

indeterminant problem. A muscle group's weighted mean mechanical advantage at a joint was calculated as $\bar{r} = r_1 \times F_1 + r_2 \times F_2 + \dots + r_n \times F_n$, where $F_1 = (A_1/A_{tot})F_{tot}$, $F_2 = (A_2/A_{tot})F_{tot}$, and $A_{tot} = A_1 + A_2 + \dots + A_n$. F_{tot} represents the total muscular force required to balance the joint moment exerted by the ground reaction force, A_{tot} is the total fiber cross-sectional area of the muscle group, and n is the number of muscles acting about the joint. In this analysis inertial effects of limb segment movement during the support phase are ignored; however, these forces are small compared to the ground reaction force during steady speed locomotion.

12. The coefficient of variation (CV) for changes in EMA during the middle third of the support period of the stride ranged from 0.06 to 0.74 for all joints in all species (overall mean CV, 0.31 ± 0.22 ; $n = 56$, eight limb joints in each of seven species). EMA was most consistent at the distal limb joints (0.15 ± 0.08 , $n = 28$) compared to the proximal limb joints (0.46 ± 0.19 , $n = 28$).
13. C. R. Taylor, *J. Exp. Biol.* **115**, 253 (1985); A. A. Biewener and C. R. Taylor, *ibid.* **123**, 383 (1986). Stride frequency at the trot-gallop transition also decreases in a regular way with increased body size, consistent with the view that animals move as resonant mass-spring systems to lower energy cost [N. C. Heglund, C. R. Taylor, T. A. McMahon, *Science*, **186**, 1112 (1974); N. C. Heglund and C. R. Taylor, *J. Exp. Biol.* **138**, 301 (1988)].
14. Available data, though limited, indicate that under conditions of steady speed locomotion, maximal ground reaction forces acting on a limb generally are between two and four times an animal's body weight, irrespective of an animal's body size [T. A. McMahon, in *Scale Effects in Animal Locomotion*, T. J. Pedley, Ed. (Cambridge Univ. Press, Cambridge, 1977), pp. 143–151; G. A. Cavagna, N. C. Heglund, C. R. Taylor, *Am. J. Physiol.* **223**, 244 (1977)]. R. McN. Alexander *et al.* [*J. Zool. Lond.* **183**, 135 (1979)] have argued, based on relative limb support time (duty factor) that, within ungulates, ground reaction forces likely decrease with increased size. However, no measurements of ground reaction forces for a broad range of these species have been made.
15. R. McN. Alexander *et al.*, *J. Zool. Lond.* **194**, 539 (1981).
16. Reported values for the maximum isometric force per fiber cross-sectional area (isometric stress) of vertebrate striated muscle measured in situ range from 150 to 300 kPa, averaging 200 kPa [R. I. Close, *Physiol. Rev.* **52**, 129 (1972); A. V. Hill, *First and Last Experiments in Muscle Mechanics* (Cambridge Univ. Press, Cambridge, 1970); A. K. Perry, R. Blickhan, A. A. Biewener, N. C. Heglund, C. R. Taylor, *J. Exp. Biol.* **137**, 207 (1988); C. L. Prosser, *Comparative Animal Physiology* (Saunders, Philadelphia, 1973); J. B. Wells, *J. Physiol. Lond.* **178**, 252 (1965); A. A. Biewener, unpublished data for cat soleus and gastrocnemius].
17. C. R. Taylor, N. C. Heglund, G. M. O. Maloij, *J. Exp. Biol.* **97**, 1 (1982).
18. N. C. Heglund, M. A. Fedak, C. R. Taylor, C. A. Cavagna, *ibid.*, p. 57.
19. M. B. Hidebrand, *Analysis of Vertebrate Structure* (Wiley, New York, 1986); G. V. Lauder, *Paleobiology* **7**, 430 (1981); J. M. Smith and R. J. G. Savage, *Zool. J. Linn. Soc.* **42**, 603 (1956); D. B. Wake and K. Liem, in *Functional Vertebrate Morphology*, M. B. Hildebrand, Ed. (Harvard Univ. Press, Cambridge, MA, 1985), chap. 17.
20. J. E. Bertram, M. C. LaBarbera, C. R. Taylor provided valuable comments on earlier drafts of this manuscript. Supported by NSF grant DCB 85-14899.

28 December 1988; accepted 10 April 1989

Scale Invariance in Food Web Properties

GEORGE SUGIHARA, KENNETH SCHOENLY, ALAN TROMBLA

The robustness of five common food web properties is examined by varying the resolution of the data through aggregation of trophic groupings. A surprising constancy in each of these properties is revealed as webs are collapsed down to approximately half their original size. This analysis of 60 invertebrate-dominated community food webs confirms the existence of all but one of these properties in such webs and addresses a common concern held by critics of food web theory that observed food web properties may be sensitive to trophic aggregation. The food web statistics (chain length; predator/prey ratio; fraction of top, intermediate, and bottom species; and rigid circuits) are scaling in the sense that they remain roughly invariant over a wide range of data resolution. As such, within present standards of reporting food web data, these statistics may be used to compare systems whose trophic data are resolved differently within a factor of 2.

