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Maintenance of biodiversity on islands

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MacArthur and Wilson's theory of island biogeography predicts that island species richness should increase with island area. This prediction generally holds among large islands, but among small islands species richness often varies independently of island area, producing the so-called 'small-island effect' and an overall biphasic species–area relationship (SAR). Here, we develop a unified theory that explains the biphasic island SAR. Our theory's key postulate is that as island area increases, the total number of immigrants increases faster than niche diversity. A parsimonious mechanistic model approximating these processes reproduces a biphasic SAR and provides excellent fits to 100 archipelago datasets. In the light of our theory, the biphasic island SAR can be interpreted as arising from a transition from a niche-structured regime on small islands to a colonization–extinction balance regime on large islands. The first regime is characteristic of classic deterministic niche theories; the second regime is characteristic of stochastic theories including the theory of island biogeography and neutral theory. The data furthermore confirm our theory's key prediction that the transition between the two SAR regimes should occur at smaller areas, where immigration is stronger (i.e. for taxa that are better dispersers and for archipelagos that are less isolated).

1. Introduction

In their seminal treatise on island biogeography, MacArthur & Wilson [1] proposed a general explanation for the maintenance of biodiversity on islands. Their theory explains how distance and area affect island species richness: larger islands and islands nearer to mainlands experience greater immigration than small, remote islands and should therefore, *ceteris paribus*, have more species at the colonization–extinction dynamic equilibrium. These predictions are generally consistent with empirical data [2], and the theory of island biogeography is among the most influential of ecological theories.

Despite the successes of their theory, MacArthur & Wilson [1] discovered empirical examples where the theory's predictions broke down. In particular, they noted that archipelagos exhibit unusual species–area relationships (SARs): below a threshold island area, island species richness apparently varies independently of area. This phenomenon has become known as the small-island effect [3–6]. The small-island effect is surprising not only because it violates MacArthur & Wilson's expectation for islands, but also because it is an exception to the putative ecological law that SARs should always be increasing functions [7–9]. The prototypical example of the small-island effect is for vascular plants in the Kapingamarangi Atoll in Micronesia [1,10], but the phenomenon is general, being observed for a wide range of taxa and biogeographic island types, including lake islands and mountain tops [3]. Ecologists have therefore sought a general theory that explains the small-island effect, while also incorporating the classic island biogeography results for larger islands [3–6].

Previous attempts to explain the small-island effect have centred around two main hypotheses [6]. The first is that extinction rates are independent of island area on small islands, because small islands are environmentally unstable and temporal turnover in species composition is rapid [1]. The idea is that small

islands are subject to major episodic disturbances (e.g. devastating storms) that eliminate most life forms and thereby prevent species diversity from reaching equilibrium. The second hypothesis is that small islands, by virtue of their smallness, have an unusual suite of habitats that is different from that on large islands [11–13]: certain types of habitat (e.g. riparian zones) are simply not available on small islands, and this limits species diversity.

But these previous hypotheses have serious shortcomings. One problem is that they make no reference to immigration. The hypotheses propose mechanisms that could indeed modify SARs in some way, but they do not explain specifically how small islands could be exempt from the general island biogeographic rule that increasing island area means more immigration and more species (i.e. how the target area effect could disappear [14]). For example, the hypothesis that catastrophic disturbances induce the small-island effect is problematic because, even if disturbances do regularly wipe out most species on small islands, the larger small islands still receive more immigrants than the smaller small islands, and the species richness on larger small islands should thus recover more quickly from disturbance and be greater on average. A second problem with existing hypotheses is that they appear to predict anomalously low diversity on small islands (relative to the SAR extrapolated from large islands), whereas the data show anomalously high diversity on small islands. A final, overarching problem with existing hypotheses is that they are qualitative: without a formulation in terms of quantitative models, it is difficult to rigorously evaluate their success at explaining the small-island effect.

Here, we present a new theory of island diversity that explains both the small-island effect and the classic MacArthur & Wilson results. Our theory does not suffer the shortcomings of previous explanations of the small-island effect. Our theory postulates that diversity on both large and small islands is maintained by two mechanisms, niche constraints and immigration, but that niche diversity increases only slowly with area, whereas immigration increases rapidly with area. The net effect is that the niche constraints dominate on small islands (where immigration is low) but immigration dominates on large islands. We test our new theory in two ways. First, we test whether this combination of mechanisms can indeed produce biphasic island SARs by analysing a mechanistic mathematical model and fitting the model to 100 archipelago datasets. Second, we use the same datasets to test the theory's key prediction that the transition between the two regimes of the SAR should occur at smaller island areas in archipelagos where immigration is greater and for taxa that immigrate to islands more easily.

