

Towards a more general species–area relationship: diversity on all islands, great and small

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Abstract

Aim To demonstrate a new and more general model of the species–area relationship that builds on traditional models, but includes the provision that richness may vary independently of island area on relatively small islands (the small island effect).

Location We analysed species–area patterns for a broad diversity of insular biotas from aquatic and terrestrial archipelagoes.

Methods We used breakpoint or piecewise regression methods by adding an additional term (the breakpoint transformation) to traditional species–area models. The resultant, more general, species–area model has three readily interpretable, biologically relevant parameters: (1) the upper limit of the small island effect (SIE), (2) an estimate of richness for relatively small islands and (3) the slope of the species–area relationship (in semi-log or log–log space) for relatively large islands.

Results The SIE, albeit of varying magnitude depending on the biotas in question, appeared to be a relatively common feature of the data sets we studied. The upper limit of the SIE tended to be highest for species groups with relatively high resource requirements and low dispersal abilities, and for biotas of more isolated archipelagoes.

Main conclusions The breakpoint species–area model can be used to test for the significance, and to explore patterns of variation in small island effects, and to estimate slopes of the species–area (semi-log or log–log) relationship after adjusting for SIE. Moreover, the breakpoint species–area model can be expanded to investigate three fundamentally different realms of the species–area relationship: (1) small islands where species richness varies independent of area, but with idiosyncratic differences among islands and with catastrophic events such as hurricanes, (2) islands beyond the upper limit of SIE where richness varies in a more deterministic and predictable manner with island area and associated, ecological factors and (3) islands large enough to provide the internal geographical isolation (large rivers, mountains and other barriers within islands) necessary for *in situ* speciation.

Keywords

Area, diversity, insular biotas, islands, small island effect, species richness, species–area.

INTRODUCTION

Larger samples, whether they are samples of molecules, ecological communities or regions of the universe, contain a

greater diversity of their fundamental elements (atomic and subatomic particles, populations and species, planets and other celestial bodies). This is a fundamental pattern of nature, and one with at least one additional feature. It is widely believed, at least among biogeographers and ecologists, that the diversity of the fundamental elements (species) increases most rapidly with increasing sample size for the smallest samples, and then more slowly for the larger ones

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(Arrhenius, 1921; Gleason, 1922; Preston, 1962; McGuinness, 1984). This pattern, referred to as the species–area relationship, is so common that it is often referred to as the closest thing to a rule in ecology (Schoener, 1976). Many hundreds if not thousands of studies have demonstrated the generality of the species–area relationship using either the semi-log or log–log models (equations 1 and 2; see also Brown & Lomolino, 1998).

$$\text{Semi-log model: } S = b_0 + b_1(\log(A)) \quad (1)$$

$$\text{log–log model: } \log(S) = b_0 + b_1(\log(A)) \quad (2)$$

where S = species richness, or number of species in a given sample, and A = area of the sample. Note that in the log–log model, b_1 is often referred to as z and has received a substantial amount of attention since Preston (1962) predicted its ‘canonical’ value to be 0.26 (Connor & McCoy, 1979; Martin, 1981; Sugihara, 1981; Wright, 1981; Lomolino, 1989; Rosenzweig, 1995). In addition to reigning as one of nature’s most general patterns, the species–area relationship is also one of its most important and insightful ones. Ecologists have used the species–area relationship as a tool to summarize patterns of diversity for a great number of taxa across a broad range of spatial and temporal scales. The relationship has served as a ‘stepping stone’ for the development of major theories in ecology, including MacArthur & Wilson’s (1963, 1967) equilibrium theory of island biogeography, and for many important developments in the fields of metapopulation biology, evolutionary ecology and macroecology (Wilson, 1961; Brown, 1995; Rosenzweig, 1995; Hanski & Gilpin, 1997). In addition, conservation biologists frequently rely on the species–area relationship to predict changes in species diversity under scenarios of habitat loss, and to develop strategies for conserving biological diversity within geographically limited reserves and fragmented ecosystems (Shafer, 1990; Brooks *et al.*, 1997, 1999a, b).

Yet, despite the many valuable and insightful applications of the species–area relationship, traditional approaches to studying this pattern may have ignored a perhaps cryptic, but potentially important feature – the small island effect (SIE; Lomolino, 2000). Detection of the SIE, in essence, implies that the species–area relationship is actually comprised of at least two distinct patterns. Beyond some minimum area, species richness increases as described by traditional models (i.e. semi-log and log–log models). On smaller islands, however, richness may vary independently of island area. Although largely ignored by most ecologists and biogeographers, SIEs were inferred or discussed as early as the 1960s by Preston (1962) and MacArthur & Wilson (1967) in their seminal monograph on the species–area relationship and patterns in insular diversity, in general (see also Wiens, 1962). Beyond the range of the SIE, richness consistently increases with island size, presumably because larger islands include a greater diversity of habitats, greater coverage of each habitat type, higher population levels and lower extinction rates of resident species and, possibly, higher immigration rates (Gilpin & Diamond, 1976;

Lomolino, 1990). Within the range of the SIE, however, it appears that these potentially beneficial effects of somewhat larger size are rendered insignificant in comparison with idiosyncratic, inter-island differences in habitat characteristics, position relative to dispersal routes, or exposure to storms and other forces that may wipe out entire populations of insular biotas (Wiens, 1962; Niering, 1963; Losos, 1998). In an overwhelming majority of studies of the species–area relationship, ecologists and biogeographers have assumed by default that SIEs are trivial, that they apply only to a small portion of the islands and archipelagoes studied and, thus, have little heuristic or practical utility. Yet this assumption, or hypothesis, has never been tested.

Here, we evaluate this hypothesis by first describing an addition to traditional methods for analysing the species–area relationship, one that incorporates both SIEs and all features of the models presented above (equations 1 and 2). We then assess the prevalence of SIEs (as proportion of islands within the range of the SIE) across a broad diversity of taxa and archipelagoes (102 data sets), and evaluate whether SIEs vary in any predictable manner. Specifically, we predict that the threshold, or upper limit of the SIE, should be highest for species groups with relatively high resource requirements (e.g. groups comprised of relatively large vs. small species, homeotherms vs. ectotherms) because they require larger islands to maintain their populations. The upper limit of the SIE should also be relatively high for species with lower dispersal abilities (e.g. non-volant mammals vs. birds and bats; animals vs. plants) because they require larger populations and lower extinction rates to compensate for relatively low immigration rates. We also predict that upper limits of SIEs should be higher for biotas of more isolated archipelagoes (e.g. oceanic archipelagoes vs. those of lakes and rivers). Persistence on isolated archipelagoes, with their relatively infrequent immigrations, requires the relatively low extinction rates characteristic of populations on larger islands (MacArthur & Wilson, 1967; Brown & Kodric-Brown, 1977; Lomolino, 1986; Hanski & Gilpin, 1997). Finally, we discuss the potential utility of an expanded species–area model (Fig. 1) that includes both an ecological threshold, corresponding to the upper limit of the SIE, and an evolutionary threshold on islands large enough to allow *in situ* speciation.