OBSERVATIONS FROM LARGE COLLECTIONS of food webs extracted from the literature have produced a number of intriguing empirical generalizations about the structure of ecosystems (1–16). These simple patterns are regarded by some investigators (4, 17, 18) as law-like and fundamental to our understanding of ecosystem architecture. They include the following well-known properties: P1, food chains are typically short, normally consisting of five or fewer trophic levels (1–3, 17, 19, 20); P2, network connectance (the number of possible linkages as a fraction of all

possible linkages in the web) declines predictably as species number increases, so that the product of species number and connectance (S·C) is roughly constant (5–7, 18, 21, 22); P3, the ratio of predator to prey species in a web is roughly constant, between 1 and 3, independent of total species number (11, 23); P4, the fraction of top predators (not preyed upon by any species in the web), basal species (pure autotrophs or detritus), and intermediate species is independent of total species number and, as such, is scale-invariant (8, 9); and P5, species trophic niches tend to be packed together closely, in

that most if not all observed consumer overlap graphs (a food web diagram in which points represent consumer species and lines (not arrows) connect pairs of points to indicate when two consumers share one or more food resources in common) are rigid circuit graphs; that is, they are paved with triangles (12–17). Technically, a rigid circuit graph is one in which all circuitous paths through more than three points are shortened by a chord (13).

Each of these properties is based in part on an ever-expanding compendium of food webs collected from the literature that now includes more than 113 cases (10, 12, 24, 25). These include a wide variety of natural environments; 23 terrestrial, 32 freshwater, and 58 marine webs. Although the prospect of acquiring an understanding of ecosystems from such general properties is attractive, critics of food web theory have expressed concern over the quality of the data being used to derive them, specifically over the lack of uniformity exercised in choosing trophic categories (4, 26–28). For example, within certain webs of this collection one finds fish resolved to the species or ontogenetic level, whereas in other webs, studied by different investigators, they may be lumped together as a single category. Moreover, this lack of uniformity in aggregation and resolution exists even for taxonomic and trophic groupings within individual webs. These rather troubling concerns about the existing food web database have cast serious doubt on the validity of the hypothesized food web generalizations (4, 21, 26–28), although, to date, such criticisms have only been supported with anecdotal and hypothetical examples (21).

To evaluate these shortcomings in the existing database directly, as they affect the derived food web properties, would require that the original field investigators reassemble each web in a more comprehensive and uniform manner. The difficulty of this task for even one system is evidenced by the fact that there are no good examples of such comprehensive food web data published for large whole systems (29). As an alternative test, one can study how systematic lumping of trophic categories in existing data affects whether one observes the claimed food web properties. That is, are the above properties sensitive to the various levels of aggregation chosen or are they “scaling” in the sense that they remain relatively constant over a wide range of food-web data resolution (30)?

To answer this question, we have examined a newly compiled set of 60 inverte-

G. Sugihara and A. Trombla, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093.
K. Schoenly, Department of Biology, University of New Mexico, Albuquerque, NM 87131.

brate-dominated community food webs (31) (Table 1). These webs extend the existing catalog of 113 and have a comparatively high level of taxonomic resolution, with

over 80% of the trophic categories resolved to the species and genus level (32–61). They span a wide range of macro- and microhabitats, from gall–gall maker–parasitoid (46,

47) and phytotelmata webs (49–55), to dungpads (39–41), plant-herbivore (56–61), carrion (42–45), and rotting wood systems (48), to stream, spring, and lake biotas (32–

Table 1. Properties and data sources of 60 invertebrate-dominated food webs.