2. Material and methods

(a) Mathematical model

To test our theory, we required a model that includes immigration and niche structure, and that allows one to specify how these vary with island area. We used a previously published model that satisfies these conditions [15,16]. The model is a simplified representation of island community dynamics, but is adequate for testing the fundamental tenets of our theory in a general and parsimonious way.

The model contains a local community, which we consider to represent a focal island, and a metacommunity, which we consider to represent other islands and the mainland. The local community will henceforth be referred to as the 'island community'. The metacommunity comprises K equal-sized non-overlapping niches, and within each niche the species competing for resources are considered to be ecologically equivalent. This means that the community dynamics within each niche follow neutral, zero-sum dynamics. At each time step, an individual is chosen at random to die in the metacommunity and is replaced by the offspring of another randomly chosen individual within the same niche. Speciation occurs in each time step with some typically very small probability. These processes lead to a speciation–extinction balance in the metacommunity and a species abundance distribution in each niche approximately equal to a log-series [17] with parameter θ/K (technically, it is asymptotically equivalent to a log-series in the limit of high diversity [15]), where θ is known as Fisher's α or the fundamental biodiversity number [8,15]. Metacommunity diversity is considered to be fixed on time scales relevant to the island community. For mathematical details of the metacommunity model, see [15].

The island community in the model obeys similar dynamics to the metacommunity except that diversity is maintained only by immigration from the metacommunity (there is no speciation on the island). The island community comprises J individual organisms in K distinct equal-sized non-overlapping niches (as in the metacommunity), so that there are $J/K \equiv J^*$ individuals in each niche. At each time step, an individual is chosen at random to die in the island community and is replaced by the offspring of another randomly chosen individual within the same niche in the island community with probability $1 - m$, or by a randomly selected immigrant from the same niche in the metacommunity with probability m . The probability m is typically small (i.e. immigrants are few and most propagules are produced locally on an island).

In the island community, the species abundance distribution within each niche in our model is given by the known neutral result [18]. Specifically, the expected number of species with abundance n in a given niche at the colonization–extinction dynamic equilibrium is

$$\langle \phi_n^* \rangle = \frac{\theta}{K} \int_0^1 P_S(n; J^*, m, x) \frac{(1-x)^{\theta/K-1}}{x} dx, \quad (2.1)$$

where

$$P_S(n; J^*, m, x) = \binom{J^*}{n} \frac{\Gamma(\gamma^*)}{\Gamma(J^* + \gamma^*)} \frac{\Gamma(J^* - n + \gamma^*(1-x))}{\Gamma(\gamma^*(1-x))} \frac{\Gamma(n + \gamma^*x)}{\Gamma(\gamma^*x)}, \quad (2.2)$$

and $\gamma^* = (J^* - 1)m/(1 - m)$.

The expected total number of species in the modelled island community at the dynamic equilibrium is obtained by summing equation (2.1) over all possible abundances n and niches i :

$$S = \sum_{i=1}^K \sum_{n=1}^{J^*} \langle \phi_n^* \rangle. \quad (2.3)$$

We simplified equation (2.3) to obtain (electronic supplementary material, appendix S1)

$$S = \theta \left\{ -\psi_0\left(\frac{\theta}{K}\right) + \frac{1}{(\gamma^*)_{J^*}} \sum_{j=0}^{J^*} |s(J^*, j)| \gamma^{*j} \psi_0\left(j + \frac{\theta}{K}\right) \right\}, \quad (2.4)$$

where $\psi_0(z)$ is the digamma function, $s(a, b)$ is a Stirling number of the first kind and $(a)_b$ is the Pochhammer symbol [19].

To turn equation (2.4) into an SAR, we had to specify how the parameters J^* , K and m scale with island area A . For the parameter J^* , which determines the community size, we assumed linear scaling with area so that $J^* = \rho A/K$, where ρ is the

number of individuals per unit area [8]. For the parameter K , niche diversity, we noted that our theory postulates that niche diversity increases only gradually with island area and therefore made the simplifying assumption that K is constant with area. An alternative approach would be to allow K to increase as, say, a power law of area, but this would add at least one free-fitting parameter to the model without greatly improving the fits to data (the fits are already very good; see Results).