METHODS

We used simple linear regression with a breakpoint transformation to estimate the upper limit of SIEs along with r^2 values and other pertinent statistical parameters (Table 1; literature sources are available from the senior author on request). The breakpoint, or piecewise regression model with two pieces, we used is described below (see McGee & Carleton, 1970; Neter *et al.*, 1996; Bersier & Sugihara, 1997).

$$Y = b_0 + b_1[(\log_{10}(A) - T_1) \times (\log_{10}(A) \geq T_1)] \quad (3)$$

where Y = species richness (S) or $\log_{10}(S)$ for semi-log and log–log versions of the model, respectively, A = island area,

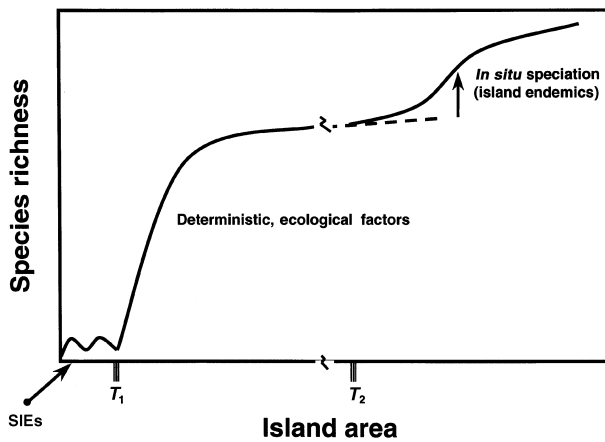


Figure 1 A general model for the species–area relationship (Lomolino, 2000) that includes the scale-dependent changes in the principal factors structuring insular communities including (1) idiosyncratic differences among islands and effects of hurricanes and other stochastic extinction forces – predominately on the small islands (i.e. those less than the ecological threshold, T_1), (2) more deterministic, ecological factors associated with habitat diversity, carrying capacity and extinction/immigration dynamics as envisioned by MacArthur & Wilson (1967) – on islands of intermediate size, and (3) *in situ* speciation – on the relatively large islands (i.e. those greater than the evolutionary threshold T_2).

here in m^2 , T_1 = the upper limit of the SIE, and $(\log_{10}(A) \geq T_1)$ = a variable that returns the logical value of 0 or 1.

Note that on islands smaller than T_1 , the independent variable equals 0 and species richness is estimated as a constant (b_0), independent of island area. On larger islands where $\log_{10}(A)$ exceeds T_1 , the independent variable equals the difference between $\log_{10}(A)$ and the breakpoint, T_1 . The data for each archipelago are not split for large vs. small islands, but included in one linear regression model (equation 3, above) for each archipelago or data set. The sample size equals the total number of islands, the estimates of the intercept, slope and coefficient of determination apply to the entire data set, and the assumptions are those of General Linear Models, which are relatively robust. The key difference between this and more traditional models is the breakpoint transformation, which essentially decreases x -values of all small islands (those $< T_1$) to 0, and decreases x -values of all larger islands by the amount T_1 , the upper limit of the SIE.

We used a maximal r^2 method to estimate the upper limit of the SIE. We ran 101 regressions for each model (semi-log and log–log) and data set, incrementing the trial breakpoint (T_i in units of $\log_{10}[A]$, m^2) by 0.1 each iteration through the range of $T_i = 0.0$ – 10.0 . For the few data sets where at least one island fell outside this range, we adjusted the initial T_i to include all islands (regressions run in Excel; file and macros available from senior author on request). We selected as the optimal breakpoint the T_i value yielding the highest r^2 value calculated to the third decimal point (in the case of ties, we

selected the largest T_i value yielding that r^2), and estimates of b_0 and b_1 were taken from regressions using this T -value. We acknowledge that the relationship may be more gradual than implied by the breakpoint model, but defining a strict T_1 value has proven instructive, especially when evaluating predictions based on this threshold of the species–area relationship. Sample results for regressions run with and without breakpoint transformations are graphed in Fig. 2.

RESULTS

Small island effects, albeit of varying magnitude, appear to be a relatively common feature of the data sets that we studied (Fig. 3). The range of the SIE included at least a fourth of the islands in 60 (59%) of the data sets, and at least a 10th of the islands in 77 (76%) of the data sets (semi-log model; respective values for regressions with the log–log model were 23 [23%] and 46 [45%]). The prevalence of detectable SIEs is surprising, especially in light of our tendency as biogeographers and ecologists to undersample small islands. That is, although frequency distributions of island or patch sizes in nature tend to be highly right-skewed and leptokurtic (dominated by the very small islands), we tend to include a disproportionately high number of the ecologically more interesting, larger islands in our surveys. Note that seven of the eleven data sets where we failed to detect SIEs (semi-log model) included only large islands (i.e. those exceeding $10^{6.3} m^2$). SIEs may be important features of diversity patterns within these archipelagoes, but only within the range of the relatively numerous, but unsampled, smaller islands.

Median values for T_1 , the upper limit of the SIE, were $10^{6.2}$ and $10^{5.6}$ for semi-log and log–log models, respectively. That is, species richness tended to vary independently of area for islands up to approximately $1 km^2$. In the 91 data sets where we did detect SIEs (semi-log model), the T_1 values ranged from $10^{1.7}$ to $10^{9.8} m^2$. The improvement in the explanatory power of species–area models (based on differences in r^2 values with and without the breakpoint transformation) ranged up to 0.663 for the semi-log model, and up to 0.207 for the log–log model (improvement in r^2 exceeded 0.10 in 28 and 12% of the 102 cases for semi-log and log–log models, respectively). We limit the following discussion of patterns in variation of T_1 values to results of semi-log regressions, which are qualitatively similar to patterns derived from log–log regressions.

The T_1 values were lowest for plants on islands of Lake Hjalmarren, Sweden ($10^{1.7}$) and for plants on near-shore islands in Prince Charlotte Bay, north-eastern Australia ($10^{1.9}$). T_1 values were highest for *Anolis* lizards of isolated islands in the Caribbean ($10^{9.8}$), non-volant mammals of the Sunda Shelf ($10^{9.8}$), primates of islands in south-east Asia ($10^{9.8}$) and ungulates of African savannas ($10^{9.7}$). Within this range, variation in T_1 values was generally consistent with predictions based on characteristics of the archipelagoes and species groups (Fig. 4). Archipelagoes of inland waters were characterized by relatively low T_1 values in comparison with those of marine systems where islands must be much larger

Table 1 Results of breakpoint regression analysis for small island effects in 102 data sets across a diversity of taxa and archipelagos. The breakpoint, species-area regression model is $Y = b_0 + b_1[(\log_{10}(A) - T_1) \times (\log_{10}(S) - T_2)]$, where Y = species richness (S) or $\log_{10}(S)$ for semi-log and log-log versions of the model, respectively. A = island area in m^2 , T_1 = the upper limit of the SIE, and $(\log_{10}(A) \geq T_1)$ = the breakpoint transformation, which returns the logical value of 0 or 1 for islands that fall below or beyond the range of the small island effect, respectively