Type of system	S	P1				P2	P3	P4			P5	
		MIN		MAX				TF	IF	BF	Rigid	Ref.
		Max. chain length	Mean chain length	Max. chain length	Mean chain length							
Thermal spring, Yellowstone Park	15	2	2	2	2	2.867	1.4	0.333	0.6	0.067	Yes	32
Deep Creek, Idaho-Utah	18	2	1.125	3	2.033	3	1.25	0.333	0.5	0.167	Yes	33
Doe Run (Station 1), KY	11	2	1.5	4	2.825	2.727	1	0.182	0.636	0.182	Yes	34
Morgan Creek, KY	24	2	1.857	6	3.726	3.917	1.167	0.25	0.625	0.125	Yes	35
Dee River, Wales	34	3	1.354	4	2.043	3.118	1.25	0.412	0.324	0.265	No	36
Aire, Nidd, & Wharfe Rivers, U.K.	60	3	2.023	4	3.337	3.083	1.293	0.317	0.567	0.117	No	37
River Clydach, S. Wales	29	2	1.675	4	2.349	3.655	1.048	0.276	0.483	0.241	Yes	38
Dung (all links), IL	17	2	2	2	2	2.059	1.778	0.471	0.471	0.059	Yes	39
Dung (common links), IL	16	2	2	2	2	1.938	1.667	0.438	0.5	0.062	Yes	39
Dung, Chihuahua Desert, U.S.	28	2	1.238	2	1.484	1.321	3.857	0.75	0.214	0.036	Yes	40
Dung (day 1, all links), NY	26	1	1	4	3	2.692	1.785	0.462	0.5	0.038	Yes	41
Dung (day 1, estab. links), NY	26	1	1	2	1.679	2.346	2.778	0.654	0.308	0.038	Yes	41
Dung (day 5, all links), NY	35	2	1.177	4	3.061	4.171	1.889	0.486	0.486	0.029	Yes	41
Dung (day 5, estab. links), NY	33	2	1.063	3	2.491	3.667	1.882	0.485	0.485	0.030	Yes	41
Toad carrion, Guan., Costa Rica	26	1	1	1	1	1.885	4.2	0.808	0	0.192	Yes	42
Toad carrion, Osa, Costa Rica	50	2	1.135	2	1.683	2.62	1.162	0.26	0.6	0.14	Yes	42
Dog carcass, Costa Rica	27	2	1.391	2	1.682	1.741	6.5	0.852	0.111	0.037	Yes	43
Carrion (day 2), Aden Crater, NM	18	2	1.125	2	1.364	1.278	8.5	0.889	0.056	0.056	Yes	44
Carrion (day 9), Hueco Mtns., TX	27	2	1.2	4	2.549	2.667	1.182	0.185	0.778	0.037	Yes	44
Carrion (day 8), White Sands, NM	21	2	1.125	2	1.611	1.905	4	0.762	0.191	0.048	Yes	44
Carrion (day 4), Chihuahua Desert	25	2	1.231	3	1.87	2.6	2	0.52	0.44	0.04	Yes	45
Carrion (day 14), Chihuahua Desert	14	2	1.1	2	1.667	2.143	3.25	0.714	0.214	0.071	Yes	45
Oak galls, Wytham Wood, U.K.	62	3	1.87	7	4.281	2.984	1.564	0.371	0.613	0.016	Yes	46
Galls (<i>A. canescens</i>), CA	36	3	2.357	5	3.292	2.25	1.591	0.389	0.583	0.028	Yes	47
Galls (<i>A. polycarpa</i>), CA	37	3	2.539	5	3.382	2	1.5	0.351	0.622	0.027	Yes	47
Felled oak logs (1 yr old), U.S.	47	3	1.686	4	2.262	1.298	2.095	0.553	0.383	0.064	Yes	48
Felled oak logs (>3 yr), U.S. #1	87	3	1.31	3	1.557	1.299	4.421	0.781	0.184	0.034	Yes	48
Felled oak logs (>3 yr), U.S. #2	2	1	1	1	1	0.5	1	0.5	0	0.5	Yes	48
Felled pine logs (1 yr), U.S. #1	75	3	1.985	3	2.245	1.824	1.972	0.514	0.446	0.04	Yes	48
Felled pine logs (1 yr), U.S. #2	15	1	1	1	1	0.933	14	0.933	0	0.067	Yes	48
Felled pine logs (>3 yr), U.S. #1	31	3	1.3	3	1.758	1.387	2.727	0.645	0.323	0.033	Yes	48
Felled pine logs (>3 yr), U.S. #2	5	1	1	1	1	0.8	4	0.8	0	0.2	Yes	48
Pitchers (<i>N. albo.</i>), Malaysia	19	3	1.667	4	2.5	1.842	1.333	0.368	0.474	0.158	Yes	49
Pitchers (<i>N. ampul.</i>), Malaysia	18	2	1.5	4	3	2.333	1.071	0.222	0.611	0.167	Yes	49
Pitchers (<i>N. dist.</i>), Sri Lanka	8	2	1.571	2	1.7	1.25	1.5	0.5	0.25	0.25	Yes	49
Pitchers (<i>N. mad.</i>), Madagascar	11	3	1.8	3	2.353	1.727	0.889	0.182	0.546	0.273	Yes	49
Pitchers (<i>N. perv.</i>), Seychelles	5	2	1.5	2	1.667	1.2	1	0.4	0.2	0.4	Yes	49
Pitchers (<i>S. purpurea</i>), SE U.S.	6	2	1.4	2	1.4	1	1.333	0.5	0.167	0.333	Yes	50
Pitchers (<i>N. mirab.</i>), Hong Kong	11	2	1.5	3	1.9	1.273	1	0.273	0.455	0.273	Yes	51
Treeholes (<i>F. sylvatica</i>), U.K. #1	3	1	1	1	1	0.667	2	0.667	0	0.333	Yes	52
Treeholes (<i>F. sylvatica</i>), U.K. #2	6	1	1	1	1	0.833	2	0.667	0	0.333	Yes	52
Treeholes (all links), Australia	12	2	1.333	7	4.563	2	0.818	0.083	0.667	0.25	Yes	52
Treeholes (obs. links), Australia	11	2	1.8	3	2.333	1.364	0.778	0.182	0.455	0.364	Yes	52
<i>Heliconia bihai</i> , Venezuela	7	1	1	1	1	1.143	1.333	0.571	0	0.429	Yes	53
<i>H. imbricata</i> , Costa Rica #1	7	1	1	1	1	1	1.333	0.571	0	0.429	Yes	54
<i>H. imbricata</i> , Costa Rica #2	2	1	1	1	1	0.5	1	0.5	0	0.5	Yes	54
<i>H. wagneriana</i> , Costa Rica	7	1	1	1	1	1.143	1.333	0.571	0	0.429	Yes	54
Wet stump hole, Alabama #1	9	2	1.5	2	1.75	1.333	1.167	0.333	0.444	0.222	Yes	55
Wet stump hole, Alabama #2	3	1	1	1	1	0.667	2	0.667	0	0.333	Yes	55
Treeholes (<i>Abies+</i>), Germany #1	3	1	1	1	1	0.667	2	0.667	0	0.333	Yes	55
Treeholes (<i>Abies+</i>), Germany #2	8	1	1	1	1	0.875	3	0.75	0	0.25	Yes	55
Tree canopies, W. Europe	25	2	2	2	2	1.12	1.917	0.52	0.4	0.08	Yes	56
<i>Bacharis fauna</i> , CA	8	2	2	3	2.8	1.875	1.167	0.25	0.625	0.125	Yes	57
<i>Rumex fauna</i> , Lancaster, U.K.	9	3	2.333	5	3.375	1.444	1.333	0.333	0.556	0.111	Yes	58
Pine fauna, Oxshott Heath, U.K.	23	3	2	4	3.568	2.087	1.105	0.174	0.739	0.087	Yes	59
Mistletoe fauna, TX	23	3	2.375	4	2.55	1.13	3.143	0.696	0.261	0.043	Yes	60
Soybean (3rd wk, all links), U.S.	7	2	2	2	2	1.429	1.2	0.286	0.571	0.143	Yes	61
Soybean (3rd wk, obs. links)	7	2	2	2	2	1.143	1.2	0.286	0.571	0.143	Yes	61
Soybean (12th wk, all links)	15	2	1.8	3	2.259	2.4	1.4	0.333	0.6	0.067	No	61
Soybean (12th wk, obs. links)	15	2	1.8	3	2.263	1.867	1.4	0.333	0.6	0.067	Yes	61

