

Niches, body sizes, and the disassembly of mammal communities on the Sunda Shelf islands

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The rising sea level at the end of the Pleistocene that created the islands of the Sunda Shelf in Indonesia and Malaysia provides a natural experiment in community disassembly and offers insights into the effects of body size and niches on abundance, distribution, and diversity. Since isolation, terrestrial mammal communities of these islands have been reduced by extinction, with virtually no offsetting colonization. We document three empirical patterns of disassembly, all of which are significantly different from null models of random assembly: (i) a diversity–area relationship: the number of taxa is strongly and positively correlated with island area; (ii) nested subset composition: species that occur on small islands tend to be subsets of more diverse communities inhabiting larger islands; and (iii) body size distributions: species of intermediate body sizes occur on the greatest number of islands, and smaller islands have smaller ranges of body sizes, caused by the absence of species of both very large and extremely small size. These patterns reveal the role of body size and other niche characteristics, such as habitat requirements and trophic status, in the differential susceptibility of taxa to extinction.

allometric scaling | assembly rules | extinction | habitat fragmentation | nested subsets

Traits of organisms determine the niches of species, and niches of species shape the composition of biota. The roles of traits and associated niches in influencing the abundance, distribution, and diversity of species are reflected in community assembly rules: empirical patterns of distribution and coexistence over space and time. Since Diamond's seminal article (ref. 1 and see also refs. 2–4), especially clear examples of assembly rules have been documented for islands and insular habitats, where breakup of large contiguous environments have resulted in reduced diversity and altered taxonomic composition in the isolated fragments (e.g., refs. 5–7).

Such cases of community disassembly typically show three kinds of nonrandom patterns indicative of underlying roles of niches. First, the fragments usually exhibit strong positive correlations between the number of taxa and habitat area. Such diversity–area relationships reflect the combined effects of total population size and ecological specialization on probability of extinction. Taxa with low abundances and specialized requirements are more susceptible to extinction and survive only in the largest fragments, whereas only the few most abundant generalist taxa persist in the smallest fragments (e.g., refs. 5 and 8–10).

Second, the taxonomic composition of the fragments often shows highly nested subset structure, in which the smaller number of taxa inhabiting successively smaller fragments tends to be subsets of the richer biotas of larger fragments. This pattern implies that each taxon requires some minimal area to support sufficient populations to resist extinction, and that it can occur in all fragments of greater than threshold area (e.g., refs. 6 and 11).

Third, the habitat fragments sometimes show distinctive distributions of body sizes, with successively smaller areas having fewer taxa of extreme size. These distributions imply that body size strongly influences traits of organisms and characteristics of niches, and these in turn influence probability of extinction (12, 13). Indeed, body size is probably the single trait of paramount ecological significance, because most characteristics of organisms vary

closely with size (14–17). Allometric equations or power laws of the form $Y = Y_0 M^b$ describe how a trait, Y , scales with body mass, M , where Y_0 is a normalization coefficient and b is the scaling exponent. In mammals, for example, (i) whole-organism metabolic rate or rate of food consumption scales as $M^{3/4}$ (18, 19); (ii) rates of biomass production and maximum population growth scale as $M^{-1/4}$ (14, 20, 21); (iii) lifespan, generation time, and fasting endurance time scale as $M^{1/4}$ (21); and (iv) population density scales as $M^{-3/4}$ (22). Thermal conductance, home range, speed of locomotion, and minimum and maximum prey size all also exhibit allometric scaling relations.

The nonvolant mammals inhabiting the islands of the continental Sunda Shelf, comprising most of the country of Indonesia and parts of Malaysia, provide an elegant “natural experiment” of the community disassembly process. Beginning at the end of the Pleistocene $\approx 11,000$ years ago, rising sea level caused by global warming and melting of ice sheets created these islands. Before sea-level rise, each island was part of the Asian mainland and had a typical continental mammal fauna. Since being isolated, each island has experienced selective extinctions of native mammal species with little subsequent colonization, because nonvolant mammals are poor over-water dispersers (23). The contemporary taxa inhabiting each island represent an assemblage that persisted and coexisted since the late Pleistocene. Here, we focus on three kinds of empirical assembly rules: diversity–area relationships, nested subset structures, and body size distributions. These are enduring legacies of the niche relationships that have shaped the composition of these biotas since the formation of the islands.

