

of deeper-level, higher-temperature fluids, resulted in gypsum replacement and later stages of silicification, carbonatization and  $K_2O$  enrichment. Where the chert caps remained intact, the formation of additional crack-seal veins may have accompanied these metasomatic events.

The results of this study indicate that these distinctive Archaean alteration zones formed initially through a complex sequence of surface and near-surface low-temperature processes. Later metasomatism and metamorphism also played a major role in their final character. Studies of this and other flow-top alteration zones may provide important clues to Archaean water and atmospheric chemistry, surface and subsurface hydrologic systems, and the relationships among volcanism, subsidence and sedimentation in greenstone belts.

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## Body size, ecological dominance and Cope's rule

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**We present data and analyses demonstrating that large species utilize a disproportionately large share of the resources within local ecosystems. Even though small species tend to have higher local population densities, these are not sufficient to compensate for their lower rates of energy use per individual. The relationship is very general; holding for example for birds, mammals, fish and plants. We suggest that several ecological advantages enable larger species and larger individuals within species to monopolize resources, and that the resulting selection pressures are responsible for the evolutionary trend towards increasing body size seen in many phyletic lineages. Our results contradict important studies<sup>1-4</sup> that have concluded that species of small body size use at least as large a proportion of the resources within ecosystems as their larger relatives.**

A goal of community ecology is to understand the patterns and processes that determine the numbers and variety of coexisting species. Are there general rules that characterize the contributions of the different species to the structure and dynamics

of ecosystems? One measure of the ecological importance of species is their relative utilization of energy and transfer of materials<sup>5,6</sup>. Within groups of taxonomically-related, ecologically similar organisms, two variables (individual body size and population density) are of primary importance in determining how energy and other limiting resources are allocated. Large individuals demand more from environmental resource pools than small ones, but also tend to occur at lower population densities. The question, then, is to what extent the greater abundance of small species compensates for their lower resource requirements per individual.

Although direct measurements of energy flow per unit area are probably not available for all species in any community, these rates can be estimated quite accurately from data on population density ( $D$ ), individual body mass ( $M$ ) in animals and photosynthetic cover ( $C$ ) in plants. In animals the average daily energy use of a free-living individual ( $U$ ) scales allometrically as approximately  $M^{0.67}$  (refs 7, 10), so total energy use per species ( $E$ ) is given as  $E = DU = DM^{0.67}$ . In plants, variation in photosynthetic rate per unit leaf surface among species is insignificant compared to the total leaf surface<sup>11,12</sup>, so the energy use of each species is directly proportional to its vegetative cover ( $C$ ).

We analysed data on  $D$  and  $M$  for local groups of birds, mammals and fish, and on  $C$  for communities of plants to determine how rates of energy use per species ( $E$ ) varies with body size. Using the results of 39 censuses of breeding land birds and data on species body mass<sup>13</sup>, we tried three different methods<sup>14</sup> to fit a linear relationship for  $\log D$  with  $\log M$  (Table 1). Depending on the method, only 3 to 10 of the 39 slopes were  $\leq -0.67$ . Pooling the data gave a slope of approximately  $-0.30$ , not greatly different from the value of  $-0.19$  reported by Peters<sup>2</sup>. If  $D$  scales as  $M^{-0.30}$  and  $U$  scales as  $M^{0.67}$ , then the rate of energy intake per species ( $E = DU$ ) increases with body mass, scaling as  $\sim M^{0.37}$ . Because the three methods of estimating slopes give comparable results, in the following analyses we present only the results of the regression method applied to log-transformed data.

For the nine species of granivorous rodents (mammals) in a Chihuahuan Desert ecosystem<sup>15</sup>, regression of  $\log D$  on  $\log M$  gave a significant positive relationship ( $r = 0.56$ , slope [ $b$ ] = 1.17,  $n = 9$ ,  $P = 0.05$ ). Consequently, in these mammals the rate of energy flow per species ( $E = DU$ ) scales positively with body mass as  $\sim M^{1.17} \times M^{0.67} = M^{1.84}$ .

We analysed three independent data sets<sup>16-18</sup> on population densities and body masses of marine fish (Table 2). The slopes of regressions of  $\log D$  on  $\log M$  averaged near zero, and only one was more negative than  $-0.1$ . Thus, if  $D$  scales as  $\sim M^{0.0}$  and  $U$  scales as  $M^{0.67}$ , then the average rate of energy use per species ( $E = DU$ ) must vary as  $\sim M^{0.67}$ .

We obtained complete census data for perennial plants in five different habitats in two desert regions<sup>19,20</sup>. Total cover ( $C$ ) of each species was used to estimate its contribution to energy flow, and cover divided by population density ( $D$ ) was taken as the effective size of an individual plant. When we regressed  $\log C$  against  $\log (C/D)$ , all the slopes were positive, with values ranging from 0.53 to 1.59 and averaging  $\sim 1.0$  (Table 3). Although the usefulness of estimating individual mass in perennial plants containing nonliving woody tissue is questionable,  $M$  should vary with individual surface area as  $\sim (C/D)^{1.5}$  and rate of energy use per species ( $E$ ) should scale as  $> M^{1.0}$ .