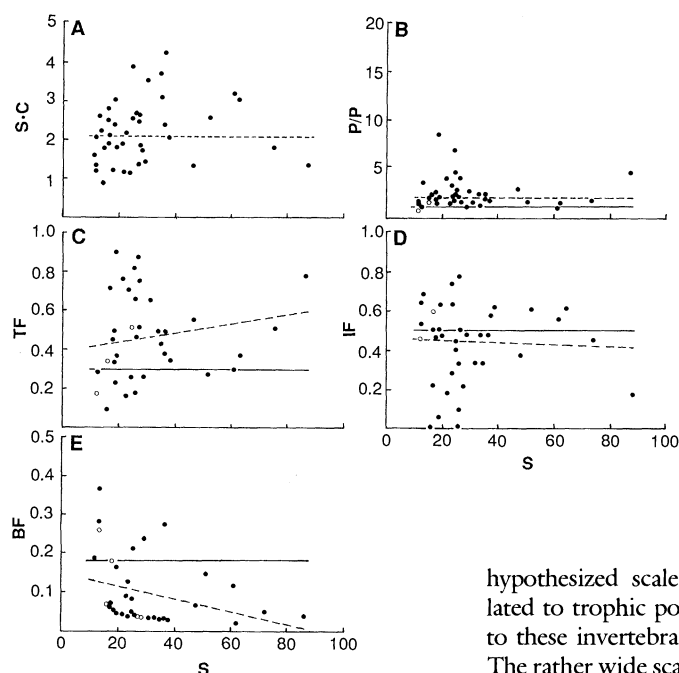


Fig. 1. (A) Plot of species number times connectance (S-C) as a function of web size of species. The fitted solid line is constrained to be horizontal. (B-E) The four trophic ratios plotted as a function of number. The horizontal lines are drawn to show the scale-invariant value given by Briand and Cohen (8). The dashed lines are regression lines [see (62) for coefficients]. All plots are for webs in Table 1 containing ten or more species. Open circles indicate coincident points.

