Optimal Form of Branching Supply and Collection Networks

Peter Sheridan Dodds*

*Department of Mathematics and Statistics, Center for Complex Systems,
and the Vermont Advanced Computing Center, University of Vermont, Burlington, Vermont 05401, USA*
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For the problem of efficiently supplying material to a spatial region from a single source, we present a simple scaling argument based on branching network volume minimization that identifies limits to the scaling of sink density. We discuss implications for two fundamental and unresolved problems in organismal biology and geomorphology: how basal metabolism scales with body size for homeotherms and the scaling of drainage basin shape on eroding landscapes.

In both natural and man-made systems, branching networks universally facilitate the essential task of supplying material from a central source to a widely distributed sink population. Branching networks also underlie the complementary process of collecting material from many sources at a single sink. Such networks typically exhibit structural self-similarity over many orders of magnitude: river networks drain continents [1–3], arterial and venal networks move blood between the macroscopic heart and microscopic capillaries [4], and trees and plants orient leaves in space taking on the roles of both structure and transportation.

We address the following questions regarding supply networks. (1) What is the minimum network volume required to continually supply material from a source to a population of sinks in some spatial region Ω? (2) How does this optimal solution scale if Ω is rescaled allometrically? (For convenience, we use the language of distribution, i.e., a single source supplying many sinks.) Our approach is inspired by that of Banavar *et al.* [5,6] who sought to derive scaling properties of optimal transportation networks in isometrically growing regions based on a flow rate argument; Banavar *et al.*'s approach followed the seminal work of West *et al.* [7] who suggested supply networks were key to understanding the metabolic limitations of organisms, and focused on network impedance minimization (see [8,9]). In contrast to this previous work, our treatment is explicitly geometric. We also accommodate four other key features: the ambient dimension, allometrically growing regions, variable sink density, and varying speed of material transportation.

We consider the problem of network supply for a general class of d-dimensional spatial regions in a $D \geq d$ dimensional space. Each region Ω has volume V and overall dimensions $L_1 \times L_2 \times \cdots \times L_d$ [see Fig. 1(a)]. We allow these length scales to scale as $L_i \propto V^{\gamma_i}$, creating families of allometrically similar regions. For isometric growth, all dimensions scale uniformly meaning $\gamma_i = 1/d$, while for allometric growth, we must have at least one of the $\{\gamma_i\}$ being different. For the general case of allometry, we

choose an ordering of $\{\gamma_i\}$ such that the length scales are arranged from most dominant to least dominant: $\gamma_{\max} = \gamma_1 \geq \cdots \geq \gamma_d$.

We assume that isolated sinks are located throughout a contiguous spatial region Ω (volume V) which contains a single source located at $\vec{x} = \vec{0}$. We allow sink density to follow $\rho \sim \rho_0(V)(1 + a\|\vec{x}\|)^{-\zeta}$ where a is fixed, $\zeta \geq 0$, and $\|\vec{x}\|$ is the distance from the source. When the exponent $\zeta = 0$, ρ is constant throughout the region (as for capillaries in organisms), but remains a function of the region's
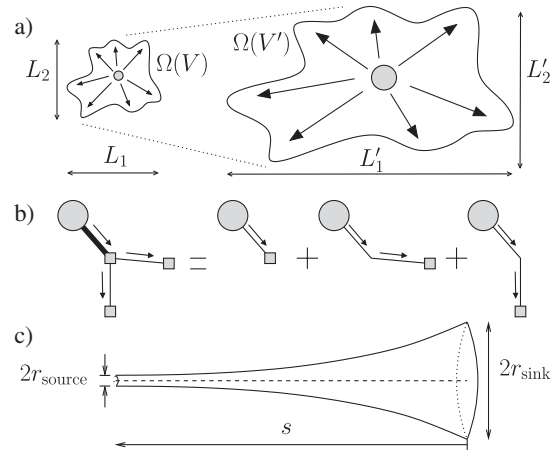

FIG. 1. (a) We consider families of d-dimensional spatial regions that scale allometrically with $L_i \propto V^{\gamma_i}$, and exist in a D-dimensional space where $D \geq d$. For the $d = D = 2$ example shown, $\gamma_{\max} = \gamma_1 > \gamma_2$, and L_1 grows faster than L_2. We require that each spatial region is star-convex, i.e., from at least one point all other points are directly observable, and the single source must be located at any one of these central points. (b) Distribution (or collection) networks can be thought of as a superposition of virtual vessels. In the example shown, the source (circle) supplies material to the three sinks (squares). (c) Allowing virtual vessels to expand as they move away from the source captures a potential decrease in speed in material flow. For scaling of branching network form to be affected, the radius r of a virtual vessel must scale with vessel length s (measured from the sink) as $s^{-\epsilon}$.

