



Scaling of Differentiation in Networks: Nervous Systems, Organisms, Ant Colonies, Ecosystems, Businesses, Universities, Cities, Electronic Circuits, and Legos

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(Received on 10 September 2001, Accepted in revised form on 25 April 2002)

Nodes in networks are often of different types, and in this sense networks are differentiated. Here we examine the relationship between network differentiation and network size in networks under economic or natural selective pressure, such as electronic circuits (networks of electronic components), Legos[™] (networks of Lego[™] pieces), businesses (networks of employees), universities (networks of faculty), organisms (networks of cells), ant colonies (networks of ants), and nervous systems (networks of neurons). For each of these we find that (i) differentiation increases with network size, and (ii) the relationship is consistent with a power law. These results are explained by a hypothesis that, because nodes are costly to build and maintain in such “selected networks”, network size is optimized, and from this the power-law relationship may be derived. The scaling exponent depends on the particular kind of network, and is determined by the degree to which nodes are used in a combinatorial fashion to carry out network-level functions. We find that networks under natural selection (organisms, ant colonies, and nervous systems) have much higher combinatorial abilities than the networks for which human ingenuity is involved (electronic circuits, Legos, businesses, and universities). A distinct but related optimization hypothesis may be used to explain scaling of differentiation in competitive networks (networks where the nodes themselves, rather than the entire network, are under selective pressure) such as ecosystems (networks of organisms).

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1. Introduction

While there is a considerable literature studying the scaling properties of network *connectivity* [e.g. see the literature springing from the papers by Watts & Strogatz (1997) and Barabási & Albert (1999), and also Changizi (2001a)], there

has been comparably little attention given to one of the most important features of networks: that nodes within networks come in different types. Our main purpose is to examine the relationship between network differentiation (i.e. the number of node types) and network size (i.e. the total number of nodes) among those kinds of network that are under selective pressure, whether it be economic or natural selection. We call such networks *selected networks*. Consider two general relationships one might *a priori* expect. The first is that there is a finite set of node

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types—a universal language—from which any network of that kind may be built, and thus differentiation does not increase as a function of network size. For example, every digital circuit, no matter its size or function, can be constructed from just two types of node (an AND gate and a NOT gate). Thus, differentiation need not increase as a function of network size for digital circuits. The second possible relationship is that there is no universal language, and, instead, larger networks tend to have more node types. As we will see below, it is this latter possibility which appears to hold for a wide variety of selected networks.

2. Hypothesis and Mathematical Preliminaries

In this section, we present a hypothesis concerning the relationship between differentiation and size in selected networks, and also introduce mathematical tools for understanding the scaling relationships.

2.1. THE INEQUALITY RELATING COMPLEXITY E AND SIZE N

Employees in a business (a network of employees) interact for the purpose of doing something for the business. And cells in an organism (a network of cells) interact to implement some useful function for the organism. More generally, nodes in a (selected) network interact in order to carry out functions for the network. We will call such functions *expressions*: expressions are a group of nodes that implement some network-level function. Let the *expression length*, L , be the average number of nodes involved in an expression for a given network. Figure 1 illustrates a simple network with $N = 18$ nodes in all (edges not shown). There are three node types: circles, squares, and triangles. Nodes interact in groups of three—i.e. expressions are of length $L = 3$. There are six expressions instantiated in the network— e_1, \dots, e_6 —as shown by the six dotted-line rectangular groupings. The number of distinct expression types is $E = 5$, since e_1 and e_5 are identical. The number of expression types, E , is a measure of the *complexity* of the network, which fits the intuition that a network is more complex if it does more kinds of things.

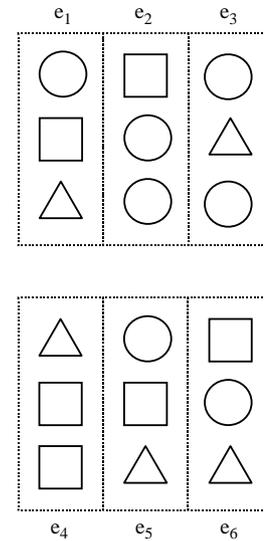


FIG. 1. Illustration of a simple network (edges not shown) with $N = 18$ nodes, where there are nodes of $C = 3$ types, and they combine into six expressions of length $L = 3$, of which there are $E = 5$ distinct expression types.

There must be sufficiently many nodes in a network to carry out the E different expression types. Since there are $L(E)$ nodes per expression, a network possessing E expression types must have at least $EL(E)$ many nodes in the network. That is, $N \geq EL(E)$. (In Fig. 1, $N = 18 \geq 15 = EL$.) This derivation is insufficiently general, however, since it presupposes that each node can participate in only one expression. More generally, we allow that each node may participate in, on average, σ expressions, where σ is the *participation constant*, and whose value will depend on the particular kind of network. (For example, employees in businesses may tend to participate in, say, ten expressions each, whereas ants in ant colonies may tend to participate in, say, five each.) In order to accommodate E expression types, each of length $L(E)$, there must now be at least $EL(E)/\sigma$ nodes in the network. That is,

$$N \geq [L(E)/\sigma]E. \quad (1)$$

For example, if each of the rows in Fig. 1 were expressions, then σ would be two, $E = 10$, and $N = 18 \geq 15 = EL/\sigma$.

2.2. THE OPTIMALITY HYPOTHESIS: RELATING COMPLEXITY E AND SIZE N

We hypothesize that for selected networks, the following *Minimal N Hypothesis* applies: *Network size N does not scale up more quickly than needed to obtain the E expression types.* Equivalently, the hypothesis is that network size N is minimized (or that E is maximized), up to a constant factor. The motivation behind this is that nodes in a selected network are costly, requiring energy of some kind to build and maintain. [For other applications of volume optimization, see Cherniak *et al.* (1999), Changizi & Cherniak (2000), and Changizi (2001a, d, in press)]. It follows that $N \sim L(E)E$. Furthermore, to minimize N , $L(E)$ must remain invariant, for if $L(E)$ increases with E , then N scales up faster than needed to obtain the E expression types. Thus, we may derive from this hypothesis that

$$L \text{ is invariant, and } N \sim E. \quad (2)$$

If networks do conform to the Minimal N Hypothesis, then, within any given kind of network, network size N may be used as a proxy for network complexity E .

Note that we do not generally expect the Minimal N Hypothesis to apply to non-selected networks. For example, a crystalline structure is a network: the number of atoms is the network size, and different expression types are the different kinds of interacting groups of atoms. Crystalline structures are not, however, under any selective pressure, and there is nothing preventing N from increasing (i.e. a bigger crystal) without any increase in the number of expression types (i.e. no increase in network complexity). The Minimal N Hypothesis therefore does not apply to crystals. Another kind of non-selected network is *competitive networks*, which are networks where there is selective pressure on the nodes themselves, not the network. Examples are ecosystems (networks of organisms) and cities (networks of businesses). Although the Minimal N Hypothesis is not plausible for competitive networks, there are sometimes other hypotheses that do plausibly apply and that serve as a replacement assumption allowing the derivation of eqn (2). We will

discuss this in subsection 3.7 when we take up ecosystems.

2.3. THE RELATIONSHIP BETWEEN COMPLEXITY E AND DIFFERENTIATION C

From the above hypothesis, we may derive the expected relationship between network differentiation and size. As a step toward this, consider how network complexity, E , relates to the number of node types, or *differentiation*, C . (Some of these notions emanate from Changizi, 2001b; see also Changizi, 2001c, in press.) With C node types, how many length- L expression types, E , are possible? The answer is $E = C(E)^{L(E)}$. For example, if there are $C = 2$ node types—labeled A and B—and expression length $L = 4$, then there are $E = 2^4 = 16$ expression types, namely AAAA, AAAB, AABA, ..., BBBB. However, this is insufficiently general for two reasons. First, only some constant fraction α of these expression types will generally be grammatical, or allowable, in the network, where this proportionality constant will depend on the particular kind of network. The relationship is, then, $E \sim C(E)^{L(E)}$. Second, the exponent, L , assumes that all L degrees of freedom in the construction of expressions are available, when only some fixed fraction β of the L degrees of freedom may generally be available due to inter-nodal constraints. Let $d(E) = \beta L(E)$. Call this variable d the *combinatorial degree*. The relationship is, then,

$$E \sim C(E)^{d(E)}. \quad (3)$$

Let us use the same example above, but suppose now that A's always occur in pairs, and that B's also always occur in pairs. The "effective components" in the construction of expressions are now just AA and BB, and the expression types are AAAA, AABB, BBAA, and BBBB. The number of degrees of freedom for an expression is just 2, not 4, and thus $E = 2^2 = 4$. Via the Minimal N Hypothesis, expression length, L , was invariant, and thus so is the combinatorial degree, d . It follows that

$$E \sim C(E)^d, \quad \text{where } d \text{ is invariant and } \geq 1. \quad (4)$$

It is important to understand the meaning of "combinatorial degree", for it will be much

discussed later. It is best interpreted as, intuitively, the “effective length of an average expression”, or, “how combinatorial the expressions are”, or “the number of degrees of freedom in an expression.” The lowest possible combinatorial degree is $d = 1$, and this means that there is effectively just one node per expression. This, in turn, means that nodes are not used in a combinatorial fashion to build expressions (despite the fact that L might be greater than one). A combinatorial degree greater than one means that nodes *are* used in a combinatorial fashion to construct expressions, and greater values mean that expressions are more combinatorial, or “effectively longer”. [The combinatorial degree is related to the Shannon–Boltzmann entropy H as follows: $H = -\sum p_i \log_2(p_i)$, where i ranges from 1 to the number of expression types E , and p_i is the probability of expression type i occurring (Ash, 1965). Assuming that the probabilities are uniform, $p = 1/E$, and thus $H = -E[(1/E)\log_2(1/E)]$, or $H = \log_2 E$. Recall that $E \sim C^{d(E)}$, and so $d = (\log_2 E)/(\log_2 C(E))$, and thus it follows that $d = H(E)/\log_2 C(E)$. That is, the combinatorial degree d is a measure of the entropy, but relative to a (possibly increasing) symbol set size C .]

