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Island area and species diversity in the southwest Pacific Ocean: is the lizard fauna of Vanuatu depauperate?

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One island group suggested to be an exception to the species–area relationship is the Vanuatu Archipelago, a group of 13 large and 80 small islands in the southwest Pacific Ocean. To test the hypothesis that the lizard fauna of the Vanuatu Archipelago does not meet the predictions of the species–area relationship, and thus is depauperate, we compare diversity among several island groups in the southwest Pacific: Fiji, the Loyalty Islands, New Caledonia, Samoa, the Solomon Islands, Tonga, and Vanuatu. We found that the lizard diversity of Vanuatu meets the pattern of diversity predicted by the species–area relationship. The Solomon Islands, the largest and least isolated oceanic archipelago considered, has the greatest species diversity and endemism of the oceanic islands. Inclusion or exclusion of island groups based on factors such as geologic history or faunal source affects the strength of the relationship between diversity, area, and history of emergence, and influences perceptions of diversity within individual archipelagos. In addition to island size, factors such evolutionary time scale, speciation, and archipelago complexity influence species richness on islands.

The relationship between species richness, island area, and island isolation is one of the most fundamental models in ecology and biogeography (Arrhenius 1921, Gleason 1922, Preston 1962, MacArthur and Wilson 1963, 1967). In general, faunas show increasing diversity with an increase in area and proximity to the mainland or faunal source. This general pattern, the species–area relationship (SAR), has been key in the development of several fields, including meta-population biology (Gilpin and Hanski 1991) and macroecology (Brown 1995), has been applied to conservation planning (Schafer 1990), and used to model extinction probabilities in the face of increasing fragmentation (Brooks 1997). The relationship between species richness, area, and isolation has been documented for a wide variety of macro- and micro-biotas occupying continental and oceanic islands as well as terrestrial habitat fragments (Lomolino 2001, Kalmar and Currie 2006, Peay et al. 2007). Island age may influence diversity: older archipelagos have greater endemism at both specific and supraspecific taxonomic levels resulting from the longer emergent time available for both colonization and phylogenetic diversification (Heaney 2000, Whittaker et al. 2008). Islands, or groups of islands, for which the expectations of the SAR pattern are not met are instructive in assessing the generality of this ecological model, and in understanding the relative importance of factors responsible for generating and maintaining species diversity (Frey et al. 2007, Baldi 2008).

One island group suggested to be an exception to the SAR is the Vanuatu Archipelago, a group of 13 large and 80 small islands in the southwest Pacific Ocean (Fig. 1). Summarizing published accounts of the herpetofauna of Vanuatu, Allison (1996) noted that previous researchers had considered the Vanuatu herpetofauna depauperate, in part due to the absence of endemic snakes and frogs (Baker 1928, 1929, Darlington 1948, Bauer 1988). Additionally, due to the perception that Vanuatu showed low endemism, it has been suggested that much of the species richness in Vanuatu is derived from the Fijian fauna (Gibbons 1985). To test the hypothesis that the lizard fauna of the Vanuatu Archipelago represents an exception to the predictions of the SAR, and thus is depauperate, we compare diversity among several island groups in the southwest Pacific. We also ask whether the inclusion of archipelagos with different faunal sources or geologic origins creates a bias in the perception of the diversity of individual archipelagos.

Biogeographic background of the southwest Pacific Ocean

The southwest Pacific Basin is tectonically dynamic, and has resulted in an ever-changing landscape due to mountain building, the formation of new oceanic islands through volcanic activity, and the generation and isolation of continental islands as they are sheared and separated from

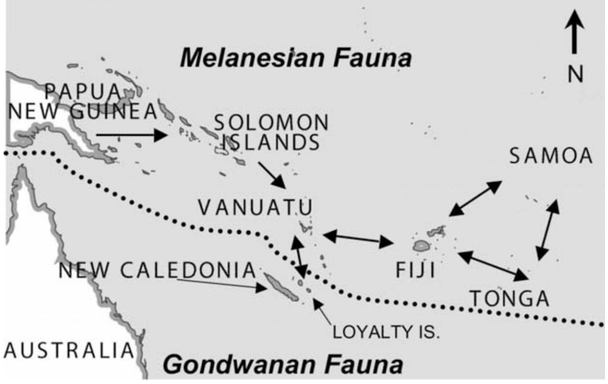

Figure 1. Location of the island groups in the southwest Pacific Ocean included in this comparison. Dispersal pathways discussed in this paper are illustrated with arrows. The distribution of the Melanesian lizard fauna (OMA fauna) is depicted with the dotted line; islands to the north of this line have a predominantly Melanesian lizard fauna, whereas those south of the line are derived primarily from a Gondwanan fauna. The fauna of the Loyalty Islands (south of the line) is a mixture of both Gondwanan and Melanesian elements.

mainland areas (Carney and Macfarlane 1982, Chase and Seekins 1988). Geologic complexity and dynamically fluctuating landforms are partially responsible for high levels of diversity and endemism in the southwest Pacific (Bauer 1999, Bauer and Sadlier 2000, Myers et al. 2000). Colonization of the island groups in the southwest Pacific and subsequent diversification within these archipelagos must be viewed in light of the geologic history of this region, as historical geology is crucial in understanding the generation and maintenance of diversity of these rich and highly endemic faunas (Parent and Crespi 2006, Gruner 2007, Whittaker et al. 2008).

The geologic process associated with the formation of an island is vital in assessing its diversity and understanding the development of its fauna (Parent and Crespi 2006, Gruner 2007). Oceanic islands result from volcanic sea floor orogeny, with their biota accumulating solely via over-water colonization and in-situ speciation (Carson and Clague 1995, Ziegler 2002). Continental islands, in contrast, are fragments severed from a continental landmass and contain mainland faunas present prior to isolation as well as organisms that have colonized by subsequent over-water dispersal or arose through speciation (Bauer and Sadlier 2000).