overall volume V. While decreasing sink density ($\zeta > 0$) does not reflect the reality of biological organisms, it is not an unreasonable postulate for other supply collection systems, and may be of use in modeling transportation to and from cities. Last, we assume each sink draws approximately the same amount of material from the source per unit time. The material traveling from the source to a specific sink takes up a certain volume of the network, and while this volume of material may not be coherent away from the sink, we can nevertheless imagine separate "virtual vessels" transporting material from the source to the sinks [see Fig. 1(b)]. (Only in the smallest, outer branches will virtual vessels coincide with physical vessels.) Material flow rate will then vary according to changes in the cross sections of these vessels.

We take the cross-sectional area of these virtual vessels to be bounded by a fixed upper limit at the sink [see Fig. 1(c)]. We allow that material speed may increase with proximity to the source, meaning these virtual vessels may taper. If the radius decreases as $r_{\text{sink}}(1 + cs)^{-\epsilon}$, where s is the length of the vessel as measured from the sink and c is a constant, then the volume of a virtual vessel grows as $v_{\text{vessel}} \sim s^{1-2\epsilon}$ for $0 \leq \epsilon < 1/2$ and $v_{\text{vessel}} \sim s^0$ for $\epsilon \geq 1/2$ (we can therefore focus on $\epsilon = 1/2$ to represent the latter case). We ignore all other possible taperings since only an algebraic decay relationship between vessel radius and length will affect the scaling of overall network volume V_{net}. If, however, there is a minimum virtual vessel radius (i.e., a limit to material speed) then vessel volume must grow linearly with length: $v_{\text{vessel}} \sim s^1$.

The overall network volume V_{net} is the sum of all virtual vessel volumes, and is evidently minimized when virtual vessels travel directly from the source to each sink—the extreme case of a star network. While real, large-scale distribution networks are branched, many examples are close to this limit in terms of path length [10]. Minimal network volume therefore grows as

$$\min V_{\text{net}} \propto \int_{\Omega_{d,D}(V)} \rho_0 (1 + a\|\vec{x}\|)^{-\zeta} \|\vec{x}\|^{1-2\epsilon} d\vec{x}, \quad (1)$$

where $0 \leq \epsilon \leq 1/2$, and we have indicated a spatial region Ω scaled to have volume V by $\Omega_{d,D}(V)$. The integral's leading order behavior gives the optimal scaling of V_{net} with V:

$$\min V_{\text{net}} \sim \rho_0 V^{1+\gamma_{\max}(1-2\epsilon-\zeta)}, \quad (2)$$

where again $\rho_0 = \rho_0(V)$. When $\epsilon \geq 1/2$, $\min V_{\text{net}} \sim \rho_0 V^{1-\zeta\gamma_{\max}}$. The scaling of minimal network volume with V is thus governed by sink density ρ, vessel scaling, and the dominant length scale through $\gamma_{\max}$, and we first address the role of the latter. Since for isometric scaling, $\gamma_{\max} = 1/d$, whereas for allometric scaling, $\gamma_{\max} > 1/d$, we immediately see that from a scaling perspective, isometrically growing regions require less network volume than allometrically growing ones, and are in this sense

more efficiently supplied. Efficiency also increases with the dimension d since network volume scales more closely with overall volume ($\gamma_{\max} = 1/d$ decreases). Furthermore, shapes that scale allometrically effectively function as lower-dimensional, isometrically scaling objects and are therefore less efficiently supplied (the equivalent spatial dimension is $1/\gamma_{\max}$).

We see from Eq. (2) that network volume straightforwardly increases linearly with ρ_0. How ρ_0 in turn scales with V depends on the specific system, and, in particular, on whether $D = d$ or $D > d$. We now specialize our general result for the two cases of blood networks and river networks.