To determine the area scaling of the parameter m , which measures the probability that a new recruit will be an immigrant [20], we first assumed that the distance between an island and the source of immigrants is much larger than the average dispersal distance, which will almost always be the case. We can write $m \propto n_{\text{imm}}/n_{\text{local}}$, where n_{imm} is the number of immigrant propagules per unit time, n_{local} is the number of locally produced propagules on the island per unit time and $n_{\text{imm}} \ll n_{\text{local}}$. We assume that the number of immigrant propagules is proportional to island area ($n_{\text{imm}} \propto A$), consistent with most previous models of island biogeography (e.g. [1,21]). Thus, because n_{local} also scales linearly with A , m is independent of A . (Note that this assumption $n_{\text{imm}} \propto A$ is most appropriate for species with undirected aerial dispersal; for species with directed or waterborne dispersal, it may be more appropriate to assume scaling with island perimeter instead, i.e. $n_{\text{imm}} \propto \sqrt{A}$).

For computational efficiency, we derived an approximation to equation (2.4) (the Stirling numbers of the first kind are difficult to compute for large arguments [22]). This approximation stemmed from the insight that the dynamics of lineages in an island community (where each lineage arises from a unique immigration event) is analogous to the dynamics of species in the metacommunity (where each species arises from a unique speciation event), and by making the approximation that the number of lineages represented on an island is constant at the dynamic equilibrium. Computing the species richness then reduces to a problem of first calculating the expected number of lineages L on the island (which, as our analogy shows, is easily calculated by translating the known formula for the expected number of species in the metacommunity [23]) and second calculating the expected number of species S represented in a sample of size L from the metacommunity (obtained as a limiting case of equation (2.4); electronic supplementary material, appendix S1). The final formula is (electronic supplementary material, appendix S1)

$$S \approx \theta \left\{ \psi_0 \left(\frac{\theta}{K} + \gamma^* (\psi_0(\gamma^* + J^*) - \psi_0(\gamma^*)) \right) - \psi_0 \left(\frac{\theta}{K} \right) \right\}. \quad (2.5)$$

See the section 'Testing accuracy of approximate species–area relationship formula' for how we tested the accuracy of this approximation (i.e. equation (2.5) versus equation (2.4)).

For small areas ($A \rightarrow 1/\rho$, corresponding to $J \rightarrow 1$) and low immigration m , the expected number of species (equation (2.5)) asymptotes to (electronic supplementary material, appendix S1)

$$S \sim K. \quad (2.6)$$

(i.e. the species richness tends to the number of niches). In the limit of large area (and thus large J), we have a different asymptotic approximation to equation (2.5) (electronic supplementary material, appendix S1):

$$S \sim \theta \log \left\{ 1 + \frac{\gamma}{\theta} \log \frac{1}{m} \right\} + \theta \left\{ \log \left(\frac{\theta}{K} \right) - \psi_0 \left(\frac{\theta}{K} \right) \right\}, \quad (2.7)$$

where $\gamma = (J - 1)m/(1 - m)$. The first term in equation (2.7) gives the non-zero-sum neutral result [24], and the second term is a correction factor that accounts for the niche constraints. The second term becomes negligible relative to the first term as area A (and thus community size J) becomes large. From equations (2.6) and (2.7), we see that in the model, diversity is maintained primarily by niche constraints on small islands but

by immigration on large islands. Importantly, this confirms that the parsimonious combination of mechanisms proposed in our theory can indeed yield a biphasic SAR.

The critical area A_{crit} at which the transition between the two regimes of the SAR occurs can be estimated by equating the first term on the right-hand side of equation (2.7) (the neutral component) to the right-hand side of equation (2.6) and solving for A :

$$A_{\text{crit}} \approx \frac{\theta(1 - m)(\exp(K/\theta) - 1)}{m\rho \log(1/m)}. \quad (2.8)$$

From the above equation, we can see that in our model the critical area at which the transition occurs is larger for systems with more niches (large K), lower metacommunity diversity (small θ), lower immigration (small m) and lower individual density (small ρ).

(b) Datasets

We compiled 100 datasets of SARs (electronic supplementary material, table S1 and appendix S2) for a range of taxa from a range of archipelago types, based on the synthesis of Lomolino & Weiser [3] (we merged four of these authors' 102 datasets into others and added two new datasets). As in [3], only archipelagos with $n \geq 10$ islands were included. Each archipelago was classified as terrestrial (8 of 100 datasets), montane (8), inland waters (18) or marine (66) (electronic supplementary material, table S1). The taxonomic group for each dataset was classified as birds (15 of 100 datasets), herpetofauna (7), invertebrates (22), mammals (37) or plants (19).

For each dataset, the number of individuals per unit area was taken from the original study or from other studies specific to the system where possible (electronic supplementary material, table S1). In most cases, system-specific density estimates were unavailable and instead default values of densities for the taxa concerned were used, based on a literature survey (electronic supplementary material, table S2).