Both oceanic and continental islands occur within the geographic region considered in this study (Fig. 1). The Fiji archipelago, the islands of Samoa, the Solomon Islands, the Tongan archipelago, and the Vanuatu archipelago are all oceanic in origin, and comprise the majority of the Outer Melanesian Arc (OMA); their development results from tectonic events ranging from 11.2 to 2.0 Mya (Kroenke and Rodda 1984). In contrast, New Caledonia is a continental fragment (Bauer and Sadlier 2000). The Loyalty Islands are a composite of both oceanic and continental elements, with the underlying geology resulting from a continental origin, while the exposed landmass that is the present day Loyalty Islands is coralline in origin and has a history of recent submergence (Bauer and Sadlier 2000); therefore, we consider the Loyalty Islands to be oceanic for the purposes of our analysis. The ages of islands in this study range from ca 2 Mya (estimated emergence history for groups like Samoa and Vanuatu) to Jurassic (isolation of New Caledonia) (Table 1). These archipelagos also vary in isolation from the source area and neighboring island groups, total archipelago land area, and the number, size, and elevation of individual islands within each island group (Table 1). The Solomon Islands occur in relatively close proximity to New Guinea, the putative source of much of the archipelago's biota, and have the greatest total land area of all the island groups considered in this study, with four relatively large islands (>3000 km^2) and many smaller ones.

In contrast to the archipelagos of the OMA, the histories and geologic origins of New Caledonia and the Loyalty Islands are much more complex. New Caledonia is a component of the Inner Melanesian Arc and associated with the breakup of Gondwanaland (Bauer and Sadlier 2000). As the origin of New Caledonia is continental, the biota of New Caledonia does not result primarily from over-water dispersal, unlike other archipelagos considered in this analysis. Since its emergence, New Caledonia has had multiple potential land-bridge connections with Australia and New Zealand (Kroenke 1996, Bauer and Sadlier 2000). The Loyalty Islands are derived from more than a single geological source; some components of this island group are of Gondwanan origin while others are oceanic (Bauer and Sadlier 2000). Additionally, the reptile faunas of New Caledonia and the archipelagos of the OMA are disparate; the reptile fauna of New Caledonia is not predominately Melanesian in origin (Bauer and Sadlier 2000). The biota of the Loyalty Islands is a mixture of Melanesian fauna, derived from New Guinea, and continental Gondwanan fauna derived primarily from New Caledonia and not shared with the oceanic islands of the OMA (Bauer and Sadlier 2000).

The colonization of the Pacific oceanic islands by reptiles is thought to have occurred by way of a stepping-stone route (Fig. 1) from the source area of New Guinea into the islands of the southwest Pacific (Brown 1991, Allison 1996), a dispersal pathway also suggested for other fauna (Simpson 1953). Dispersal along this pathway generates the expectation that faunas will become more impoverished eastward with increasing distance from the source region, as organisms with limited vagility are not able to colonize these more remote archipelagos (Crombie and Steadman 1986, Woodroffe 1987). Under this scenario, assuming roughly equal area among all archipelagos, the fauna of the Solomon Islands should be the most diverse because of its proximity to New Guinea. The fauna of the Vanuatu Archipelago should have moderate diversity, as components of the fauna with a more limited ability for over-water dispersal would have been filtered out during dispersal from New Guinea via the Solomon Islands. Likewise, Fiji should have faunal diversity lower than the Vanuatu Archipelago, as dispersal to Fiji from New Guinea occurred by way of the Solomon Islands and Vanuatu, with each archipelago acting as both stepping-stone and faunal filter (Fig. 1). The most remote island groups in this study, Tonga and Samoa, should have the lowest faunal diversity, as fewer species would have dispersal capabilities great enough to colonize these archipelagos (Fig. l).

Table 1. Geologic history, size, elevation, and diversity for archipelagos in this study. Diversity is a conservative estimate of true native lizard diversity for each island group. Because of their association with human-modified landscapes, *Hemidactylus frenatus, Hemidactylus garnotii* and *Lepidodactylus lugubris* were considered introduced in all island groups. We used personal observations from faunal surveys, unpublished molecular data, personal communications, and literature sources (Supplementary material, Appendix 1) to determine species diversity. The primary source for the data on island size and elevation is an online database maintained by the UN Earthwatch Coordination Unit of UNEP <http://islands.unep.ch/isldir.htm> based on data tabulated by Dahl (1986, 1991). Sources for geologic data are provided as footnotes. As the Loyalty Islands and New Caledonia do not have predominantly Melanesian fauna, some comparisons are not relevant and, therefore, omitted.

Island group	Solomon Islands	Vanuatu Archipelago	Fiji Archipelago	Samoan Islands	Togan Archipelago	Loyalty Islands	New Caledonia
Geologic origin	Oceanic	Oceanic	Oceanic	Oceanic	Oceanic	Oceanic	Continental
Emergence history [a]	11.2	2	7.75[b]	2.75 [c]	14	1.8	150
Total land area (km^2)	27 556	12 190	18 272	3132	699	2000	17 103
Number of islands	138	81	322	14	67	8	28
Area of largest island (km^2)	5353	3955	10531	1820	257	1150	16760
Islands >100 km^2	20	14	6	3	2	3	2
Islands >1000 km^2	6	2	2	2	0	1	1
Islands >3000 km^2	4	1	2	0	0	0	1
Speciation:immigration index	44.3	32.4	88.2	0	0	0	97.9
Archipelago complexity	0.5	0.7	1.8	0.4	9.6	0.4	0.2
Islands with elevation >500 m	17	19	7	3	1	0	1
Islands with elevation >1000 m	2	1	3	2	1	0	1
Islands with elevation >1500 m	2	1	0	1	0	0	1
Maximum elevation (m)	2447	1837	1324	1857	1033	138	1628
Distance to faunal source (km)	710.8	1623.8	2757.4	4040.6	3789.4	2060.6	
Distance to neighbor (km)	171.9 (VU)	171.9 (SI)	718.1 (TO)	849.8 (FJ)	718.1 (FJ)	259.3 (NC)	259.3 (LI)
Number of species	50	20	18	10	14	12	78
Percent of total OMA species	68%	27%	24%	14%	19%	–	
Number of genera	18	9	8	4	8	7	23
Percent of total OMA genera	72%	36%	32%	16%	32%	–	
Number of families	4	2	3	3	3	2	3
Number of endemic species	29	7	7	2	2	1	67
Endemism rate	58%	35%	39%	20%	14%	8%	86%
Percent of OMA endemics	62%	15%	15%	4%	4%		
Total no. species/emergence	4.46	10.0	2.32	3.64	1.00	6.67	0.52
Number endemics/emergence	2.59	3.50	0.90	0.73	0.14	0.56	0.45

[a] Data on island emergence history are from the following: Solomon Islands (Hackman 1973, Kroenke and Rodda 1984); Vanuatu (Greene and Wong 1988, Macfarlane et al. 1988); Fiji (Ewart 1988, Zug 1991); Samoa (Dickinson 2006, pers. comm.); Tonga (Dickinson 2006, pers. comm., Dickinson and Burley 2007); Loyalty Islands (Kroenke and Rodda 1984, Kroenke 1996, Bauer and Sadlier 2000).