38). The results in Table 1 and Fig. 1 show that these webs have many of the same characteristics with regard to food web structure as the earlier catalog. Maximal food chain length, P1, was calculated in two different ways in Table 1, depending on whether chain length was reckoned as the length of the longest maximal path (MAX) connecting a top predator to autotroph or detritus or as the length of the longest minimal path (MIN) connecting a top and bottom species in a web. The average MIN length is the average of all minimal paths between top predators and basal species, whereas the average MAX length is the average of all possible paths between top predators and basal species. The MAX calculation is the convention used by earlier investigators (4, 8–10, 17, 23, 24). The range of average MAX values in Table 1 is 1 to 4.56 with a mean of 2.10 trophic links, which is similar to that reported by Briand and Cohen (24) for webs from planar habitats, that is, a range of 2 to 4.28 trophic links with a mean of 2.65. The invertebrate-dominated webs as a whole appear to be slightly shorter than those reported by Briand and Cohen, a feature that appears to be largely due to the carrion webs (Table 1).

Following precedent (8, 24), we attempt no formal statistical tests of differences here because of uncertainties about the extent to which the webs in either collection form a random sample from a well-defined statistical universe of webs. Figure 1A shows that S-C is roughly independent of species number. That is, network connectance in webs containing more than ten species falls approximately as the number of trophic species. Figures 1, B through E, shows how the

hypothesized scale-invariant properties related to trophic position, P3 and P4, apply to these invertebrate-dominated webs (62). The rather wide scatter shown here is similar to that observed by Briand and Cohen (8, 17). Although the predator/prey ratios (P/P), P3, are slightly higher here, they appear to be independent of the number of species in the web, as are the fraction of top (TF) and intermediate species (IF), P4. The fraction of basal species (BF), on the other hand, rises slightly as webs contain fewer species; however, the trend is not conclusive. All but three of the webs in Table 1 have the rigid circuit property (P5), which agrees with the fact that all of the original 40 webs (12) and almost all of the 113 webs in the presently expanded collection of Briand and Cohen (24) are rigid circuit in the consumer overlap graph (17). Thus, with the possible exception of lack of scale invariance in BF, the five common food web properties listed above extend to the present collection of 41 of the 60 additional webs.

To study the effect of lumping and loss of resolution in the data, we aggregated trophic categories for each of the webs in Table 1 stepwise, using a simple clustering algorithm based on increasing trophic similarity (63). The similarity of two species is measured as the quotient of the numbers of predators and prey shared in common, over the total number of predators and prey in their union. Each step of this hierarchical clustering procedure involves lumping the two trophic categories that are most similar in terms of their predators and their prey (64). Hence, the aggregates are formed as the union of the constituent species, and clusters are linked with feeding arrows if one or more members share an arrow. The webs of Table 1 are lumped one step at a time until the reduced web contains the greater of either half of the original number of species or ten species. We restrict this analysis to

webs containing more than ten species in order to avoid the obvious artificial biases that must occur in very small webs.

Results of this analysis for P1, P2, P3, and P4 are summarized in Fig. 2. Similar results were obtained when webs were reduced to 80 and 70% of the original number of species. Figure 2 shows the distribution of the maximum fractional error and coefficient of variation of food web properties P1 through P4 as webs are collapsed in aggregation. Maximum fractional error represents the largest deviation from the original web encountered during any step of the aggregation procedure. Remarkably, none of these properties appears to be highly sensitive to lumping or to the degree of resolution in the data, although some minor systematic trends were observed, especially in the coarsest aggregates (most aggregated webs). This is reflected in the maximum deviations, where small but systematic errors were most apparent for P2, which tended to fall slightly with increasing aggregation, and for P4-BF, which tended to rise slowly toward 1/3 with increasing aggregation. Paine's anecdotal examples of rocky intertidal webs show P2 (connectance) to be fairly robust to certain arbitrary decisions about aggregation with a possible slight tendency for P2 to increase with aggregation [see tables 2 and 3 in (21)]. Predator/prey ratios were more variable with lumping; however, they did not show a clear systematic trend.

Perhaps the greatest surprise of this analysis is the relative constancy of food chain lengths. Computations of chain length based on the MIN criterion for distance (a metric based on the shortest path between top and basal species) appears to be more robust to variability in data resolution than the conventional MAX criterion (reckoned from the longest path between species and the average of all paths) and as such may be a better scaling statistic for cross-system comparisons. Of the properties P1 through P4, the MIN chain length statistic appears to be the most robust, and the connectance (P2) and trophic position properties (P3 and P4) appear to be the most fragile. In particular, of P4, the proportion of basal species appears to be most sensitive to trophic aggregation. Nonetheless, the coefficient of variation for each of these properties is relatively small.

Much of the apparent robustness of the directed graph properties P1 through P4 is due in part to the presence of trophically equivalent species or species with identical diets and predators (8, 12). When web categories are aggregated beyond the level of trophically equivalent species, the average coefficient of variation increases slightly for each of these properties: P1-MIN = 0.01,

P1-MAX = 0.03, P2 = 0.06, P3 = 0.08, P4-TF = 0.09, P4-BF = 0.13, P4-IF = 0.08. Thus, once webs are aggregated beyond the level of trophically equivalent species, the food web properties P1 through P4 become more fragile to data resolution. This is true with the possible exception of food chain length based on minimal paths (P1-MIN), which emerges as the most robust of these directed graph properties.

