules is very low, which can occur due to some combination of low source-pool species diversity and limited dispersal. In such situations, the sampling phase should end at areas substantially smaller than those at which the dispersal-structured phase begins, and the niche-structured phase should be visible (Fig. 1b).

Here, we test the hypothesis that the niche-structured phase of the SAR should emerge in a system with low, large-scale diversity, using mangrove tree communities as a model system. Mangroves are an appropriate study system because, though confined to the tropics, subtropics, and warm temperate zones, they have a largely pan-longitudinal distribution (Duke 2017), allowing for the construction of a local-to-global SAR. Further, mangroves have evolved within a narrow range of coastal environmental settings (Woodroffe et al. 2016), which minimises habitat complexity differences among mangrove forests (Ellison 2002). They also have low, large-scale species diversity: while estimates vary globally there are thought to be only approximately 73 true mangrove and mangrove hybrid species (Spalding et al. 2010). Mangroves are a disparate group of taxa across multiple families, with at least 27 independent evolutionary origins linked to rapid sea-level changes in the geological record (He et al. 2022). As a result, most mangrove species have developed a range of species-specific adaptations to biophysical stresses such as tidal inundation and hydrodynamic energy (Krauss et al. 2008). We used a recently compiled global dataset on mangrove tree diversity to calculate empirical SARs and fit a mechanistically derived SAR model to the data to explore how the SAR slope varies across scales.

Material and methods

Dataset compilation

We based our dataset on a recently compiled large field-based dataset on mangrove forest structure and biomass (Rovai et al. 2021, Rovai 2023). In its raw form, the dataset is a compilation of summary data for 3497 mangrove plots distributed globally across 67 countries, synthesised from approximately 500 different sources (both published and unpublished). We removed 1433 plots for which mangrove species identities and species richness were not available, leaving 2064 plots. A total of 54 mangrove and mangrove-associated tree taxa were represented at these plots (i.e. roughly 74% of the global total).

Our goal was to construct SARs that are, as far as possible, based on accurate taxonomy, based on true mangrove tree species, and representative of natural conditions without anthropogenic influence. To this end we performed several data curation steps. We updated the name of *Avicennia lanata* to *Avicennia rumphiana*. We removed from the dataset species that are not considered true mangroves and merged synonymous taxa (as per the World Register of Marine Species). This resulted in the purging of three species considered mangrove associates (*Cerbera odollam*, *Intsia bijuga* and *Pterocarpus officinalis*) and the merging of five taxa with synonymous taxa (*Avicennia africana* was absorbed into *Avicennia germinans*; *Bruguiera decandra* into *Ceriops decandra*; *Excoecaria ovalis* into *Excoecaria agallocha*; *Rhizophora brevistyla* into *Rhizophora harrisonii*; and *Xylocarpus mekongensis* into *Xylocarpus moluccensis*). After these changes, the

number of species in our dataset was reduced to 46. In addition, the dataset contained errors in which the wrong mangrove species was recorded in a small number of plots. This was determined by checking for distributional outliers against known mangrove distribution patterns by biogeographical region (Spalding 2010). There were 20 plots with such errors (Supporting information). These errors were corrected to account for likely misidentifications where possible, but two plots with particularly dubious occurrences (*Laguncularia racemosa* in a plot in the Philippines and *Avicennia marina* in a plot in Venezuela) were deleted.

We removed from the dataset a further seven mangrove plots that had no remaining species after deletions. Plots containing only introduced mangrove species were also removed from the dataset. There were ten such plots, all in Hawaii. Our final dataset thus comprised 2045 plots.

Compilation of the species–area data

We constructed the SAR from scales of 4 m^2 (a small plot) to the entire Earth. The SAR at small scales was constructed by treating each plot as a single data point. Plot areas were taken from the original sources where available (242 plots) and ranged from 4 to 2500 m^2, with 19 unique values of area. We refer to these unique values of area as A_i with $i \in \{1,2,\ldots 19\}$, and the mean species richness of plots with area A_i as $\bar{S}_i$.