(c) Model fitting

For each archipelago dataset, we fitted equation (2.5) to the SAR data by finding the best-fit values of our model's three free parameters: the niche diversity K , the fundamental biodiversity number θ and the immigration parameter m . We did this by systematically considering all values of K between 1 and S_{max} , where S_{max} is the maximum species richness recorded on an island in the archipelago. For each K , a least-squares algorithm was used to find the best-fit values of m and θ (NonLinearModelFit in Wolfram MATHEMATICA 10). Initial guesses for m and θ were

$$\hat{m} = \frac{J}{\rho A_{\text{med}} W_{-1}(-K/\rho A_{\text{med}})}$$

and

$$\hat{\theta} = \frac{S_{A_{\text{max}}} \hat{\gamma} \log \hat{m}}{S_{A_{\text{max}}} - \hat{\gamma} \log \hat{m} W_{-1}((S_{A_{\text{max}}}/\hat{\gamma} \log \hat{m}) \exp(S_{A_{\text{max}}}/\hat{\gamma} \log \hat{m}))},$$

where $\hat{\gamma} = (\rho A_{\text{max}} - 1)\hat{m}/(1 - \hat{m})$, $W_{-1}(z)$ is the lower branch of the Lambert W function [19], A_{med} is the median area of islands in the archipelago, A_{max} is the maximum island area in the archipelago and $S_{A_{\text{max}}}$ is the species richness on this largest island. The formula for \hat{m} comes from inverting the approximate formula for the critical area (equation (2.8)). The formula for $\hat{\theta}$ comes from inverting the neutral species–area formula [24]. After finding best-fit values of m and θ for each K , we chose the m and θ and the corresponding K that gave the highest R^2 .

For a few small islands where the estimated number of individuals was less than the number of niches ($J < K$), we constrained the modelled species richness to be equal to the number

of individuals ($S = J$) during the fitting procedure, because it is biologically impossible to have more species than individuals.

(d) Testing accuracy of approximate species–area relationship formula

We compared the exact species–area equation (equation (2.4)) with the approximate species–area equation (equation (2.5)) to assess the error in the latter. We achieved this by taking the best-fit parameter values for each dataset and evaluating both the exact and approximate formulae for those islands with estimated community size $J = \rho A < 10\,000$ (34% of all islands satisfied this criterion; we did not perform the comparison for larger J because, as mentioned, the exact formula becomes computationally expensive). The percentage error was then computed as $100 \times |S_{\text{approx}} - S_{\text{exact}}|/S_{\text{exact}}$.

(e) Estimating critical area

For each archipelago dataset, we estimated the critical area A_{crit} at which the transition from the niche-structured to the colonization–extinction regime occurs by evaluating equation (2.8) for the fitted values of K , θ and m . This is a rigorous and repeatable method of estimating the critical area, but similar results could be obtained by other methods (e.g. [3]).

We used the estimated critical area values to test our theory's key prediction that the critical area should be larger in archipelagos that are more isolated (e.g. marine archipelagos) and for taxa that are more dispersal-limited (e.g. mammals). We ran a multiple regression with $\log(A_{\text{crit}})$ as the dependent variable, and archipelago type and taxonomic group (using the coarse classifications defined in the section 'Datasets') as categorical explanatory variables (i.e. we ran a two-way ANOVA). It is important to note that there is no circularity here because the information on archipelago type and taxonomic group was used neither to fit the model nor to estimate A_{crit} . The test is thus a strong test of our theory's predictive capabilities.

3. Results

The fits of our model to the 100 archipelago datasets had mean $R^2 = 0.91$, and adjusted mean adjusted $R^2 = 0.89$ with standard deviation 0.09 and range 0.55–0.99 (electronic supplementary material, tables S1–S2 and appendix S3). Figure 1 shows the fit to Niering's [10] classic plant data; figure 2 shows the fits to the bird [25], herpetofauna [26], invertebrate [27] and mammal [28] datasets with the most data points. The median value of the fitted fundamental biodiversity number θ was 3.9; the median fitted immigration parameter m was 1.5×10^{-5} ; and the median fitted number of niches K was 2. Of the three fitted parameters (m , θ , K), the immigration rate m was the most variable across datasets (electronic supplementary material, figure S1; median m was 1.5×10^{-5} , with range 2.7×10^{-12} –0.44). Correlations between the four model parameters (the three fitted parameters m , θ and K , and the independently estimated parameter ρ) were weak to moderate (electronic supplementary material, figure S2). The strongest correlation was between K and θ (Spearman's $r_s = 0.51$, $p = 8 \times 10^{-8}$; see the electronic supplementary material, appendix S4 for discussion of these results).