Taxonomic group	Archipelago	Type of archipelago	Source	Number of islands	Richness (range)	$\log_{10}(\text{Area})$ (m^2 , range)
Amphibians	Lake Erie, USA	Inland waters	King <i>et al.</i> (1997)	19	0-12	3.7-7.6
Amphibians	West Indies	Marine	Hedges (1999)	40	1-63	7.1-11.0
Ants	Frisian Islands, North Sea	Marine	Boomsma <i>et al.</i> (1987)	18	0-35	5.4-8.2
Ants	N. Australian Islands	Marine	Woinarski <i>et al.</i> (1998)	37	1-45	3.8-8.4
Beetles	Faroe Islands	Marine	Enckell <i>et al.</i> (1987)	18	9-65	5.9-8.6
Beetles (carabid)	Vargskar, Baltic Sea	Marine	Niemela <i>et al.</i> (1987)	13	3-24	3.7-5.7
Beetles (carabid)	Lake Saimaa	Inland waters	Niemela <i>et al.</i> (1987)	13	1-12	3.3-5.8
Beetles (carabid)	Swedish lake	Inland waters	Nilsson <i>et al.</i> (1988)	17	4-28	3.8-5.9
Beetles (carabid)	Tvarminne, Baltic Sea	Marine	Niemela <i>et al.</i> (1987)	16	1-11	2.5-4.9
Beetles (carabid)	Baltic Islands	Marine	Ås (1984)	10	6-29	2.7-5.2
Beetles (carabid)	Stockholm, Baltic Sea	Marine	Niemela <i>et al.</i> (1987)	12	1-12	3.6-6.2
Beetles (carabid)	Florida Keys, USA	Marine	Peck & Howden (1985)	21	1-121	5.8-11.2
Beetles (scarab)	Pymatung Lake, USA	Inland waters	Coleman <i>et al.</i> (1982)	30	0-35	3.0-5.8
Birds	Krunnit Islands, Finland	Marine	Vaisanen & Jarvinen (1977)	18	0.2-10.6	2.8-6.3
Birds	Hawaiian Islands	Marine	Amerson (1975)	18	1-23	2.6-4.8
Birds	Vargskar, Baltic Sea	Marine	Haila <i>et al.</i> (1983)	43	1-56	3.7-6.8
Birds	British Isles	Marine	Reed (1981)	73	1-79	3.9-8.0
Birds	Sea of Cortez	Marine	Cody (1983)	25	1-30	5.0-9.1
Birds	Faroe Islands	Marine	Bengston & Bloch (1983)	22	7-60	5.0-8.6
Birds	New Zealand Islands	Marine	Williams (1981)	23	3-50	6.0-11.1
Birds	New Hebrides	Marine	Diamond & Marshall (1977)	28	16-50	6.4-9.6
Birds	Mountains, Baja and CA	Montane	Kratter (1992)	20	7-48	4.0-9.0
Birds	SW Australian Islands	Marine	Abbott (1978)	20	1-15	6.9-10.8
Birds	West Indies	Marine	Gotelli & Abele (1982)	19	16-79	7.9-11.1
Birds	Paramo, Northern Andes	Montane	Vuilleumier (1970)	15	4-65	7.4-9.5
Birds	Great Basin Mountains	Montane	Johnson (1975)	20	16-60	7.2-9.2
Birds	Galapagos Islands	Marine	Connor & Simberloff (1978)	15	6-20	6.4-9.7
Butterflies	West Indies	Marine	Davies & Smith (1997)	68	8-202	5.5-11.0
Butterflies	Great Basin Mountains	Montane	Wilcox <i>et al.</i> (1986)	18	3-84	8.1-9.5
Earthworms	Faroe Islands	Marine	Enckell <i>et al.</i> (1987)	18	3-10	5.9-8.6
Harvestmen	Faroe Islands	Marine	Enckell <i>et al.</i> (1987)	18	1-4	5.9-8.6
Isopods	Aegean Islands	Marine	Sfenthourakis (1996)	43	5-38	4.5-8.7
Isopods	Lake Erie, USA	Inland waters	Dexter <i>et al.</i> (1988)	22	2-11	2.5-7.6
Land snails	Swedish lake	Inland waters	Nilsson <i>et al.</i> (1988)	17	9-27	3.8-5.9
Land snails	Faroe Islands	Marine	Enckell <i>et al.</i> (1987)	17	6-19	6.4-8.6
Land snails	Hawaiian Islands	Marine	Cowie (1995)	14	1-282	5.3-10.0
Land snails	Aegean Islands	Marine	Heller (1976)	61	1-5	6.5-9.9
Mammals (bats)	Western New Guinea	Marine	Lawlor (1986)	23	1-19	6.7-10.2
Mammals (bats)	Solomon Islands	Marine	Lawlor (1986)	23	1-9	6.8-9.9
Mammals (bats)	West Indies	Marine	Lawlor (1986)	21	3-27	7.1-11.0
Mammals (bats)	American Southwest	Montane	Sidner & Davis (1995)	10	1-8	8.0-9.2

Mammals (large)	African Savannah	Terrestrial reserves	Western & Ssemakula (1981)	19	15-31	7.7-10.3
Mammals (large)	SE Asian Islands	Marine	Harcourt (1999)	31	1-13	7.3-11.9
Mammals (small to large)	Thousand Island Region	Inland waters	Lomolino (1982)	19	0-11	0.6-4.8
Mammals (small to large)	Lake Huron	Inland waters	Lomolino (1994)	25	0-15	3.0-8.5
Mammals (small to large)	Wisconsin Forests, USA	Fragmented forests	Matthiae & Stearns (1981)	22	4-13	3.6-5.6
Mammals (small to large)	Olympic Peninsula, WA	Fragmented forests	Lomolino & Perrault (2000)	20	1-8	4.0-5.8
Mammals (small to large)	Lake Michigan	Inland waters	Hatt <i>et al.</i> (1948)	14	0-5	4.0-8.2
Mammals (small to large)	Western Australia	Marine	Lawlor (1986)	11	1-12	6.3-8.8
Mammals (small to large)	Coastal Marine	Marine, near shore	Growell (1986)	24	1-29	3.5-8.4
Mammals (small to large)	British Columbia, Canada	Marine	Lawlor (1986)	75	1-16	5.9-10.5
Mammals (small to large)	American Southwest	Montane	Lomolino <i>et al.</i> (1989)	27	1-16	6.8-10.0
Mammals (small to large)	Channel Islands, CA, USA	Marine	Lawlor (1986)	12	1-5	4.7-8.4
Mammals (small to large)	Alexander Arch., Alaska	Marine	Conroy <i>et al.</i> (1999)	24	3-17	7.0-9.76
Mammals (small to large)	Kimberly Is., W. Australia	Marine	Lawlor (1986)	18	1-7	6.7-8.3
Mammals (small to large)	Bass Straits	Marine	Lawlor (1986)	21	1-25	6.3-10.8
Mammals (small to large)	Western New Guinea	Marine	Lawlor (1986)	17	1-7	6.7-10.2
Mammals (small to large)	British Isles	Marine	Lawlor (1986)	64	1-26	6.1-11.4
Mammals (small to large)	West Indies	Marine	Lawlor (1986)	20	0-5	6.4-11.0
Mammals (small to large)	Japanese Islands	Marine	Lawlor (1986)	15	1-32	6.7-11.3
Mammals (small to large)	N. Australian Islands	Marine	Lawlor (1986)	11	2-21	7.7-9.8
Mammals (small to large)	Philippines	Marine	Lawlor (1986)	17	2-28	7.4-11.0
Mammals (small to large)	Sunda Shelf	Marine	Lawlor (1986)	27	5-120	6.9-11.9
Mammals (small to large)	Panama Islands	Marine	Lawlor (1986)	13	1-9	6.6-8.7
Mammals (small to large)	National Parks, Canada	Terrestrial reserves	Glenn (1990)	36	4-36	7.2-10.7
Mammals (small to large)	National Parks, Western US	Terrestrial reserves	Newmark (1986)	24	30-59	7.9-10.3
Mammals (small to medium)	Southern Australia	Marine	Lawlor (1986)	17	1-17	6.0-9.7
Mammals (small to medium)	Great Basin Mountains	Montane	Brown (1971, 1978)	18	3-13	8.1-9.5
Mammals (small)	Basswood Lake, MN; USA	Inland waters	Beer <i>et al.</i> (1954)	31	1-7	2.6-6.2
Mammals (small)	Lake Erie, USA	Inland waters	Jackson (1988)	14	0-4	4.3-7.6
Mammals (small)	New England, MA, USA	Marine, nearshore	Adler & Wilson (1985)	33	1-7	3.7-10.4
Mammals (small)	Sea of Cortez	Marine	Lawlor (1986)	34	1-13	5.6-9.1
Plants	Lake Hjalmarren, Sweden	Inland waters	Rydin (1988)	37	5-115	1.7-4.4
Plants	Prince Charlotte, NE Australia	Marine, nearshore	Buckley (1985)	61	1-45	0.0-3.6
Plants	Lakes Western Ireland	Inland waters	Roden (1998)	29	16-113	1.9-4.5
Plants	SW Australian Islands	Marine	Abbott & Black (1980)	78	0-103	0.3-5.2
Plants	Lake Mockeln, Sweden	Inland waters	Nilsson & Nilsson (1982)	41	21-95	2.5-4.3
Plants	des Hybrids, Canada	Marine	Deshaye & Morriset (1988)	34	0-259	1.7-6.0
Plants	Shetland Isles	Marine	Kohn & Walsh (1994)	47	0-71	2.5-6.0
Plants	Swedish Lake	Inland waters	Nilsson <i>et al.</i> (1988)	17	18-32	3.8-5.9
Plants	Caroline Islands	Marine	Niering (1963)	33	4-60	2.1-5.5
Plants	Hawaiian Islands	Marine	Amerson (1975)	18	0-12	2.6-4.8
Plants	Sea of Cortez	Marine	Cody <i>et al.</i> (1983)	33	4-298	5.0-9.1
Plants	Arizona	Terrestrial reserves	Bowers & McLaughlin (1982)	20	195-1574	6.1-9.7
Plants	Galapagos Islands	Marine	Johnson & Raven (1973)	29	2-440	4-9.7
Plants	British Isles	Marine	McCoy & Connor (1976)	42	62-1666	5.7-11.4
Plants	Thousand Island Region	Inland waters	McNeill & Cody (1978)	17	116-500	4.2-6.6
Plants	Adirondack Mts., NY, USA	Montane	Riebesell (1982)	13	3-16	2.5-5.0

