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The maximal body mass–area relationship in island mammals

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ABSTRACT

Aim A positive power relationship between maximal body mass and land area has previously been reported of the form $M_{\max} \propto \text{Area}^{0.5}$ whilst allometric scaling theory predicts either $M_{\max} \propto \text{Area}^{1.33}$ or $M_{\max} \propto \text{Area}^1$. We provide an analysis of the maximal mass–area relationship for four island systems, to test the hypothesis that community relaxation following isolation converges in each case to a slope of $\text{Area}^{0.5}$.

Location Islands of the Japanese archipelago, the western Mediterranean, the Sea of Cortés and Southeast Asia.

Methods We calculated the relationship between island area and the maximal body mass of the largest mammal species on the island using linear regression models with log-transformed variables, and tested the hypothesis that the slopes were not significantly different from 0.5.

Results We found a slope of 0.47 within the Japanese archipelago, 0.42 for western Mediterranean islands, 0.73 for the Sea of Cortés islands and 0.50 for Southeast Asian islands. None of these slopes were significantly different from 0.5.

Main conclusions Our results provide further empirical support for previous findings of a general maximal body mass–area relationship of $M_{\max} \propto \text{Area}^{0.5}$, but they deviate from theoretical predictions. We hypothesize that this mass–area relationship was the ultimate end point of community relaxation initiated by the isolation of the mammal communities. Maximal body mass on each island today probably reflects the interaction between energetic constraints, home range size and island area.

Keywords

Body mass, community relaxation, extinction, island area, island evolution, mammal, maximal body mass.

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INTRODUCTION

Body mass is a fundamental characteristic that affects diverse aspects of a species' physiology, ecology and evolution (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984), including the question of the area of habitat required for a species to sustain a viable population size (Harcourt, 2002). In general there is a positive relationship between land mass area and the maximum body mass of a species that can be sustained there (Marquet & Taper, 1998; Burness *et al.*, 2001; Marquet *et al.*, 2005; Okie & Brown, 2009).

Marquet & Taper (1998) reported a positive relationship between the log(land mass area) and the log(body mass) of mammal assemblages from three archipelago-like areas (the

Great Basin mountaintops, 20 islands in the Sea of Cortés and the seven continents). Replotting their data with area as the explanatory variable gives a slope of $\text{Area}^{0.53}$. In another study based on 31 land masses, Burness *et al.* (2001) also reported a positive power-law relationship between maximal body mass and land area for some mammals, but also birds and reptile species, that was not significantly different from $\text{Area}^{0.50}$ (Burness *et al.*, 2001). Okie & Brown (2009) reported a very similar value of $\text{Area}^{0.56}$ for mammals on some islands on the Sunda Shelf. All reported analyses to date thus indicate a consistent slope for maximum body mass and area of $\text{Area}^{0.50}$.

Surprisingly, there is a marked divergence in the empirical values reported by these studies and the slope predicted by allometric theory (Marquet & Taper, 1998; Marquet *et al.*,

2005; Okie & Brown, 2009). Okie & Brown (2009) derived an allometric relationship of $M_{\max} \propto \text{Area}^{1.33}$, whilst Marquet & Taper (1998) derived $M_{\max} \propto \text{Area}^1$. In both cases larger mammals with larger home ranges will require a larger land area to achieve the minimum viable population size required for long-term persistence (Marquet & Taper, 1998; Jetz *et al.*, 2004; Marquet *et al.*, 2005). The differences in the theoretical predictions arise because Marquet & Taper (1998; see also Marquet *et al.*, 2005) assumed that home range area scaled as M^1 , while Okie & Brown (2009) assumed instead that population density scaled as $M^{-0.75}$. However, in their study, Marquet *et al.* (2005) also predicted that the minimum viable population density should be independent of body mass. This last prediction is supported by a review of 212 plant and animal species for which body size explained very little of the variation observed in the minimum viable population size (Traill *et al.*, 2007). Clearly, further research is needed to address the disparity between theory and data. Here we contribute new data to evaluate the robustness of the empirical pattern of $M_{\max} \propto \text{Area}^{0.5}$.