2.4. THE RELATIONSHIP BETWEEN DIFFERENTIATION C AND SIZE N

At this point, we have related network size N and network (expressive) complexity E via eqn (2), and we have related E to differentiation C via eqn (4). Combining these equations we may derive

$$N \sim C^d, \quad \text{where } d \text{ is invariant and } \geq 1. \quad (5)$$

That is, we have derived from the Minimal N Hypothesis that we expect network size, N , to relate to network differentiation, C , as a power law with exponent $d \geq 1$. We will see in Section 3 that this appears to be the case for selected networks. For each kind of network, we compute the inverse of the best-fit slope of C vs. N on a log–log plot, for this provides an estimate of the combinatorial degree, d . In this way, (i) we acquire a measure of how combinatorial that kind of network is, and (ii) the combinatorial degree provides us with a clue as

to what the expressions might be in that kind of network. [Note that eqn (5) implies that $C \sim N^{1/d}$, and thus that the number of components of any given type will scale as $N/C \sim N/(N^{1/d}) = N^{1-1/d}$. In non-combinatorial organizations where $d = 1$, the number of components of any given type is invariant; whereas as d gets large, N/C approaches proportionality with N .]

2.5. TYPE-NETWORKS

As just discussed, plots of differentiation C vs. size N provide us with interesting information about a kind of network; in particular, from such plots one is able to measure the combinatorial degree. One may also extract useful information via the examination of “type-networks”. Let u_1, \dots, u_C be the C node types in some network J . A *type-network* for network J , labeled J_{type} , is built as follows: for each type u_i , a vertex w_i is placed into J_{type} representing that type; and, an edge is placed between vertices w_i and w_j in J_{type} just in case there are nodes in J of types u_i and u_j that are connected. (Note that to help to avoid ambiguities, I am using “vertex” to refer to nodes in a type-network, and “nodes” for nodes in networks.) Consider electronic circuits as one example, where the type-network consists of one vertex for each type of electronic component in the circuit, and an edge connects two vertices in the type-network just in case there exists a physical connection (a wire) between two individuals of the respective types. As another example, consider ecosystems (i.e. networks of organisms), where a type-network consists of one vertex for each organism type, and an edge connects two vertices just in case there is a trophic interaction between them—that is, a type-network for ecosystems is just a food web.

Suppose that, for some given kind of network, the average edge-degree δ —i.e. the number of edges emanating from a vertex—in type-networks scales as the total number of vertices C to the power of a constant v —i.e., $\delta \sim C^v$ —where v ranges from 0 to 1. If expressions in the network are of length L , then how many possible expression types E are there? Any of the C vertices can participate with one of δ

many other vertices, which can, in turn, participate with one of δ others, and so on until L vertices have participated in the chain. Thus, there are $E \sim C(\delta^{L-1})$ many possible expression types. Since $\delta \sim C^v$, we may write

$$E \sim C^{vL-v+1}. \quad (6)$$

For selected networks we expect $E \sim N$, and thus $N \sim C^{vL-v+1}$. Furthermore, we expect eqn (5) to hold, or $N \sim C^d$ with d invariant, and we may conclude that

$$d = vL - v + 1, \quad (7)$$

where d , L , and v are constants (i.e. not a function of E). Equation (7) is of interest for two reasons.

First, it may be used to independently determine if the network is acting combinatorially. If the expression length $L = 1$, then $d = 1$, and thus it is not combinatorial. Since $d > 1$ in the networks we study below, it must be that $L > 1$ (since $L \geq d$). If $L > 1$, then there are two possibilities. The first is that $v = 0$ —i.e. the edge-degree δ does not increase with the size C of the type-network—in which case $d = 1$, and the system is again not combinatorial. The second possibility is that $v > 0$, in which case $vL - v > 0$, and thus the network is acting combinatorially since $d > 1$.

Second, we may also use eqn (7) to compute the length of an expression *if* we already know the combinatorial degree d . Solving for L in eqn (7), we get

$$L = (d + v - 1)/v. \quad (8)$$

That is, if we know that the edge-degree $\delta \sim C^v$, where $v > 0$, and that the combinatorial degree is d via a plot of C vs. N , then we may compute the length L of an expression. For example, if $v = 1$ —i.e. if the edge-degree δ scales up linearly with the size C of the type-network—then $L = d$. Intuitively, $v = 1$ implies that all possible degrees of freedom are used in expressions; or, expressions are no longer than absolutely necessary. Lower values of v , but still with $v > 0$, imply longer expression lengths compared to the combinatorial degree. For example,

$v = 1/2$ implies $L = 2d - 1$; that is, it implies that, for large d , d is roughly half of L .

3. Results

In this section, we discuss the scaling of differentiation in a number of distinct kinds of selected network (and two kinds of competitive network). Differentiation C increases disproportionately slowly as a function of network size N in all the kinds of network below, and we compare the fit under both a power-law assumption ($\log C \sim \log N$) and a logarithmic assumption ($C \sim \log N$). The relative magnitude of the correlations under the two assumptions informs us as to which is the better fit, but does not serve as a statistical test for the rejection of a model. A statistical test for fits under these two models was carried out by searching for non-randomness in the serial dependence of the signs of the residuals about the best-fit line (see Appendix C for details). For each kind of network studied below, we compute the probability under the two models that there is no serial dependence of the signs of the residuals; low p values ($p < 0.05$) mean that the residuals do show serial dependence, and thus that the model is not a good fit. p_{power} and p_{log} refer to the serial-dependence probabilities under, respectively, the power-law and logarithmic models.

We will find that in each kind of selected network studied, the relationship between differentiation and network size is well described by a power law, and in most cases a logarithmic relationship can be discounted. Thus, in every case the relationship is consistent with the optimality hypothesis presented earlier, and we will be able to measure the combinatorial degree from the inverse of the slope of $\log C$ vs. $\log N$.

3.1. ELECTRONIC CIRCUITS: NETWORKS OF ELECTRONIC COMPONENTS

Electronic circuits are an advantageous starting point because they are very well understood. The number of component types C and total number of components N were recorded from 373 electronic circuit diagrams (obtained from the sources listed in Appendix A), ranging in size N from 2 to 265, and in differentiation C from 2 to 26. We treated as a component any

pre-fabricated electrical component in a circuit diagram. Example component types include resistor, capacitor, inductor, diode, Zener diode, npn transistor, pnp transistor, MOSFET, NOT gate, AND gate, op amp, and specialized microcircuits. Figures 2(a) and (b) show log-log and semi-log plots of differentiation C vs. circuit size N . The first observation to make is that C increases with N . This is surprising, since, like digital circuits, any circuit can, in principle, be built from just a small, fixed number of node types (e.g. resistor, capacitor, inductor, diode, and transistor). *A priori*, then, it was possible that C would remain constant at around, say, 5. That it does not remain constant is *not* a fact implied by any laws of electronics. Rather, the increase in differentiation with size is probably due to general organizational principles *de facto* followed among circuit designers. The second observation about Figs 2(a) and (b) is that the quantitative relationship between differentiation and size in electronic circuits is best described by a power law, namely $C \sim N^{0.44}$ ($p_{\text{power}} = 0.05$ and $p_{\text{log}} = 4 \times 10^{-5}$). The combinatorial degree d is therefore invariant, and can be estimated as the inverse of the power-law exponent, and thus $d \approx 2.3$. Because $d > 1$, electronic circuits are combinatorial networks, i.e. they use their nodes as words, and combinatorially make functional expressions out of them. The fact that the combinatorial degree is a little over two means that, whatever the expressions are, there exists only around two degrees of freedom in their construction.

Let us now consider how, for electronic circuits, the connectivity scales within type-networks. We built type-networks for 109 circuits in Horowitz & Hill (1989), ranging in total number of edges G from 1 to 96, and in total number of component types C from 1 to 14. An edge in the type-network exists between two types just in case there exists a wire connecting two components of those respective types. Figure 2(c) plots $\log C$ vs. $\log G$, and one can see that $C \sim G^{0.52}$, or $G \sim C^{1.92}$ (where an exponent of 2 here is the maximum possible). The average edge-degree (i.e. number of edges at a vertex) $\delta \equiv G/C$, and thus $\delta \sim C^{0.92}$. That is, the exponent relating δ and C is $v = 0.92$. In other words, the total number of edges scales

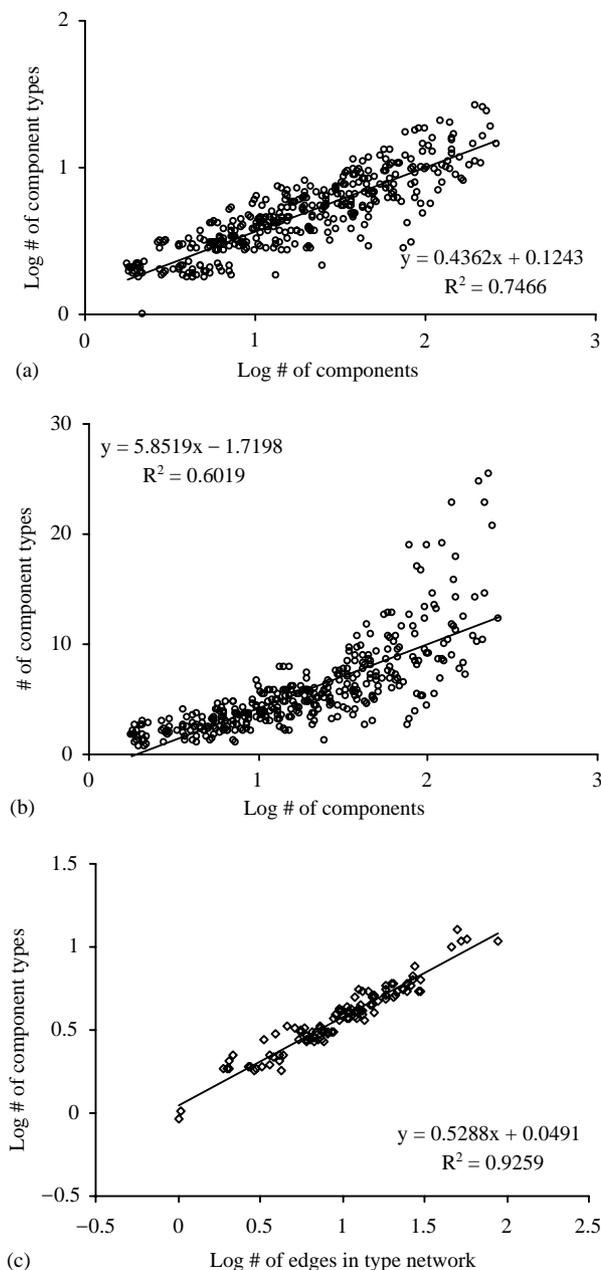


FIG. 2. (a) Logarithm (base 10) of the number of electronic component types vs. the logarithm of the total number of components ($n = 373$). To make sure each point in the plot is visible, x and y values were each perturbed by adding a random number in the interval $[-0.05, 0.05]$. (b) Number of electronic component types vs. the logarithm of the total number of components ($n = 373$). y -axis values were perturbed by adding a random number in the interval $[-1, 1]$, and x -axis values using the interval $[-0.05, 0.05]$. (c) Logarithm of the number of electronic component types vs. the logarithm of the total number of edges in the type-network ($n = 109$). x and y values were each perturbed by adding a random number in the interval $[-0.05, 0.05]$. Best-fit line (via linear regression) and correlation shown for each plot (as is the case in every plot in this paper).