Table 1 continued

Taxonomic group	Archipelago	Type of archipelago	Source	Number of islands	Richness (range)	log ₁₀ (Area) (m ² , range)
Plants (grasses)	SW Australian Islands	Marine	Abbott (1992)	30	0-8	1.3-7.0
Plants (herbs)	Nui Atoll, Central Pacific	Marine	Woodruffe (1985)	20	2-19	2.0-6.1
Plants (shrubs)	Nui Atoll, Central Pacific	Marine	Woodruffe (1985)	20	1-8	2.0-6.1
Plants (trees)	Nui Atoll, Central Pacific	Marine	Woodruffe (1985)	20	3-14	2.0-6.1
Plants (weeds)	Vacant Lots	Habitat patches	Crowe (1979)	26	9-69	2.0-3.9
Reptiles (lizards)	Guam Fringing Islands	Marine	Perry <i>et al.</i> (1998)	22	0-10	2.7-5.6
Reptiles (lizards)	Gulf of California	Marine	Case (1975)	24	2-11	5.8-9.1
Reptiles (lizards)	Bahamas	Marine	Losos (1998)	53	1-4	5.2-9.3
Reptiles (lizards)	Sea of Cortez	Marine	Murphy (1983)	20	1-9	5.8-9.1
Reptiles (lizards)	West Indies	Marine	Losos (1998)	83	1-54	5.2-11.0
Reptiles (snakes, turtles, lizards)	Lake Erie, USA	Inland waters	King (1988)	33	0-14	4.6-8.2
Reptiles and amphibians	Sea of Cortez	Marine	Murphy (1983)	43	1-25	5.0-9.1
Spiders	Lake Erie, USA	Inland waters	Beattie (1988)	22	5-162	2.5-7.6
Spiders	Faroe Islands	Marine	Enckell <i>et al.</i> (1987)	18	2-31	5.9-8.6

Results of breakpoint regression analysis using the semi-log model

Results of breakpoint regression analysis using the log-log model

$R^2_{w/o}$ breakpoint	Breakpoint (T_1 value)	$R^2_{w/}$ breakpoint	Improvement in R^2	Proportion w/in SIE	b_0 , or sill	Semi-log slope	$R^2_{w/o}$ breakpoint	Breakpoint (T_1 value)	$R^2_{w/}$ breakpoint	Improvement in R^2	Proportion w/in SIE	b_0 , or sill	log-log slope
0.789	5.1	0.861	0.072	0.47	0.697	4.879	0.723	3.7	0.723	0.000	0.05	-0.921	0.605
0.634	9.5	0.948	0.314	0.90	2.268	36.952	0.634	8.7	0.762	0.128	0.75	0.243	0.720
0.163	5.4	0.163	0.000	0.06	3.827	4.815	0.215	5.4	0.215	0.000	0.06	0.221	0.400
0.718	6.0	0.847	0.129	0.62	5.500	16.195	0.689	4.8	0.741	0.052	0.17	0.580	0.311
0.675	7.4	0.755	0.080	0.44	23.058	37.740	0.625	7.0	0.636	0.011	0.28	1.303	0.336
0.808	3.9	0.816	0.008	0.15	6.355	8.759	0.742	3.9	0.759	0.017	0.15	0.782	0.353
0.604	4.0	0.690	0.086	0.38	3.578	6.041	0.375	3.8	0.444	0.069	0.31	0.461	0.400
0.575	4.3	0.632	0.057	0.24	7.678	14.708	0.556	4.3	0.619	0.147	0.69	0.393	0.955
0.484	4.3	0.673	0.189	0.69	2.549	10.118	0.472	4.3	0.619	0.063	0.24	0.878	0.463
0.519	4.7	0.763	0.244	0.70	10.460	32.215	0.532	4.5	0.584	0.052	0.70	1.006	0.825
0.612	< 3.6	-	0.000	0.00	-	-	0.528	< 3.6	-	0.000	0.00	-	-
0.874	8.4	0.979	0.105	0.90	4.304	42.289	0.688	6.0	0.689	0.001	0.14	0.253	0.376
0.856	3.7	0.937	0.081	0.43	1.805	15.835	0.578	3.0	0.579	0.001	0.07	-0.119	0.725
0.771	4.0	0.820	0.049	0.39	1.486	4.032	0.493	< 2.8	-	0.000	0.00	-	-
0.658	4.1	0.789	0.131	0.44	4.966	25.296	0.801	< 2.6	-	0.000	0.00	-	-
0.855	4.9	0.919	0.064	0.49	6.338	25.270	0.852	3.7	0.852	0.000	0.05	0.361	0.499
0.641	5.2	0.674	0.033	0.27	5.530	16.871	0.692	< 3.9	-	0.000	0.00	-	-