In our numerical investigations, the error associated with using the approximate formula for species richness (equation (2.5)) instead of the computationally expensive but exact equation (2.4) was on average 1.6% and at most 8.3% (based on 961 observations). This shows that equation (2.5)

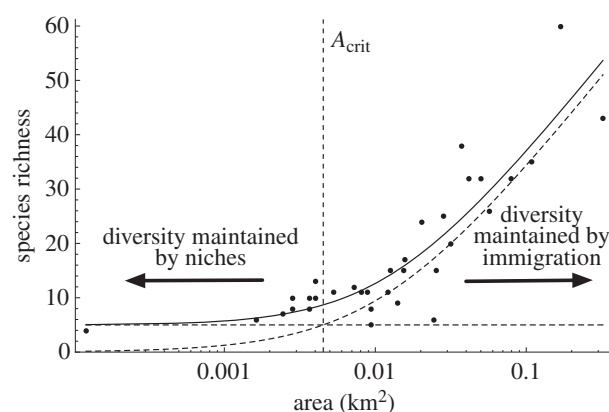


Figure 1. SAR for vascular plants on islands in the Kapingamarangi Atoll [10] (points) along with the fitted SAR from the model (solid curve; $n = 33$, $\theta = 15.2$, $m = 6.9 \times 10^{-5}$, $K = 5$, $R^2 = 0.93$). The horizontal dashed line and dashed curve show the diversity predicted by, respectively, the niche and neutral components of the model in isolation. The transition between the two regimes occurs at area $A_{\text{crit}} = 0.0045 \text{ km}^2$ (grey dashed vertical line; equation (2.8)).

is a reasonable approximation to the equilibrium species richness in our model.

There were marked differences in the average critical area, A_{crit} , across archipelago type and taxonomic group (figure 3). The multiple regression of A_{crit} on archipelago type and taxonomic group (which satisfied the normality and homoscedasticity assumptions) quantified these effects and upheld the key prediction that the critical value of island area A_{crit} should be smaller where immigration is greater (i.e. for taxa that disperse well and for archipelagos that are less isolated; table 1). For example, the model estimates that the critical area is on average $e^{4.17} = 64.7$ (95% CI [4.85, 862.6]) times greater for mammals than for birds, and on average $e^{6.49} = 658.5$ [72.2, 6002.9] times greater for marine archipelagos than for inland-water archipelagos. Overall, taxonomic group and archipelago type explained 51% of the variance in $\log A_{\text{crit}}$ (table 1).

4. Discussion

We have proposed a unified theory of island diversity that can explain both the classic MacArthur & Wilson [1] result of increasing diversity with island area among large islands, and the small-island effect [3] of roughly constant diversity among small islands. According to our theory, the regime at small areas arises from niche constraints and the regime at large areas arises from a colonization–extinction balance. A mechanistic model of the relevant processes [15] accurately fits 100 SARs from a broad range of archipelago types and for a broad range of taxa (figures 1 and 2; electronic supplementary material, table S1).

The model we used to test our theory is, to the best of our knowledge, the first mechanistic model fitted to datasets exhibiting the small-island effect. Past fits to similar data have been based on phenomenological models and the quality of the fits has been poorer. For example, Lomolino & Weiser [3] fit piecewise linear models to almost the same data and achieved a mean R^2 of 0.69, compared with a mean R^2 of 0.91 for our model with the same number of free parameters. Though our model ignores much biological