[b] An intermediate date of 7.75 Mya is used; published estimates range from 5.5 to 10 Mya (Ewart 1988, Zug 1991).

[c] Fragments of present day Upolo and Savai'i date to the late Pliocene to early Pleistocene (2.75–1.55 Mya); the majority of these two islands (as well as all of the Manu'a group) are <1.0 Mya, Tutuila dates primarily to the middle Pleistocene, 1.5 to 1.0 Mya (Dickinson 2006, pers. comm.).

Materials and methods

To determine whether the lizard fauna of the Vanuatu Archipelago represents an exception to the SAR, we examine the species-level lizard diversity of the Vanuatu Archipelago and compare this to neighboring island groups. We have restricted this comparison to lizards because they are one of the most diverse terrestrial vertebrate groups throughout the Pacific. In addition, lizards possess three other characteristics that make this group well-suited for studies of Pacific island biogeography: 1) they have moderate vagility, i.e. intermediate between organisms with extremely limited over-water dispersal ability (amphibians) and highly vagile groups (birds); 2) they are conspicuous members of the fauna of Pacific islands and are relatively easy to survey; and 3) the contemporary distribution of lizard faunas in the Pacific does not result primarily from anthropogenic causes. In contrast, recent evidence from mammals and birds has shown that the modern distributions and consequent patterns of species diversity of these two vertebrate groups have been drastically altered by human-mediated introductions and extinctions (Pregill and Dye 1989, Steadman 1995, Matisoo-Smith et al. 1998, Austin 1999a, b, Austin and Zug 1999, Steadman et al. 1999, 2002). We considered a species introduced if a previous worker indicated that the distribution was likely the result of introduction and provided supporting data (Supplementary material, Appendix 1).

To evaluate whether the lizard fauna of Vanuatu is an exception to the diversity patterns expected under the SAR, we used the model $\log S = z \log A + \text{Log } c$ or $S = cA^z$ (where S = number of species, A = area, c = intercept of the y-axis, z = slope of the relationship betweeen (log) species richness and (log) area, of MacArthur and Wilson (1967) to predict numbers of species (S in the equation above) occurring in each archipelago. We compiled species lists (Supplementary material, Appendix 1) for each island group using available literature sources and personal field observations and determined the number of species endemic to each island group. It is important to note that our understanding of the reptile faunas of these archipelagos is still incomplete; for example, 20 species of lizards have been described from the southwest Pacific since 2000 (see references in Supplementary material, Appendix 1). We included all published species as of 1 August 2008. We considered a species endemic if its distribution was restricted to a single archipelago or island group. We compared diversity values calculated under the expectations the SAR to native lizard diversity each island group. The proportion of the overall OMA lizard diversity that occurs in Vanuatu was compared to the proportion that occurs in the Solomon Islands, Fiji, Samoa, and Tonga. Four measures of diversity were calculated for each archipelago: 1) representative species diversity – the number of species in each island group/the total number of OMA species; 2) representative generic diversity – the number of genera in each island group/the total number of OMA genera; 3) representative endemism – the number of species endemic to each island group/the total number of species endemic to a single archipelago within the OMA; and 4) percent endemism – the percentage of an island group's fauna that is endemic to that island group. These diversity measures, as well as total number of species, genera, and endemic species occurring in each archipelago, were regressed against three factors suggested to be important in predicting species richness: total archipelago area, archipelago age (based on the earliest date of continuous emergence), and isolation using SAS. Island age data were determined from the literature, and the source for each island group is provided in Table 1. Data on island size and elevation are from an online database maintained by the UN Earthwatch Coordination Unit of UNEP <http://islands.unep.ch/isldir.htm> based on data tabulated by Dahl (1986, 1991). We used "total land area" as our value for archipelago area. We used the Lambert conformal projection for the southwestern Pacific in ArcGIS to calculate two separate measures of isolation: 1) distance from the faunal source and 2) distance from the nearest neighbor. Distances were measured as a straight-line distance from the most adjacent points of neighboring islands. For example, to calculate distance from the faunal source (New Guinea) to Vanuatu, we compared multiple straight-line distances between the southeastern tip of New Guinea, Milne Bay Province, and the northernmost islands in Vanuatu, the Torres Island group. The shortest distance between these points was used. Due to the small number of data points we did not expect these relationships to be statistically significant, but R^2 values allow us to make cautious inferences about the relative strength of various relationships.

To examine the relationship between species diversity, endemism, and biogeographical factors not explicitly considered in the SAR, we generated two additional measures of archipelago features for comparison among island groups, as attributes of islands themselves may influence species diversity, community composition, and speciation in divergent ways (Parent and Crespi 2006). The result of these divergent processes generates variation in the relative roles of within-island speciation, interisland speciation, and immigration in shaping the species richness of an island or archipelago (Losos and Schluter 2000, Parent and Crespi 2006). Based on the observation that 3000 km^2 is a critical size for islands above which the rate of within-island speciation exceeds the rate of immigration (Losos and Schluter 2000), we calculated a speciation: immigration index. This index is simply a measure of the amount of overall archipelago area that consists of islands large enough so that the within-island speciation rate would be predicted to exceed the immigration rate (Losos and Schluter 2000). We expect this measure to be positively correlated with the rate of endemism. The speciation:immigration index is calculated as:

$$[\text{Total area of islands } (\text{km}^2) > 3000\ \text{km}^2 / \text{total archipelago area } (\text{km}^2)] \times 100$$

The structure of an archipelago is expected to influence the generation of diversity as well; small peripheral islands adjacent to a much larger island would be expected to result in a different fauna than several large islands lacking small peripheral islands between them. To examine the differences in species diversity and endemism associated with the structure of archipelagos, we calculate a second measure, archipelago complexity. Archipelago complexity provides a way to examine the structure of the archipelago in terms of the number of islands, when controlling for the overall area of an archipelago. A higher value indicates a greater number of smaller islands, whereas a low number would indicate that the majority of land area in the archipelago is contained within a lower number of large islands. Archipelago complexity is calculated as:

$$[\text{Total number of islands} / \text{total archipelago area } (\text{km}^2)] \times 100$$

We consider archipelagos rather than individual islands within archipelagos as our unit of comparison for two primary reasons. First, the island groups in this analysis are remote and have historically been poorly studied. As a result, for many islands species lists are either not available or are expected to not be sufficiently comprehensive. Second, as the distance among islands within an archipelago is significantly less than the distance between any of the archipelagos considered in this study, we consider each archipelago to function as a biogeographic unit. Because we were interested in comparing diversity among archipelagos, we considered $A =$ total archipelago area.