At larger scales we constructed the SAR by placing nested concentric circles around each plot and counting the species present in all plots within each circle (Supporting information). Specifically, we collated the latitude and longitude of all 2045 plots in the final dataset and computed the distances between all pairs of plots using the haversine method. To define the scales at which the SAR would be constructed, we specified 20 distances (d_i with $i \in \{20,21,\ldots 39\}$, equally spaced on a logarithmic scale between the minimum inter-plot distance of $d_{20} = 12.7$ m and half the circumference of the Earth ($d_{39} = \pi R_{\text{Earth}} = 20\ 037.5$ km). Using more than 20 distances makes little difference to our final results (not shown). We then computed the corresponding areas A_i from the formula for the area of a spherical cap ($A_i = 2\pi {R_{\text{Earth}}}^2(1 - \cos(d_i/R_{\text{Earth}}))$). For each plot j and each distance i we then determined $S_{i,j}$, the combined number of species in all plots (including plot j) within that distance. We discarded any values of $S_{i,j}$ where going from distance d_{i-1} to d_i did not lead to any new plots being included, because including such plots could lead to underestimation of species richness and could unfairly bias the results in favour of our hypothesis. We acknowledge that this only partially corrects the under-sampling problem inherent to our analysis.

Model fitting

The data exhibited substantial spatial autocorrelation: SARs centred on plots closer in distance tended to be more similar. This autocorrelation was stronger for larger areas A_i, because two large nearly concentric circles will inevitably have very similar species richness (in the extreme case of the largest circle, which corresponds to the entire Earth, the species richness value is the same regardless of the focal point). We dealt with this by fitting a generalised least squares model (function *gls()* in the 'nlme' package in R; Pinheiro and Bates 2000, Pinheiro et al. 2025, http://www.r-project.org) with spherical autocorrelation to estimate a mean species richness $\bar{S}_i$ for each value of A_i (preliminary analyses, not shown, demonstrated that spherical autocorrelation produced better fits than other types of spatial autocorrelation). Accounting for spatial autocorrelation effectively downweights observations in heavily sampled regions, and, because sampling has historically been concentrated in more species-rich regions (Fig. 2), this tends to depress the SAR relative to one based on unweighted mean species richness values. We confirmed that our final qualitative conclusions are robust to using an unweighted mean across focal points to calculate species richness (not shown). Note also that because the generalised least squares procedure is applied independently at each focal area and spatial autocorrelation structure varies with scale, it is possible for estimated mean species richness to decrease occasionally with area, but such effects should be slight and should not preclude the fitting of increasing SAR formulas.

In preliminary analyses on the entire dataset, we found that the generalised least squares procedure sometimes failed to converge, which we attributed to divergent SARs arising from distinct biogeographical patterns and differences in species diversity between the world's two major mangrove regions: the Atlantic-East Pacific (AEP), which extends from the Americas to western Africa, and the Indo-West Pacific (IWP), which extends from eastern Africa to the western Pacific Ocean (Fig. 1a). This split is consistent with long-standing concepts in mangrove biogeography (Duke 1992): the AEP and IWP regions are delineated by geological history and geological and contemporary dispersal barriers, which have resulted in distinct species assemblages. We therefore ran the entire analysis pipeline separately for each region. For each region, we discarded any values of A_i for which the generalised least squares fitting procedure still did not converge, and additionally, for the small-scale data, we discarded any values of A_i with fewer than five observations, i.e. values of area for which there were fewer than five plots (because plot sizes are fairly standard across studies, this involved discarding only about 10% of the single-plot observations). Note that the largest area, A_{39}, is the same for both regions and equal to the surface area of the entire Earth (i.e. the two empirical SARs converge to the same point at maximum area). Further details on the generalised least squares fitting procedure can be found in the Supporting information.

We fitted to the mangrove SAR data (mean species richness $\bar{S}_i$ at each unique value of area A_i) a mathematical formula to evaluate how the slope of the SAR changes across scales. Many formulas have been proposed for describing SARs (Triantis et al. 2012). Most such formulas have been phenomenological: an advantage of phenomenological formulas is that they can be mathematically very simple (e.g. straight lines or power laws; Triantis et al. 2012), but a major disadvantage is that they give limited insight into