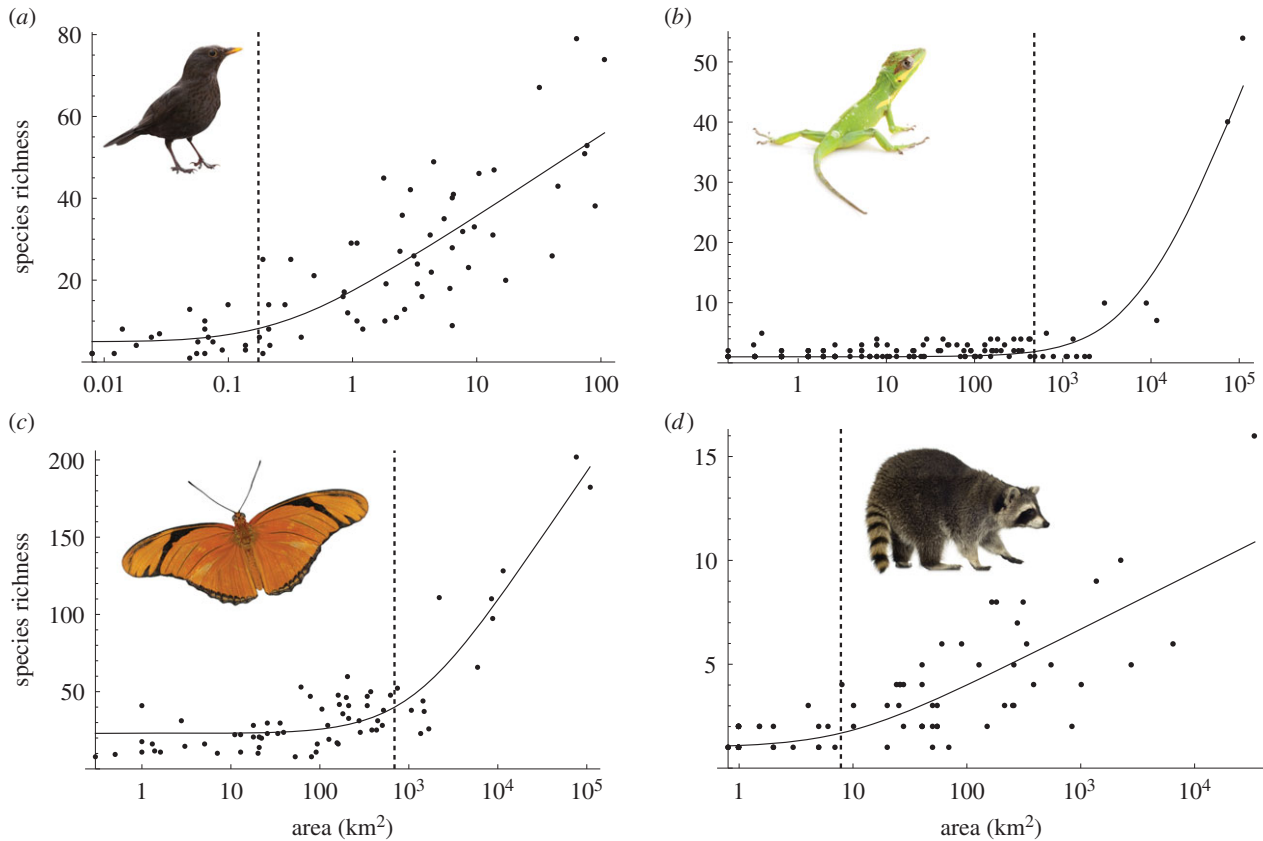


Figure 2. SARs for four datasets (points), with best-fit models (solid curves): (a) birds, British Isles ($n = 73$, $\theta = 8.6$, $m = 0.012$, $K = 5$, $R^2 = 0.87$); (b) anoline lizards, West Indies ($n = 136$, $\theta = 16.6$, $m = 1.1 \times 10^{-9}$, $K = 1$, $R^2 = 0.93$); (c) butterflies, West Indies ($n = 68$, $\theta = 37.2$, $m = 2.3 \times 10^{-9}$, $K = 23$, $R^2 = 0.92$); and (d) mammals, Islands of British Columbia ($n = 75$, $\theta = 1.2$, $m = 1.8 \times 10^{-5}$, $K = 1$, $R^2 = 0.84$). As in figure 1, a transition from a niche-structured regime to a colonization–extinction regime occurs in each panel as area increases past a critical area A_{crit} (dashed vertical lines; equation (2.8)). Inset images (obtained with permission from www.shutterstock.com) show common blackbird (*Turdus merula*), Knight anole (*Anolis equestris*), Julia heliconian (*Dryas iulia*) and common raccoon (*Procyon lotor*). (Online version in colour.)

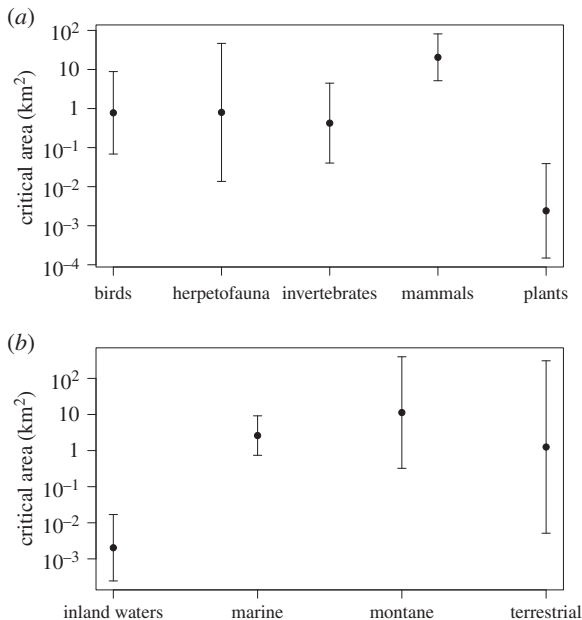


Figure 3. Critical area by (a) taxonomic group and (b) archipelago type. Points show means on a log scale; whiskers show estimated 95% CIs using a normal approximation on a log scale.

detail, it verifies our main hypothesis that a biphasic archipelago SAR can arise if niche diversity increases only slowly (or not at all) with area but the total number of immigrants increases rapidly with area.