In the SAR, the rate at which species richness accumulates with an increase in area is the slope of the relationship between (log) species richness and (log) area, and is represented in the equation as z. Preston (1962) found $z = 0.301$ for amphibians and reptiles in the West Indies, and subsequent work has suggested that, for islands, the value of z is generally around 0.30 and does not vary greatly among taxa or with geography (MacArthur and Wilson 1963, 1967, Lomolino and Weiser 2001). Based on these previously reported values of z, we used $z = 0.30$ in our calculations. Because the value of z can influence the predicted species richness of an area, we used one value for z across archipelagos to reduce bias.

To determine what value to use for c (the value of the y-axis intercept in the SAR), we estimated the likely range of c-values from lizards distributed in other Pacific archipelagos (Table 2). Specifically, for these archipelagos we generated estimates of c using the SAR. We took the number of species (represented by S) and area (A) reported in the literature, and a z value of 0.30 as previously explained. Using the SAR, we solved for c for each island group. The obvious problems inherent in computation of c values from literature sources, such as the likelihood of incomplete faunal lists or erroneous data, make these values appropriate only as a guideline for generating a value of c for our islands and taxa of interest. We do not expect

Table 2. C values for lizards from other Pacific islands and archipelagos from literature sources. These c values are used as a guideline in the selection of a value for c for our analysis, and in the generation of a set of confidence intervals.

Archipelago	Species	Area (km^2)	c	Source
Admiralty Islands	30	2072	3.0	Allison 1996
Bismarck Islands	40	49 700	1.6	Adler et al. 1995
Kapingamarangi Atoll	4	1.3	3.7	Buden 1998
Marshall Islands	9	181	1.9	Adler et al. 1995
Mariana Islands	5	471	0.8	Adler et al. 1995
Mortlock Islands	9	12	4.3	Buden 2007a, b
New Britain	32	39807	1.3	Allison 1996
New Ireland	23	7405	1.6	Allison 1996
Niue	5	259	0.9	Adler et al. 1995
Palau	23	415	3.8	Crombie and Pregill 1999
Pitcairn Islands	3	43	1.0	Gill 1993b
Wallis and Futuna	8	177	1.7	Gill 1995

a priori the five island groups considered in this analysis to have identical c values as c is influenced by isolation (MacArthur and Wilson 1967, Lomolino and Weiser 2001), and degree of isolation and distance from potential source populations vary greatly among the island groups in our analysis. The relative strength of the influence of isolation or environmental quality on the parameter c is unclear. Therefore, we used a single c value for all island groups considered in this analysis. We used $c = 2.13$, the mean of the c-values for lizard species from other Pacific archipelagos (Table 2). We generated an estimate of error ($c \pm 2.45$) equal to two standard deviations of the mean c-value and estimated potential diversity for each island group for $c \pm 2.45$.

Our primary analysis is restricted to five island groups (Fiji, Vanuatu, the Solomon Islands, Samoa, and Tonga) for three reasons: 1) these archipelagos result from the same general geologic processes (oceanic origin) and are components of the OMA (Bregulla 1991, Zug 1991, McCoy 2006); 2) none of these archipelagos have a confounding historical association with the mainland or with each other (Bregulla 1991, Zug 1991, McCoy 2006); and 3) these archipelagos all have the same putative faunal source (Allison 1996). This third point (faunal source) is especially critical, as it eliminates the possibility that differences in lizard species richness recovered in these archipelagos are a result of differences in richness among source faunas or variation in dispersal capacity (as a result of phylogenetic constraint or other factors) among source populations. The inclusion of neighboring island systems enabled a comparison of islands of differing sizes, geologic histories, degrees of isolation, and proximity to source populations.

To understand the influence of inclusion or exclusion of island groups in this analysis, we performed these same comparisons including two additional island groups: New Caledonia and the Loyalty Islands. Despite their geographic proximity, New Caledonia and the Loyalty Islands differ from the OMA archipelagos with respect to geologic history, patterns of colonization, and faunal origin.

Results

There is a positive relationship between total archipelago land area and species richness (Fig. 2), as predicted by the SAR. The species diversity of New Caledonia and the Solomon Islands exceeds the level of species diversity predicted by archipelago area alone, and all other island groups (Samoa, Tonga, Fiji, Vanuatu and the Loyalty Islands) have fewer species than expected (Fig. 2). For all island groups analyzed, however, observed species richness falls within the 95% confidence intervals (Fig. 2).

Archipelago area is a relatively good, but not statistically significant, predictor of the proportion of OMA species ($R^2 = 0.75$, $p = 0.059$) and OMA endemics ($R^2 = 0.78$, $p = 0.046$) that occur within an archipelago (Table 3); the diversity of both OMA species and OMA endemic species increases with area (Fig. 3A). The Solomon Islands, and perhaps Tonga, appear to have a greater proportion of OMA diversity than predicted by this relationship, and the diversity in Fiji appears lower than expected (Fig. 3A). Both Vanuatu and Samoa appear to have roughly the level of

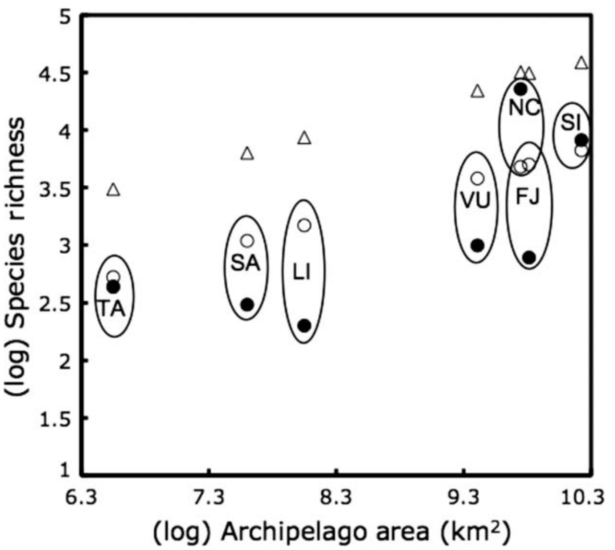

Figure 2. Observed lizard species richness (closed circles) for each island group and the lizard species richness (open circles) for each group expected under the species–area relationship (SAR). Expected values were calculated using a value of 2.13 for the parameter c. The 95% maximum confidence interval (triangles) was calculated with $c \pm 2.45$, which is the mean value of c for reptiles in other Pacific island groups ± two standard deviations (Table 2). Minimum confidence intervals are not shown, as they are zero for all island groups in this study. Archipelago abbreviations: Fiji (FJ), Loyalty Islands (LI), New Caledonia (NC), Samoa (SA), Solomon Islands (SI), Tonga (TO), and Vanuatu (VU).