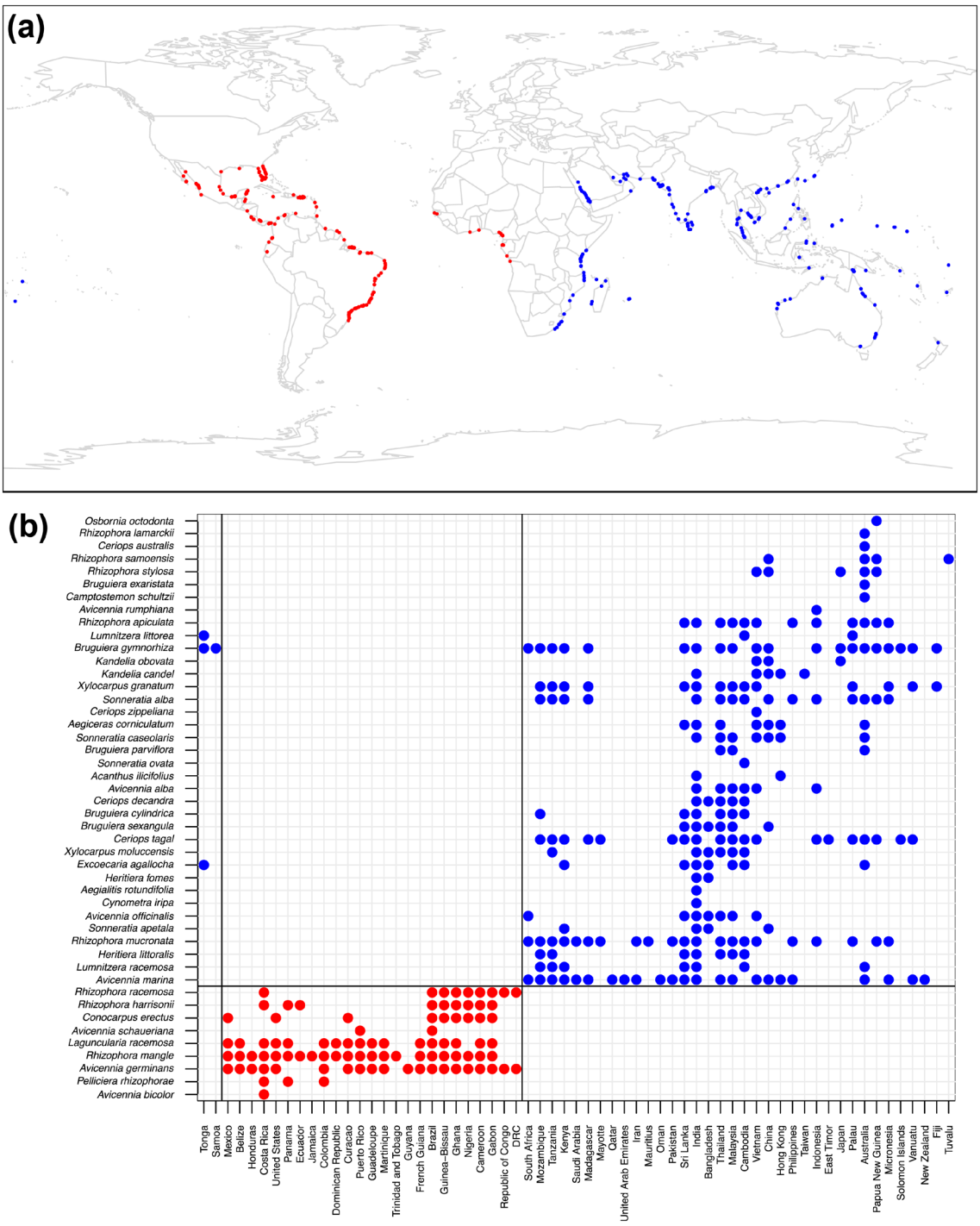

Figure 2. (a) Geographical distribution of mangrove plots in our database. Red points indicate plots in the Atlantic-East Pacific region; blue points indicate plots in the Indo-West Pacific region. (b) Species-by-country co-occurrence matrix. Countries (horizontal axis) are ordered by longitude. Points are coloured as in panel (a).

underlying mechanisms. We therefore opted instead to fit a recently derived SAR from a mechanistic model (Chisholm and Fung 2021). In the model there is a fixed number n^* of non-overlapping niches with neutral drift occurring within each niche. The diversity of the community within each niche at any given focal scale is maintained by a combination of speciation within the focal scale and immigration from a larger metacommunity. The model predicts a tetraphasic SAR, via the mechanisms described in the Introduction. The model is spatially implicit but gives good correspondence with simulations from a spatially explicit model (Chisholm and Fung 2021). Although the model is conceptually simple

and has few parameters, the resulting formula is fairly complicated; the Supporting information describes the model in more detail and gives the SAR formula. The formula has four free parameters that must be fitted to the data: the number of niches n^*, the metacommunity diversity θ, the per-capita speciation rate ν, and an immigration scaling constant k. We fit the formula by minimising the sum of squared differences between empirical and model logged species richness ($\log \bar{S}_i$), using the function *optim()* in R.

To generate confidence intervals on the fitted SAR and the four fitted parameters, we sampled $\bar{S}_i$ values from the output of the generalised least squares model for each value of A_i assuming normally distributed errors, and reran the SAR fitting procedure for the sampled values. We repeated this 1000 times and computed the confidence intervals from quantiles on the resulting output. We discarded repeats for which the fitting procedure did not converge (0/1000 repeats for AEP; 194/1000 repeats for IWP).