Our analyses show that in four different taxonomic groups (birds, mammals, fish and plants) species comprising large individuals account for most of the energy flow and resource use within local ecosystems. These results contradict those of two influential recent studies. Damuth<sup>1</sup> claimed that population densities of mammals scale as  $M^{-0.75}$ , so that rates of energy use per species are essentially independent of body size ( $E$  scales as  $\sim M^{0.0}$ ). Peters<sup>2-4</sup> compiled data which suggest that population density ( $D$ ) often scales as  $M^{-1.0}$  so that energy use per

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**Table 1** Slopes of log population density and log body mass<sup>13</sup> for land birds in different habitats

Habitat	log data	log normal data		Correlation coefficient	No. of species	
	regression	regression	RMA			
Savanna	-0.53	-0.64	-1.11	-0.40	17	
Grassland	0.19	-0.18	1.36	0.45	19	
Deciduous forest	1.08	2.47	7.29	0.48	15	
Managed forest	-0.05	-0.25	-1.40	-0.04	35	
Douglas fir	-0.90	-1.03	-1.93	-0.57	21	
Clearcut forest	-0.31	-0.99	-2.86	-0.26	15	
Ponderosa pine	-0.18	-0.18	-0.32	-0.26	21	
Logged ponderosa	{ -0.44	-0.57	-0.60	-0.47	22	
	{ -0.31	-0.33	-0.44	-0.39	23	
	{ -0.04	-0.07	-0.10	-0.06	19	
Clearcut forest	-0.72	-0.18	-0.12	-0.50	6	
Spruce	{ -0.41	-0.20	-0.20	-0.25	16	
	{ -0.51	-0.17	-0.09	-0.34	21	
Spruce/jackpine	-0.58	-0.31	-0.37	-0.32	22	
Spruce forest edge	-0.60	-0.32	-0.21	-0.35	12	
Spruce/jackpine edge	-0.59	-0.35	-0.44	-0.31	21	
Spruce riparian	-0.50	-0.46	-0.40	-0.24	18	
Beech/maple	{ -0.37	-1.34	-1.62	-0.41	29	
	{ -0.37	-1.51	-1.23	-0.51	24	
Urban woodlot	{ 0.39	0.73	5.15	0.36	20	
	{ 0.17	1.73	-0.28	0.20	17	
Pine/oak seral	-0.18	-0.15	-0.51	-0.09	23	
Pine/oak mature	-0.67	-0.66	-2.32	-0.31	23	
Cove forest	-0.17	-0.14	-0.35	-0.11	31	
Hemlock/deciduous	-0.63	-0.33	-0.28	-0.45	26	
Chestnut oak	-0.36	-0.13	-0.13	-0.23	32	
Red oak	-0.31	-0.10	-0.09	-0.29	25	
Pine heathland	-0.57	-0.13	-0.09	-0.39	14	
Gray beech	-0.08	-0.17	-0.20	-0.06	13	
Spruce/fir	{ early	-1.05	-5.68	-5.14	-0.35	11
	{ middle	-0.34	-4.37	-4.34	-0.25	10
	{ late	0.10	-0.24	0.34	0.07	14
	{ climax	-0.37	-0.60	-0.54	-0.23	15
Grassland	-0.01	-0.13	-0.26	-0.01	13	
Brushland	-0.49	-0.27	-0.24	-0.40	14	
Savanna	0.02	-0.11	0.56	0.01	14	
Shrubland	0.03	-0.31	1.22	0.02	15	
Aspen	-0.11	-0.02	-0.01	-0.13	28	
Savanna	-0.17	-0.44	-1.34	-0.11	12	
Pooled data	-0.30	-0.12	-0.40	-0.27	197	

Three methods of calculation were used: linear regression on log-transformed data, linear regression and reduced major axis (RMA) fitted to log-normally distributed data<sup>14</sup>. Note that only 3-10 slopes were < -0.67.

These 39 censuses were taken from the published literature; the references are available from the authors on request.

**Table 2** Regression analyses of log population density on log body mass for fish

Habitat	Slope	Standard error	Intercept	Correlation coefficient	No. of species
Caribbean coral reef <sup>16</sup>	-0.05	0.08	0.76	-0.08	53
Gulf of California tide pool <sup>17</sup>	0.04	0.22	2.26	0.04	25
Newport Bay, California <sup>15</sup>					
bag seine	-0.08	0.36	1.18	-0.05	27
seine/bay	0.32	0.65	1.22	0.12	19
seine/shallows	-0.07	0.98	1.96	-0.03	8
drop net	-0.48	0.35	0.89	-0.37	14
enclosure	0.24	0.46	1.11	0.25	6
otter trawl	0.16	0.12	0.60	0.22	35
gill net	-0.03	0.26	0.88	-0.03	22

Note that none of the slopes are more negative than -0.50.

species should scale negatively with body mass (as  $M^{-0.33}$ ). The results of Damuth and Peters can probably be attributed to a sampling bias inherent in their data collection procedures. Their analyses are based on published values of population densities for species from different, scattered localities. These data probably neglect the numerous rare species of small body size that occur within local ecosystems, because ecologists tend to study

conspicuous and abundant species. We have been careful to avoid this and other possible biases by using only complete censuses of local biotas.