The result reported by Burness *et al.* (2001) is compelling because of the range of organisms (endothermic and ectothermic, herbivores and carnivores), masses (2.7–6000 kg), time span (during the last 65,000 years) and land areas (0.12 to $5 \times 10^7 \text{ km}^2$) examined. However, as the authors suggest, an important test of the generality of their result would be achieved if this mass–area relationship were to be established for communities isolated on separate islands of varying size within the same archipelago (Burness *et al.*, 2001; Okie & Brown, 2009). In this context we may view land-bridge islands (newly formed islands previously connected to a nearby continent) as providing a natural macroecological ‘experiment’

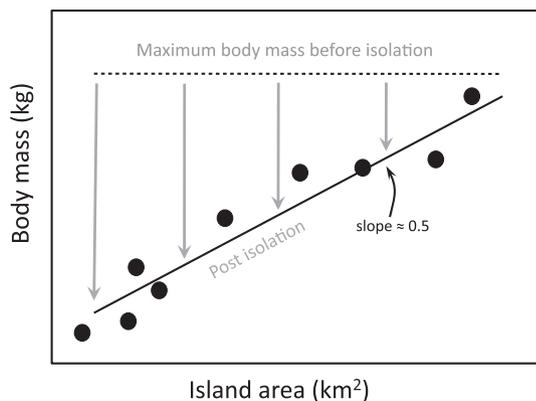


Figure 1 An hypothesis for the evolution of the relationship between log(maximal body mass of mammals) and log(land mass area) during the process of community relaxation initiated by isolation. The extinction of large-bodied species is driven by the reduction in surface area associated with insularization. Previous empirical research suggests that the slope of the relationship should attain a value of 0.5, although theoretical predictions from body size allometry range from 1.0 to 1.33 (see Introduction for details). There is currently no precise theoretical explanation for the empirical relationship $M_{\max} \propto \text{Area}^{0.5}$.

in which we would predict an increase in the mass–area slope as the newly isolated fauna adjusted (by rapid extinction and/or evolution to smaller body size) to the energetic constraints of the new island system (Fig. 1). Such a relaxation dynamic (*sensu* Diamond, 1984) should result in a modern fauna exhibiting a maximal mass–area relationship with a slope of 0.50 if the empirical findings of Burness *et al.* (2001) are general. Here we report the result of such a test for four insular systems: the Japanese archipelago, the western Mediterranean islands, the Sea of Cortés islands and Southeast Asian islands. Our aim was to test the hypothesis of community relaxation, and establish whether a maximal mass–area relationship of *c.* 0.50 was obtained following significant increases in the isolation of islands resulting from late Quaternary sea-level rise in these four systems.

MATERIALS AND METHODS

We sampled a number of islands from four distinct island systems. The number of islands, sources of species lists, body mass and area are detailed below. Our sampling was limited by our ability to recover from the literature the faunal lists for individual islands, and the body masses of the largest species for each island. We did not include introduced species for any of the islands considered. The taxonomic status of all species was checked with the list provided in Wilson & Reeder (2005).

The Japanese archipelago is a long chain of islands located off the eastern coast of Asia that extends over a distance of about 2000 km. The archipelago comprises more than 3900 islands of widely differing area, ranging from less than 1 km^2 to more than $230,000 \text{ km}^2$. All the Japanese islands, except the Ryukyu Islands, are land-bridge islands *sensu* Lawlor (1986), i.e. they were connected to the Asian mainland during the Pleistocene (Dobson, 1994; Millien-Parra & Jaeger, 1999). We considered 12 islands with areas ranging from 4 to $230,000 \text{ km}^2$; a 60,000-fold range in island area. There are 90 species (distributed over seven orders) of extant terrestrial mammals in the Japanese archipelago, of which 40% are endemic (Abe, 1994; Wilson & Reeder, 2005). The list of the terrestrial mammalian fauna used here was that reported by Millien-Parra & Jaeger (1999). We used the maximum recorded body mass of the heaviest native species present within the complete fauna for each of the 12 islands considered (Nowak & Paradiso, 1983; Abe, 1994).