Table 1. Effects of taxonomic group and archipelago type on \log_{10} (critical area) ($\log_{10} A_{crit}$) from multiple regression on the 100 archipelago datasets ($F_{92,7} = 13.94$, $p = 3.4 \times 10^{-12}$, $R^2 = 0.51$; adjusted $R^2 = 0.48$). The critical area is the area at which the transition from the niche-structured regime to the colonization–extinction regime occurs (figure 1; equation (2.8)). Positive effect sizes indicate a larger critical area than the base case (birds, inland waters); negative effect sizes indicate a smaller critical area than the base case. The results show that effect sizes are positively related to taxon dispersal limitation and to archipelago isolation, (i.e. the critical area is smaller where immigration is stronger).

	estimated effect on $\log A_{crit}$ (km^2) [95% CI]		p -value
intercept (birds, inland waters)	−6.59	[−9.56, −3.62]	2.9×10^{-5}
taxonomic group			1.4×10^{-9}
herpetofauna	1.73	[−2.10, 5.55]	0.37
invertebrates	0.65	[−2.15, 3.45]	0.65
mammals	4.17	[1.58, 6.76]	0.0019
plants	−4.11	[−7.03, −1.19]	0.0062
archipelago type			8.3×10^{-7}
marine	6.49	[4.28, 8.70]	8.2×10^{-8}
montane	7.88	[4.28, 11.48]	3.5×10^{-5}
terrestrial	4.72	[1.11, 8.32]	0.011

Our theory also makes the key prediction that the critical area (where the transition between the niche-structured regime and the colonization–extinction regime occurs) should be smaller where immigration is stronger. For example, it is usually easier for birds and plants to immigrate to islands than it is for mammals, and therefore our theory predicts A_{crit} to be smaller on average for birds and plants. Similarly, it is usually easier for organisms to immigrate to islands in inland waters than to oceanic islands, and so our theory predicts A_{crit} to be smaller on average for islands in inland waters. These predictions are largely borne out by the data (table 1 and figure 3). For mammals, the average critical area (geometric mean) is 20 km², but for birds it is 0.78 km². For marine archipelagos, the average critical area is 2.6 km², but for archipelagos in inland waters it is a tiny 0.0020 km². The multiple regression model confirmed these results (table 1). Overall our model can account for roughly half the variance in the critical area (on a log scale) observed in island SARs, given only coarse information about taxonomic group and archipelago type. Previous explanations for the small-island effect cannot account for these patterns.

A satisfying feature of our new theory is that it encompasses two contrasting bodies of ecological theory (figure 1) [29]: the niche-structured regime corresponds to classic deterministic niche theories; the colonization–extinction regime corresponds to stochastic community theories such as the theory of island biogeography [1] and neutral theory [8,30]. In the niche-structured regime, the identity of an island's component species may change over time, but the total species richness is roughly equal to the niche diversity and could in principle be predicted by studying the abiotic properties of the system. As an example, consider a simplified caricature of an oceanic island, where one posits the presence of a tree niche, a grass niche, a salt-tolerant shrub niche, and so on, up to K niches. Then, under low immigration, our theory (in common with deterministic niche theories) predicts the long-term coexistence of K species. The identities of these species may change over time, as very occasional colonization and extinction events occur within each niche, but the total number of species remains roughly equal to K . By contrast, in the colonization–extinction regime, the species richness is not predictable from the abiotic niche structure of the environment (which reflects climate, disturbance regimes, nutrient levels, geology, etc.); instead, average species richness could be predicted, in principle, from stochastic dynamic models parametrized with measured immigration and extinction rates.

The implications of our results go beyond island biogeography to mainland systems. A fundamental difference between island communities and mainland local communities is that mainland communities receive much greater immigration. In the framework of our theory, this implies that the critical area, A_{crit} , on mainlands is very small, and that mainland local communities at most spatial scales should therefore be firmly in the colonization–extinction regime. Thus, if we want to understand why, for example, hundreds of species can coexist within a few hectares of tropical forest [31], a fruitful strategy might include a renewed focus on immigration and the mechanisms promoting regional diversity over geological time scales [32,33], in addition to the traditional focus on small-scale niche mechanisms such as Janzen–Connell effects and resource partitioning [31,34].