roughly as quickly as is possible (i.e. it is approximately the case that $G \sim C^2$), and thus δ scales nearly as fast as possible (i.e. approximately as $\delta \sim C$). Recall that $v > 0$ implies that the network is acting combinatorially; this provides another confirmation of this conclusion made earlier. Also, using eqn (8) we may compute L from d and v : $L = (d + v - 1)/v$, and thus $L = (2.3 + 0.92 - 1)/(0.92) \approx 2.43$. Because $v \approx 1$, it follows that $L \approx d$, and both L and d are a little over 2.

Expressions in electronic circuits therefore tend to be built out of around two components, and since the combinatorial degree is also around two, it means that all the possible degrees of freedom are utilized. What might expressions in electronic circuits actually be? Introductory electronics books spend considerable time introducing just such circuits. For example, functional circuits found in Horowitz & Hill (1989) include the following (with number of components and number of component types within the circuit in parentheses):

resistors in series (2, 1), resistors in parallel (2, 1), voltage divider (2, 1), adjustable voltage divider (2, 1), Zener regulator (2, 2), tunnel diode amp (2, 2), RC discharge (2, 2), integrator/low-pass filter (2, 2), differentiator/high-pass filter (2, 2), LC resonant/bandpass filter (3, 3), LC notch filter (3, 3), half-wave rectifier (1, 1), full-wave bridge rectifier (4, 1), full-wave rectifier using center-trapped transformer (3, 2), dual-polarity supply (6, 2), voltage doubler (4, 2), diode voltage clamp (2, 2), dc restoration (2, 2), diode limiter (3, 2), diode drop compensation (4, 2), blocking inductive kick (2, 2), RC snubber (3, 3), emitter follower (2, 2), Zener voltage regulator (2, 2), constant-amplitude phase shifter (2, 2), common-emitter amp (2, 2), classic bipolar-transistor matched-pair current mirror (2, 1), improved current mirror (5, 2), push-pull emitter follower (2, 2), Darlington transistor configuration (2, 1), Sziklai connection (2, 2), classic transistor differential amp (7, 2), NMOS logic inverter (2, 2), PMOS logic inverter (2, 2), CMOS logic inverter (2, 1), CMOS NAND gate (4, 1), CMOS linear amp A (3, 3), CMOS linear amp B (5, 3), CMOS linear amp C (5, 3), inverting amp (3, 2), noninverting amp (3, 2), Howland current source (5, 2), classic differential amp (5, 2), op-amp peak

detector (4, 3), integrator with op-amp (3, 3), negative-impedance converter (3, 2).

One can see that the number of components in most of these is around two (and that the number of types never exceeds three). Our claim is that the combinatorial degree and length of around two is the fingerprint of the existence in circuits of these kinds of basic functional entities, or expression types. In less well-understood kinds of network, the basic functional entities may be unknown, and knowing the combinatorial degree and length may help to discover what they are.

3.2. LEGOS: NETWORKS OF ATTACHABLE PARTS

Legos are networks of attachable parts, and we ask how the number of node types relates to network size within Legos. Only Lego structures that are intended to build something particular were considered (i.e. not buckets of generic pieces, or sets of replacement parts). Some examples are “Santa Claus”, “Air Patrol”, “Spy Boat”, and “Cargo Crane”. Figure 3 plots the number of Lego™ piece types vs. the total number of pieces in 389 such Lego™ sets (obtained from <http://www.peeron.com/inv/sets>). The first observation is that the number of Lego piece types increases as a function of structure size. Furthermore, a power-law relationship $C \sim N^{0.71}$ appears to fit the data better than a logarithmic relationship ($p_{power} = 0.09$ and $p_{log} = 10^{-7}$). The combinatorial degree is therefore invariant, and is approximately 1.4.

One straightforward hypothesis for what an expression is in Legos (and assembled structures more generally) is this: an expression just is a physical connection between two pieces. For example, piece A might connect to B, and B might connect to C. AB and BC would then be two expressions (recall that a single node can participate in multiple expressions). The expression length L would thus be 2. Because the combinatorial degree d must be less than or equal to L , $d \leq 2$. If, up to a constant factor, any Lego piece is physically connectable to every other piece, then the combinatorial degree will equal 2. If, however, the fraction of pieces a piece may connect with falls in larger Lego sets, the combinatorial degree may be

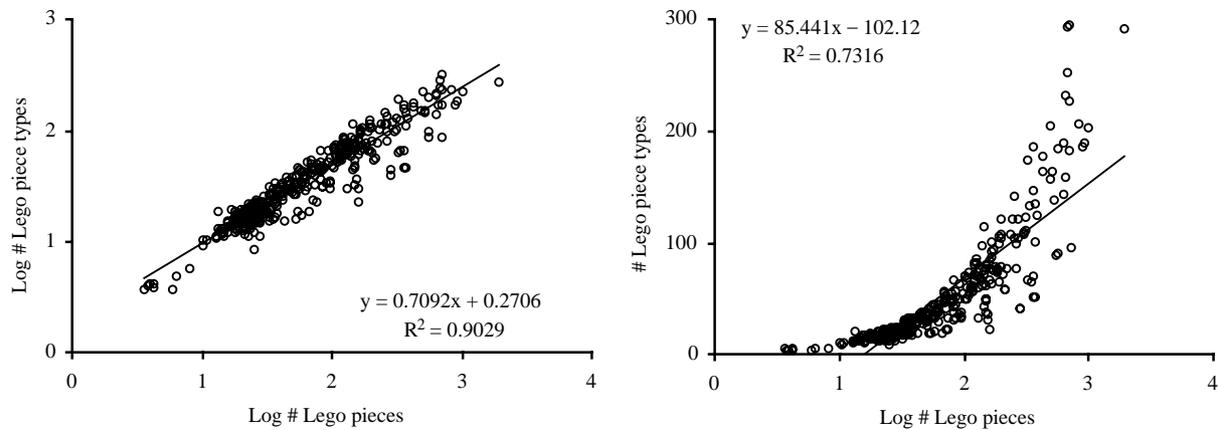


FIG. 3. Log–log (base 10) (left) and semi-log (right) plots of the number of Lego piece types vs. the total number of parts in Lego structures ($n = 391$). To help to distinguish the data points, logarithmic values were perturbed by adding a random number in the interval $[-0.05, 0.05]$, and non-logarithmic values were perturbed by adding a random number in the interval $[-1, 1]$.

lower than 2, and this may explain the lower combinatorial degree of around 1.4. Via similar reasoning, if a network possessed attachments for which m (rather than 2) pieces must simultaneously physically connect, we would expect a maximum combinatorial degree of m .

3.3. BUSINESSES AND UNIVERSITIES: NETWORKS OF PEOPLE

There exists a long tradition of looking at differentiation as a function of business size (e.g. Simmel, 1902; Caplow, 1957; Hall *et al.*, 1967; Pugh *et al.*, 1968; Blau, 1970; Blau & Schoenherr, 1971; Childers *et al.*, 1971; and see reviews by Kimberly, 1976; Slater, 1985), but these researchers commonly only report the correlation of degree of differentiation and organization size. In the few cases where degree of differentiation is plotted against organization size (e.g. Blau, 1970; Blau & Schoenherr, 1971; Childers *et al.*, 1971), log–log plots were not used, and the possibility that the data may conform to power laws was not investigated. Figure 4 shows log–log and semi-log plots of degree of differentiation vs. organization size: two are for military organizations [(a) and (b)] [using data from Childers *et al.* (1971, Fig. 2)], one from universities as businesses (c) [using data we obtained ourselves by going to university web sites: total number of employees was

often obtainable from university “at-a-glance” pages; the number of employee types was (less often) obtainable at human resources sites, where each job type at the university is listed], and one from employment insurance companies (d) [using data from Blau & Schoenherr (1971, Figs 3-2)]. Differentiation increases in each kind of network as a function of size. Although each plot is, in terms of the correlation, better described by a power law than by a logarithmic model, the logarithmic model can be rejected only in military vessels; in the other three kinds of business, neither the power law nor logarithmic model can be rejected. (See p_{power} and p_{log} values in Table 1.) The exponents are 0.63 for military vessels (combinatorial degree $d = 1.6$), 0.88 for military offices ($d = 1.14$), 0.73 for universities ($d = 1.37$), and 0.33 for employment insurance companies ($d = 3$).