The western Mediterranean islands are all found in the portion of the Mediterranean Sea between the European and African mainland, west of the Italian Peninsula. All these islands became isolated from the mainland, and from each other, following the Last Glacial Maximum (LGM). However, the level of species endemism on these islands is very low, due to the replacement of the Pleistocene fauna by a modern fauna composed of mainland species introduced to the islands by humans (Cheylan, 1984; Vigne, 1987, 1992). A total of 45 islands and islets were included in the data set, with island area ranging from 0.3 to $25,660 \text{ km}^2$. The faunal data we used were

from Sarà (1998), whilst the body mass and island area data were from Sarà (1998) and Sarà & Morand (2002).

The islands in the Sea of Cortés are located in the Gulf of California, between the Baja California peninsula and the Sonoran mainland. The peninsula of Baja California began to separate from the mainland as early as the late Miocene, around 5 Ma and became fully isolated during the Late Pliocene, around 3 Ma (Case *et al.*, 2002; Lawlor *et al.*, 2002). Many islands in the Sea of Cortés are thought to have originated as land-bridge islands and they have remained isolated from each other and from the adjacent mainland since the sea-level rise which followed the LGM. A total of 22 islands located in the Gulf of California and ranging from 0.3 to 1224 km² were included. Half of the islands are oceanic islands, while the other islands in the data set are land-bridge islands (Lawlor *et al.*, 2002). The distribution record of species on islands was based on Lawlor *et al.* (2002) and Álvarez-Castañeda & Ortega-Rubio (2003). Species recently extinct due to human activities were included in the data set (*Peromyscus guardia* on Granito and Mejia islands, and *Neotoma bunker* on Coronados) because these extinction events were not considered the natural result of community relaxation.

There are over 15,000 islands in Southeast Asia, making this island system the largest in the world (Heaney, 1986, 2000). A sample of 110 islands from the Sundaland and the Wallacean (Indonesia), the Philippines and the Australian biogeographical regions were included here. The geological history and palaeogeography of Southeast Asia is extremely complex, and a number of land-bridge connections occurred in the area during the LGM, although some land-bridge islands have been isolated for as long as *c.* 165,000 years (Heaney, 1984, 1986; Voris, 2000; Meijaard, 2003; Bird *et al.*, 2005). As an illustration of this complexity, of the 31 islands from the Philippines included in our data set, six were from the Palawan region. Based on a study of the mammalian fossil record in this region, Piper *et al.* (2011) concluded that the Palawan region was connected to the Asian mainland via Sundaland during the Middle Pleistocene. The remaining islands from the Philippines are all considered oceanic islands (i.e. they have never been connected to continental land masses). Similarly, most islands in Wallacea are considered oceanic islands, while Sundaland was connected to the Asian mainland during periods of low sea level in the Pleistocene (Voris, 2000). Species occurrences for this region were assembled from

several sources (Heaney, 1986; Corbet & Hill, 1992; Heaney *et al.*, 1998, 2010; Meijaard, 2003). Body mass data were obtained from Smith *et al.* (2003), using the 'insular' value whenever possible. When missing from this reference, we used other sources for body mass data (Silva & Downing, 1995; Myers *et al.*, 2006). The mass for *Sus ahoenobarbus* was assumed to be the same as the published mass for *Sus barbatus* because *S. ahoenobarbus* was considered a synonym of *S. barbatus* until recently (Lucchini *et al.*, 2005). Island area for this data set ranged from 5 to 7,659,861 km².

We used a least-squares linear regression on log(Area) and log(Mass) and a one-sample test of slope to test the hypothesis that the observed slope for the mass–area relationship in each of the four islands systems was not statistically different from 0.5. An analysis of covariance (ANCOVA) was then used to compare the slopes and the intercepts of the relationships calculated above for the four island groups. We also compared the slope of the regression lines across the four biogeographical regions of Southeast Asia (Sundaland and Wallacea in Indonesia, the Philippines and Australasia) using the same method. Lastly, we evaluated by Student's *t* mean comparison tests whether the inclusion of oceanic islands in some of the data sets had an effect on the slope of the regression line. All statistical analyses were performed in R v.2.9.2 (R Development Core Team, 2009).