This disassembly process offers general insights into the impact of global climate change on the geographic distributions of species and on the effects of habitat fragmentation on the extinction of species. Characterizing the empirical rules for this case of community disassembly should contribute importantly to informing conservation management and policy in a context of global, regional, and local environmental change. In particular, this case of disassembly caused by natural processes of habitat fragmentation and isolation may hold important lessons for human-caused changes, offering insights into conservation on islands and other fragmented landscapes. Similar rules of disassembly may apply even though the changes in climate and sea level that occurred at the end of the Pleistocene were much greater than have occurred so far in the present episode of global warming.

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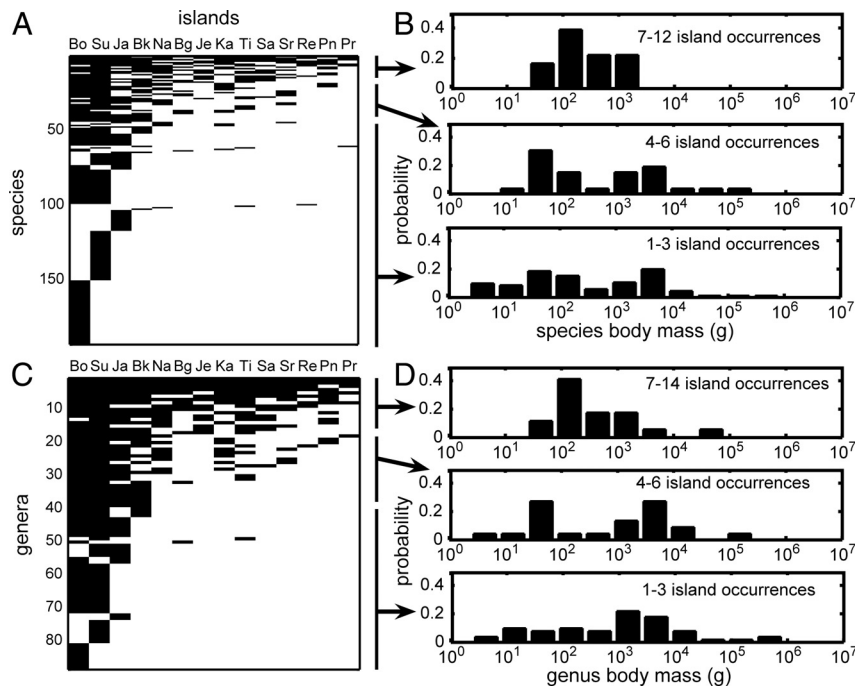


Fig. 2. The nested subset structure of the faunas of the Sunda Shelf islands as revealed by ordered presence–absence matrixes. (A and C) Presence–absence of taxa was ordered vertically by number of occurrences and horizontally by island area for species (A) and genera (C). (B and D) We plotted the associated body size distributions of species (B) and genera (D) having differing frequencies of islands occurrences. Each island and taxon is labeled by a code that references data in [Dataset S1](#). Bo, Borneo; Su, Sumatra; Ja, Java; Bk, Bangka; Na, Natuna Besar; Bg, Banggai; Je, Jemaja; Ka, Karimata Besar; Ti, Tioman; Sa, Siantan; Sr, Sirhassan; Re, Redang; Pn, Penebangan; Pr, Perhentian Besar.

More quantitatively, the maximum body size, M_{max} , for a given number of island occurrences, I , scales with I as $M_{max} \propto e^{-0.75I}$ ($R^2 = 0.73$) at the species level and as $M_{max} \propto e^{-0.56I}$ ($R^2 = 0.61$) at the genus level. The minimum body size for the species and genus level scales as $M_{min} \propto e^{0.44I}$ ($R^2 = 0.73$) and $M_{min} \propto e^{0.29I}$ ($R^2 = 0.49$), respectively. The scalings of extreme body sizes with the number of island occurrences intersect at intermediate body sizes of 437 and 418 g for species and genera, respectively.