We may also look at universities not as networks of employees generally, but rather as networks of faculty, where two faculty are considered the same type if they are members of the same department. The number of departments is used as the measure of the number of faculty types. The number of students is used as the measure of the number of faculty, since across universities they scale nearly proportionally; namely, the number of faculty scales against the number of students as a power law with exponent 0.987 ($n = 89$, $R^2 = 0.743$) [this plot is not shown here; and the data for it are taken

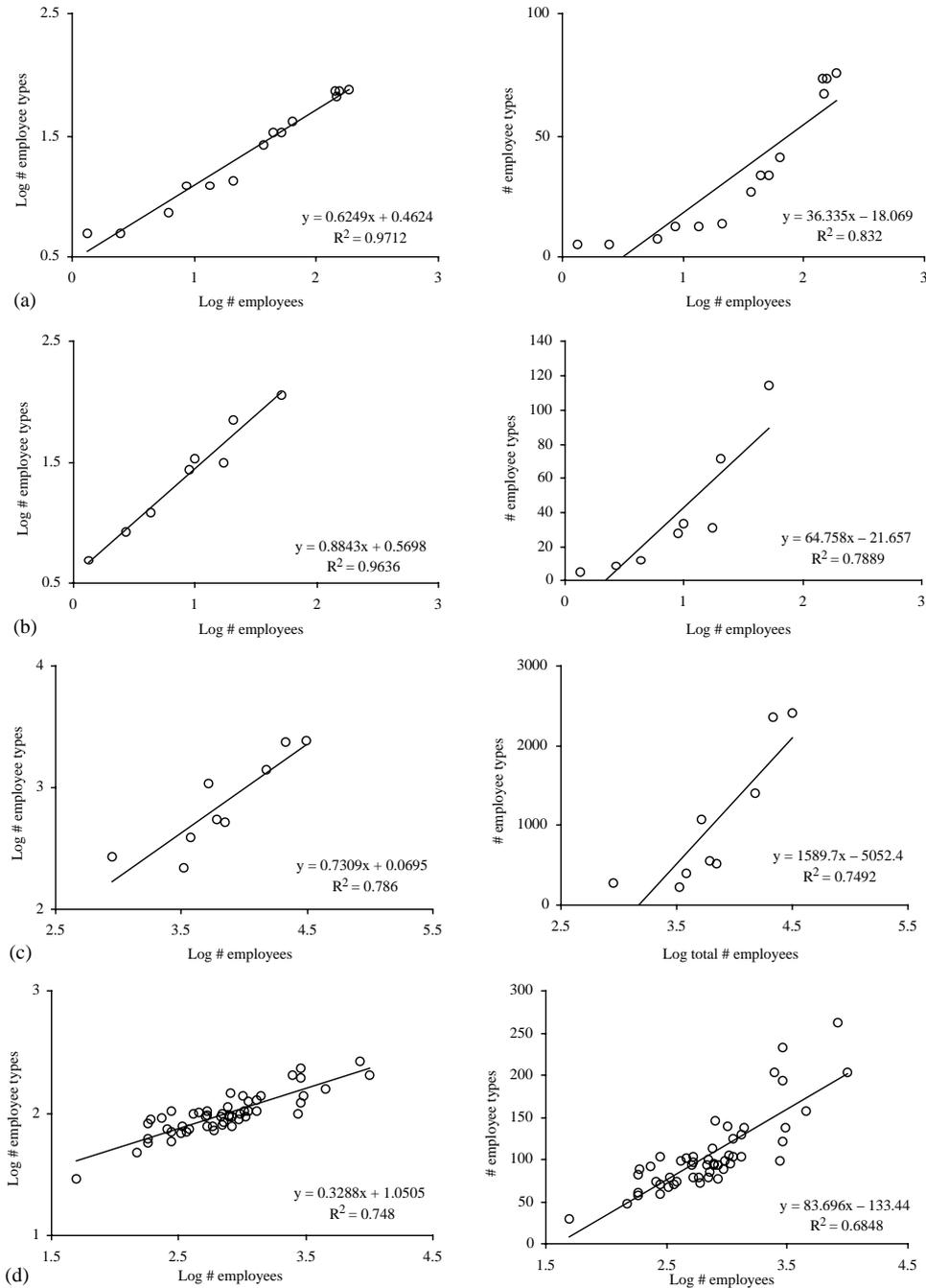


FIG. 4. Log–log (base 10) (left) and semi-log (right) plots of the number of employee types vs. the total number of employees for four kinds of business organization. (a) and (b) Trends for, respectively, military vessels ($n = 13$) and military offices ($n = 8$). (c) Trend for universities ($n = 9$). (d) Trend for employment insurance companies ($n = 52$).

from universities listed in *World of Learning*, 2000]. Log–log and semi-log plots of degree of differentiation vs. total number of faculty for a number of colleges and universities reveal that they are related by a power law with exponent nearly $1/2$ [Fig. 5(a)]. In particular, $C \sim N^{0.55}$

($p_{power} = 0.09$ and $p_{log} = 0.01$). The relationship also appears to fit a power law with slope of $1/2$ for Duke University studied through time [Fig. 5(b)]; however, the logarithmic relationship cannot be rejected ($p_{power} = 0.09$ and $p_{log} = 0.05$).

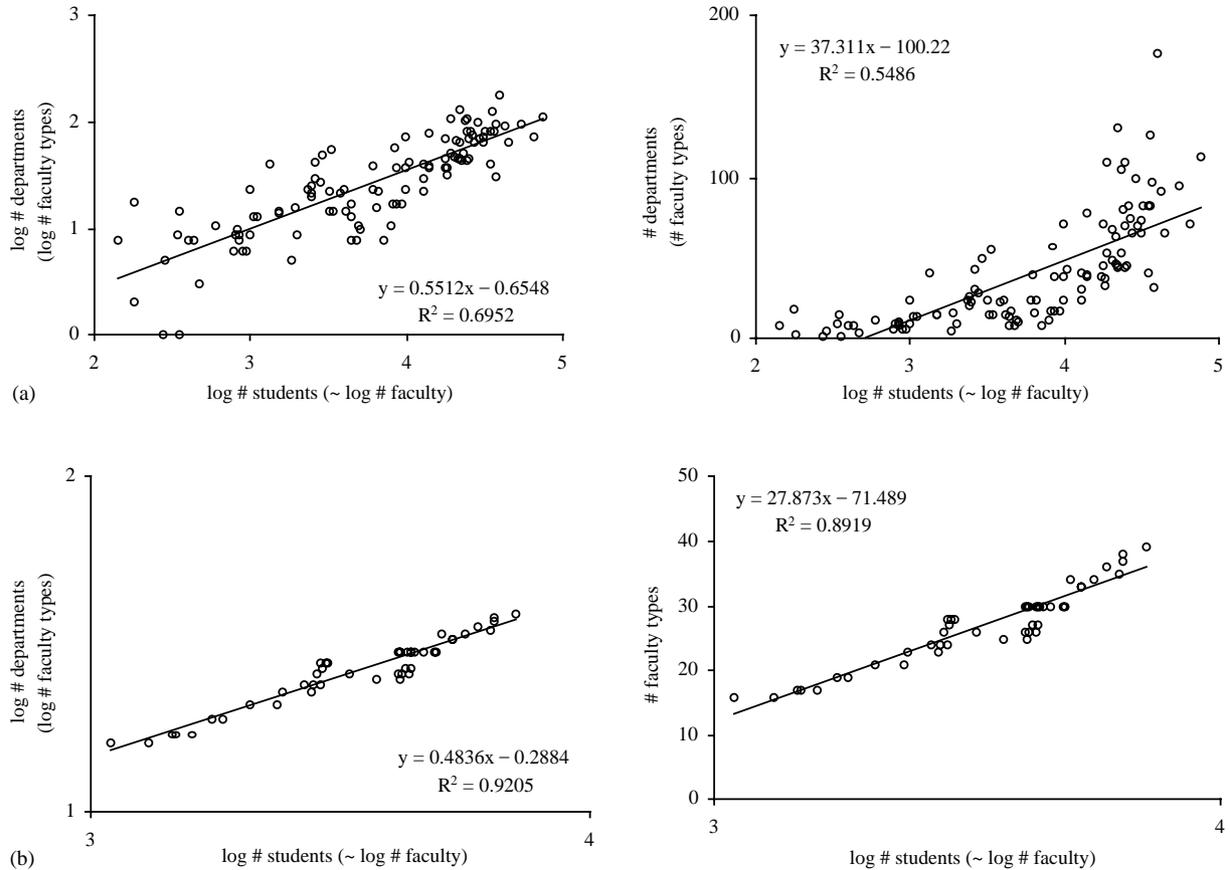


FIG. 5. Log-log (base 10) (left) and semi-log (right) plots of the number of faculty types vs. the total number of faculty. (a) The trend across many different colleges and universities, 89 taken from World of Learning (2000) (and plotted first in Changizi, 2001b) and 23 from Holdaway *et al.* (1975). (b) The trend for Duke University for the 46 years from 1924 (when Duke became a university) to 1971 (which we obtained from the Duke archives).

3.4. ANT COLONIES: NETWORKS OF ANTS

For ant colonies, how internal complexity changes with colony size has been studied (Bonner, 1993; Karsai & Wenzel, 1998; Bourke, 1999; Anderson & McShea, 2001), but the quantitative manner in which differentiation scales with colony size has not been considered. We acquired estimates from the literature of the number of physical size castes in colonies of 46 species (see Appendix B). Figure 6(a) shows that differentiation scales as a power law against colony size ($p_{power} = 0.11$ and $p_{log} = 0.04$). We also used the ratio of the worker maximum to minimum linear size as a second measure of differentiation [Fig. 6(b)], and it also appears to fit a power law ($p_{power} = 0.17$ and $p_{log} = 0.04$), having similar slope to the physical caste plot,

namely, the slopes are near 0.12. The combinatorial degree for ant colonies is therefore on the order of 10, which probably reflects the fact that ants are highly social, and that colony functional expressions are carried out by the mutual cooperation of many (i.e. perhaps around 10 or more) ants. This is in sharp contrast to the much lower combinatorial degrees for businesses and universities, where smaller numbers of employees (between 1 and 3) are probably sufficient to implement expressions.