RESULTS

The body mass of the heaviest species from each island in Japan ranged from 500 g (*Rattus norvegicus*) to 250 kg (*Ursus arctos*), a 500-fold range in body mass (Appendix S1 in Supporting Information). The range of maximal body mass of mammals in the western Mediterranean islands was smaller, ranging from 122 g (*Rattus rattus*) to 175 kg (*Cervus elaphus*). Mammals from the Sea of Cortés islands were even smaller, ranging from 16.5 g (*Chaetodipus intermedius*) to only 59 kg (*Odocoileus hemionus*). In Southeast Asia, the smallest mammal in the data set weighed 60 g (*Rattus exulans*) and the largest over 3000 kg (*Elephas maximus*).

The body mass of the heaviest species in the mammal fauna of each island increased with increasing island area in Japan, the Mediterranean islands, the Sea of Cortés islands and in Southeast Asia (Table 1, Fig. 2). For all these data sets, the slope was not significantly different from the predicted value of

Table 1 Results from linear models with log(maximum body mass) of mammals as the dependent variable and log(island area) as the independent variable, for all four island systems considered. The slope was not significantly different from 0.5 in any of these models.

	Regression statistics						Slope difference from 0.5	
	<i>n</i>	Intercept	Slope	<i>t</i>	<i>P</i>	<i>r</i> ²	<i>R</i>	<i>P</i>
Japan	14	0.31	0.47	3.66	0.003	0.53	−0.07	0.80
Mediterranean	45	−0.29	0.42	5.35	< 0.0001	0.40	−0.14	0.35
Sea of Cortés	22	−3.81	0.73	4.04	< 0.0001	0.45	0.27	0.22
Southeast Asia	110	−1.03	0.51	7.09	< 0.0001	0.31	0.01	0.90

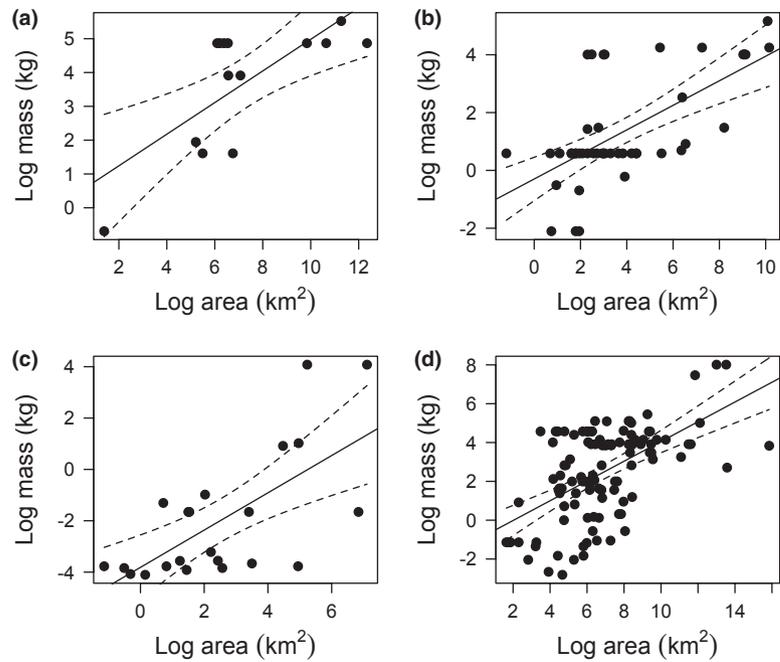


Figure 2 The power relationship between $\log(\text{body mass})$ (kg) of the largest mammal species identified from existing data and $\log(\text{area})$ (km^2) of islands in (a) the Japanese archipelago ($n = 14$), (b) the western Mediterranean islands ($n = 45$), (c) the Sea of Cortés ($n = 22$), and (d) Southeast Asia ($n = 110$). Maximal body mass increases with island area in all systems, with slopes of 0.47, 0.42, 0.72 and 0.53, respectively. The dotted lines represent the 95% confidence interval for each relationship.

0.5. An ANCOVA showed that the slope of the relationship between body mass and island area did not vary across the four biogeographical regions (all $P > 0.12$), although the intercepts were different across these regions (all $P < 0.005$) (Fig. 3).

Within Southeast Asia, the slope of the relationship between body mass and island area ranged from 0.52 in the Philippines

to 0.73 in Sundaland. However, an ANCOVA with biogeographical region as a factor indicated that there was no difference in the slope values within Southeast Asia (all $P < 0.5$). Similarly, the intercepts ranged from -4.77 in Australasia, to intermediate values in Wallacea and Sundaland (-2.32 and -1.82 , respectively), up to -1.07 in the Philippines. ANCOVA also indicated that these differences were not statistically significant (all $P > 0.15$).