An interesting feature of our island species–area formula (equation (2.7)) is that, even at large island areas, it does not exhibit the classic power-law phase with exponent ≈ 0.2 – 0.3 [7]. We attribute this to the spatially implicit structure of our model, which actually appears to be the appropriate structure for modelling archipelago systems, given our good fits to data and, indeed, previous failures to find consistent power-law fits to these data [3]. This stands in contrast to the situation on mainlands, where only spatially explicit models can accurately reproduce empirical SARs with their strong power-law phase [35,36]. Future work is required to formalize these insights and unify island and mainland SAR theory.

Our theory also makes predictions for aquatic ecosystems, such as systems of freshwater lakes and systems of coral reefs, that are essentially island archipelagos in that they comprise distinct communities connected by occasional dispersal of propagules. Specifically, we predict a small-island effect and a biphasic SAR for these systems as has been observed in terrestrial archipelagos. We can also make predictions about the extent to which different kinds of aquatic ecosystems will tend to be in the niche-structured regime versus the colonization–extinction regime. Coral reefs provide an instructive example—these typically have tens to hundreds of coral species that provide habitat for diverse communities of fish and other invertebrates [37], and can be found fringing oceanic atolls or as large contiguous stretches on continental shelves. Spawning reef species produce propagules that can disperse across tens to hundreds of kilometres [38,39], but brooding species can have very short dispersal distances of typically less than a metre [40]. Our theory predicts that oceanic reefs that are close to continental shelves and dominated by spawning species should usually be in the colonization–extinction regime. This prediction can be tested quantitatively by looking at whether the critical area for reefs dominated by spawning species is indeed smaller than that for reefs dominated by brooding species, and whether the critical area for reefs close to continental shelves is indeed smaller than that for reefs far from continental shelves.

Another implication of our results is that the abundance of a group of species exploiting the same niche (i.e. a guild) should be much more strongly regulated than the abundance of a single species. If we could only identify the niches and the guilds occupying them, then high-diversity systems, both in the marine and terrestrial realms, might be rendered predictable to an extent that has so far eluded ecologists. Choosing an appropriate niche or guild structure for a given system would be non-trivial and would require detailed data on traits and population dynamics. And appropriate models for studying guild dynamics will, in general, be more complicated than our model, and may include, for example, overlapping or unequally sized niches [41] and environmental variance [42,43].

This brings us to the limitations of the simple model we used to illustrate our island biogeographic theory [15,16]. Our model makes simplifying assumptions regarding not only the niche structure of the island (niches are static, equal-sized and non-overlapping), but also spatial structure (there is no dispersal limitation within an island) and speciation (there is no speciation on islands). Future studies should relax these assumptions. But we anticipate that the general principles of our theory will be robust—namely, the transition from a niche-structured regime to a colonization–

extinction regime with increasing island area (figures 1 and 2), and a transition at smaller critical areas in systems where immigration is stronger (table 1 and figure 3).

What are the implications of our results for conservation? Human activities worldwide are fragmenting forests and other mainland ecosystems, in the process creating many artificial small habitat islands [44–46]. Isolation of fragments leads to biodiversity loss through both reduced immigration and changes to niche structure through changes to the abiotic environment [45], but the relative importance of each is uncertain. Our theory predicts that reduced immigration is likely to be more important. Fragmentation will severely reduce diversity in mainland habitat patches by driving communities away from the colonization–extinction regime and towards the niche-structured regime. Species loss in a fragment is predicted to be large even if local ecosystem processes, including niche mechanisms, are intact. This reinforces the notion that local biodiversity conservation depends fundamentally on restoring landscape connectivity [46]. Similar arguments apply to coral reefs, which are also being fragmented and degraded [47,48].

In summary, our new theory explains maintenance of diversity on islands as arising from a combination of niches

and immigration. Niches are the dominant force on small islands, where immigration is very low; immigration is the dominant force on larger islands. Together, these effects explain the biphasic island SAR observed by MacArthur & Wilson [1] half a century ago, and also explain variation in the SAR across taxa and archipelago types. The consequences of these results extend beyond islands to mainland systems and their conservation.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material, appendix S2.

Authors' contributions. R.A.C. conducted mathematical analysis, collated data, fitted the model and wrote the paper; T.F. conducted mathematical analysis and wrote the paper; D.C. collated data; J.P.O. conducted mathematical analysis and wrote the paper. All authors gave final approval for publication.

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