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OPINION

Haldane's God and the honoured beetles: The cost of a quip

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Haldane's God

God must be crazy – crazy about beetles! Why else should He create a beetle in every four of the species He gave life to on the earth! – thus wondered Haldane. Of the estimated 1.82 million species described so far[1], about 400,000 species are beetles. This relative abundance of beetle species apparently prompted Haldane to quip about the nature of the Creator: **God must have an inordinate fondness for beetles.** The meaning of this statement, the veracity of its attribution to Haldane (versus Huxely) and the circumstances that led Haldane to utter these words have all been thoroughly thesesed and have served staple for several writers[2–4]. Pages have been written examining whether Haldane's quip was 'inordinate fondness for beetles' or 'special preference for beetles'[2,5]. In fact there is an inordinate fondness among biologists to quote Haldane's quip. In the process the fascinating diversity of the beetles has been eulogized.

Often the most celebrated statements such as this by Haldane that get established due to the authority commanded by their authors, stand as strong and opaque barriers between our beliefs and the reality. This is especially true if these statements are personal opinions inferred from hard facts and not the laws that can be falsified. While the facts on which the opinion rests, offer quite a strength to the statement, the authority of the owner of the statement shields the inferences drawn such that the quip lives longer than its utility and conveys a different meaning than is probably implied by the facts. Haldane's quip on the nature of God appears to be one such statement that is strongly perpetuating an yet untested and possibly a dubious belief about beetles that they possess an 'unparalled diversity'[2]. It is indeed surprising and unfortunate that, in the process of 'tracing the history of this canonical one liner'[2], the most important implication of the quip for the biologists has been sidelined. As it is said, the silence serves as a sign of unspoken approval; and in this sense the silence of the biologists has also contributed to the perpetuation of this belief. The fact is that it is not known if the beetles exhibit an unparalleled diversity compared to other insects or organisms. Consider, for instance, the following alternate interpretation of the same facts.

The other God

God must be crazy and crazy about redundancy of life He created. Why else should He create a beetle in every four of the species He gave life to on the earth! While the 400,000 species of beetles fall into a mere 138 groups (families), 125,000 flies (Diptera) fall into almost equal number of (115) families: the butterflies and moths that constitute less than half the number of species of beetles (about 150,000) fall into about 108 different groups (families; Table 1). Thus there are more species in any family of beetles than in that of flies or of butterflies. Since each family constitutes a group of species that share a common set of features different from other families, there must be many more species of beetles that are almost similar among themselves than are flies or butterflies. In other words, there appears to be a lot of redundancy in His creation of beetles than in other groups. God seems to have run out of ideas to inject diversity while creating beetles.

Diversity versus redundancy

Thus two contrasting opinions may be derived from the same facts: one suggesting that beetles are more diverse and the other suggesting that they exhibit a lot of redundancy. But Haldane's quip is perpetuating the first of these alternate interpretations and it is imperative that we assess the two alternatives seriously.

In fact Haldane's quip could not have emerged had he thought that God was fond of abundance and redundancy. After all, sand particles are more abundant than beetles and Haldane did not say that God has an inordinate fondness for sand particles (though he is supposed to have stated God's fondness for stars too.) Apparently Haldane equated the number of species with the variety among beetles. Supporting this view, for

Table 1. Number of species and families in different orders of insects

Order	Species/order* (India)	Species/order** (World)	Families/order† (World)
Embioptera	33	200	7
Protura	20	260	3
Strepsiptera	8	300	5
Mecoptera	15	350	7
Diplura	16	355	4
Thysanura	23	1250	5
Dermaptera	320	1800	5
Isoptera	300	2000	6
Siphonaptera	52	2000	7
Mantodea	161	2000	6
Plecoptera	113	2100	8
Ephemeroptera	94	2146	12
Phasmida	60	2500	
Psocoptera	85	2500	27
Phthiraptera	400	3000	16
Blattria	156	4200	
Neuroptera	315	5000	17
Collembola	200	5000	5
Odanata	491	5500	24
Thysanoptera	691	6000	5
Trichoptera	812	7000	25
Orthoptera	759	14491	15
Hemiptera	6500	80000	102
Diptera	6093	96600	115
Hymenoptera	5000	100000	71
Lepidoptera	13000	142500	108
Coleoptera	15000	350000	138

*From Ghosh[17].
**From Ghosh[17], but the values used in the text are from Gould[2] and Romoser[18].
†Compiled by Viraktamath from Meckerrsas[19].