We compared the fits of the full tetraphasic SAR formula to those of a triphasic SAR formula that is obtained by setting the niche diversity parameter to one ($n^*=1$) in the general mechanistic model (Supporting information), thus eliminating the distinct niche-structured SAR phase.

Results

The plots in our dataset were broadly distributed across the world's two main mangrove biogeographic regions: 1141 plots were in the AEP and 904 plots were in the IWP (Fig. 2a). Consistent with existing knowledge of mangrove biogeography, species richness was lower in the AEP region (nine species) than in the IWP region (37 species) (Fig. 2b).

The SAR formula (Supporting information) provided an excellent fit to the data in both regions (AEP $R^2=0.977$; IWP $R^2=0.921$; Fig. 3), although we had to exclude the 40 plots in western Africa when fitting the SAR model to the AEP region to achieve model convergence (the SARs centred on these plots were qualitatively consistent with those of other AEP plots but increased more steeply at scales of around 10^7 km^2 because of their greater proximity to the IWP region). The parameter estimates in the SAR model fits

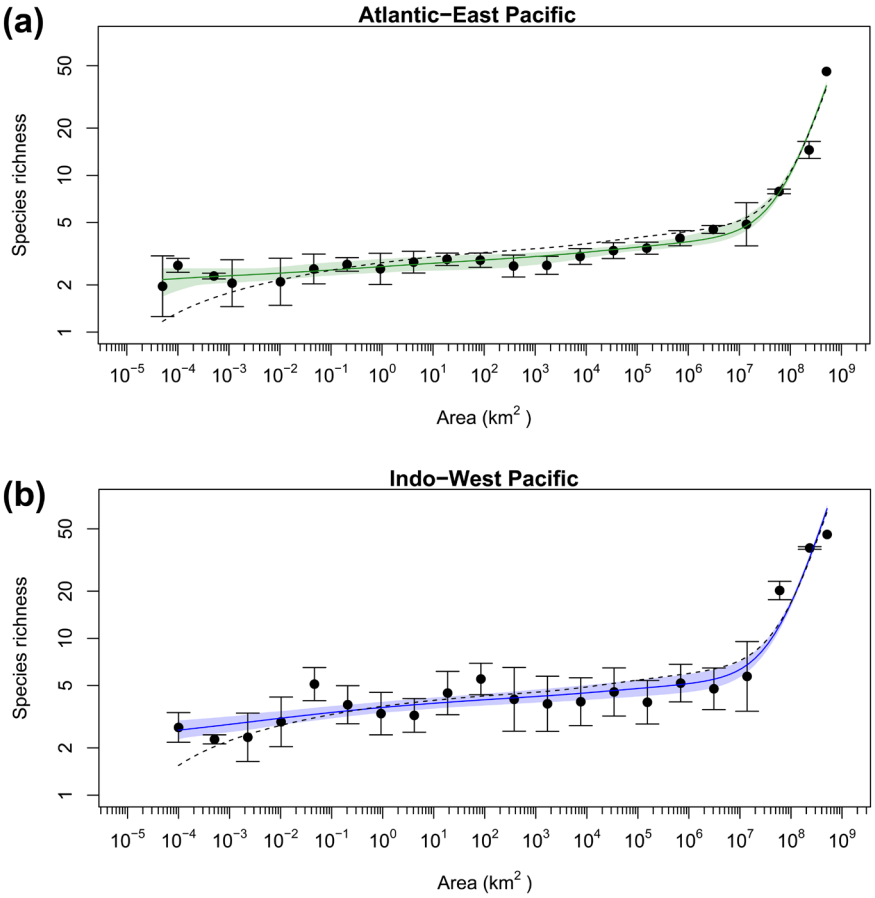

Figure 3. Global species–area relationships for mangrove trees starting from focal points in (a) the Atlantic-East Pacific region and (b) the Indo-West Pacific region. Each point with 95% confidence intervals indicates mean species richness at a given value of area, estimated as described in the main text. Coloured curves with 95% shaded confidence intervals indicate fits of the mechanistic model (Supporting information) to the data, as described in the main text. Dashed curves indicate fits of the alternative model without niches ($n^*=1$; Supporting information). Fitted parameter values are given in Table 1.

Table 1. Parameter estimates from fits of the tetraphasic SAR to the mangrove data for the two regions.