Size–Area Relationship. As might be expected from the above patterns, the distributions of body sizes vary systematically with island area and species richness, such that smaller islands have fewer species of extreme size (Fig. 4 B and D). The size of the largest species and second-largest species decreases with decreasing island area as a power law with exponents of 0.56 and 0.62 ($R^2 = 0.74$ and 0.90), respectively. Likewise, the largest and second-largest genera scale with area with exponents of 0.55 and 0.60 ($R^2 = 0.73$ and 0.90), respectively. The smallest and second-smallest body sizes decrease with island area: exponents of -0.23 and -0.24 ($R^2 = 0.64$ and 0.88) and similarly for genera: exponents of -0.17 and -0.20 ($R^2 = 0.43$ and 0.89), respectively. Interestingly, however, the median body masses are relatively invariant with respect to area (e.g., the exponent for species is 0.11, not significantly different from zero, $P = 0.057$; the exponent for genera is 0.19, $P = 0.002$). Consequently, extrapolating the scaling relations for these median sizes and for the smallest and largest species and genera gives lines that converge between 102 and 248 g (except for the genus maximum size–area relationship and genus median size–area relationship, which intersect at 53 g).

We evaluated the statistical significance of these scaling relationships by drawing species at random without replacement from the source pool until each island had the empirically observed number of species and repeated this exercise 10,000 times to generate expected null distributions based on random assembly (following ref. 13). These tests reject the null hypoth-

eses for largest and second-largest species (all $P \ll 0.01$ for both slopes and intercepts). In contrast, the observed slopes for the smallest and second-smallest species body size scaling relations, -0.23 and -0.24 , are not significantly different from the null model based on random sampling (slopes of -0.14 and -0.16 , $P = 0.1089$ and 0.0654 for smallest and second-smallest, respectively). The observed intercepts are, however, significantly higher than the null intercepts, 90.5 and 224.0 g, compared with the null model's 25.6 and 61.8 g ($P = 0.0071$ and 0.0102).

Discussion

Disassembly Rules and Niches. The contemporary terrestrial mammal communities of the islands of the Sunda Shelf have been derived by selective extinctions of species. The roles of niches in this disassembly process are indicated by three nonrandom patterns of biodiversity.

Diversity–area relationship. More species and genera have gone extinct on small islands than large ones, resulting in highly significant power law diversity–area relationships with z -values of 0.23 and 0.19. Using Heaney's (23) species–area relationship for nonisolated areas on the mainland of the Malay Peninsula, we estimate that the largest islands of Borneo, Sumatra, and Java retained the majority (85%, 87%, and 52%, respectively) of their Pleistocene fauna, whereas the five smallest islands have lost ≈ 75 –88% of their species since their isolation. The areas of the islands vary by five orders of magnitude, from 8 to 743,244 km². Such large reductions in island area can cause decreased diversity not only directly through reductions in total abundance of widespread generalist species, but also indirectly through the complete loss of certain habitat types required by specialized species. For example, the large islands have large mountains with diverse high-elevation habitats and unique resources that are completely absent on the smallest islands. So the effect of island area on diversity reflects the combined effects of abundance, specialization, and other niche attributes on extinction.

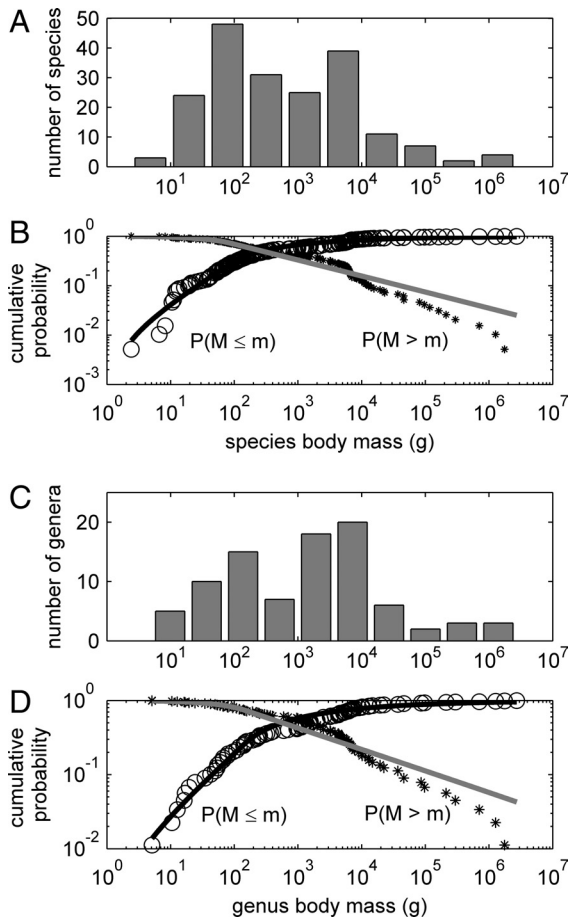


Fig. 3. Frequency distributions of body sizes of species and genera of the Sunda Shelf islands. (A and C) Log-binned histograms for species and genera comprising the entire pool of species occurring on all islands. (B and D) Cumulative frequency distributions for species and genera (circles and stars) and double power law fits to these distributions using maximum-likelihood estimation (bold and gray lines). Note that the cumulative distributions plot the proportion of species larger or smaller than a given body mass, resulting in curves that cross at the median size.