The rigid circuit property, P5, is present in all of Cohen and Briand's original collection of 40 webs (12, 13), and in almost every web of the subsequently expanded catalog of 113 webs (17). Our analysis shows that it is observed in 57 of the 60 additional consumer overlap graphs reported in Table 1. Without exception, if a web was initially rigid, it remained so for every web at every subse-

quent step of the aggregation procedure. Of the three webs that were initially not rigid, two remained nonrigid throughout the aggregation procedure (as the web was reduced to half its starting size or ten species through 30 and 7 steps), and one became rigid only after being reduced to less than 60% of its original size [after 14 steps; Dee River (36)]. Thus, both the presence and the absence of rigid circuits appears very robust to lumping. Unlike properties P1 through P4, this robustness is unaffected as one goes beyond the level of trophically equivalent species, making rigid circuits the sturdiest of the food web regularities tested. The robust behavior of this property to trophic aggregation has been predicted on theoretical grounds (12).

Each of the five common food web prop-

erties examined here appears insensitive to the degree of resolution of the data and to the coarseness of the trophic categories chosen. As such, the consequent food web regularities, which now appear in the present collection of 173 webs, may be legitimate despite understandable worries about the nonuniformity of trophic resolution in the data. Moreover, because these food web statistics exhibit apparent constancy with respect to the degree of resolution, it may be justifiable to use them to compare systems whose trophic data are resolved differently within a factor of 2.

Notwithstanding, and to underscore the need to assemble better data, it would be highly informative to repeat these analyses on at least one carefully resolved whole system containing a more realistic and complete complement of species. This procedure would allow a more conclusive test of the apparent robustness of these food web properties over a wider and more informative range of data resolution and would provide a better benchmark as to when a property such as food chain length is truly limited by the environment or simply by the quality of the data.

REFERENCES AND NOTES

1. C. S. Elton, *Animal Ecology* (new impression with additional notes, Macmillan, New York, 1935).
2. S. L. Pimm and J. H. Lawton, *Nature* **268**, 325 (1977).
3. —, *ibid.* **275**, 542 (1978).
4. S. L. Pimm, *Food Webs* (Population and Community Biology Series, Chapman & Hall, London, 1982).
5. S. J. McNaughton, *Nature* **274**, 251 (1978).
6. D. DeAngelis et al., in *Current Trends in Food Web Theory*, D. DeAngelis, W. Post, G. Sugihara, Eds. (Report 5983, Oak Ridge National Laboratory, Oak Ridge, TN, 1983), pp. 1–10.
7. P. Yodzis, *Nature* **284**, 544 (1980).
8. F. Briand and J. E. Cohen, *ibid.* **307**, 264 (1984).
9. F. Briand, in *Current Trends in Food Web Theory*, D. DeAngelis, W. Post, G. Sugihara, Eds. (Report 5983, Oak Ridge National Laboratory, Oak Ridge, TN, 1983), pp. 22–25.
10. J. E. Cohen, *Food Webs and Niche Space* (Monographs in Population Biology No. 11, Princeton Univ. Press, Princeton, NJ, 1978).
11. M. J. Jeffries and J. H. Lawton, *Freshwater Biol.* **15**, 105 (1985).
12. G. Sugihara, thesis, Princeton University (1983).
13. —, *Proc. Symp. Appl. Math.* **30**, 83 (1984).
14. —, in *Current Trends in Food Web Theory*, D. DeAngelis, W. Post, G. Sugihara, Eds. (Report 5983, Oak Ridge National Laboratory, Oak Ridge, TN, 1983), pp. 25–35.
15. —, in *International Symposium on Mathematics in Biology*, E. Teramoto, Ed. (Springer-Verlag, Berlin, 1987), pp. 53–59.
16. J. H. Lawton and P. H. Warren, *Tree* **3** (no. 9), 242 (1988).
17. J. E. Cohen, in *Perspectives on Ecological Theory*, J. Roughgarden, R. M. May, S. Levin, Eds. (Princeton Univ. Press, Princeton, NJ, in press).
18. — and C. M. Newman, *Ecology* **69**, 1655 (1988).
19. S. L. Pimm, in *Ecological Communities: Conceptual Issues and the Evidence*, L. G. Abele, D. R. Strong, Jr., D. S. Simberloff, A. Thistle, Eds. (Princeton Univ. Press, Princeton, NJ, 1983), pp. 397–412.
20. P. Yodzis, *Oecologia (Berlin)* **65**, 86 (1984).
21. R. T. Paine, *Ecology* **69**, 1648 (1988).
22. S. L. Pimm and R. L. Kitching, *ibid.*, p. 1669.