3.5. ORGANISMS: NETWORKS OF CELLS

Using data from Bell & Mooers (1997), Fig. 7 shows that differentiation in organisms scales up as a power law ($p_{power} = 0.08$ and $p_{log} = 0.02$) with an exponent of around 0.06 (see also

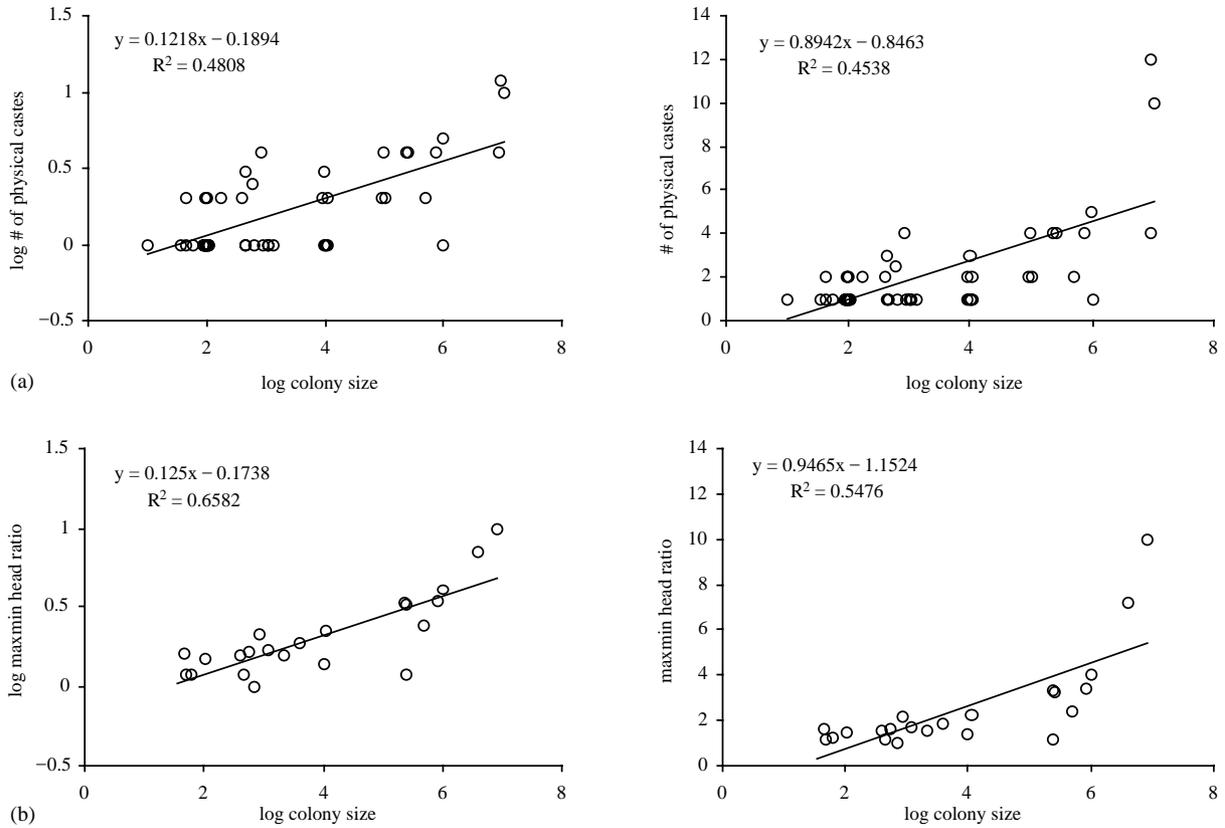


FIG. 6. Log-log (base 10) (left) and semi-log (right) plots of differentiation in ant colonies vs. colony size. (a) The number of physical castes is used as the measure of differentiation ($n = 46$). x -axis values were perturbed by adding a random number in the interval $[-0.05, 0.05]$. (b) The ratio of the maximum to minimum worker head width is used as the measure of differentiation ($n = 22$).

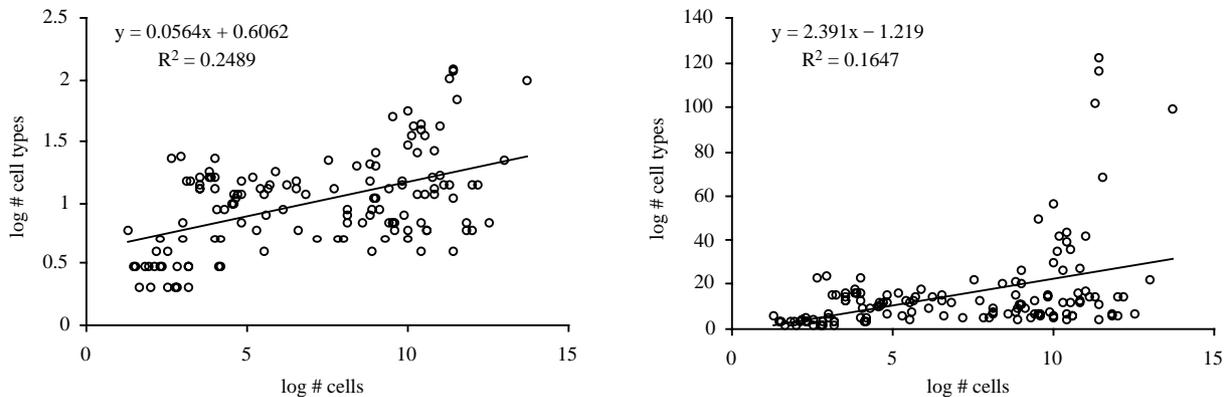


FIG. 7. Log-log (base 10) (left) and semi-log (right) plots of the number of cell types vs. the total number of cells, for 134 species of multicellular organism falling in 31 phyla (plant, animal, fungi, Chlorophyta, Phaeophyta, Rhodophyta, Ciliata, Acrasiomycota, and Myxomycota) (data from Bell & Mooers, 1997).

Bonner, 1988, 1993; Changizi, 2001b,c). The combinatorial degree is therefore on the order of 15 or so, meaning that the construction of expressions in organisms occurs via the simulta-

neous action of many (i.e. more than a dozen) nodes. It was conjectured in Changizi (2001b) that tissues may be the appropriate component, not the cell, and that tissues combine in

conglomerations of roughly a dozen (i.e. in the range of 10–20). A combinatorial degree this high for organisms is in marked contrast to Legos™, where expressions may be built by merely a pair of physically connecting components, rather than built by more than a dozen physically proximal tissues.

It is expected that similar combinatorial principles apply at the lower hierarchical level where each cell type within an organism is considered an expression type built from lower-level components in a subcellular network (McShea, 2002; McShea & Anderson, 2002). Consider gene networks as the subcellular networks. If B is the number of genes and C the number of cell types in an organism, then as in eqn (3), we expect $C \sim B(C)^{d(C)}$ (where C now is playing the role of the number of expression types, and B the number of node types). How does the number of genes relate to the number of cell types across organisms? Gene counts were obtained from the public domain (see, e.g. Liu & Rost, 2001, for compilation), and cell types from Bell & Mooers (1997): *Escherichia coli* [4285 genes, 1 cell type], *Saccharomyces cerevisiae* [6307, 3], *Caenorhabditis elegans* [18 944, 24], *Drosophila melanogaster* [14 218, 50], Human [22 887, 102]. There exist gene counts for many procaryotes, ranging from about 600 (*Ureaplasma urealyticum*) to that of *E. coli* of 4285; only *E. coli* is shown in the plot [Fig. 8(a)], but is not used for the linear regression because (i) it may be inappropriate to treat procaryotes as single-cell organisms with which multicellular eucaryotic organisms are compared, and (ii) even if it were appropriate, it is not clear which procaryote would be representative. One may, then, plot the number of genes vs. the number of cell types, and doing so leads to the preliminary conclusion that, indeed, proteins act combinatorially in the construction of cell types, with a combinatorial degree on the order of magnitude of three [Fig. 8(a)]. Although few data points for multicellular organisms currently exist, the range of the data is nearly as wide as it will get, and thus the scaling exponent of around 1/3 is not likely to drastically change as more genomes are sequenced (i.e. it is unlikely to be 1/10 or 1). Thus, although hundreds or thousands of genes may be simultaneously involved in the construc-

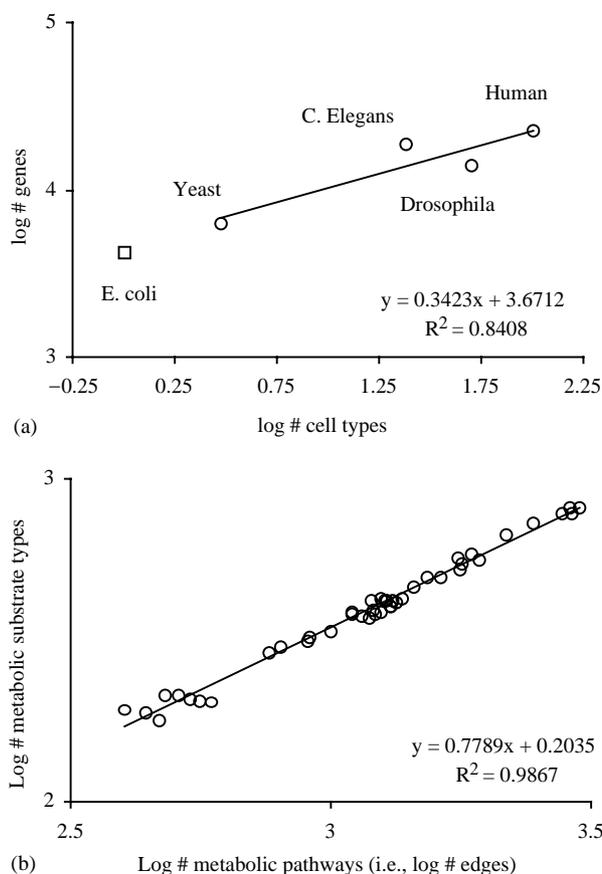


FIG. 8. (a) Logarithm (base 10) of the number of genes vs. the logarithm of the number of cell types. (b) Log–log (base 10) plot of the number of substrate types involved in metabolic pathways vs. the number of metabolic pathways in which they are involved, for 43 organisms (data from Jeong *et al.* (2000); only ingoing links are included here, and plot looks nearly identical for outgoing links).

tion of a cell type, there are only on the order of several degrees of freedom. Because of the meager number of data points, we cannot determine whether the combinatorial degree is invariant (i.e. a power law) or whether it is decreasing (i.e. a logarithmic). Another way to confirm that subcellular components are used combinatorially is by examining type-networks. Jeong *et al.* (2000) created type-networks for substrates involved in metabolic activity for 43 organisms (six archaee, 32 bacteria, and five eucaryotes), where two substrate types are connected just in case they participate in a metabolic pathway. Figure 8(b) shows a log–log plot of the number of vertices in the type-network vs. the number of edges for each of

these organisms, and one can see that the number of subcellular node types B scales as the number of edges G in the type-network to the power of 0.78, or $G \sim B^{1.28}$ (where, recall, an exponent of 2 is the maximum possible). The average edge-degree (i.e. the number of edges at a vertex) $\delta \equiv G/B$, and thus $\delta \sim B^{0.28}$. Therefore, $v = 0.28$, and since $v > 0$ it implies that metabolic networks act combinatorially.