0.842	5.7	0.865	0.023	0.12	2.473	6.592	0.768	5.0	0.768	0.000	0.12	0.363	0.292
0.853	6.1	0.889	0.036	0.23	7.964	18.591	0.928	5.3	0.930	0.002	0.05	0.857	0.286
0.942	6.3	0.944	0.002	0.22	7.360	9.021	0.747	6.1	0.747	0.000	0.04	0.888	0.188
0.702	6.4	0.702	0.000	0.04	17.275	9.061	0.650	< 6.4	-	0.000	0.00	-	-
0.511	7.4	0.758	0.247	0.35	11.799	21.076	0.682	6.3	0.758	0.076	0.15	5.589	11.761
0.690	7.5	0.708	0.018	0.25	1.160	4.274	0.587	7.1	0.589	0.002	0.15	0.047	0.366
0.897	8.1	0.898	0.001	0.16	21.800	20.420	0.777	< 7.9	-	0.000	0.00	-	-
0.516	8.2	0.595	0.079	0.33	12.599	23.746	0.459	8.2	0.560	0.101	0.33	1.086	0.440
0.290	8.5	0.477	0.187	0.55	26.312	28.342	0.275	8.5	0.472	0.197	0.55	1.405	0.382
0.745	< 6.4	-	0.000	0.00	-	-	0.703	< 6.4	-	0.000	0.00	-	-
0.532	9.0	0.819	0.287	0.82	27.040	83.933	0.589	7.1	0.620	0.031	0.19	1.181	0.260
0.352	< 8.1	-	0.000	0.00	-	-	0.201	< 8.1	-	0.000	0.00	-	-
0.558	6.7	0.572	0.014	0.17	4.699	2.606	0.549	6.5	0.554	0.005	0.17	0.652	0.167
0.535	7.1	0.677	0.142	0.44	1.868	1.320	0.460	7.0	0.603	0.143	0.28	0.287	0.196
0.841	5.9	0.903	0.062	0.19	6.210	9.080	0.903	5.6	0.919	0.016	0.14	0.815	0.240
0.408	< 2.5	-	0.000	0.00	-	-	0.461	< 2.5	-	0.000	0.00	-	-
0.362	3.8	0.362	0.000	0.06	11.237	5.502	0.365	3.8	0.365	0.000	0.06	1.061	0.147
0.494	6.4	0.494	0.000	0.06	9.982	2.935	0.494	6.4	0.494	0.000	0.06	0.996	0.107
0.559	7.8	0.661	0.102	0.43	2.130	94.221	0.886	6.4	0.911	0.025	0.29	0.110	0.674
0.282	8.1	0.395	0.113	0.72	1.063	1.249	0.324	8.2	0.444	0.120	0.74	0.062	0.784
0.358	7.1	0.361	0.003	0.09	1.172	4.155	0.421	0.8	0.421	0.000	0.09	0.059	0.314
0.563	7.2	0.573	0.010	0.26	2.924	3.681	0.550	7.1	0.559	0.009	0.22	0.436	0.256
0.808	8.2	0.828	0.020	0.24	5.570	6.140	0.813	7.1	0.813	0.000	0.00	-	-
0.562	< 8.0	-	0.000	0.00	-	-	0.524	< 8.0	-	0.000	0.00	-	-
0.060	9.7	0.156	0.096	0.79	19.864	9.726	0.052	9.7	0.156	0.104	0.79	1.291	0.196
0.590	9.8	0.788	0.198	0.84	1.888	4.491	0.497	9.5	0.564	0.067	0.65	0.231	0.360
0.677	2.8	0.899	0.222	0.63	1.305	5.220	0.701	< 0.6	-	0.000	0.00	-	-
0.889	4.1	0.895	0.006	0.44	1.107	3.075	0.507	3.0	0.507	0.000	0.04	-0.360	0.392
0.638	4.1	0.708	0.070	0.23	5.110	4.886	0.586	4.0	0.623	0.037	0.18	0.709	0.257
0.079	5.1	0.090	0.000	0.35	3.729	2.051	0.116	4.8	0.162	0.046	0.15	0.501	0.224
0.857	5.2	0.915	0.058	0.29	0.040	1.768	0.802	4.3	0.804	0.002	0.14	-0.980	0.515
0.399	6.7	0.404	0.005	0.27	1.363	2.744	0.513	7.1	0.514	0.001	0.55	0.212	0.395
0.673	6.9	0.849	0.176	0.71	3.120	14.784	0.859	4.8	0.868	0.009	0.27	0.270	0.302
0.555	7.1	0.603	0.048	0.44	1.601	2.674	0.586	6.3	0.586	0.000	0.27	0.166	0.221
0.715	7.2	0.728	0.013	0.22	1.621	4.505	0.698	7.0	0.710	0.012	0.07	0.219	0.384
0.631	7.3	0.789	0.158	0.50	0.999	2.549	0.781	6.9	0.903	0.122	0.50	0.041	0.357
0.304	7.4	0.306	0.002	0.08	4.045	3.363	0.424	< 7.0	-	0.000	0.00	-	-
0.534	7.4	0.765	0.231	0.61	1.621	5.736	0.378	7.4	0.562	0.184	0.61	0.220	0.722
0.896	7.6	0.937	0.061	0.62	1.936	6.939	0.874	< 6.3	-	0.000	0.00	-	-
0.324	7.6	0.335	0.011	0.12	1.687	1.254	0.329	7.6	0.329	0.000	0.12	0.225	0.181
0.515	7.7	0.562	0.047	0.56	2.653	4.462	0.417	6.1	0.417	0.000	0.02	0.159	0.220
0.373	8.3	0.522	0.149	0.30	1.036	1.036	0.200	8.2	0.339	0.139	0.20	-0.760	0.425
0.878	8.4	0.949	0.071	0.27	2.481	10.272	0.917	6.8	0.917	0.000	0.07	0.076	0.343
0.672	8.4	0.697	0.025	0.64	5.764	8.820	0.613	8.4	0.697	0.084	0.64	0.731	0.405
0.544	9.6	0.622	0.078	0.59	9.055	11.798	0.454	8.2	0.468	0.014	0.06	0.794	0.202
0.793	9.8	0.951	0.158	0.85	13.223	49.242	0.840	7.3	0.840	0.000	0.11	0.854	0.259
0.266	< 6.6	-	0.000	0.00	-	-	0.322	< 6.6	-	0.000	0.00	-	-