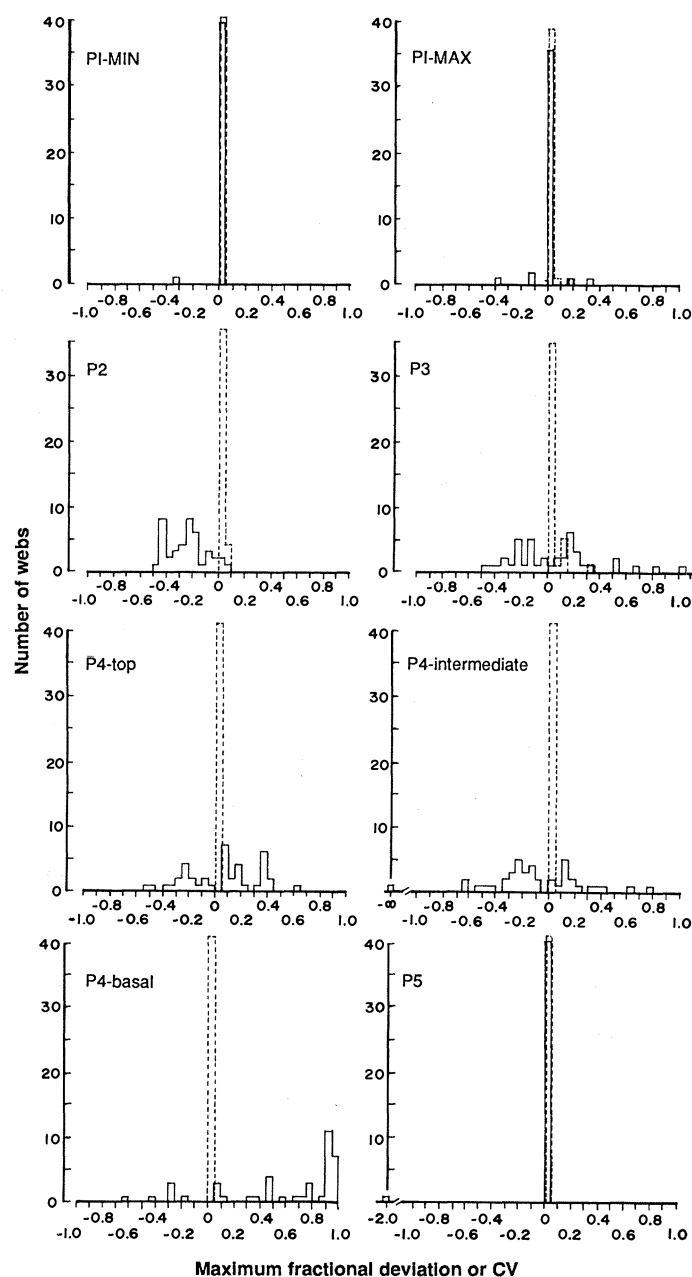


Fig. 2. The distributions of the maximum percent error (solid line) and coefficient of variation (CV) (dashed line) for the food web properties P1 through P5 introduced by lumping. Maximum error is the maximum fractional deviation from the disaggregated web. We computed CV in the usual way for each web, using all of the values obtained from the lumping procedure. To compute these statistics for the rigid circuit property, values of +1 (rigid) and -1 (not rigid) were used. All five food web properties are robust to trophic aggregation.