3.6. NERVOUS SYSTEMS: NETWORKS OF NEURONS

In an effort to acquire the number of neuron types in neocortex across a variety of mammals, it is important to confine oneself to counts within a single counting methodology. Although there is a considerable literature concerned with classifying neurons in neocortex, the primary effort has been on categorization for mammals as a whole, not on comparisons between mammals. One recent exception emanates from the work of Hof and colleagues, who have used immunoreactive staining and morphological criteria to compare the neuron types in mammals from nine orders (Hof *et al.*, 1999), and in great ape (Nimchinsky *et al.*, 1999). For each mammalian order, indices of encephalization P (i.e. the brain mass after normalizing for body size) were computed from brain and body weights (grams) for all species in that order found in the following references: Hrdlicka (1907), and Bonin

(1937), Crile & Quiring (1940) and Hofman (1982a, b). Since brain mass scales as body mass to the $3/4$ power (Allman, 1999; Changizi, 2001a), P is defined as brain mass divided by body mass to the $3/4$ power. Averages were then taken within families, and the family averages, in turn, averaged to obtain the average for an order. Index of neuron encephalization Q (i.e. the number of neurons after normalizing for body size) was computed as $Q = P^{2/3}$, since the number of neurons in neocortex scales as brain volume to the $2/3$ power (see Changizi, 2001a). Figure 9 shows plots of the number of neuron types as a function of the number of neurons in the neocortex (after correcting for body size), and one can see that the number of neuron types increases in larger brains. We cannot refute either the power-law model ($p_{power} = 0.16$) or the logarithmic model ($p_{log} = 0.16$). (Without the stray Chiroptera point, the correlations under log-log and semi-log become identical.) The combinatorial degree is approximately 5. [One conjecture for what determines this combinatorial degree is that expressions are invariant sized minicolumns (Mountcastle, 1957; Rockel *et al.* (1980); Tommerdahl *et al.*, 1993; Peters, 1994; Mountcastle, 1997; Jones, 2000), or groups of on the order of 100 neurons spanning the thickness of the neocortex. There are five cell-body-rich neocortical layers (in most mammals), and the neurons in a minicolumn that fall within each

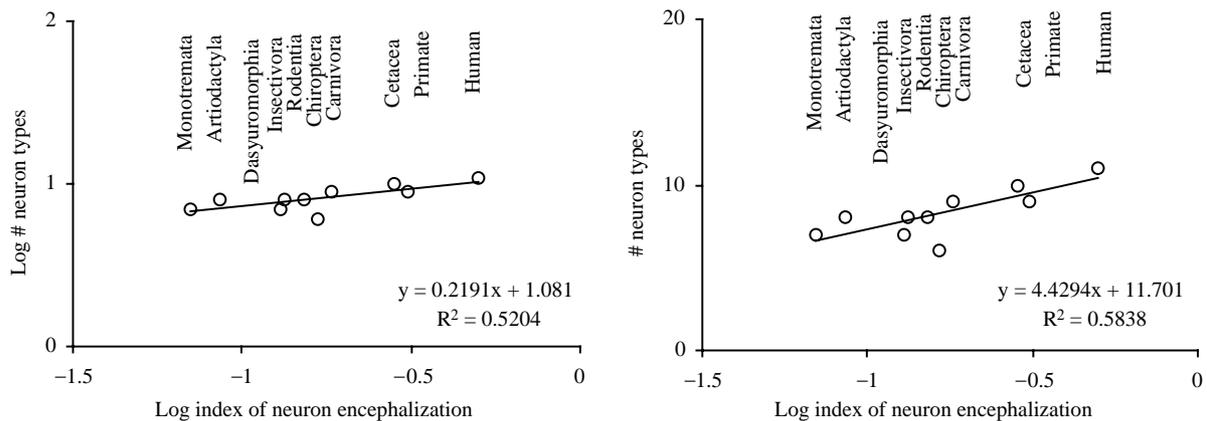


FIG. 9. Log-log (base 10) (left) and semi-log (right) plots of the number of morphologically and immuno-reactivity defined neuron types as a function of index of neuron encephalization (see text) in 9 mammalian orders (Hof *et al.*, 1999) as well as great ape (Nimchinsky *et al.*, 1999). Number of neuron types and index of neuron encephalizations are as follows: Monotremata (7, 0.0699), Artiodactyla (8, 0.0860), Dasyuromorphia (7, 0.1291), Insectivora (8, 0.1339), Rodentia (8, 0.1522), Chiroptera (6, 0.1664), Carnivora (9, 0.1830), Cetacea (9, 0.3094), Primate (not great apes) (10, 0.2826), Great Ape (11, 0.4968).

layer may serve a distinct role in the functioning of a minicolumn. The conjecture is, then, that these five layers provide five degrees of freedom in the construction of a minicolumn, which is reflected in the way the number of neuron types scales with brain size.]

Another nervous system for which considerable data exist on the number of neuron types is the vertebrate retina. As was the case for the neocortex, less attention has been paid to comparing the number of neuron types across different animals, but the research of Kalloniatis and Marc provides a single methodology in which counts have been made for three animals. The method uses pattern recognition of amino acid signals to make the classifications, and counts are nine neuron types for goldfish (*Carassius auratus*) (Marc *et al.*, 1995), 12 for cat (Marc *et al.*, 1998), and 15 for primate (Kalloniatis *et al.*, 1996). [These counts do not include retinal pigment epithelial cells or glial cells (e.g. Muller cells).] The index of neuron encephalizations for the three animals are, respectively, 0.0689, 0.1830, 0.3374 (computed from data in the sources and in the manner given above for neocortex). A log–log plot of number of retinal types vs. index of neuron encephalization (not shown) gives a best-fit equation of $y = 0.319x + 1.322$, and $R^2 = 0.9965$. Because of the small number of data points, and because index of neocortical neuron encephalization is not an appropriate measure of the number of neurons in the retina, we attempt no analysis of these data, except to say that it is clear that the number of neuron types does appear to increase in retina of more complex animals.

3.7. COMPETITIVE NETWORKS: ECOSYSTEMS AND CITIES

The scaling of differentiation has received considerable attention in ecosystems, where there is a long history of studying how the number of organism types (i.e. species) scales up with the area of the land, going back at least to Watson in 1859 (Williams, 1964; Rosenzweig, 1995). Since land area A scales proportionally to the number of organisms N , species–area plots serve as plots of the number of organism types C

vs. the total number of organisms N . There are many kinds of species–area plot (e.g. see Rosenzweig, 1995, p. 8), and we are here only interested in those which study how differentiation scales *across* networks of different sizes, in contrast to studies of larger and larger subsets of a single network (as in quadrat studies) where the governing principles can be distinct. What is an ecosystem network? The best candidate is an island biota, as (i) an island is a well-demarcated network of organisms, (ii) archipelagos usefully serve to identify a group of such networks of similar kind, and (iii) island species–area studies are not beset with sampling issues as is the case in some of the other kinds of species–area studies. Accordingly, we wish to know how the number of species scales up as a function of island size among islands within an archipelago. Many such studies have been carried out, usually focusing on just one class of organism (e.g. Wilson, 1961; MacArthur & Wilson, 1963; Johnson *et al.*, 1968; Brown, 1971; Diamond, 1972, 1974; Power, 1972; Johnson & Simberloff, 1974; Case, 1975; Johnson, 1975; Diamond & Mayr, 1976; Simberloff, 1976; Connor & McCoy, 1979; Wright, 1981; Lomolino, 1982; Heaney, 1984; Losos, 1996; Nieminen, 1996; Holt *et al.*, 1999; Losos & Schluter, 2000). On the whole, such species–area plots conform to power laws with slopes in the approximate range of 0.2–0.4 (Rosenzweig, 1995). For example, Connor & McCoy (1979) cataloged 100 such slopes from the literature, and among the roughly 60 island slopes, the average is about 0.3.

Why is differentiation and network size related by a power law in island biota networks? We explained the power-law relationship for selected networks via the Minimal N Hypothesis, but as discussed then, the hypothesis is only plausible for selected networks. Island biota networks are competitive networks (where selection acts at the level of the nodes, not at the level of the entire network), not selected networks, and the Minimal N Hypothesis is inappropriate. However, there is another hypothesis that is plausible for island biota networks. Before stating the hypothesis, consider that a group of organisms can interact in such a way as to fill a habitat. That is, some particular group of

organisms may be able, by virtue of their interactions, to invade a certain kind of habitat, whereas another group of organisms (made up of different organism types) may not be able to. These habitat-filling groups of organisms are expressions in the network. We make the following *Habitat-Filling Hypothesis*, which states that, *up to a constant proportion, every habitat type is filled by an expression type (i.e. filled by a type of group of interacting organisms)*. The motivation for this hypothesis is that, because of competition in the network, every kind of habitat will be invaded. From this we may derive that the number of habitat types, H , will scale proportionally with the number of expression types, E (i.e. E is the number of different ways groups of organisms interact to fill habitats). That is, $H \sim E$. Since islands with twice the area, A , tend to have roughly twice the number of habitat types, H , we may derive that $A \sim E$. Recalling that island area, A , is proportional to network size, N , we may conclude that $N \sim E$. (Note also that since $N \geq [L(E)/\sigma]E$ from eqn (1), it follows that L is invariant.) Recall that this was eqn (2). In a manner identical to that in Section 2, we may now go on to derive that, for island biota networks, eqn (5) holds. Namely,

$$N \sim C^d, \quad \text{where } d \text{ is invariant and } \geq 1.$$

We have arrived at the same conclusion as we did for selected networks, but we have done so using a different explanation. A power-law relationship holds for island biota networks not because such networks optimize their size subject to the “needed” network complexity (as was the case for selected networks), but, rather, because these networks maximally fill every available habitat (up to a constant factor) on the island. [This explanation of the species–area relationship has certain affinities with Williams (1964) and Simberloff (1972) in that the number of organism types is hypothesized to increase because of the increase in the number of habitat types.]