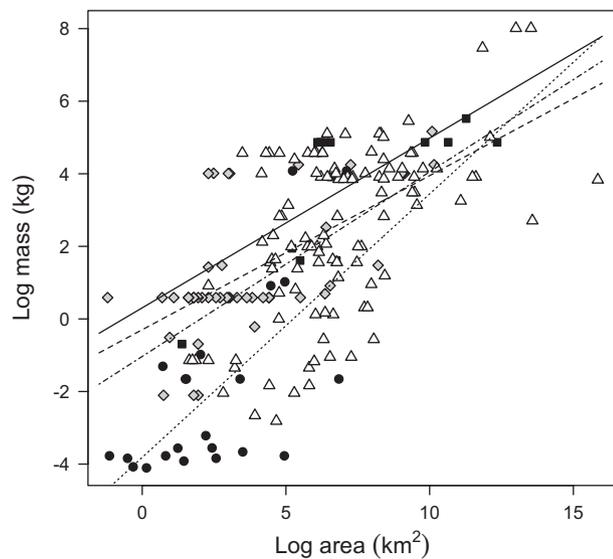


Figure 3 The power relationship between $\log(\text{body mass})$ (kg) of the largest mammal species identified from existing data and $\log(\text{area})$ (km^2) of islands in the Japanese archipelago (black squares and solid line; $n = 14$), the western Mediterranean (grey diamonds and dashed line; $n = 45$), the Sea of Cortés (black circles and dotted line; $n = 22$) and Southeast Asia (open triangles and dot-dash line; $n = 110$). None of the slopes differed from 0.5, but the intercepts of the relationship varied across the four island systems.

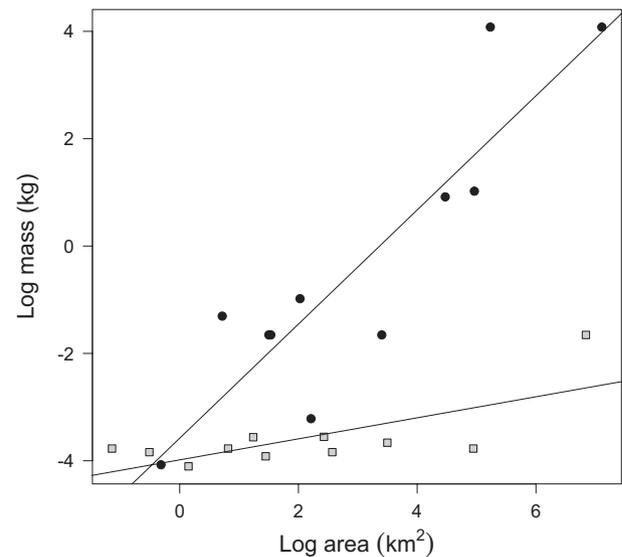


Figure 4 The power relationship between $\log(\text{body mass})$ (kg) of the largest mammal species identified from existing data and $\log(\text{area})$ (km^2) of islands in the Sea of Cortés for land-bridge islands (black circles) and oceanic island (grey squares). The slopes of the two regression lines are 1.06 ($t = 5.95$, $P = 0.0002$) and 0.19 ($t = 3.01$, $P = 0.01$), respectively.

The islands from the Palawan island group in the Philippine islands are land-bridge islands, while the remaining Philippine islands are all oceanic. The bearded pig, *Sus ahoenobarbus*, is the second largest species in our data set and occurs on all the six land-bridge islands. So on average, the maximum body mass was larger on land-bridge islands than on oceanic islands in the Philippines (average mass 96.67 kg and 8.97 kg on land-bridge and oceanic islands, respectively; $t = 5.37$, $P < 0.0001$).