Table 3. Results of diversity comparisons among archipelagos. *Significant when α-level of 0.05 is adjusted using the sequential Bonferroni correction (Rice 1989). Strongest predictor for each measure of diversity is highlighted in bold, even if the relationship is not statistically significant at the adjusted α-level.

Diversity measure	R^2	p	Figure
Percentage of OMA species present			
Archipelago area	**0.75**	**0.059**	3A
Emergence	0.13	>0.l	3B
Distance from source	**0.76**	**0.056**	3C
Isolation	0.55	>0.l	3D
Percentage of OMA genera present			
Archipelago area	**0.78**	**0.046**	3A
Emergence	0.10	>0.l	3B
Distance from source	0.73	0.064	3C
Isolation	0.50	>0.l	3D
Endemism rate			
Size of largest island	**0.79**	**0.007***	4A
Speciation: immigration index	0.71	0.017	4B
Total number of species			
Maximum elevation	**0.54**	**>0.l**	5C
Size of largest island	0.07	>0.l	5E
Total number of endemic species			
Maximum elevation	**0.59**	**>0.l**	5D
Size of largest island	0.10	>0.l	5F

OMA diversity that would be predicted by the total archipelago area (Fig. 3A). The relationship between these measures of diversity and archipelago emergence history is very weak; island emergence history is a poor predictor of the proportion of OMA lizard fauna present in an archipelago (Table 3). In general, older archipelagos tend to have greater diversity (Fig. 3B), although there are clear exceptions (i.e. Tonga). The proportion of OMA species and endemics decreases with both distance from the faunal source of New Guinea (Fig. 3C) and the nearest neighbor (Fig. 3D); proximity to the faunal source explains more of the variation in diversity for OMA species and OMA endemics than the proximity of the nearest neighbor, but these relationships are not statistically significant (Table 3). The Solomon Islands appear to have a greater component of both OMA species diversity and OMA endemism than this relationship predicts, and the OMA lizard diversity appears to be lower than expected for Vanuatu based on its proximity to the faunal source of New Guinea (Fig. 3C), and the Solomon Islands, its nearest neighbor (Fig. 3D).

A positive, statistically significant relationship was found between the endemism rate of an archipelago and the size of the largest island (Fig. 4A; Table 3); the relationship between endemism rate and the speciation:immigration index was also positive, but was not statistically significant after α was adjusted using a sequential Bonferroni (Fig. 4B; Table 3). Vanuatu had a higher endemism rate than expected when either the size of the largest island (Fig. 4A) or the speciation:immigration index (Fig. 4B) were considered. Based on the size of the largest island in an archipelago, Vanuatu, the Solomon Islands, and New

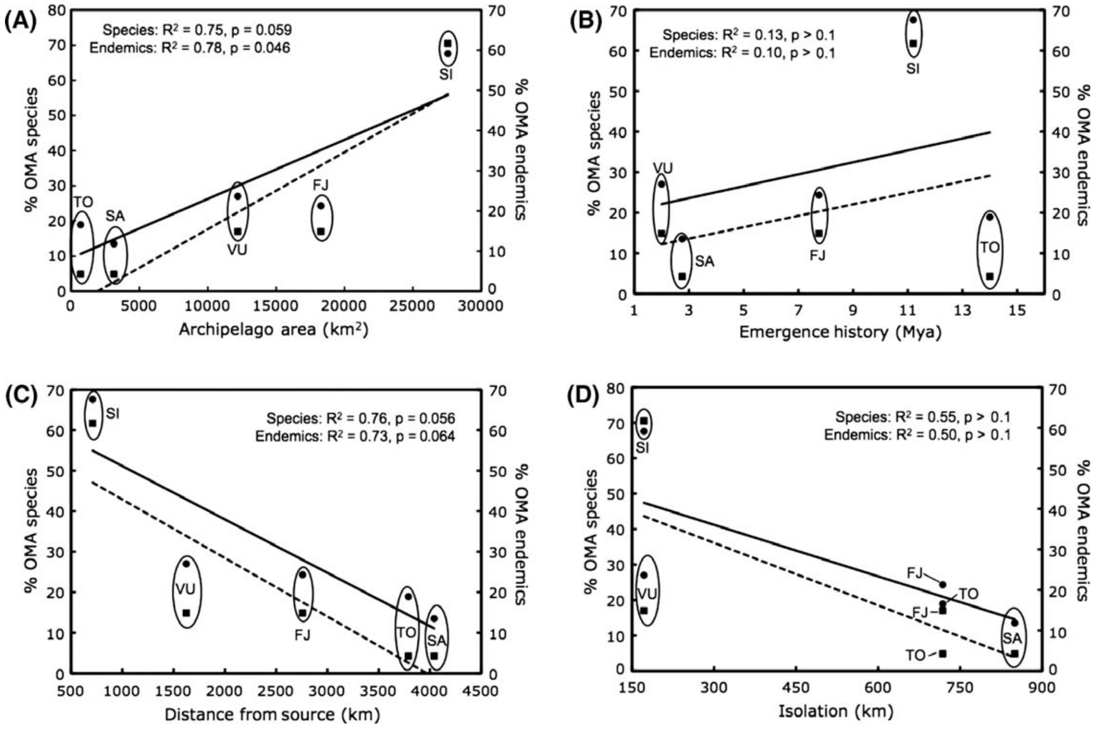

Figure 3. The percentage of the total Outer Melanesian Arc (OMA) lizard fauna occurring in each island group and the percentage of the OMA lizard species endemic to each island group. These diversity measures are shown in relation to four archipelago features: (A) total archipelago area (km^2), (B) length of time the archipelago has been continually emergent (Mya), (C) distance from the faunal source of New Guinea (km), and (D) distance from the closest point of the nearest neighboring island group (km). For all panels closed circles represent species richness and closed squares represent the percentage of the endemic lizard fauna restricted to each archipelago. Solid lines are associated with species richness values; dotted lines with percentage of endemic species in each archipelago. Archipelago abbreviations: Fiji (FJ), Loyalty Islands (LI), New Caledonia (NC), Samoa (SA), Solomon Islands (SI), Tonga (TO), and Vanuatu (VU). R^2 values and p-values for all regressions are presented in Table 3.