Although we have just provided an explanation for why species–area plots conform to power laws, we have not explained the magnitude of the exponent. As mentioned earlier, the

power-law exponents for species–area plots tend to be approximately 0.3, and thus the combinatorial degree values are around 3 (ranging from about 2.5 to 5, depending on the study). We now put forth an explanation for why combinatorial degrees are in this range. A combinatorial degree of around 3 means that there are three degrees of freedom in expressions, recalling that expressions are habitat-filling groups of organisms. We hypothesize that such habitat-filling groups are of the following nature: each group consists of a predator, a herbivorous prey, and so on down through the trophic levels. That is, we hypothesize that expressions are food chains, and it is food chains that fill habitats. Furthermore, we hypothesize that there is a degree of freedom for each trophic level in the chain, and thus that the combinatorial degree is determined by food chain length. This hypothesis makes several predictions.

One straightforward prediction is that, since the combinatorial degrees are roughly 3 (i.e. somewhere between 2.5 and 5), food chain lengths should also be around 3 on average (i.e. somewhere between 2.5 and 5). Food chain lengths have been measured in a variety of kinds of food web (Pimm & Lawton, 1977; Briand, 1983; May, 1983; Cohen *et al.*, 1986, 1990; Newman & Cohen, 1986; Schoener, 1989; Sugihara *et al.*, 1989; Warren, 1989; Martinez, 1991; Pimm *et al.*, 1991; Polis, 1991; Schoenly *et al.*, 1991; Goldwasser & Roughgarden, 1993, 1997; Cabana & Rasmussen, 1996; Vander Zanden *et al.*, 1999; Post *et al.*, 2000), and, indeed, their lengths tend to be in the range of about 3–5 (for longer estimates see Polis, 1991; Martinez, 1991). For example, of 113 webs in Cohen *et al.* (1990), the average of the average food chain length within a web is 2.88 (S.D. 0.87), and the average maximum chain length is 4.21 (S.D. 1.51). More recent isotope methods for determining the number of trophic levels (in aquatic systems) have concluded that there are between 3 and 5 (Cabana & Rasmussen, 1996; Vander Zanden *et al.*, 1999; Post *et al.*, 2000). These food chain length estimates are, then, consistent with the hypothesis that it is food chains that are the expressions, and that the combinatorial degree is determined by the food chain length.

A second prediction of this “combinatorial degree $d \approx$ food chain length L ” hypothesis is that, since the combinatorial degree is invariant, food chain length should not vary as a function of island area. Although food chain length does appear to increase somewhat as a function of species richness (Briand, 1983; Hall & Raffaelli, 1991; Vander Zanden *et al.*, 1999; Post *et al.*, 2000), we are unaware of any documented trend in food chain length as a function of island size.

We may make a third prediction by recalling eqn (7) from Subsection 2.5, which stated that $d = vL - v + 1$, where v is the scaling exponent relating edge-degree δ to the number of vertices C in a type-network. This may be manipulated to become $v = (d - 1)/(L - 1)$. Our hypothesis that $d \approx L$ (and each is > 1) for island biota networks predicts that $v = 1$. For ecosystems, type-networks are food webs, and edges are trophic links. Our prediction is therefore that, in food webs, the number of trophic links per species, or edge-degree δ , scales proportionally with the number of species in the web, C . The earliest studies of edge-degree scaling argued that $\delta \sim C^0$ (e.g. Pimm, 1982; Cohen & Briand, 1984; Sugihara *et al.*, 1989; Cohen *et al.*, 1990; Warren, 1990), meaning $v = 0$. (This would imply that island biota networks are not combinatorial at all.) Later researchers, however, suggested that such edge-degree invariance may primarily be due to “artistic convenience” in drawing food webs, and that more detailed food webs reveal that $v > 0$: for example, Pimm *et al.* (1991) give $v = 0.3$ or 0.4 , Havens (1992) gives $v = 0.4$, and Martinez (1992), Deb (1995), and Havens (1997) argue that $v = 1$. These most recent estimates are consistent with our prediction. If, however, v is sometimes lower than 1, then it would imply that food chain length is greater than the combinatorial degree [again, as related by eqn (7)].

Finally, notice that if this “combinatorial degree \approx food chain length” hypothesis is true, then archipelagos with longer food chains are predicted to have lower species–area slopes, all things equal. This is because biota with longer chains have more combinatorial room to build novel expression types with which to fill new habitat types without the need for new species;

biota with shorter chains exhaust their possible expression types more quickly, and a new organism type (via speciation or invasion) is needed in order to have new expression types capable of adjusting to novel habitat types. A counterintuitive consequence of this is that if healthier biotas tend to have longer food chains (e.g. of length 5 rather than, say, 3), then healthier biotas should scale up the number of species *less* quickly than less healthy biota with shorter chains, all things equal.

Another kind of competitive network is cities, or networks of businesses. Using web-accessible business directories (i.e. online yellow pages), for 82 cities we measured the number of businesses in the city N and the number of types, or categories, of business C . The cities were chosen arbitrarily, the only guide being to acquire a large range of city sizes. Data were obtained via the online search engine www.superpages.gte.net. The search engine allows one to search for all businesses and all business types among businesses whose first letter is a certain character. Searches via very common first-letter characters lead to too many listings and the engine responds with an “error”, so we carried out searches using the relatively less common first-letter characters ‘j’ and ‘k’. Figure 10 shows the results for ‘j’ (the plots for ‘k’, not shown, look nearly identical), and the differentiation of a city increases roughly as $C \sim N^{0.64}$. Note that this kind of scaling law is important to know for those wishing to use economic diversity measures to diagnose a city’s economic health: any good measure of economic diversity would have to account for the diversity that is due simply to the city being as large as it is, and an appropriate measure might accordingly be $C/N^{0.64}$. We do not take up here possible explanations for this scaling relationship.

4. Discussion and Conclusion

Consider some of the generalizations we may make about the scaling of differentiation in selected networks. The first, and most central, generalization is that differentiation increases with size. This is not some kind of tautology, for as discussed in Section 1, it is *a priori* possible that a fixed set of node types could serve as

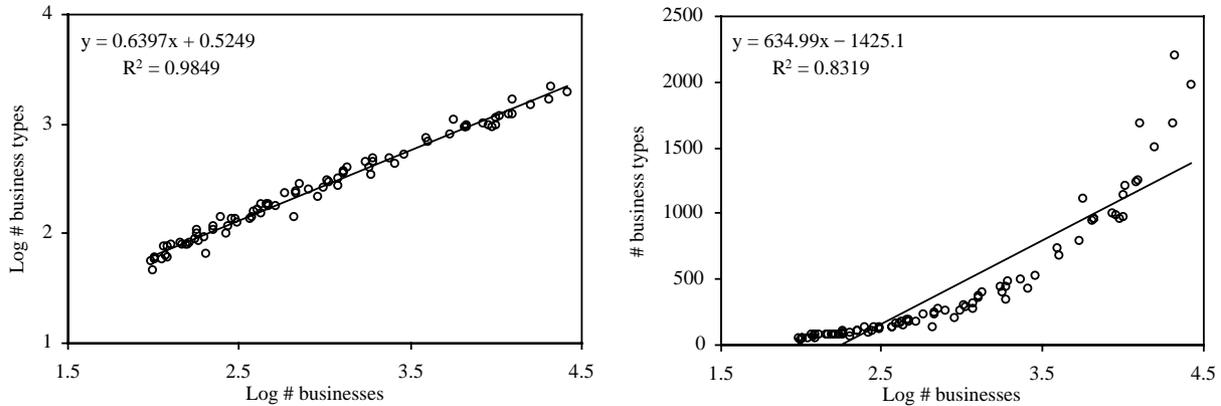


FIG. 10. Log–log (base 10) (left) and semi-log (right) plots of number of business types vs. the total number of businesses, for 82 cities in the United States.

a universal language from which all possible expression types could be built. If this “universal language” strategy were taken, increases in network complexity, E , would be achieved by increasing the average length of an expression. Selected networks do not, then, take the “universal language” approach. Instead, selected networks appear to be governed by an optimization hypothesis—the Minimal N Hypothesis—so that network complexity is economically accommodated by the network. Increasing expression length as a function of network complexity would lead to an unnecessarily large and costly network size. Therefore, expression length (and combinatorial degree) is kept invariant in selected networks, and increased complexity must come entirely from increased differentiation. It follows that selected networks should not only increase differentiation with network size, but that they should be related by a power law. Indeed, we saw that for each of the 12 kinds of selected network studied above, differentiation fits a power-law relationship (see Table 1). In a majority of the cases (7 of 12) a logarithmic relationship could be rejected; and of the five cases where a logarithmic relationship could not be rejected, four of the five (all but nervous systems) had lower correlations under a power-law model. Furthermore, except possibly for military offices, the combinatorial degrees are greater than one in each case, meaning that each kind of network acts combinatorially. An alternative optimization hypothesis—the Habitat-Filling Hypothesis—was used to explain why

differentiation follows a power law in networks of competing organisms. That is, we explained why species–area plots follow power laws, and argued that the power-law exponent in these plots may be due to the average food chain length.