Table 2. Body length variations* in different orders and their relative range ratios expressed as the proportion of their range with that in Coleoptera

Order	Range in the body length min.–max. (mm)	Range (mm)	Relative ratios†
Ephimeroptera	2–25	23	0.18
Odonata	20–135	115	0.93
Phasmida	15–180	165	1.33
Orthoptera	4–75	71	0.57
Mantodea	–100	–	–
Blattaria	3–51	48	0.39
Isoptera	6–110	104	0.84
Dermaptera	4–30	26	0.21
Hemiptera	1–100	99	0.798
Homoptera	2–150	148	1.19
Diptera	1–70	69	0.55
Lepidoptera**	1–250	249	2.00
Hymenoptera	1–40	39	0.31
Coleoptera	1–125	124	1.00

*Ranges of the body length of different orders were compiled from Borror *et al.*[20].
**The range refers to wing spread and not to body length.
†The relative ratios represent the ratio of range of the order to that of the Coleoptera.

example, Gould[2] states: '... our world is incredibly strange and therefore supremely fascinating (the key point ... behind Haldane's quip that ultimate meaning must reside in the unparalleled diversity of group that rarely rivets our attention)...'.

Though more frequently Haldane's quip is described to represent his awe at the incredibly large number of species of beetles, the message perpetuated is that Haldane was awed by the 'unparalleled diversity' that he thought, this group exhibits. In fact in the recent past after the invention of the term 'biodiversity' and its equation with the number of species, there is a greater danger that Haldane's quip would be equated to mean that beetles, to be precise, the **Coleoptera are more diverse.**

Are beetles more diverse?

Are beetles really more diverse than other groups of insects? Is their diversity proportional to the number of species in them? In the context of Haldane's quip, does the high number of species in Coleoptera mean that there is more fascination in them than in other groups of organisms? Unfortunately the literature in biodiversity abounds with the suggestions that more the species more the diversity. The well-known formulations to estimate diversity are so constructed that the value of the estimate increases with the species numbers – a necessary relation that has outlived its utility. It is only recently that this view has been found inadequate and suggestions are being made that while measuring biological diversity, the species should not be viewed merely as statistical equivalents[6,7]. It has been argued that the number of species of a sample *per se* does not represent its biological diversity; rather, any estimate of biological diversity has to essentially incorporate the total biological variation existing in the sample.

For example, consider two independent samples of beetles each having 100 species. Assume that one of them has all the one hundred species belonging to only one family and the other sample has its 100 species from 10 different families. Obviously, despite the similarity in the species richness between the two samples, the second sample is biologically more diverse than the first. The second sample has high biological diversity because of the variation in morphological features associated with the different families represented in it. Thus the biological diversity of a group or order depends not only on the number of species in it but also on the extent of diversity they exhibit in the morphological and other biological features.