	Atlantic-East Pacific (AEP)		Indo-West Pacific (IWP)	
Parameter	Estimate	95% Confidence interval	Estimate	95% Confidence interval
n^*	2.22	1.95, 2.57	2.72	2.38, 3.11
k	6.56×10^{-4}	2.16×10^{-6}, 1.04×10^{-2}	0.0100	0.00676, 0.0104
ν	3.95×10^{-11}	2.60×10^{-11}, 5.06×10^{-11}	9.03×10^{-11}	8.45×10^{-11}, 9.61×10^{-11}
θ	0.186	0.115, 0.498	0.209	0.132, 0.304

were well constrained, except for the parameter k in the AEP region (Table 1). The estimates of both the metacommunity parameter θ and the per capita speciation rate parameter ν (Table 1) are around two orders of magnitude lower than typical estimates for tropical terrestrial forests (Volkov et al. 2007, Hubbell 2015), which makes biological sense given the much lower diversity of mangrove forests. The estimates of the parameter k, though uncertain, together with the estimates for θ (Table 1), imply realistic new species arrival rates (via formulas in Condit et al. 2012) giving, for example, a 2% per-generation probability of a new species arriving to a 250 × 1000 m patch of mangroves, which seems plausibly low, although the data for precise verification do not exist.

The confidence intervals on the fitted SARs were narrow (Fig. 3). Consistent with IWP's known higher mangrove diversity, the SAR for the IWP was generally higher than that for the AEP, although this was only strongly evident at large areas. The fitted SAR for the AEP region underpredicted species richness at the scale of the entire Earth (Fig. 3a), while the IWP overpredicted it (Fig. 3b). The poor fit to this one data point, attributable to the higher richness of the IWP region relative to the AEP region, does not affect our interpretations, which are focussed on the shape of the SAR at scales below 10^6 km^2.

The niche-structured phase was clearly visible, with the SARs for both regions consistently stuck at an average of around two to three species over several orders of magnitude of area (AEP $n^* = 2.22$, 95% CI [1.95, 2.57]; IWP $n^* = 2.72$, 95% CI [2.38, 3.11]). In accordance with this, the estimated SAR slopes were very low (less than 0.04) up to scales of 10^6 km^2 (Fig. 4). The alternative triphasic SAR formula gave poorer fits to the data (AEP $R^2 = 0.896$; IWP $R^2 = 0.884$) and in particular was unable to capture the long nearly flat SAR phase (Fig. 3, dashed curves).

Discussion

The mangrove tree SAR exhibits a long, nearly flat phase that is highly anomalous in ecology. Mangrove tree species richness barely changes over about ten orders of magnitude of area (Fig. 2), with the estimated log–log SAR slope over these scales being less than 0.04 (Fig. 4); for comparison, a typical SAR at intermediate scales has a slope of 0.25 (Lomolino 2000), implying that over ten orders of magnitude of area the number of species should increase by a factor of about 300 (i.e. $(10^{10})^{0.25}$). Even if we deliberately choose from among the lower previously observed values of this exponent and take $z = 0.15$ (as observed for, e.g. birds in Australia; Storch et al. 2012), we would predict that species richness should increase by a factor of about 30 over this range of scales. Crucially, the species richness in this nearly flat phase of the mangrove SAR does not simply asymptote to a value of one as area becomes small, which would be easily reconciled with typical SARs (and with models lacking stabilising niches) by noting that species richness is constrained to integer values. Rather, average richness is persistently maintained at between two and three species. In the subsections below, we seek to explain this anomalous SAR and reconcile it with standard SAR theory. We also discuss implications for our understanding of community assembly processes in mangroves and more broadly.

Explaining the nearly flat phase of the mangrove SAR

What explains the mangrove SAR's anomalous long, nearly flat phase, where species richness is maintained at an average of between two and three species? Because our analysis is based on nested SARs, this nearly flat phase implies not only that species richness is roughly constant over a broad range of areas but that there is also very little turnover. One hypothesis might be that the unusual SAR has something to do with the unusual spatial distribution of mangroves, which tend to exist in a series of long, almost linear strips. But we can dismiss this because other habitat types with a similar spatial distribution exhibit typical SARs (e.g. bird species in South African coastal forests; Olivier et al. 2013).