Table 1 continued

Results of breakpoint regression analysis using the semi-log model						Results of breakpoint regression analysis using the log-log model							
$R^2_{w/o}$ breakpoint	Breakpoint (T_1 value)	$R^2_{w/}$ breakpoint	Improvement in R^2	Proportion w/in SIE	b_0 , or sill	Semi-log slope	$R^2_{w/o}$ breakpoint	Breakpoint (T_1 value)	$R^2_{w/}$ breakpoint	Improvement in R^2	Proportion w/in SIE	b_0 , or sill	log-log slope
0.569	< 7.2	-	0.000	0.00	-	-	0.631	< 7.2	-	0.000	0.00	-	-
0.690	< 7.9	-	0.000	0.00	-	-	0.683	< 7.9	-	0.000	0.00	-	-
0.753	7.7- 9.7 ^a	0.981	0.228	0.94	1.188	- ^a	0.664	7.7- 9.7 ^a	0.833	0.169	0.94	0.087	- ^a
0.679	< 8.1	-	0.000	0.00	-	-	0.679	< 8.1	-	0.000	0.00	-	-
0.383	3.3	0.394	0.011	0.26	1.304	1.416	0.383	< 2.6	-	0.000	0.00	-	-
0.892	4.9	0.924	0.032	0.29	-0.019	1.498	0.735	4.4	0.736	0.001	0.14	-0.997	0.585
0.228	5.0	0.245	0.017	0.09	2.331	0.517	0.179	5.0	0.245	0.066	0.09	0.374	0.060
0.484	7.6	0.632	0.148	0.68	1.728	5.109	0.510	5.8	0.510	0.000	0.06	0.062	0.244
0.837	1.7	0.837	0.000	0.03	13.255	36.058	0.722	1.7	0.722	0.000	0.03	1.261	0.358
0.701	1.9	0.781	0.080	0.49	4.958	20.256	0.822	0.5	0.830	0.008	0.03	0.256	0.405
0.769	2.1	0.769	0.000	0.03	17.491	32.064	0.842	< 1.9	-	0.000	0.00	-	-
0.444	2.8	0.788	0.344	0.85	2.314	40.195	0.484	0.4	0.484	0.000	0.05	-0.964	0.711
0.763	3.1	0.817	0.054	0.27	33.374	47.652	0.705	3.0	0.744	0.039	0.17	1.512	0.370
0.845	3.5	0.954	0.109	0.26	6.124	93.619	0.840	1.7	0.840	0.000	0.03	-0.702	0.853
0.875	3.5	0.915	0.040	0.40	4.173	23.195	0.542	2.9	0.568	0.026	0.06	0.157	0.696
0.593	3.8	0.593	0.000	0.06	19.495	5.672	0.581	< 3.8	-	0.000	0.00	-	-
0.648	4.0	0.817	0.169	0.45	9.005	28.939	0.719	2.9	0.743	0.024	0.03	0.640	0.421
0.369	4.3	0.586	0.217	0.56	1.117	17.410	0.274	4.2	0.325	0.051	0.56	-0.459	2.141
0.807	6.0	0.837	0.030	0.24	17.702	66.706	0.665	5.6	0.687	0.022	0.03	1.201	0.397
0.324	6.2	0.324	0.000	0.05	198.349	178.929	0.364	< 6.1	-	0.000	0.00	-	-
0.624	7.0	0.753	0.129	0.55	19.014	130.747	0.795	4.0	0.795	0.000	0.03	0.424	0.404
0.591	7.8	0.703	0.112	0.52	237.168	356.124	0.478	5.9	0.480	0.002	0.05	2.091	0.213
0.892	< 4.2	-	0.000	0.00	-	-	0.785	< 4.2	-	0.000	0.00	-	-
0.703	< 2.5	-	0.000	0.00	-	-	0.686	< 2.5	-	0.000	0.00	-	-
0.575	2.6	0.592	0.017	0.20	0.554	1.218	0.550	2.0	0.567	0.017	0.13	-0.305	0.240
0.872	3.0	0.908	0.036	0.20	3.202	4.099	0.796	2.9	0.815	0.019	0.15	0.538	0.233
0.701	2.0	0.701	0.000	0.05	2.322	1.518	0.614	2.0	0.614	0.000	0.05	0.364	0.159
0.844	3.1	0.884	0.040	0.25	3.849	2.823	0.813	2.8	0.836	0.023	0.15	1.218	0.395
0.438	2.4	0.454	0.016	0.15	17.738	28.396	0.442	2.3	0.458	0.016	0.15	1.218	0.395
0.612	3.8	0.714	0.102	0.50	1.417	4.503	0.308	< 2.7	-	0.000	0.00	-	-
0.515	5.9	0.515	0.000	0.04	2.287	2.299	0.497	< 5.8	-	0.000	0.00	-	-
0.194	7.3	0.210	0.016	0.55	1.182	0.785	0.193	7.3	0.204	0.011	0.55	0.084	0.153
0.308	7.4	0.327	0.019	0.55	2.989	2.780	0.319	5.7	0.319	0.000	0.00	-	-
0.290	9.8	0.953	0.663	0.95	1.881	38.913	0.380	9.1	0.587	0.207	0.93	0.252	0.787
0.289	4.7	0.289	0.000	0.03	1.097	1.927	0.245	5.0	0.247	0.002	0.06	0.028	0.307
0.723	6.2	0.752	0.029	0.42	2.723	7.047	0.668	5.6	0.675	0.007	0.05	0.315	0.344
0.395	3.6	0.405	0.010	0.18	10.189	23.531	0.646	< 2.5	-	0.000	0.00	-	-
0.642	7.2	0.772	0.130	0.44	6.625	15.066	0.528	7.0	0.632	0.104	0.28	0.773	0.451

Less than symbol indicates that the upper limit of the small island effect may be less than that of the smallest island studies.
^aNo islands were included within this range of island area, so breakpoints are reported as a range and slopes, which varied within this range, are not reported.

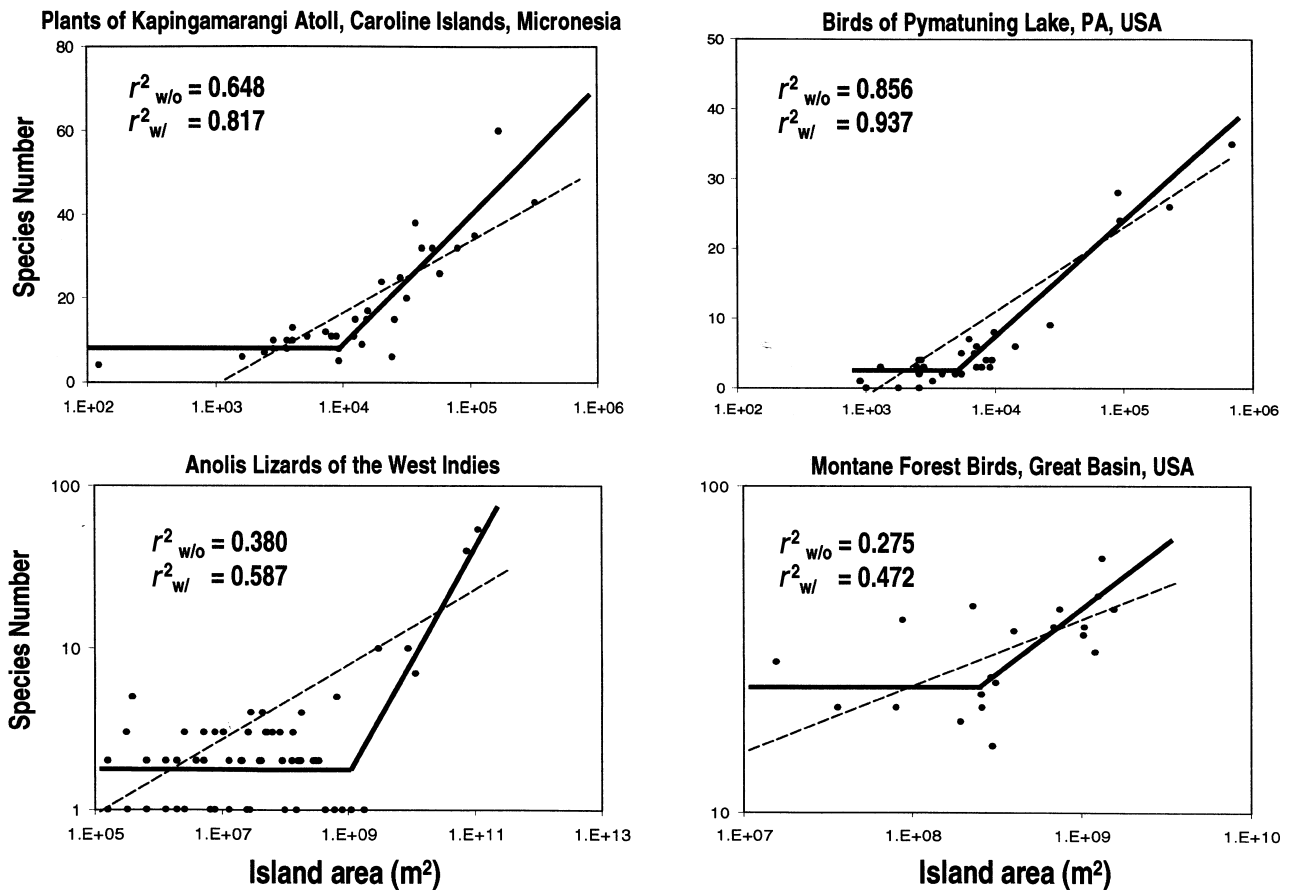


Figure 2 Sample results of breakpoint and traditional species–area regression analysis for four insular biotas. Solid and dashed lines indicate predicted species–area curves using breakpoint and traditional methods, respectively (top two graphs based on semi-log models, bottom two based on log–log models). Note that in all of these examples, the slope of the species–area relationship is underestimated unless breakpoint methods are used to control for small island effects. The $r^2_{w/o}$ and $r^2_{w/}$ refer to coefficients of determination without and with breakpoint transformations, respectively.

to maintain populations in the face of relatively infrequent immigrations. Fragmented terrestrial ecosystems and patches of terrestrial habitats such as vacant lots also tended to have relatively low T_1 values, while those of montane forests exhibited T_1 values within the range of marine biotas. This latter result is consistent with Brown's (1971) assertion that intermontane habitats, which are dominated by desert and other xeric habitats, are as isolating to montane forest species as the waters of marine archipelagoes.