Blood networks [$D = d = 3$].—If material is costly, as in the case of blood, then we expect that isometric scaling ($\gamma_{\max} = 1/d$) to be attained by evolution. We take $\zeta = 0$ because capillaries (the sinks) are distributed relatively uniformly. Furthermore, since blood velocity in both the aorta and in capillaries changes little with V during resting states [7,11], we have $\epsilon = 0$. Lastly, it is well observed that the volume of blood scales linearly with organismal volume [12], $V_{\text{net}} \propto V$. (In general, for $D = d$, we must have $V_{\text{net}} \propto V$ as otherwise we would have the nonsensical limits of $V_{\text{net}}/V \to 0$ or ∞ as $V \to \infty$.) Since we already have that $V_{\text{net}} \propto \rho_0 V^{1+1/d}$, the additional constraint $V_{\text{net}} \propto V$ means sink density must decrease as volume increases: $\rho_0 \propto V^{-1/d}$, where ρ_0 for resting organisms now refers to the effective or active sink density (organisms at rest have a substantial proportion of inactive capillaries that are called into use during higher rates of overall activity [13]).

It follows that P_{rest}, the average rate of energy use in a resting state (basal power), which is proportional to the number of active sinks in Ω, can at best scale as $P_{\text{rest}} = \rho V \propto V^{-1/d} V \propto M^{(d-1)/d}$, where we have assumed that V scales as body mass M. For three-dimensional organisms, we therefore have

$$P_{\text{rest}} \propto M^{2/3}. \quad (3)$$

If organism shapes obey instead an allometric scaling then power scales more slowly as $P_{\text{rest}} \propto M^{1-\gamma_{\max}}$ with $\gamma_{\max} > 1/3$, contrary to McMahon's theory of elastic similarity [14].

We note that in detail, blood networks do not appear to have universal forms [15], showing substantial variation in branching structure across and within species; we therefore argue that it is only the system level that matters and that branching networks need only approximate star networks.

Crucially, the scaling law of Eq. (3) balances with the standard one based on organismal surface area S. For homeothermic organisms, who must constantly balance heat loss to maintain a steady internal temperature, we have that $P_{\text{rest}} \propto S$ (due primarily to radiation but also convection [16]). For isometrically scaling organisms, $S \propto M^{2/3}$, and this is well supported empirically [12]. Moreover, it is easy to show that only isometrically grow-

ing shapes balance P_{rest} since the $(d-1)$-dimensional surface area of a growing region Ω scales as $V^{1-\gamma_{min}}$, and therefore $\gamma_{max} = \gamma_{min} = 1/d$. Thus, the most efficient network in terms of minimal volume is also the one that precisely balances radiative heat loss.

Our seemingly reasonable result, which was empirically observed over a century ago by Rubner [17], runs counter to nearly 80 years of reports that $P_{rest} \propto M^{3/4}$. Kleiber [18] first suggested the exponent might be 3/4 in the 1930s after measuring a value of 0.76 for 13 mammals (his practical reason for choosing 3/4 was to simplify slide rule calculations [19]). In the decades following, a general but not universal consensus on a "3/4-law of metabolism" was reached [7,20,21]. The issue remains controversial both theoretically [8,22–24] and empirically: some recent statistical analyses have shown that a 2/3 exponent is well supported by large data sets for warm-blooded organisms (both birds and mammals) [8,25–27] while others have found evidence in favor of a 3/4 exponent or no simple scaling relationship [8,28–31]; and for cold-blooded organisms, plants, and invertebrates, a much broader range of exponent values has been measured empirically and predicted from theory [32–35].

Perhaps the most important aspect of the 2/3 versus 3/4 debate is that, from an optimization point of view, the lower the scaling of resting metabolism the better. A scaling of $M^{3/4}$ (or any power exceeding 2/3) would point to either a fundamental scaling limitation for warm-blooded organisms or to the existence of a cost other than volume minimization, such as impedance [7]. Where a higher exponent would be desirable is in the scaling of maximal power P_{max}, which is unsustainable and depends on stored energy, and indeed, P_{max} scales almost linearly with mass [33].

River networks $[D = 3 > d = 2]$.—The patterns of large-scale river networks have long drawn scientific interest, naturally from hydrologists and geomorphologists [1,2], but also from statistical physicists seeking evidence of universality in nature [36–39]. In our framework, river networks are collection systems: water flows from many sources (channel heads [40]) to a single sink, the outlet of the network's main stream. The description of river network geometry has often focused on Hack's law [41] which relates the area a of a drainage basin to the length l of its longest stream: $l \propto a^h$. Various studies of small-scale basins, starting with Hack's initial work [2,41], have suggested that the "Hack exponent" h exceeds 1/2, indicating an anomalous allometric scaling of basin shape wherein large basins are relatively long and thin compared to smaller ones (provided that the longest stream exhibits no or sufficiently weak fractality). Indeed, for sufficiently small, homogeneous landscapes, there may be a universal value of $h > 1/2$, yet to be fully understood theoretically [36,38,39,42]. However, the most comprehensive data sets robustly show that $h = 1/2$ for large-scale networks; in

particular, Montgomery and Dietrich [40] found that over 12 orders of magnitude variation in basin area, $l \propto a^{0.49}$ (their data set mixed both Euclidean overall basin length L and main stream length l; generally, $l \propto L^\beta$ with β very close to, if not equal to, unity).