Examination of the combinatorial degree values in Table 1 reveals two starkly distinct regimes among selected networks: the networks undergoing natural selection have high combinatorial degrees (about 5 for neocortex, 8 for ant colonies, 17 for organisms), and all the others have relatively low combinatorial degrees (between 1 and 3). [It also appears to be low (around 2) in single-community societies, such as Tasmanians, Bushmen, and the Maori (see Carneiro, 1967; Bonner, 1993).] All the low combinatorial degree selected networks are human constructions—circuits, Legos, businesses, and universities—and we speculate that the reason for the difference in scaling exponents is that it is easy to acquire new types among human-oriented networks. Humans can quickly build a new electronic component type or Lego piece type, and humans can themselves quickly *become* a new employee or faculty type—humans may be trained in a few weeks or years, and, at worst, in one generation new employee types or faculty types can be output from the educational system. In short, humans are plastic and inventive, and it is thus inexpensive to increase the number of node types in systems for which human ingenuity is at the base. For nervous systems, ant colonies, and organisms,

TABLE 1
Summary of results*

Network	Node	No. data points	Range of $\log N$	Log-log R^2	Semi-log R^2	p_{power}/p_{log}	Relationship between C and N	Comb. degree	Exponent v for type-net scaling	Figure in text
<i>Selected networks</i>										
Electronic circuits	Component	373	2.12	0.747	0.602	0.05/4e-5	Power law	2.29	0.92	2
Legos™	Piece	391	2.65	0.903	0.732	0.09/1e-7	Power law	1.41	—	3
<i>Businesses</i>										
military vessels	Employee	13	1.88	0.971	0.832	0.05/3e-3	Power law	1.60	—	4
military offices	Employee	8	1.59	0.964	0.789	0.16/0.16	Increasing	1.13	—	4
universities	Employee	9	1.55	0.786	0.749	0.27/0.27	Increasing	1.37	—	4
insurance co.	Employee	52	2.30	0.748	0.685	0.11/0.10	Increasing	3.04	—	4
<i>Universities</i>										
across schools	Faculty	112	2.72	0.695	0.549	0.09/0.01	Power law	1.81	—	5
history of Duke	Faculty	46	0.94	0.921	0.892	0.09/0.05	Increasing	2.07	—	5
<i>Ant colonies</i>										
caste = type	Ant	46	6.00	0.481	0.454	0.11/0.04	Power law	8.16	—	6
size range = type	Ant	22	5.24	0.658	0.548	0.17/0.04	Power law	8.00	—	6
Organisms	Cell	134	12.40	0.249	0.165	0.08/0.02	Power law	17.73	—	7
Neocortex	Neuron	10	0.85	0.520	0.584	0.16/0.16	Increasing	4.56	—	9
<i>Competitive networks</i>										
Biotas	Organism	—	—	—	—	—	Power law	≈ 3	0.3 to 1.0	—
Cities	Business	82	2.44	0.985	0.832	0.08/8e-8	Power law	1.56	—	10

*(1) The kind of network, (2) what the nodes are within that kind of network, (3) the number of data points, (4) the logarithmic range of network sizes N (i.e. $\log(N_{max}/N_{min})$), (5) the log-log correlation, (6) the semi-log correlation, (7) the serial-dependence probabilities under, respectively, power-law and logarithmic models, (8) the empirically determined best-fit relationship between differentiation C and organization size N (if one of the two models can be refuted with $p < 0.05$; otherwise we just write “increasing” to denote that neither model can be rejected), (9) the combinatorial degree (i.e. the inverse of the best-fit slope of a log-log plot of C versus N), (10) the scaling exponent for how quickly the edge-degree δ scales with type-network size C (in those places for which data exist), (11) figure in this text where the plots are presented. Values for biotas represent the broad trend from the literature.

on the other hand, the creation of a new node type is costly and difficult: natural selection is required. Having a greater combinatorial degree drastically reduces the rate at which new node types must be added. However, this comes with a cost: each expression itself must be more complex. That is, more components must interact in a coordinated, or social, manner in order that an expression be implemented. This is one reason that even small nervous systems, ant colonies, and organisms are so much more difficult to understand than, say, (similarly sized) electronic circuits: their expressions are longer, and the rules governing the formation of expressions are accordingly more difficult to infer.

The authors thank Drs Daniel McShea, Richard Burton, Warren G. Hall, and Zhi-Yong Yang for valuable discussions and comments.

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APPENDIX A

Data for electronic circuits were acquired from the following places:

- Horowitz & Hill (1989)
- members.aol.com/beacoqui/main/partlist.htm
- members.aol.com/stanpope2/khamm/parts.html
- optics.caltech.edu/billgr/tec-control/teccparts.html
- videogames.org/html/PongStuff/PartsList.html
- www.bloblulent.com/hp300/peripherals
- www.ee.washington.edu/circuit_archive/circuits/
- www.electronics_projects.net
- www.hiviz.com/tools/triggers/makeown.htm
- www.interq.or.jp/japan/se_inoue/e_samp11.htm
- www.math.niu.edu/~behr/RC/KW/kw-low-schem.pdf
- www.nostalgiaair.org/NostalgiaAir/Schematics/schem_SCT.htm
- www.paia.com
- www.pjrc.com/tech/8051/board3/schematic.html
- www.plitron.com/Pages/Products/Audio/circuit.htm
- www.portlandrobotics.org
- www.solorb.com/gfc/elect
- www.space-rockets.com/Altparts.html
- www.velleman.be/kits
- www.xs4all.nl/~sbolt/e-foto

APPENDIX B

Data for 52 species of ants were obtained from the following sources, where after the citation we have placed the species name and, in square brackets, the logarithm of maximum colony size, the number of castes, and the maximum-to-minimum head ratio ('n' means "no data"). Brandao (1978): *Formica perpilosa* [2.65, 3, n]. Brandao (1983): *Ondontomachus affinis* [2.65, 1, n]. Beshers & Traniello (1994): *Trachymyrmex septentrionalis* [3.08, 1, 1.67]. Carlin (1981), Corn (1980), Franks (1985), Franks & Norris (1986), Kaspari & Vargo (1995): *Orectognathus versicolor* [2.02, 2, 1.47], *Cephalotes atratus* [4.05, 2, 2.2], *Eciton burchelli* [5.92, 4, 3.37], *Leptothorax longispinosus* [1.66, 1, 1.66], *Pheidole dentata* [2.98, 4, n]. Fowler *et al.* (1986) and Wilson (1980): *Atta sexdens* [6.90, 4, 20]. Jaffe (1987): *Atta laevigata* [7, 12, n], *Atta cephalotes* [7, 10, n], *Acromyrmex octospinosus* [5, 4, n], *Acromyrmex landolti* [4, 3, n], *Trachymyrmex urichi* [3, 1, n], *Mycocepurus* sp. [2, 1, n], *Myrmecocrypta* sp. [2, 1], *Crematogaster sumichrasti* [5, 2, n], *Myrmica rubra* [4, 1, n], *Leptothorax unifasciatus* [2, 1, n], *Eurhopalothrix heliscata* [2, 1, n], *Novomessor albisetosus* [2, 1, n], *Ectatomma ruidum* [3, 1, n], *Neoponera apicalis* [2, 1, n], *Odontomachus bauri* [3, 1, n], *Pseudomyrmex triplarinus* [4, 1, n], *Pseudomyrmex termitarius* [2, 1, n], *Oecophylla longuinoda* [5, 2, n], *Camponotus rufipes* [4, 2, n], *Gigantypus destructor* [1, 1, n], *Azteca foreli* [6, 1, n], *Conomyrma biconis* [4, 1, n], *Nothomyrmecia macrops* [2, 1, n]. Longhurst & Howse (1979): *Megaponera foetens* [2.93, n, 2.13]. Moffett (1985): *Acanthomyrmex notabilis* [1.7, 2, n]. Moffett (1986a): *Oligomyrmex overbecki* [2.60, 2, 1.55]. Moffett (1986b): *Proatta butteli* [4.00, 1, 1.37]. Moffett (1988): *Pheidologeton diversus* [5.40, 4, 3.25]. Traniello (1982): *Amblyopone pallipes* [1.54, 1, n]. Traniello & Jayasuriya (1985): *Aneuretus simoni* [2.03, 2, n]. Wheeler (1984): *Procryptocerus scabriusculus* [1.79, 1,

1.19], *Zacryptocerus christopherseni* [3.60, n, 1.87]. Wheeler (1986): *Azteca chartifex* [2.75, 2.5, 1.65], *Azteca trigona* [5.70, 2, 2.41]. Wilson (1978): *Solenopsis geminata* [6.00, 5, 4.03], *Solenopsis invicta* [5.36, 4, 3.33]. Wilson (1985): *Atta cephalotes* [6.60, n, 7.14]. Wilson (1986): *Erebomyrma nevermanni* [2.26, 2, n]. Wilson (1987): *Formica exsectoides* [5.38, n, 1.19], *Prenolepis imparis* [3.34, n, 1.54]. Wilson & Fagen (1974): *Leptothorax curvispinosus* [2.00, 1, n]. Wilson & Brown (1984): *Eurhopalothrix heliscata* [2.67, 1, 1.17]. Wilson & Holldobler (1986a): *Basiceros manni* [1.70, n, 1.18]. Wilson & Holldobler (1986b): *Prionopelta amabilis* [2.85, 1, 1].

APPENDIX C

In order to distinguish between the power-law ($\log C \sim \log N$) and logarithmic ($C \sim \log N$) models, a statistical test was carried out, which we describe here. If a model fits the data, then the sign of the residuals about the best-fit line should not vary in a systematic fashion as a

function of $\log N$. Suppose the data are partitioned into subsets, or groups, of size m of adjacent data. Thus, suppose that g_1 is the first set of m adjacent residuals (i.e. the m residuals at the low end of $\log N$), g_2 the subsequent set of m adjacent residuals, and so on. Let r_i be the average value of the residuals in g_i . If the model is a good fit, then the signs of the average residuals for nearby groups should be independent of one another. In particular, the probability should be $1/2$ that r_i and r_{i+1} have the same sign. Let $h_i = 0$ if r_i and r_{i+1} have the same sign, and $h_i = 1$ otherwise. The binary sequence $\langle h_1, h_2, \dots, h_{k-1} \rangle$ thus summarizes the serial dependence of the signs of the average residuals within the k groups. We may then compute the probability of this sequence being generated at random. That is, the probability of getting r 0's in the binary sequence of length k is $C_r^k (1/2)^k$. Because we are primarily interested in identifying large-scale deviations from the models, we *a priori* chose to create approximately 40 groups for each data set. (When the total number of data points, n , was less than this, n groups of size one were used.)