Nested subset composition. There is a strong tendency for species and genera inhabiting smaller islands with lower diversity to be subsets of taxa occurring on larger islands with more diverse faunas. This means that each taxon has a relatively deterministic threshold area requirement. Although it is possible *a posteriori* to estimate a minimal island size for each species and genus from Fig. 4 B and D, we cannot say what sets these thresholds without additional detailed information on the niches of the species and the ecology of the islands. Supertramps make up one group of taxa that are conspicuous deviations from nested subset structures (1). Examples of supertramps are bird species that are excellent over-water dispersers and tend to occur only on small islands with few other species. The absence of supertramp mammals is consistent with our assumption that the mammal faunas of the Sunda Shelf islands are derived primarily by extinction with minimal over-water dispersal. **Body size distributions.** Distributions of body sizes on the islands reveal two interrelated patterns. There is a triangular body size–incidence relationship (Fig. 4 A and C). The taxa that occur on only one or a few islands include the entire range of body sizes, from shrews weighing <10 g to elephants and rhinos weighing >1,000 kg. In contrast, the taxa that occur on the largest number of islands span a much narrower range, from 100 g to 1 kg. There is a complementary triangular body size–area relationship (Fig. 4 B and D). The entire range of body sizes is represented on the largest islands,

but the range becomes progressively more restricted on smaller islands. This trend is reflected in a significant decrease in the sizes of the largest and second-largest taxa and a consistent increase in the smallest and second-smallest taxa with decreasing island area. Interestingly, the median or modal size remains largely invariant with island area. The triangles in Fig. 4 depicting the body size–incidence and body size–area relations are closely coincident, converging to a similarly narrow range of 140 to 440 g for the highest incidence species and the smallest islands. We interpret these patterns to mean that a few species and genera in this special size range have generalist niches and high abundances, and these attributes have allowed the taxa to have the lowest extinction rates and hence to persist in the smallest areas and on the largest number of islands.

For the Sunda Shelf island fauna, the ecologies of the high incidence species and genera reveal the importance of niche breadth, habitat, and diet in the disassembly process. The 10 species with the highest number of island occurrences were *Maxomys surifer*, *Callosciurus notatus*, *Galeopterus variegatus*, *Macaca fascicularis*, *Tragulus javanicus*, *Rattus tiomanicus*, *Tupaia glis*, *Ratufa affinis*, *Petaurista petaurista*, and *Nycticebus coucang*. Six of these are arboreal (two are gliders), two are likely semiarboreal, and only two are surface-dwelling. At least seven have omnivorous diets. It is not surprising that arboreal, omnivorous mammals have low probabilities of extinction on islands where the predominant habitat is tropical forest. It is also not surprising that dietary specialists, especially carnivores, have lower incidences reflecting higher extinction probabilities and presumably lower population densities (see ref. 27).

Allometric Relationships. The body size–area relationship documented here for the restricted case of the Sunda Shelf islands is strikingly similar to that reported by Marquet and Taper (13) for mammals on continents, islands of the Sea of Cortéz, and American Southwest mountaintops. They observed that maximum body size decreases and minimum body size increases with decreasing landmass area, converging on a mass of 70–200 g on the smallest islands with only one terrestrial mammal species. This pattern can be readily understood from the perspective of allometry. In general, smaller mammals have lower resource requirements and thus can maintain higher population densities with lower probabilities of extinction. There is evidence, however, that the highest population densities and rates of population growth occur at intermediate body sizes of ≈ 100 g, rather than at the very smallest sizes (12, 28). A similar and undoubtedly related pattern is Foster's rule, the tendency of large mammals to evolve dwarf forms and small mammals to evolve giant forms when isolated on islands (29). So, there appear to be some traits unique to some intermediate-sized mammals that are reflected in their niches and expressed in high abundances, wide distributions, and evolutionary trajectories. Interestingly, the effect of body size on niche characteristics results in very different assembly rules for insular and continental mammal faunas. Local communities in nonisolated habitats on continents do not show the loss of extreme sizes and convergence toward an intermediate size as seen on islands; instead, the local communities tend to exhibit virtually the entire range of sizes found in the continent-wide pool (30, 31).