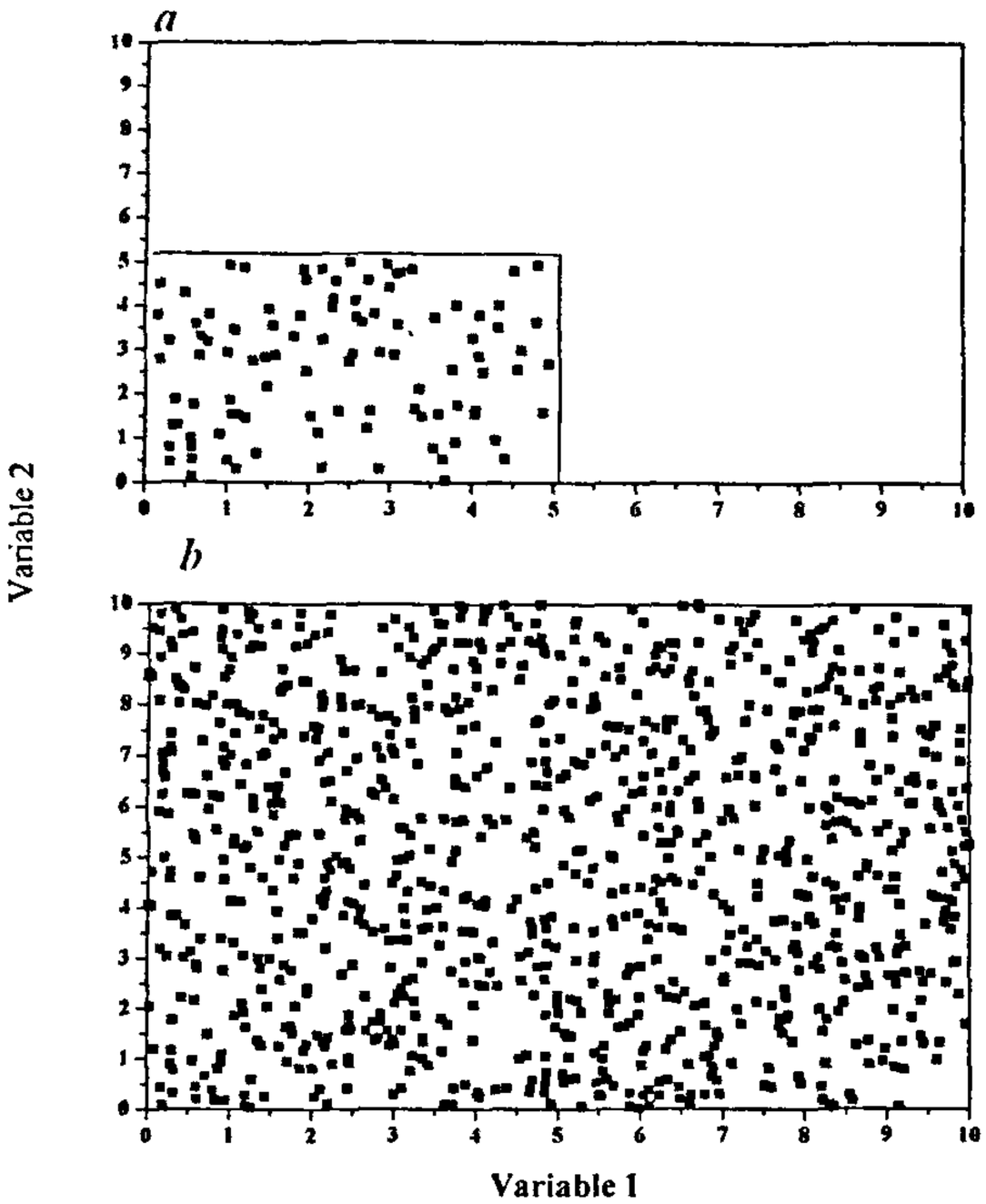

Figure 1. The morphospaces of different sizes of two orders (*a*) and (*b*), with same density of species. The total biological diversity of the order with large morphospace (*b*) is higher than the one with smaller morphospace (*a*).

Further, the morphological diversity of orders need not be a linear function of the number of species in them as argued below.

Morphospaces and diversity of orders

Taxonomy is hierarchical in that a given specimen is assigned to a species or genus or family based on hierarchically increasing set of morphological features. Accordingly, all the species can be arranged in a multidimensional space defined by the morphological traits used in the classification of the group. For simplicity assume two such dimensions defining the morphospace of an order in which all its species are distributed. The number of species accommodated in the order increases due to any of the following two factors:

Increased morphospace. Consider two orders with different sizes of their morphospaces[8]. Given the same density of species in the morphospaces, the larger among the two would contain more species and exhibits more biological diversity than the smaller (Figure 1 *a* and *b*). In other words, both the number and biological diversity increase with increase in the size of the morphospace. Consequently, in such situations, the biological diversity of different orders increases linearly with their species numbers; an order with less number of species can be expected to have relatively less diversity compared to those with many species.

Dense packing of species in the morphospace. Number of species in an order can also increase with the density with which the species are packed in the morphaspace (Figure 2 *a* and *b*). Keeping the size of the morphospace constant (i.e. diversity space being constant) an order can contain more species due to relatively denser packing. Such a process obviously does not yield a strong relationship between the number of species and biological diversity; in fact this relation could plateau after a certain density.