The T_1 values also exhibited some clear patterns of variation among species groups (Fig. 4), tending to be lowest for plants (with their relatively low resource and space requirements, and high dispersal abilities), intermediate for reptiles, beetles and birds, and highest for non-volant mammals. Within the latter group, the highest T_1 values observed were those for the two groups comprised solely of large mammals (again, $10^{9.7}$ and $10^{9.8}$ for ungulates of African savannas and primates of south-east Asian islands). In contrast, T_1 values for species groups comprised solely of small mammals (those < 1 kg) ranged from $10^{3.3}$ to $10^{5.0}$ for

those on islands of inland and near-shore archipelagoes (Basswood Lake, MN, USA, Lake Erie, and coastal islands near Boston, MA, USA) to $10^{7.6}$ for small mammals on islands of the Sea of Cortez (all other mammalian biotas we studied were comprised of combinations of small to large sized species).

Comparisons among different taxa within the same archipelago are also instructive. Again, plants and birds tended to exhibit relatively low intra-archipelago T_1 values, while non-volant mammals, reptiles and amphibians, exhibited relatively high T_1 values (Fig. 5). For example, on islands in the Sea of Cortez, T_1 values were lowest for birds ($10^{5.7}$) followed by plants ($10^{6.0}$), herptiles ($10^{6.2}$), reptiles ($10^{7.4}$), and then non-volant mammals ($10^{7.6}$). Birds also exhibited the lowest intra-archipelago T_1 values for the Hawaiian Islands ($10^{4.1}$ vs. $10^{4.3}$ and $10^{7.8}$ in plants and land snails), the Galapagos ($10^{<6.3}$ vs. $10^{7.0}$ for plants), the West Indies ($10^{8.1}$ vs. $10^{8.2}$, $10^{8.3}$, $10^{9.0}$, $10^{9.5}$ and $10^{9.8}$ for bats, non-volant mammals, butterflies, amphibian and reptiles), the Faroe Islands ($10^{6.1}$ vs. $10^{6.4}$, $10^{6.7}$, $10^{7.1}$, $10^{7.2}$ and $10^{7.4}$

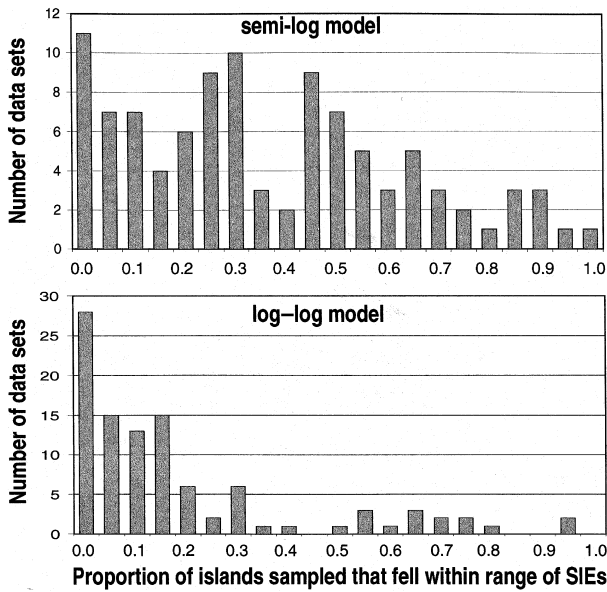


Figure 3 Frequency distributions of the relative prevalence of small island effects (as proportion of islands sampled within each archipelago that fell within the range of small island effects) among 102 data sets of insular and otherwise isolated biotas.

for land snails, earthworms, harvestmen, spiders and beetles) and the British Isles ($10^{5.2}$ vs. $10^{7.7}$ and $10^{7.8}$ for mammals and plants). While these intra-archipelago comparisons are limited and preliminary to more expanded data sets and analyses, the observed tendencies are consistent with the predictions that the upper limit of SIEs should be highest for

groups comprised of species with relatively high resource requirements and/or low dispersal abilities (e.g. non-volant mammals vs. birds and plants).

The prevalence of SIEs (detected for at least one island in 89 and 73% of cases using semi-log and log-log models, respectively) calls for a re-evaluation of traditional approaches to studying one of nature’s most fundamental patterns. To more fully evaluate the relative importance of SIEs, we should compare frequency distributions of actual island sizes (not just those surveyed) with the upper limit of the SIE. Again, because biogeographers tend to undersample relatively small islands, SIEs may be more common than it appears based on the results presented here. To date, we have made this comparison of frequency distributions of available islands with the range of SIEs for just one archipelago, but the results are illustrative of the general approach and utility of such comparisons (Fig. 6).

What we are recommending is not a radical change, but an enhancement of the species–area research programme: one that now includes the potential importance of SIEs along with all the features of traditional models. We are modifying the two traditional models by adding the breakpoint transformation. If all islands sampled fall above the range of SIEs, then the breakpoint transformation is zero and the model reduces to the semi-log or log–log models traditionally used for decades. The breakpoint transformation, however, has several advantages. It allows us to test the implicit assumption of previous studies that SIEs are trivial. It provides an objective means to estimate the range of the SIE within an archipelago and to explore patterns of variation in the upper limit of that range among species groups and archipelagoes. The breakpoint species–area