Our interpretation of the nearly flat SAR phase is that there are typically between two and three stabilising niches for mangrove trees, and these are associated with distinct tidal ranges. Most mangrove stands exhibit species patterning across tidal ranges at plot-to-landscape scales, with pioneer species such as *Avicennia alba* and *Sonneratia alba* able to tolerate more seaward and inundated locations (Friess et al. 2012), and other species able to tolerate less-flooded conditions further inland. Intra-plot species differences in mangrove species' distributions are generally determined by species-specific tolerances to physical conditions such as tidal inundation, with different species having evolved distinct adaptation mechanisms to flooding stress. While many species have wide inundation niches, species still show patterning across gradients of elevation (Leong et al. 2018, Ellison et al. 2022) and other biophysical factors, which can translate to niche differentiation (Ndayambaje et al. 2021). We infer that this niche differentiation prevents the number of species at a plot form dropping below the number of stabilising niches

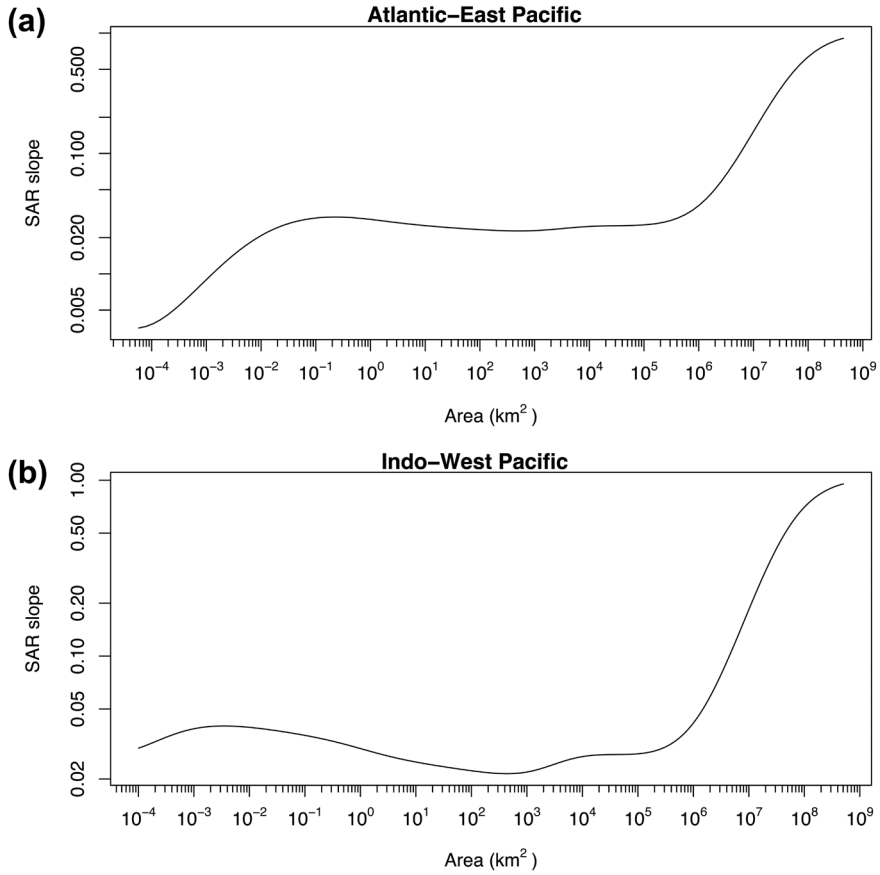

Figure 4. Estimated log–log slopes of the SARs from Fig. 3 as a function of area for (a) the Atlantic-East Pacific region and (b) the Indo-West Pacific region. Note that a typical SAR slope at intermediate scales would be in the range 0.15–0.35 (Storch et al. 2012), whereas the slopes observed here at such scales are about an order of magnitude lower.

(monoculture mangrove stands are typically only seen in plantations, Chen et al. 2012).

We expect that most ecologists will find the above explanation intuitive and easy to accept. But we have thus far sidestepped the bigger conundrum of why the mangrove SAR is anomalous. The above logic seemingly applies to any ecological community, which all have their own sets of niches and yet almost all exhibit strongly increasing SARs. Why is the mangrove SAR different? One could perhaps argue that while in other communities the number of niches increases with area, in mangrove tree communities it does not. But this, at best, just shifts the original question from the SAR to the niche–area relationship. We propose below an alternative explanation for why the mangrove SAR is anomalous. To motivate this, we first review existing theoretical explanations for typical increasing triphasic SARs.

Theoretical explanations for the typical triphasic SAR

As first noted by Preston (1960), when viewed across a broad range of scales, a typical SAR is triphasic, with all three phases being strongly increasing. Recent theoretical work (O'Dwyer and Cornell 2018) using neutral models (i.e. models without niches) has attributed these three phases to sampling, dispersal, and speciation processes, respectively.