Thus, a given order can have more species either due to increase in the size of the morphospace or due to dense packing of the species in it (or both). While the former leads to an increase in the total morphological diversity of the order, the latter leads to more redundancy among the species of an order; in fact in the latter, the diversity does not increase in proportion to the number of species and hence it is important to analyse the processes by which the Coleoptera as an order has more number of species.

But it is difficult to examine the first alternative because the variables that define the morphospace of Coleoptera could be entirely different from those that define the morphospace of the Diptera or Lepidoptera or any other order; the scales and the dimensions are not always comparable[9].

Nevertheless, certain generalizations can be conveniently reached and these might help in assessing the possibilities. Though number of species of beetles and weevils are more, it does not seem that they are extraordinarily large or small in their size. In fact on the basis of the length of the insects, Phasmida, Homoptera, Odonata and Lepidoptera (on wing spread) show more variation than the beetles and weevils (Table 1). There is also no data suggesting that beetles occur in extraordinarily different habitats that are not occupied by the members of the other orders at least not to the extent that their numbers represent. While these *per se* do not rule out the possibility of wider morphological diversity of beetles, as of yet there are no specific morphological structures identified in beetles that are unusually wider in range and diversity that could be listed as features enhancing their morphospace. If anything there appears to be a frustration in finding a common factor that explains their diversity: 'The basic characters of Coleoptera suggest no obvious reason for the remarkable success of this particular insect pattern'[9,10].

Since comparing morphospaces across orders is difficult, we can resort to treating the number of families in an order as a proxy for the morphological diversity[11]. As argued earlier, family represents a group of species that share