We have calculated the slopes of allometric equations to reveal differences between our results and those of Damuth and Peters. However, the low correlation coefficients of our regressions suggest that no allometric equation adequately characterizes the

**Table 3** Regression analyses of log cover on log (cover/population density) for perennial plants in five different habitats in two desert regions of southwestern North America

Habitat	Slope	Standard error	Intercept	Correlation coefficient	No. of species
Sonoran Desert <sup>19</sup>					
Goldeneye	0.55	0.18	0.91	0.53	27
Agave	0.53	0.14	0.67	0.56	33
Mojave Desert <sup>20</sup>					
Shadscale	1.32	0.26	3.40	0.76	21
Bladder-sage	1.25	0.17	3.19	0.87	19
Spiny menodora	1.59	0.13	4.36	0.93	23

Note that all the slopes are greater than 0.50.

relationship between population density and body size. Our qualitative result that on average small species use proportionally less energy than large ones can be corroborated using a robust nonparametric technique. We divide the species in a census into those above and below the median body mass for species in that census. Then if population energy use ( $E$ ) is on average greater for larger than for smaller species, then  $\bar{E}_s < \bar{E}_l$ , where  $\bar{E}$  represents mean energy use of the smaller (s) and larger (l) species. For animals in which individual energy use scales as  $M^{0.67}$ , we can substitute  $\bar{D}\bar{M}^{0.67}$  for  $\bar{E}$ , so  $\bar{D}_s\bar{M}_s^{0.67} < \bar{D}_l\bar{M}_l^{0.67}$ . Because the probability that any one census obeys this relationship by chance is 0.5, whenever we have a sufficient number of censuses we can use a binomial test to evaluate the hypothesis that the collection of censuses exhibits the expected pattern. For the bird censuses in Table 1, 35 out of 39 showed the predicted relationship (one-tailed test,  $p < 0.0001$ ).

We have shown that on a per species basis, within trophic levels and taxonomic groups, organisms of large individual size account for most of the energy flow through local ecosystems. This has important ecological and evolutionary implications. There are several ecological advantages of large body size. Large species are usually dominant in interspecific aggression<sup>21</sup>, which may result in exclusion of small species from preferred resources; they tend to have more efficient homeostatic mechanisms and greater mobility<sup>2,8,10</sup>, so they are able to tolerate a wider range of environmental conditions and to seek out more favourable locations. An increase in size enables an individual to spend less energy per unit biomass on maintenance and to become more efficient at extracting usable energy from low-quality foods<sup>2,22</sup>. Consequently, the same amount of available energy can support a greater biomass of a large species than of a small one. Finally, size may be important in avoiding predators<sup>23</sup>. Our data suggest that these advantages enable large species to dominate the resource allocation in ecosystems, leaving smaller species to divide up the remainder.

The ecological consequences of body size provide a mechanistic explanation for the evolutionary cycle known as Cope's rule<sup>23,24</sup>. Phylogenetic lineages usually begin with relatively small organisms that give rise to larger forms. Ultimately giant forms are produced, but these frequently become extinct, creating new opportunities for another lineage as it in turn evolves organisms of larger size. Presumably the ecological advantage of monopolizing resources provides the selective pressure that promotes evolution of greater size. Individuals of large size are favoured by intraspecific natural selection, because they can dominate resource use and consequently leave more offspring than their smaller relatives. However, this increase in body size is accompanied by a higher probability of extinction, which may be attributed to lower population density, smaller population size, slower population growth and perhaps other factors<sup>23,24</sup>. Thus Cope's rule is the result of two opposing evolutionary processes, one operating at the level of individuals within populations, and the other at the level of species within ecosystems<sup>25</sup>.

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## Mach bands are phase dependent

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The prevailing explanation of Mach bands, the paradoxical bands of light and dark seen where luminance gradients meet plateaux, is that they are due to lateral inhibition in the visual system<sup>1-4</sup>. This explanation equates Mach bands with distortions in a processed luminance distribution due to selective attenuation of low frequency components. But square waveforms exhibit no Mach bands<sup>2,5,6</sup>, although they should also be distorted after processing. Measurements of the contrast required to see Mach bands in trapezoidal waveforms and manipulations of their spectra lead us to conclude that phase relationships between Fourier components are important to the structure we perceive. A model based on the odd and even symmetry of visual receptive fields explains our results.