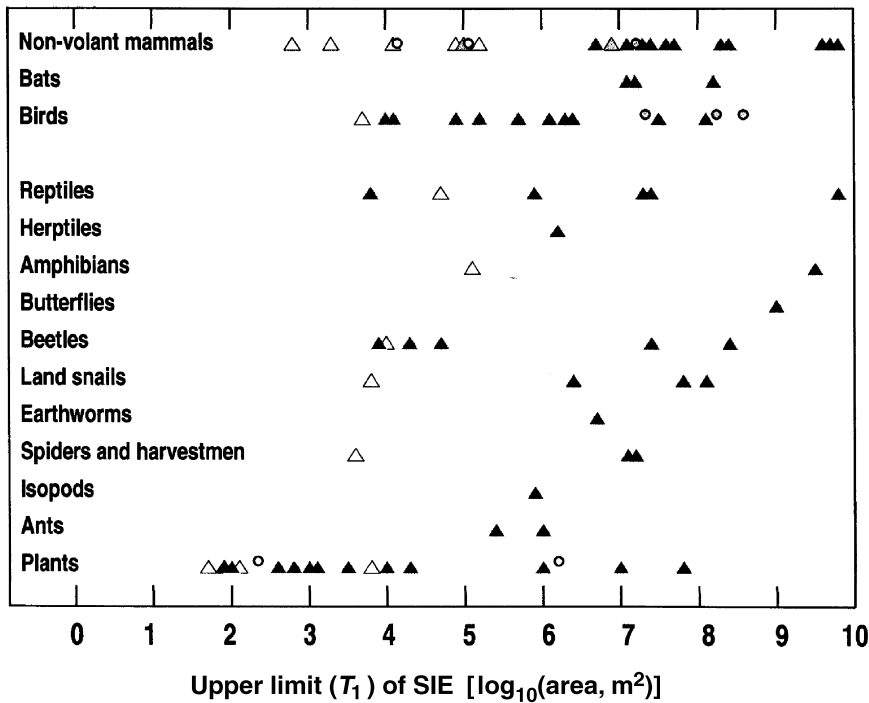


Figure 4 Patterns of variation in the upper limit of the small island effect (T_1 , in units of $\log_{10}(\text{Area}, \text{m}^2)$) among a diversity of taxonomic groups and types of archipelagoes. Key to symbols: white, grey and black triangles represent inland, nearshore and marine archipelagoes, respectively; white and grey dots refer archipelagoes of anthropogenic fragments, and montane archipelagoes, respectively.

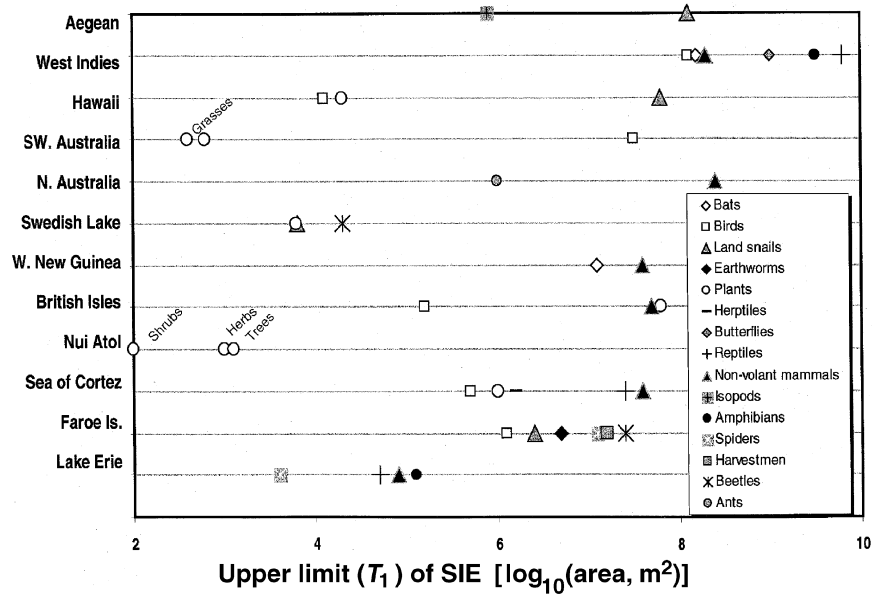


Figure 5 Patterns of variation in the upper limit of the small island effect (T_1 , in units of $\log_{10}(\text{Area})$, m^2) among various taxonomic groups surveyed within the same archipelago.

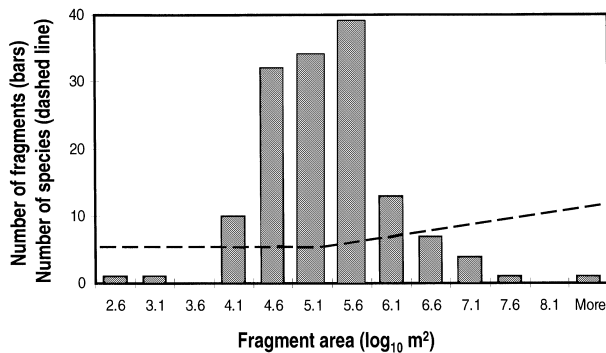


Figure 6 Comparison of the frequency distribution of available (mapped), old-growth forest fragments of the Hoodport District, Olympic National Forest (WA, USA) to the extent of the small island effect (fragment sizes ranged from $10^{2.57}$ to $10^{8.19}$ m^2). Seventy-eight (55%) of the 143 mapped fragments fell within the range of small island effects (i.e. were $< 10^{5.1}$ m^2 ; see Lomolino & Perault, 2000, 2001; Perault & Lomolino, 2000).

model has three readily interpretable, biologically relevant parameters: b_0 , an estimate of the ‘sill’ or species richness for relatively small islands; T_1 , an estimate of the breakpoint, or upper limit of the SIE in units of $\log_{10}(A)$ and b_1 , an estimate of the semi-log or log–log slope of the species–area relationship on the larger islands. The breakpoint model also provides a means to study patterns in slopes and intercepts of semi-log or log–log models after adjusting for SIEs. Where SIEs are important, the slope of the semi-log or log–log relationship (b_1 or z) may be underestimated unless a breakpoint transformation is included in the regression model (see scatter plots of Fig. 1, dashed vs. solid lines for regression results without and with breakpoint transformations, respectively).

In addition to its potential heuristic value, the breakpoint species–area model can be an important tool for conservation biologists attempting to predict diversity of prospective nature reserves, predict the loss in diversity following reduction of native ecosystems or develop management strategies for relatively small reserves. If species–area slopes on larger islands are actually steeper than those estimated by traditional relaxation models (see Fig. 2), then species extinctions will exceed estimates based on those models. On smaller islands, changes in fragment or reserve area should be a poor predictor of changes in species richness. Incremental additions to existing reserves that fall within the range of SIEs are less likely to promote increased diversity than are alternative efforts to optimize habitat quality and manage populations within those reserves. On the other hand, habitat and population management at local scales are unlikely to yield significant increases in diversity of relatively large reserves unless these measures are applied at a very broad geographical scale and preferably combined with other measures of landscape-scale management such as establishing and managing dispersal corridors among reserves. It is ironic that the benefits of increasing reserve size are only likely to be effective where such measures will be most expensive, i.e. on the intermediate to large reserves – those which fall beyond the range of SIEs. In all such applications, it is important to determine which reserves fall within or beyond the range of the SIE: the breakpoint species–area model provides a means to do this.

CONCLUSIONS

The approach we have described here may provide some important insights for developing a more general understanding of this fundamental pattern of nature, and for conserving biological diversity. We repeat an earlier call by

the senior author (Lomolino, 2000) to focus our attention on key thresholds of the species–area relationship (Fig. 1). Two thresholds delineate three fundamentally different realms in island area where richness is most strongly influenced by (1) idiosyncratic differences among islands, and hurricanes and other stochastic forces – predominately on the small islands; (2) more deterministic, ecological factors including increased habitat diversity, increased carrying capacity and extinction/immigration dynamics as envisioned by MacArthur & Wilson (1967) – on islands of intermediate size; and (3) evolution – on islands larger enough to provide internal geographical isolation (larger rivers, mountain ranges and other barriers necessary for *in situ* speciation; see Heaney, 2000; Losos & Schluter, 2000). As Munroe (1953, p. 53) stated, ‘Where speciation is important, as in large islands and continents, the expected size of the fauna is exceeded, but the relationship between area and size of fauna is not lost, but accentuated’ (see Fig. 1, curve for islands larger than the evolutionary threshold, T_2).

While the conceptual model of Fig. 1 is certainly more complex than traditional models of this very general pattern, we believe it is a more accurate and insightful one, and a more powerful tool for understanding and conserving biological diversity on islands and other isolated ecosystems.

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BIOSKETCHES

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