For the Sea of Cortes islands, we found that on average, the mass of the largest species was greater on land-bridge islands than on oceanic islands (average mass 667.5 g and 27.7 g on land bridge and oceanic islands, respectively; $t = 3.84$, $P = 0.003$). More interestingly, the slope for oceanic islands (1.06) was larger than the slope for land-bridge islands (0.20) ($t = -4.66$, $P = 0.0002$). For a given island size, the mass of the heaviest species was greatest on land-bridge islands. However, this was only true for the largest islands because the intercepts for the two regression lines were not significantly different ($t = -0.64$, $P = 0.53$; Fig. 4).

DISCUSSION

Our results provide further empirical support for previous findings of a general maximal body mass–area relationship of $M_{\max} \propto \text{Area}^{0.5}$. The slopes of island mass–area relationships we report here correspond well to those observed over continental scales by Burness *et al.* (2001). Moreover, the slopes did not differ significantly across the island groups. This result in itself is suggestive of the generality of the processes operating to generate the island mass–area relationship (Kay *et al.*, 2005).

The theoretical explanation for a general relationship for a maximal body mass–area relationship of $M_{\max} \propto \text{Area}^{0.5}$ is not easily derived from simple rules of allometry (Peters, 1983; Brown, 1995; Marquet & Taper, 1998; Kelt & Van Vuren, 2001; Jetz *et al.*, 2004; Marquet *et al.*, 2005). More generally, however, the result supports the area-scaling hypothesis of Marquet & Taper (1998), which stresses the importance of individual energetic constraints. In their view, food and foraging requirements set a limit to the number of individuals that can be sustained per unit area (a minimum area requirement), which in turn limits local population density and thus influences the probability of the extinction of a species (Brown, 1995). Large species with large foraging requirements (large home ranges) will have low population densities (Damuth, 1993; Marquet & Taper, 1998) and thus a higher extinction probability (Griffen & Drake, 2009). The area-scaling hypothesis suggests therefore that the maximum body size will be area dependent (assuming equal productivity per unit area) as corroborated by the result presented here.

In addition, of particular interest is the speed with which the mass–area relationship observed here would seem to have been established following isolation at the end of the Late Pleistocene. The slope of the maximum body size–area relationship may have been adjusted by a process of community relaxation, evolutionary change in body size (Lomolino, 1985; Marquet &

Taper, 1998) or a combination of both. An evolutionary decrease in body size would permit a large species to reduce its energetic requirements (Marquet & Taper, 1998; McNab, 2002), resulting in a greater number of individuals per island and hence a lower extinction risk (Damuth, 1993). Dramatic decreases in size are well documented for large mammals on Quaternary islands, for example the Irish elk of Jersey (Lister, 1996), dwarf elephants in the Mediterranean region (Sondaar, 1977) or dwarf mammoths of northern Pacific islands (Vartanyan *et al.*, 1993; Guthrie, 2004). The reduction in body size would reflect the spatial constraints imposed by the island and a larger size reduction would be expected to occur on the smaller islands (Marquet & Taper, 1998; McNab, 2002; Millien, 2011). If such a scenario were to be repeated across a range of island sizes within an archipelago then a positive mass–area relationship would be expected. It is also known that evolutionary changes can occur at a greater rate on smaller islands (Millien, 2011). Yet, some of the best examples of evolutionary change on islands reveal that island dwarfs such as the elephants of Crete, the mammoth of Wrangel island or the pygmy hippopotamus of Cyprus – all now extinct – were still too large bodied for the island area they evolved on, under the model of $M_{\max} \propto \text{Area}^{0.5}$ (Burness *et al.*, 2001). Although probably a contributory factor, the evolutionary explanation alone is not sufficient to explain the empirical mass–area relationship described here.

Our understanding of the history of the island systems studied here would suggest that a rapid process of faunal relaxation which pre-dated the introduction of exotic species to Japan by humans is most likely. In Japan, the present mass–area relationship is almost certainly the result of many post-glacial extinctions that induced a shift from palaeocommunities dominated by large mammals (Artiodactyla, Perissodactyla) to modern communities dominated by small mammals (Rodentia, Insectivora and Lagomorpha; Millien-Parra & Jaeger, 1999). For example, 77% of the artiodactyl Quaternary fauna is absent from the modern fauna. The perissodactyls (*Rhinoceros*, *Dicerorhinus* and *Equus*), although present in the Middle and Late Pleistocene, all suffered extinction during the Holocene.