The empirical observation that $h = 1/2$ accords with our result that with respect to network volume minimization, isometrically growing regions are most efficient; with our optimality argument, this becomes a stronger statement than appealing only to dimensional analysis.

Beyond isometry, we have the scaling of network volume to consider. We now take ρ_0 to be constant and again set $\zeta = 0$, meaning we assume that, when averaged over time, rain falls approximately uniformly across a landscape. We also assume $\epsilon = 0$ for the continental-scale networks we examine below. In contrast to the case of cardiovascular networks, the constraint that network volume must scale as overall volume (or basin area a) cannot apply to river networks, since Eq. (2) now gives $V_{net} \propto \rho_0 V^{1+1/d} \propto V^{3/2} = a^{3/2}$. The reason is simple: river networks lie on a $d = 2$ dimensional surface embedded in $D = 3$ dimensions, and the presence of a third dimension allows the total water in the network to grow faster than if the embedding dimension was $D = 2$.

In Fig. 2 we show that V_{net} scales as $a^{3/2}$ for four continental-scale networks: the Mississippi, the Amazon, the Congo, and the Nile [43]. The scaling holds over 6 and 10 orders of magnitude in area and network volume, respectively, indicating that self-similar drainage basins most efficiently drain large-scale landscapes.

While we have argued that the optimal scaling corresponds to the case of $h = 1/2$, we can directly see this connection arising from known scaling laws of river networks [36,37]. As put forward in [39], network volume
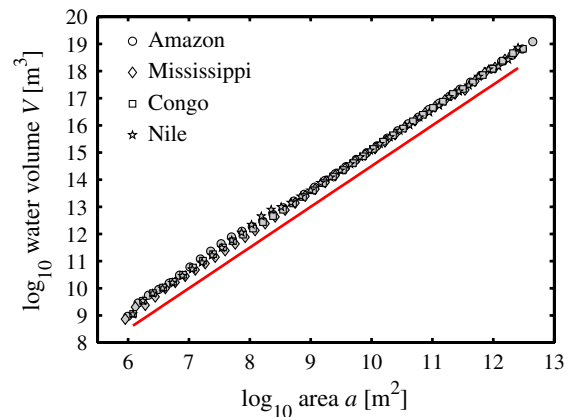

FIG. 2 (color online).   The scaling of network volume versus basin area for four continental-scale river networks. The solid line indicates a scaling of 3/2. Network volume is estimated for an idealized steady-state, uniform rainfall condition normalized such that $V_{net} = \sum_{ij} a_{ij}$, where a_{ij} is the area of the basin draining into the ijth cell on a coarse-grained version of a landscape, and the data are binned in log space [5].

scales with basin area as $V_{net} \propto a^{1+h}$, showing that for the optimal case, we indeed have $h = 1/2$.

We acknowledge that a stronger optimization may be at work for eroding landscapes. In particular, previous theoretical analyses suggest that in terms of energy minimization, landscapes may reach local, dynamically accessible minima [38,39], though sufficient self-averaging inherent in larger landscapes may render such minima indistinguishable from the global one. Nevertheless, our argument and data analysis show that for large-scale networks on heterogeneous landscapes, far exceeding the typical correlation length for precipitation events, a kind of optimal volume minimization is achieved.

With suitable modifications, our findings may be found relevant to other systems, in particular to plants (when seen as two connected branching networks), as well as to the scaling limits of episodic movement such as the transportation of people in and out of city centers. (Assuming constant flow as we do here, then a decay of sink density with $\zeta = 1$ follows for growing cities where transportation remains unchanged with city size.) While we have demonstrated that empirical evidence supports a geometric optimality for two kinds of large-scale natural branching networks, not all systems will be optimal or may be optimized. For example, if allometric scaling of organismal shape is demanded by some other constraints (e.g., due to the effects of gravity), then blood volume will be forced to obey a poorer scaling with overall volume [9].

*peter.dodds@uvm.edu

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