The scaling of ecologically relevant traits with body size provides a basis for exploring the disassembly rules more quantitatively and mechanistically. Here, we use the empirical ecological scaling relations reported above (see Introduction), to suggest more explicit mechanisms linking these traits, extinction probability, and body size–area relationships.

Maximum body size and extinction probability. The data show that the maximum body mass on an island (M_{\max}) increases with increasing area as approximately $M_{\max} \propto A^{1/2}$. If we assume: (i) average species population density or number of individuals per unit area, K , scales

areas required for persistence of species and genera. Selective extinctions of species are related to island area and body size, resulting in the distinctive body size–incidence and body size–area relationships. The patterns of disassembly on the Sunda Shelf are generally similar to those documented for other isolated landmasses. The role of niche attributes in conferring resistance to extinction and the resulting persistence of medium-sized taxa on very small islands have important implications for conservation, because habitat fragmentation is a major cause of endangerment.

Methods

We started by constructing a species list for the entire recent terrestrial, nonvolant mammal fauna of 14 well-surveyed islands. For all islands except Borneo, we used the species lists assembled by Heaney (23, 34), which we updated by incorporating more recent data on occurrences and taxonomy from Wilson and Reeder (35). For Borneo, we used Payne et al. (36) and Wilson and Reeder (35). Our list for each island includes both extant species and species that went extinct during historic times because of human impacts and excludes human-introduced species.

We constructed a database of body masses, using a single estimated value for each species. For the vast majority of species, we used the mean body mass or the average of male and female mean body masses from the “Macroecological database of mammalian body mass”, MOM Version 3.6.1 (37). For most of the species not found in MOM, we used the midpoints of the body mass range given in *Walker's Mammals of the World* (38). Additional data were compiled from Payne et al. (36), Alderton (39), and Wilson and Reeder (35). For the few species for which we were unable to find any published measurement of body mass, we used either: (i) the geometric mean of the body masses of extant congeneric species, because body sizes of congeners tend to be very similar (40) or (ii) when masses of congeneric species could not be found, taxon-specific allometries to estimate body mass from available body length data (following ref. 41). For genus-level analyses we used the geometric mean body masses of the congeneric species in our database.

Ideally we would have used direct data on the body mass of each population on each island, but such data are simply not available. Fortunately, the effects of

insular body size evolution are small and intraspecific variation among islands is usually less than interspecific variation. L. Heaney (personal communication) suggests that intraspecific variability is at most comparable to that documented for the tri-colored squirrel (26). This idea is similar to the finding of Lomolino (29) that extant insular populations deviate from their closest relatives on continents by at most a factor of 2–3 or ± 0.50 log units. Given the 10^6 range in body masses across all species and the 10^2 to 10^3 range in extreme body masses, we are confident that our results are robust to the small effect of insular body size evolution.

We ordered the species and genus presence–absence matrices by area and number of island occurrences. The nested subset temperature of each matrix was calculated by using the algorithm and program of Rodriguez-Girones and Santamaria (ref. 42, but see ref. 43), an improvement over the original, seminal works of Patterson and Atmar (6, 44). We calculated *P* values based on three different null models, including the original null model of Atmar and Patterson (44). The calculations were based on 10,000 randomized matrices.

We used ordinary least-squares regression on log-transformed data to characterize diversity–area, size–area, and size–incidence relationships. All regression models had approximately normally distributed residuals.

We developed a null model similar to Marquet and Taper's (13) to evaluate the null hypothesis that the scaling of extreme body masses can be accounted for simply by randomly sampling from the source pool consisting of all species inhabiting Sunda Shelf islands. For each island, we drew at random and without replacement the number of species occurring on the island and recorded their associated body masses. Expected null values of scaling exponents and normalization coefficients were estimated by fitting regressions to these data. This procedure was repeated 10,000 times, producing expected distributions of parameters for the null model, and allowing one-sided tests of the null hypothesis with associated *P* values.

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