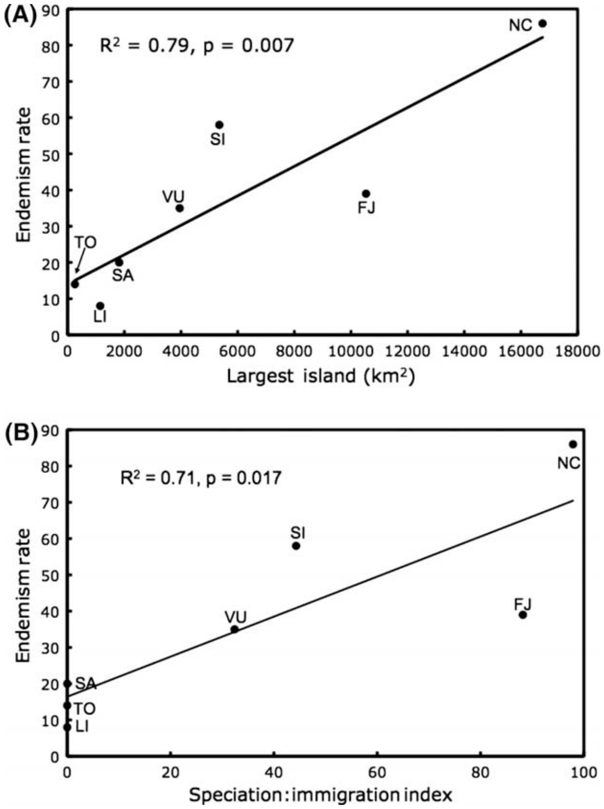

Figure 4. Endemism rate for each island group in this study when two measures suggested to influence the contribution of speciation relative to immigration in faunal accumulation on islands (Losos and Schluter 2000) are considered: (A) endemism rate (the percent of the total archipelago fauna endemic to the archipelago) for each archipelago regressed against the size of the largest island within the archipelago; (B) endemism rate for each archipelago regressed against our speciation: immigration index. Island groups with a high speciation:immigration index are predicted to have a greater proportion of endemic species. Archipelago abbreviations: Fiji (FJ), Loyalty Islands (LI), New Caledonia (NC), Samoa (SA), Solomon Islands (SI), Tonga (TO), and Vanuatu (VU). R^2 values and p-values for all regressions are presented in Table 3.

Caledonia appear to have greater diversity than predicted, the Loyalty Islands and Fiji appear to have lower diversity than expected, and the diversity of Samoa and Tonga meet predicted values (Fig. 3A). A similar pattern is seen with respect to the species:immigration index: the Solomon Islands and New Caledonia appear to have elevated diversity, Fiji and the Loyalty Islands appear to show reduced diversity, and Vanuatu, Samoa, and Tonga seem to meet the predictions of this model (Fig. 4B).

When the number of species and the number of endemic species in an archipelago are compared with respect to archipelago area (Fig. 5A, B), maximum elevation (Fig. 5C, D), and size of the largest island (Fig. 5E, F), the relationship between diversity and archipelago features is stronger, but not statistically significant, when the analysis excludes islands that do not share a faunal source and geologic origin (Fig. 5A–D). The addition of New Caledonia and the Loyalty Islands improves the relationship between the size of the largest island and the total number of species (Fig. 5E) and endemic species (Fig. 5F) in an archipelago. The islands included in an analysis have an affect on the perception of diversity within an island group (Fig. 5); Tonga and Fiji appear to have lower diversity than would be expected by the maximum elevation if the analysis contains all islands; when the analysis is restricted to OMA archipelagos, Fiji and Tonga appear to be more diverse than expected (Fig. 5C, D).

There is a clear difference in lizard species diversity between the Solomon Islands, a large archipelago (50 native species), and the smaller archipelagos of Vanuatu (20), Fiji (18), Tonga (14), the Loyalty Islands (12), and Samoa (10). The highest lizard species diversity occurs in New Caledonia (78 species). Despite having less total archipelago land area than Fiji, Vanuatu is slightly more representative of the overall OMA lizard diversity, with 27% of the native OMA lizard species and 24% of the endemic species occurring in this archipelago (Fig. 3A). The largest component of the OMA lizard fauna occurs in the Solomon Islands; 68% of the OMA native lizard fauna occurs in the Solomon Islands (Table 1). Additionally, a large component (58% species-level endemism) of the lizard fauna of the Solomon Islands is endemic (Table 1). Endemism is noticeably lower for the other island groups considered in this study: Vanuatu (35%) and the Fijian archipelago (39%) have species-level endemism values roughly comparable to each other (Table 1). In archipelagos located farther from the source of New Guinea endemism is lower; 20% of the Samoan fauna and 14% of the Tongan fauna are endemic (Table 1).

Archipelago complexity ranged from 0.2 (New Caledonia; most of the area restricted to a single, large island) to 9.6 (Tonga; 67 islands, the largest of which is only 257 km^2), and was not correlated with either species diversity ($R^2 = 0.10$, $p > 0.1$) or endemism ($R^2 = 0.10$, $p > 0.1$). Three archipelagos (Samoa, Tonga, and the Loyalty Islands) had a speciation: immigration index of 0, as no island in the group was > 3000 km^2 (Table 1). Index values ranged from 32.4 (Vanuatu) to 97.9 (New Caledonia) for the remaining archipelagos. As predicted, endemism was higher in the island groups with a higher speciation:immigration index than in the three islands with an index of 0 ($R^2 = 0.71$, $p = 0.017$; Fig. 4B), although this relationship was not statistically significant after α was adjusted using a sequential Bonferroni correction (Rice 1989, Table 3).

Discussion

The biotic composition of an island is influenced by myriad factors, including past and present geologic circumstances. Islands with different geologic histories may have drastically different faunas as a result of the influence of island age, timing of island emergence, and mode of island origination. These factors are important in explaining the differences in the composition and species diversity of their lizard faunas, as opportunities for colonization and speciation change through time and space.