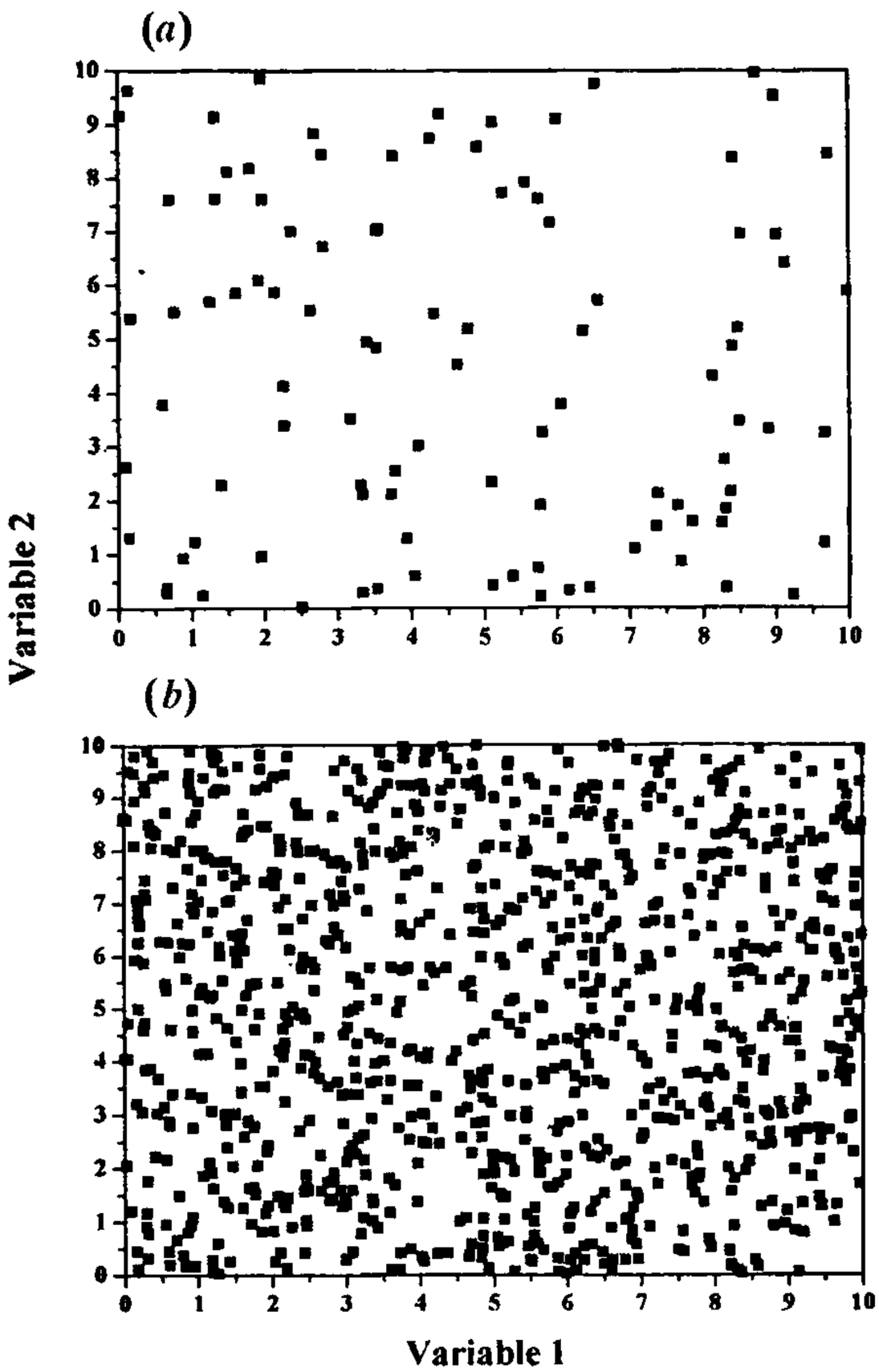

Figure 2. Morphospaces of same size but with different densities of the species in them. The morphospace with less density (*a*) shall have less number of species than the one with high density (*b*). Note that the total biological variation would be same for two orders. Coleoptera has more number of species mostly due to such high density of species in the morphospace.