The transition from the sampling phase to the dispersal-structured phase is predicted to occur at a scale corresponding to the mean dispersal distance (O'Dwyer and Cornell 2018): below this scale, communities are close to well mixed and the SAR slope approaches a value of one as the area becomes small; above this scale, the SAR is close to a power law with a slope of approximately 0.25. Consistent with this, there is a clear drop in the slope at around 10^4 m^2 for terrestrial tropical forest trees (Chisholm 2024), implying a plausible mean dispersal distance on the order of 100 m, and at around 10^5–10^6 m^2 for birds (Preston 1960), implying a plausible mean dispersal distance of 600–1000 m.

The transition from the dispersal-structured phase to the speciation-structured phase, manifested by the SAR slope rising and approaching one for large areas, is predicted to occur at a scale corresponding to the typical species range size (Grilli et al. 2012, O'Dwyer and Cornell 2018). Consistent with this, Preston's (1960) bird data exhibit the predicted

sharp rise in the SAR slope at around 10^6 km^2, roughly corresponding to the average species range size for birds. Data compiled by Storch et al. (2012) confirm this phenomenon for a broad range of taxa.

These theoretical explanations do not work for mangroves. The average dispersal distance of a mangrove propagule is likely on the order of tens to hundreds of meters. Although the propagules of some genera (e.g. *Rhizophora, Heritiera*) can remain buoyant for months (Van der Stocken et al. 2019) and although trans-oceanic dispersal is possible (Takayama et al. 2013), most propagules leading to successful recruitment travel short distances due to propagule trapping within the donor plot, variation in vector speed and direction, discontinuities in suitable habitat after long-distance dispersal, and decreased long-term propagule viability (Binks et al. 2019, Van der Stocken et al. 2019). Most mangrove tree species' distributions span multiple continents, and thus average range sizes are on the order of 10^6–10^8 km^2. Thus, standard theory would predict two transitions in the mangrove SAR, the first coinciding with a sharp drop in the SAR slope at around 10^{-4}–10^{-2} km^2 and the second coinciding with a sharp rise in the SAR slope at around 10^6–10^8 km^2. But only the second of these is apparent from the data (Fig. 4).

Why is the mangrove SAR anomalous?

The mangrove SAR does not fit the classic paradigm of an increasing triphasic SAR because, as noted above, its slope is far too shallow over ten orders of magnitude of area. As we also explained above, we attribute this nearly flat phase to niche structure, but the outstanding question is why this phase is observed only in the mangrove SAR and not in other ecological communities. To explain this, we invoke the very low metacommunity diversity of mangrove trees. We propose that in most non-mangrove systems, metacommunity diversity is sufficiently high that propagule input to communities at all scales is diverse enough to overwhelm the niches. In this view, it is high metacommunity diversity and dispersal, not niches, that produce the increasing SAR observed in most systems, and in most systems, there is a large excess of species over niches. Only in exceptional systems with low metacommunity diversity, such as mangroves, is the diversity of input propagules over a large range of scales too low to overwhelm the niche structure, with the result that the observed number of species approximately reflects the number of niches.

Recent theoretical work confirms that the above mechanisms can produce a long, nearly flat niche-structured SAR phase in systems with low metacommunity diversity (Chisholm and Fung 2021). In such situations, the overall SAR is tetraphasic, with the niche-structured phase appearing between the sampling and dispersal-structured phases (Chisholm and Fung 2021). This phase is hidden in most systems because of high metacommunity diversity. Although we acknowledge that one cannot clearly distinguish all four phases of the theoretical tetraphasic SAR in the mangrove data (Fig. 3), we propose that the observed long, nearly flat phase is indeed the theoretical, typically hidden, niche-structured phase.

We note that there are exceptions to the general pattern of low species diversity in mangrove communities, particularly in the IWP region. For example, although the average richness across our 35 plots in Malaysia was only 3.8, five of these plots had seven or more species (Faridah-Hanum et al. 2012, Goessens et al. 2014, Rozainah et al. 2018). We attribute such unusual cases to the fact that mangrove tree diversity in the IWP region is approximately four times higher than in the AEP region. Thus, the immigrant pool is also more diverse and the niches are overfilled at some plots. Although plots with more than a few species are unusual among mangrove tree communities, they are, of course, the norm for most guilds in terrestrial communities. This includes terrestrial tropical forest tree communities, where hundreds of species may be found in a single hectare (Wright 2002), a point to which we return below.