The SAR does not consider all the relevant, and perhaps most important, components of biodiversity such as speciation, which is crucial to the evolution of island biotas (Heaney 2000). Because of the isolated nature of oceanic Pacific islands, speciation is essential in the development of island faunas. In addition to speciation, other factors such as island emergence history and additional components of

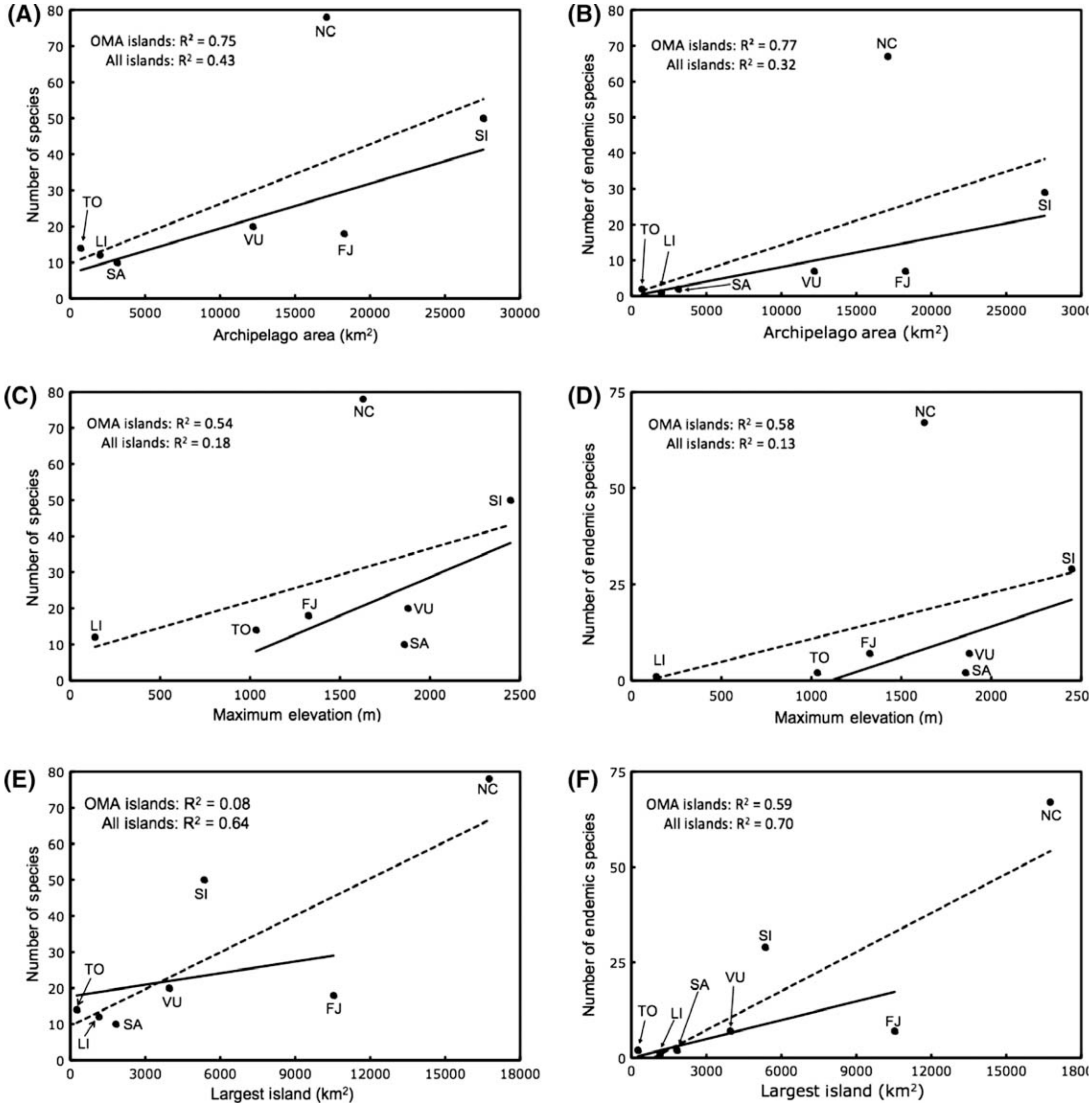

Figure 5. Influence of archipelago inclusion on the perception of diversity in relationship to archipelago area, maximum elevation of an archipelago, and the size of the largest island in an archipelago. Lizard species diversity (A) and endemism (B) within each archipelago shown in relation to total archipelago area. Panels (C) and (D) show the relationship between diversity and maximum elevation within an archipelago for both (C) number of lizard species in an archipelago and (D) the number of lizard species endemic to each archipelago. The relationship between diversity and the size of the largest island is depicted in panels E and F: (E) relationship between the size of the largest island in an archipelago and the number of lizards species found in that archipelago, (F) relationship between the size of the largest island in an archipelago and the number of lizards species endemic to that archipelago. For all panels, the solid line represents the relationship between diversity and area when the analysis is excluded to the five archipelagos that share a faunal origin (OMA islands), whereas the dotted line shows the relationship between diversity and area when New Caledonia and the Loyalty Islands are included (all islands). R^2 values are shown for OMA islands and all islands. Regressions were conducted for the relationships between diversity and OMA islands with respect to maximum elevation (C and D) and the size of the largest island (E and F); p-values are provided in Table 3. Other relationships were not evaluated statistically, but their inclusion in this figure allows a visual, qualitative effect of the influence of archipelago choice on the perception of diversity.

archipelago complexity are likely to be significant in determining the species diversity and level of endemism observed on islands (Gruner 2007), and the contemporary fauna must be evaluated in light of these processes. Archipelago complexity, a concept that encompasses disparate components such as the number of islands within an archipelago, the distance among islands, the degree of variation in size and elevation of islands, and even factors influencing dispersal across the archipelago matrix (such as ocean currents and changes in sea level) likely plays a key role in shaping patterns of species richness in oceanic archipelagos by influencing colonization, speciation, and extinction. We have attempted to examine the diversity of these archipelagos taking speciation and archipelago complexity into consideration, if only using coarse comparisons. We found the level of endemism in an island group increased as the size of the largest island in the group increased; the size of the largest island accounted for 79% of the observed variation in the level of endemism. The relationship between the proportion of an archipelago that consisted of islands ≥ 3000 km^2 and archipelago endemism was also positive, and although not significant statistically ($p = 0.017$), explained 71% of the variation and likely represents a biologically relevant relationship. Archipelagos in which a greater proportion of the total area was made up of larger islands (i.e. the Solomon Islands and New Caledonia)

had higher endemism, and those with large numbers of small islands and no really large islands (i.e. Tonga and the Loyalty Islands) had lower levels of endemism. As the relationship between size of an island and the relative contribution of immigration and speciation to faunal accumulation has been previously examined for lizards (Losos and Schluter 2000), we did expect to find this positive relationship between island size and endemism.

