

resource inventory in the transportation network also to increase as it awaits metabolization. Equating the rate of flow through the inventory volume to the rate of flow through the metabolizing volume provides a relation determining the scaling behaviour of the metabolization rate. Thus, if a three-dimensional metabolizing system contains two volumes, one,  $V_M$ , within which metabolization of resources occurs, and one,  $V_I$ , within which the resource is inventoried, and if these volumes are sequentially connected and the resource is incompressible and conserved, then  $V_M/\tau = V_I/T$ , where  $\tau$  is the residence time of resource in the metabolizing volume, and  $T$  is the residence time of the resource in inventory. The metabolic rate is  $B \propto V_M/\tau$ .

If metabolization occurs in small volumes,  $V_{met}$ , of fixed size, then  $V_M \propto V_{met}(L/l)^3$ , where  $l$  is the average spacing between metabolizing volumes. The inventoried resource for each metabolizing volume  $V_{met}$  is distributed in a queue that extends across the length of the system  $L$ , with  $L/l$  units of inventory volume  $V_I$  earmarked for each volume  $V_{met}$ . If  $V_I$  is independent of  $L$  (which would be expected in systems where the rate-limiting process was metabolization rather than transport), then  $T/\tau$  is proportional to  $L/l$  (that is, the ratio of average velocities  $U/u$  in the two volumes  $V_I$  and  $V_M$  is independent of  $L$ ). The total inventory volume then scales as  $V_I \propto (L/l)^4$  (that is,  $l \propto L^{1/4}$ ), so that  $L/l \propto V_I^{1/4}$ , and metabolic rate is given by  $B \propto V_I^{3/4}/\tau$ .

Three-quarter-power scaling of total metabolic rate as a function of system size follows under the additional assumptions<sup>1</sup> that  $V_I$  ('blood' volume) is proportional to system ('whole animal') volume (or mass), and that  $\tau$  is independent of system size. It is worth noting that, in the geometric argument presented here, the distribution of metabolic units,  $V_{met}$ , is taken to be uniform for purposes of counting, but the actual spacing can be highly non-uniform without affecting the overall scaling argument.

If allometric scaling of the kind found for animals has almost universal applicability to resource distribution systems, as suggested by Banavar *et al.*<sup>1</sup>, it ought to apply to rivers, an application they consider. Consider the particular case of sediment transport in rivers, in which the metabolic rate of a drainage basin of area  $A$  is the rate at which sediment is delivered by the trunk stream to the lower end of the drainage basin. An analogue of blood volume  $V_I$  is the total sediment volume in transport,  $V_{sed}(L/l)^2(T/\tau)$ , where  $V_{sed}$  is the volume of sediment delivered from hillslopes to stream channels from a small hillslope area  $l^2$  during time  $\tau$ , and  $T$  is the residence time of such sediment in the channel system of drainage basin  $A$  with linear dimension  $L$ .

However, in fluvial systems there is no

apparent basis for assuming that the velocity ratio  $U/u$  is independent of  $A$ . It is also difficult to identify a fluvial analogue of the constraint<sup>1</sup> that blood volume is proportional to animal volume. One difference between rivers and organisms in this regard is that, in rivers, sediment can be easily stored laterally and vertically in flood plains. Flood plains, lying outside the channels themselves, occupy a third volume representing a kind of long-term storage. Such 'loss' of sediment between hillslope and river mouth can be a significant effect<sup>4</sup> in fluvial sediment budgets. The relation equating rates of flow in inventory and metabolizing volumes is valid only if there is no third volume for storing resources. Models of the kind proposed by Banavar *et al.*<sup>1</sup> for biological organisms do not appear to be sufficient for deriving scaling relations for river (sediment) metabolism; such models potentially apply only to distribution of an incompressible resource in a system with 'two-volume' geometry.

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*Banavar et al. reply* — The idea behind our theorem<sup>1</sup> is simple. It can be illustrated by using airline travel as an example. Consider a stream of people (blood) leaving London (heart) at a steady rate and fanning out to all parts of the world (body). The number of people leaving London each day and arriving elsewhere at their final destinations (metabolic rate) is denoted by  $B$ . Assuming that the people travel along a locally connected network and that the transit time for each local hop is the same (say, 1 day), the number of people in transit at any given time (blood volume) is proportional to  $B$ , but with a proportionality constant that is given by the mean number of hops from all the destination cities to London.

This additional factor arises because if, for example, there are  $P$  people who arrive in, say, Paris (let us assume Paris is two hops from London — London–Brussels–Paris) each day, there are  $2P$  passengers in transit at any given time whose final destination is Paris ( $P$  of them are en route from London to Brussels and the other  $P$  are travelling from Brussels to Paris). In a  $D$ -dimensional space, if  $B$  scales as  $L^D$ , our theorem asserts that because the mean number of hops must itself scale at least as  $L$ , the total number of people in transit must scale at least as  $L^{D+1}$ .

Haff points out the difference between the scaling properties of water flow and sediment transport in rivers and that river sediments can be stored in flood plains. Although water flow at a given point is proportional to the area of the sub-basin draining into it, the sediment discharge is

not, because the source of sediments is not uniform in space, unlike the rainfall in landscape-forming events<sup>5</sup>. Rather, sediment production is scattered in space and time, and not isochrone with the main transport mechanisms in the network. In fluvial systems, scaling networks are stationary structures derived from the evolutionary dynamics of the topography of landscapes<sup>6</sup>.

Painter's exercise of the parallelepiped, showing that the mean number of hops from the origin,  $\langle L_x \rangle$ , is proportional to  $L$  is in accord with our theorem. Painter assumes that the blood in the network is proportional to the number of links — or, by analogy, that the total number of people in transit is proportional to the number of operating flights — but this assumption is wrong because there are many more people crammed into flights originating from London than in those from cities distant from London. The number of flights is indeed proportional to the number of destinations and the metabolic rate  $B$ . The branching network in Painter's last paragraph is a Cayley tree which, for large enough sizes, cannot exist in any finite-dimensional space. The observation that in an  $N$ -site Cayley tree the average distance from the origin scales as  $\ln N$ , which is what would be expected for a  $D$ -dimensional lattice in the infinite  $D$  limit, agrees with our theorem.

We do not believe that fractal-like networks effectively endow life with an additional fourth dimension<sup>3</sup>. Allometric scaling comes built in with any system in which the flow is directed and the circulation time is proportional to circulation length, irrespective of size<sup>1</sup>. The fact that nature, in spite of her extreme diversity, exhibits allometric scaling to the extent she does in plants, animals and river networks suggests that optimality associated with directedness is quite common.

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