Similar Holocene extinctions in the Mediterranean islands have occurred, resulting in the replacement of the Holocene autochthonous fauna (e.g. the endemic genera *Megaloceros*, *Prolagus* or *Rhagamys*) by a modern fauna composed of introduced species from the European mainland. This faunal turnover has been largely attributed to the colonization of the Mediterranean islands by human populations (Cheylan, 1984; Vigne, 1987, 1992). Yet, a slope of 0.5 was still apparent in this highly disturbed system, making this pattern robust.

The region of the Gulf of California was less disturbed but has suffered the greatest number of recent extinctions in Mexico, probably due to the introduction of exotic species onto the islands by humans (Álvarez-Castañeda & Ortega-Rubio, 2003). The origin of the mammalian fauna is to be sought among mainland forms, via dispersal events from the Baja Peninsula or the Mexican mainland during low sea-level

events of the Pleistocene (Hafner *et al.*, 2001; Lawlor *et al.*, 2002). There is no evidence in the fossil record for the presence of larger mammals on the islands. However, the terrestrial fauna of the land-bridge islands in the Sea of Cortés was found to be significantly nested (Lawlor *et al.*, 2002). A nested distribution describes the situation whereby less rich insular assemblages show a significant tendency to be a subset of the species found on all other islands possessing a larger number of species (Patterson & Atmar, 1986). This pattern can be the signature of community relaxation towards a new dynamic equilibrium (Patterson & Atmar, 1986). Nested patterns are strongest for assemblages from land-bridge island archipelagos, but they have also been found for assemblages thought to be more strongly structured by colonization and dispersal (Patterson, 1990; Wright *et al.*, 1998; Ulrich *et al.*, 2009). Our results corroborate the hypothesis that the body size structure of mammalian communities can be the result of both selective colonization and community relaxation. Yet we found that within the Sea of Cortés islands, the body size of the largest mammal for a given island area was greater on land-bridge islands than on oceanic islands. This suggests that land-bridge islands represent an intermediate stage on the continuum of community sorting from an initial mainland assemblage to oceanic islands that would represent the theoretical end point on this continuum. According to our results, community filtering appears to be even stronger for oceanic islands (colonization and dispersal) than for land-bridge archipelagos (predominantly shaped by selective extinctions).

The mammal fauna of Southeast Asia is unique, with over 70% of the species being endemic (Heaney, 1986). Heaney (1986, 2000) estimated that extinctions occurred very rapidly following isolation in Indonesia and the Philippines, especially on young islands that became isolated following the sea-level rise, about 10,000 years ago. For example, as many as four different large mammal species (the carnivores *Cuon alpinus* and *Panthera tigris*, and the perissodactyls *Tapirus indicus* and *Rhinoceros sondaicus*) became extinct during the Late Pleistocene in Borneo (Louys *et al.*, 2007). In Java, as many as 14 large mammals became extinct since the Late Pleistocene, including the proboscideans *Stegodon trigonocephalus* and *Elephas hysudrindicus* (Louys *et al.*, 2007). There is no single cause identified for the extinction of large mammals on islands in Southeast Asia, and Louys *et al.* (2007) concluded the extinctions were probably due to a combination of different factors, including climate change and human disturbance. One exception may be seen in the survival on Flores of the pygmy stegodon, *Stegodon florensis* (van den Bergh *et al.*, 2001; Morwood *et al.*, 2004).

The consistent pattern found across various land masses world-wide in Burness *et al.* (2001) and for different sets of islands within the same archipelago reported here suggest that a relationship of $M_{\max} \propto \text{Area}^{0.5}$ is rather general. Further work is needed to align expectations from allometric theory with these data. Natural defaunation and community relaxation events represent an end state where the size of the largest mammal species found on each island today reflects the

interaction between energetic constraints, minimum viable population size and home range area. The post-isolation adjustments apparent in all four island mammal faunas examined here emphasize the importance of individual energetic constraints and suggest in particular their importance at a very general level in the generation of macroecological patterns (Brown, 1995; Gaston & Blackburn, 2000; Kay *et al.*, 2005).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 A list of the heaviest mammal species found on islands in Japan, the western Mediterranean, the Sea of Cortés and Southeast Asia, used to calculate body mass–area relationships.

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