We attempted to evaluate the role of archipelago complexity (AC) on patterns on diversity. We did not expect to see a directional pattern (i.e. smaller value for archipelago complexity would predict lower diversity, or vice versa) with respect to our crude measure of AC; rather we expected that archipelagos with similar AC values would also have similar endemism rates or other measures of diversity. As this was not the case (Table 1), it is likely that our simple measure of AC cannot capture the complex interaction between the relative areas and number of individual islands within an archipelago, as well as the distance among islands and the difficulty in crossing the intra-archipelago dispersal matrix, affected by factors such as ocean currents and historical changes in sea level, resulting in increases or decreases in intra-archipelago distances and in the size of islands themselves. These variables are difficult to quantify, but future studies focusing on insular patterns of species richness should consider the role of archipelago complexity.

Patterns of southwest Pacific biogeography

Previous research on patterns of insular diversity in the southwest Pacific indicate a high proportion of the mammal fauna has an Austral-Papuan affinity (Carvajal and Adler 2005), as do lizards. Archipelago species richness of mammals is driven by isolation (negative relationship) and archipelago area (positive relationship) (Carvajal and Adler 2005). The pattern we recovered for lizards was similar; a positive relationship was found between archipelago area and both species diversity and endemism (Fig. 2, 3A), as well as between endemism rate and the size of the largest island in an archipelago (Fig. 4A). We also found a negative relationship between lizard species richness and distance from the faunal source (Fig. 3C) as well as distance from the nearest neighboring landmass (Fig. 3D), although this relationship was not as strong as distance from the source.

Like lizards, OMA mammals have their highest diversity in the Solomon Islands (Carvajal and Adler 2005). This diversity results from proximity to the faunal source and the relatively larger size of individual islands (promoting both relatively low levels of extinction and subsequent intra-archipelago speciation). We suggest these same factors generate the higher lizard diversity we report for the Solomon Islands. For both mammals and lizards, intra-archipelago speciation is a significant contributor to the high species diversity and endemism of the Solomon Islands fauna. These patterns are congruent with the idea that larger islands should have greater endemism, and provide partial support for the predictions that endemism should be greatest on larger, isolated islands, and that an insular size threshold exists above which speciation becomes the significant contributor to species diversity (Losos and Schluter 2000, Johnson et al. 2000). Our data, and data for mammals, do not provide support for the relationship between endemism and isolation alone. Island size, rather than isolation, seems to be more important for lizards and mammals, perhaps due to their intermediate vagility. Perhaps there is some lower bound of isolation required to promote speciation by reducing gene flow, likely related to the vagility of the taxon, and some upper bound of isolation above which initial colonization and subsequent extinction become less and more likely, respectively.

Molecular phylogenetic data have recently provided novel insights to the patterns of speciation and diversification within Pacific Island birds. These data revealed two geographically distinct radiations (Filardi and Moyle 2005). One radiation was the historically expected pattern of island taxa resulting from continental forms, whereas the second radiation resulted from diversification occurring on islands within the tropical Pacific. No comparable work has been published for reptiles to allow us to make comparisons with our results, but the patterns of species diversity and high levels of endemism in island groups such as Vanuatu, the Solomon Islands, and Fiji suggest that a similar diversification history may exist for Pacific Island reptiles. Further research on the phylogenetic relationship of Pacific Island lizards is necessary for an accurate assessment of the evolutionary and biogeographic history of these lineages.

Is Vanuatu a depauperate outlier?

Lizard diversity in the Vanuatu Archipelago, and all other archipelagos in this study, meets the pattern predicted by the SAR (Fig. 2). Vanuatu has approximately the proportion of the OMA fauna (Fig. 3A) and number of species (Fig. 5A) and endemic species (Fig. 5B) expected given the total archipelago area, and a greater proportion of this fauna than expected given the recent emergence history of this archipelago (Fig. 3B). Vanuatu has a lower proportion of the OMA diversity than would be expected given its distance from the faunal source (Fig. 3C) and degree of isolation (Fig. 3D). Total number of native species and endemic species in Vanuatu are higher than expected based on the size of the largest island in the archipelago (Fig. 4E, F), but lower than expected based on the maximum elevation of the archipelago (Fig. 4C, D).

Overall, these results do not support the suggestion that Vanuatu has a depauperate fauna. When the archipelagos were compared with respect to their ability to generate diversity through speciation as opposed to immigration, we found that Vanuatu has the expected rate of endemism (Fig. 4B). Furthermore, the ratio of both number of species and endemic species to the amount of time since emergence for Vanuatu is almost twice that for all other island groups considered in this study (Table 1). The development of high species richness over a short geologic timescale as seen in the Vanuatu Archipelago does not support the suggestion that the lizard fauna is depauperate. Rather, the lizard fauna of Vanuatu appears to fit the expectation for diversity relative to other OMA archipelagos.

It is important to note that our understanding of the reptile faunas of these archipelagos is still incomplete. Since 2000,18 new species of lizards have been described from New Caledonia and two from the Solomon Islands (Supplementary material, Appendix 1). The lizard fauna of Vanuatu has historically received less attention than most of the other island groups in this study; Vanuatu and Tonga are the only groups lacking a reptile field guide or monograph (Schwaner 1979, Bauer and Vindum 1990, Zug 1991, Bauer and Sadlier 1993, 1994, 2000, Gill 1993a, Bauer 1999, Morrison 2003, McCoy 2006). Recent collections in the Vanuatu archipelago and ongoing molecular work indicate that the actual diversity and endemism of the lizard fauna of Vanuatu is greater than currently described (Hamilton and Austin unpubl.), providing even more support for the rejection of the historical characterization of the Vanuatu herpetofauna as depauperate.

Does choice of island groups influence perceptions of diversity?

Inclusion or exclusion of archipelagos and island groups does influence the strength of the pattern recovered by the SAR (Fig. 5). Comparisons that contain multiple source faunas or islands with differing geologic origins confound the relationship between archipelago area, maximum elevation, and species richness and number of endemic species (Fig. 5A–D). Perhaps more importantly, choice of inclusion or exclusion of archipelagos based on their geologic history or the source of their lizard fauna altered the expected relationship between the number of species and endemic species in an island group and total archipelago area, maximum elevation, and size of the largest island, thus influencing perception of the diversity within each archipelago considered (Fig. 5). This perception bias may explain the historical perception that the Vanuatu Archipelago has a depauperate reptile fauna. The geographic proximity of Vanuatu to New Caledonia, an ancient continental landmass with a dissimilar, but species rich and highly endemic, fauna lends itself to a direct comparison of diversity between these two faunas, although the lack of a shared source fauna and the different geologic processes responsible for the formation of these islands renders such a comparison not valid.

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