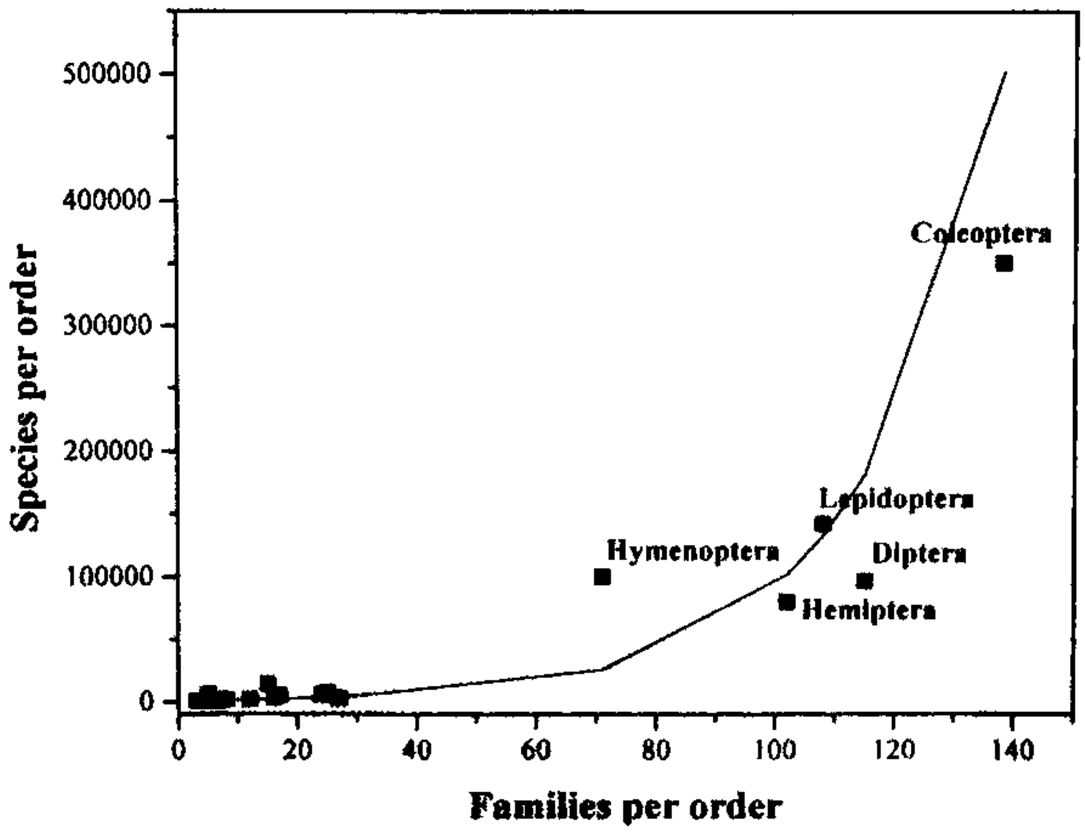

Figure 3. Relation between the number of species in an order and the number of families in it. Note that Coleoptera has proportionately more number of species than the number of families in it. In other words, beetles are more packed in their morphospace.

common traits but are different from those belonging to other families within the order and in this sense the morphological diversity can be considered to increase with the number of families. Accordingly, Coleoptera does have more families (138) than Diptera (115) and Lepidoptera (108). However, as argued earlier, note that the number of families are far less in comparison to the relatively vast number of species in Coleoptera: These 138 families accommodate 400,000 species of beetles while almost the same number of families in Diptera (115) contain only 125,000 species. In other words, though Coleoptera appear to have a wider morphological space, the diversity reflected by the number of species in it appears greatly overstated. Also it appears that one significant reason for the increased number of beetle species is their dense packing in the morphospace. This is also supported by the relation between the number of species per order and the number of families per order (Figure 3). Especially for Lepidoptera, Diptera and Coleoptera, the slope of the relation between the number of species per order with the number of families increases steeply; i.e., the rate or density of species per family is higher for Coleoptera than other orders.

This has another interesting and deleterious consequence to the belief that beetles are more diverse: Diversity can be defined as the *probability and the extent* to which any two randomly chosen species from a pool are different[7]. The dense packing of the beetles compared to other orders (say Diptera) suggests that any two randomly-chosen species in Coleoptera are likely to be more similar among themselves than two randomly-chosen species of Diptera. In other words, the *extent* to which the randomly chosen species differ, would be less for beetles than for flies or moths or butterflies for example. Beetles thus seem more redundant in their morphology than thought.

How densely could the species be packed in a morphospace?

Density of species cannot indiscriminately increase in a morphospace. Any two species need to be isolated by a minimum threshold of the morphospace such that they maintain their reproduc-

tive identity and reduce the extent of interspecific competition between them. Hutchinson[12] and other workers following him suggested that sympatric species exhibit such limiting similarities[13,14]. For example a number of workers found that the ratio of the morphological features of the larger to the smaller of any two coexisting species is 1:1.3 (refs 12–15). If such a ratio does exist and if it is constant across the taxa, then assuming that any available niche in the morphospace is always filled and that the extinction of the species is random across the taxa, all the orders are expected to exhibit an equal density of packing. However, it is not clear if the ratio is consistent across the taxa. It is also not clear if these ratios would depend on the biology and morphology of the species. Several studies have shown that these ratios are not consistent and hence no specific limits are suggested[16]. The relative differences in the packing of insects of different orders are probably suggestive of differences in such ratios among taxa. Accordingly, beetles seem to have the lower range of such threshold for isolation ratios. In fact one family, Curculionidae is known to contain almost 30% of the species of Coleoptera and hence could suggest the lowest range for such thresholds.

There is no immediate data to test this, and it would be interesting to examine if beetles and weevils indeed have lower Hutchinson ratios than other insects and organisms. If that be true, it leaves us with another special and probably a more fascinating question about beetles than their mere dominance in numbers of species: **What special biology of beetles renders them more tolerant for coexistence?** It is likely that their tolerance to coexist would be true not only among themselves but probably also with other organisms.

In any case, it appears that our fascination for beetles does not die even if their diversity is overstated by their species numbers. Rather they seem to become more enigmatic with respect to their yet unknown biological features that make them abundant in species numbers. By shifting the issue from Haldane's awe about the richness of the beetles to **Why are there more species of beetles** we only have gone one long circle to agree with Haldane that **God has an inordinate fondness for tickling us.** This time He has chosen beetles to tickle us with! We shall enjoy this tickling of course.

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