To summarise this subsection, we interpret the long, nearly flat phase of the mangrove SAR as a niche-structured phase, and we attribute the fact that we see this phase uniquely in mangroves to the very low metacommunity diversity of mangroves. We attribute the low metacommunity diversity of mangroves, in turn, to mangroves being widespread but having a small total area – today the total global area of mangroves is less than 1% of terrestrial lowland tropical forest – and to mangroves having suffered substantial range contractions associated with sea level changes over geological time, as also evidenced from very low within-species genetic diversity (Guo et al. 2018).

Implications for community assembly and limitations

Assuming our interpretations of the niche-structured mangrove SAR are correct, the results presented here have implications for our understanding of biogeography and community assembly. Firstly, they help reconcile the mainland SARs with the island archipelago SARs, where a nearly flat SAR phase is more commonly observed and has been attributed to niche assembly predominating on islands with low immigration (Chisholm and Fung 2021). Secondly, our results suggest that the number of stabilising niches in local ecological communities may often be surprisingly low, often fewer than ten at a given trophic level. Of course, many ecological communities, such as tropical forest tree communities, exhibit much greater species diversity, but we attribute this not to high niche diversity but to continued immigration of individuals from diverse regional source pools. Only if the source pool is species-poor, as for mangroves, or if immigration is very low, as on small islands (Chisholm et al. 2016), or if immigration is reduced experimentally (Loke and Chisholm 2023), is the true niche diversity revealed. Evidence from past studies, corroborates our conclusion that niche diversity is typically low (Fig. 3; Chisholm et al. 2016, Loke and Chisholm 2023).

There are a few limitations to our analysis. The first is that some mangrove areas are underrepresented in our dataset (e.g. Indonesia and the Philippines). Several species in the IWP region are missing entirely from our dataset. Such omissions will tend to lead to underestimates of the true SARs. However, we do not expect that the addition of more plots would qualitatively change our results. Our results for the better-sampled AEP region (Fig. 3a, 4a) are qualitatively similar to those for the under-sampled IWP region (Fig. 3b,4b). Even if we restrict our SAR focal points to very well-sampled subregions (e.g. Brazil, with 820 plots), we observe a similar SAR (Supporting information). Moreover, although species omissions could affect the overall magnitude of the SAR, this effect should manifest itself across the full range of areas; it should not by itself produce a nearly flat SAR phase (Fig. 3) as some kind of artefact. Nevertheless, we encourage the continued collection of large-scale mangrove data to refine our understanding of the mangrove SAR and the processes that generate it.

A second limitation is that although the evidence for a nearly flat SAR phase in the mangrove data is unequivocal and consistent with theory that predicts a tetraphasic SAR, not all four phases are clearly distinguishable in the data. A more comprehensive dataset with a finer gradation of area values and extension of the SAR to smaller scales (ideally the scale of a single mangrove tree) would be needed to test the idea of a tetraphasic SAR (Fig. 1b) more rigorously and thereby provide further support for the theory (Chisholm and Fung 2021). A more comprehensive dataset would also facilitate testing the theory against a broader range of patterns, such as species turnover (Condit et al. 2002). Further technical work is needed to derive an SAR formula for a spatially explicit version of our spatially implicit model (O'Dwyer and Cornell 2018, Chisholm and Fung 2021).

The theoretical ideas explored here can be tested using other datasets. Can the niche-structured SAR phase (and perhaps the full tetraphasic SAR) be observed in other systems? Boreal forest tree communities are an obvious candidate, as they also have low metacommunity diversity (Svenning and Skov 2007). Theory also predicts the niche-structured SAR phase to appear in communities of taxa with very short dispersal distances. A question with major implications for our understanding of community assembly is whether there are any systems with niche diversity substantially higher than that observed here. The emerging picture is that niche diversity is usually low, and communities are primarily niche-assembled only in special cases, e.g. mangrove tree communities, small isolated islands (Chisholm et al. 2016), and experimental communities with artificially low immigration (Loke and Chisholm 2023). In most other contexts, evidence suggests that dispersal assembly dominates.

Acknowledgements – We thank Tak Fung for comments on the manuscript.
Funding – RAC was supported by a grant from the James S. McDonnell Foundation (no. 220020470).

Author contributions

Ryan A. Chisholm: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Writing – original draft (lead). **Nicholas Z. W. Fong**: Data curation (equal); Formal analysis (equal); Writing – review and editing (supporting). **Daniel A. Friess**: Conceptualization (supporting); Writing – review and editing (supporting). **Andre S. Rovai**: Conceptualization (supporting); Data curation (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0zpc86788 (Chisholm et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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