23. J. E. Cohen and C. M. Newman, *Proc. R. Soc. London Ser. B*, **224**, 421 (1985); *ibid.*, p. 449.
24. F. Briand and J. E. Cohen, *Science* **238**, 956 (1987).
25. F. Briand, *Ecology* **64**, 253 (1983).
26. R. T. Paine, *J. Anim. Ecol.* **49**, 667 (1980).
27. ———, in *Current Trends in Food Web Theory*, D. DeAngelis, W. Post, G. Sugihara, Eds. (Report 5983, Oak Ridge National Laboratory, Oak Ridge, TN, 1983), pp. 11–15.
28. R. M. May, *ibid.*, pp. 127–129.
29. E. Pianka, *Evolutionary Ecology* (Harper & Row, New York, ed. 4, 1988).
30. N. Martinez, thesis, University of Wisconsin (1988).
31. K. Schoenly, R. A. Beaver, T. A. Heumier, unpublished data.
32. N. C. Collins *et al.*, *Ecology* **57**, 1221 (1976).
33. D. G. Koslucher and G. W. Minshall, *Trans. Am. Microsc. Soc.* **92**, 441 (1973).
34. W. L. Minckley, *Wild. Monogr.* **11**, 1 (1963).
35. G. W. Minshall, *Ecology* **48**, 139 (1967).
36. R. M. Badcock, *J. Anim. Ecol.* **18**, 193 (1949).
37. E. Percival and H. Whitehead, *J. Ecol.* **17**, 282 (1929).
38. J. R. E. Jones, *J. Anim. Ecol.* **18**, 142 (1949).
39. C. O. Mohr, *Ecol. Monogr.* **13**, 276 (1943).
40. E. Schoenly, *Ann. Entomol. Soc. Am.* **76**, 790 (1983).
41. I. Valiela, *Am. Midl. Nat.* **92**, 370 (1974).
42. B. W. Cornaby, *Biotropica* **6**, 51 (1974).
43. L. F. Jiron and V. M. Cartin, *J. N.Y. Entomol. Soc.* **89**, 158 (1981).
44. M. McKinnerny, *Southwest. Nat.* **23**, 563 (1978).
45. K. Schoenly and W. Reid, *J. Arid Environ.* **6**, 253 (1983).
46. R. R. Askew, *Trans. Soc. Br. Entomol.* **14**, 237 (1961).
47. B. A. Hawkins and R. D. Goeden, *Ecol. Entomol.* **9**, 271 (1984).
48. H. E. Savelly, *Ecol. Monogr.* **9**, 321 (1939).
49. R. A. Beaver, *Ecol. Entomol.* **10**, 241 (1985).
50. W. E. Bradshaw, in *Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities*, J. H. Frank and L. P. Lounibos, Eds. (Plexus, London, 1983), pp. 161–189.
51. B. Corker, thesis, University of Hong Kong (1984).
52. R. K. Kitching, in *Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities*, J. H. Frank and L. P. Lounibos, Eds. (Plexus, London, 1983), pp. 205–222.
53. R. F. Seifert and F. H. Seifert, *Ecology* **60**, 462 (1979).
54. ———, *Am. Nat.* **110**, 461 (1976).
55. R. L. Kitching and S. L. Pimm, *Proc. Ecol. Soc. Aust.* **14**, 123 (1986).
56. M. Rejmanek and P. Stary, *Nature* **280**, 311 (1979).
57. D. C. Force, *Science* **184**, 624 (1974).
58. M. J. G. Hopkins, *Entomol. Mon. Mag.* **120**, 187 (1984).
59. O. W. Richards, *J. Ecol.* **14**, 244 (1926).
60. P. L. Whittaker, *Southwest Nat.* **29**, 435 (1984).
61. M. A. Mayse and P. W. Price, *Agro-Ecosystems* **4**, 387 (1978).
62. Least-squares regression equations for each plot are: $y = 2.082 + 0.005x$, $P = 0.552$, $SE_{slope} = 0.0074$ for S-C, Fig. 1A; $y = 2.524 - 0.003x$, $P = 0.88$, $SE_{slope} = 0.0224$, P/P, Fig. 1B; $y = 0.395 + 0.002x$, $P = 0.289$, $SE_{slope} = 0.0021$, TF, Fig. 1C; $y = 0.452 - 0.0004x$, $P = 0.816$, $SE_{slope} = 0.0018$, IF, Fig. 1D; $y = 0.153 - 0.002x$, $P = 0.024$, $SE_{slope} = 0.0008$, BF, Fig. 1E.
63. Trophic aggregation was performed on 41 webs listed in Table 1. The number of steps to the reduced, aggregated web across all webs ranged from 2 (33, 48, 50, 51) to 44 (47). Webs listed in Table 1 with ten or fewer taxa have lower percentages of actual taxa (65%), and aggregation in these smaller systems, if attempted, would give trivial results; for example, webs with fewer than seven taxa are trivially rigid. If the smallest webs are included, the trivial bias would make the properties. S-C, fraction intermediate, and fraction basal appear to vary systematically with web size.
64. One should be mindful that this procedure of trophic aggregation is not equivalent to lumping based on taxonomic similarity.
65. Supported by NSF grant BSR88-07404. We thank R. Beaver for assistance in the compilation of data sets. We are grateful to J. Cohen, J. Enright, R. May, R. Paine, and S. Pimm for comments on an earlier draft.

9 January 1989, accepted 12 April 1989

The *Diageotropica* Mutant of Tomato Lacks High Specific Activity Auxin Binding Sites

GLENN R. HICKS, DAVID L. RAYLE, TERRI L. LOMAX*

Tomato plants homozygous for the *diageotropica* (*dgt*) mutation exhibit morphological and physiological abnormalities which suggest that they are unable to respond to the plant growth hormone auxin (indole-3-acetic acid). The photoaffinity auxin analog [³H]5N₃-IAA specifically labels a polypeptide doublet of 40 and 42 kilodaltons in membrane preparations from stems of the parental variety, VFN8, but not from stems of plants containing the *dgt* mutation. In roots of the mutant plants, however, labeling is indistinguishable from that in VFN8. These data suggest that the two polypeptides are part of a physiologically important auxin receptor system, which is altered in a tissue-specific manner in the mutant.

THE PLANT GROWTH HORMONE AUXIN [indole-3-acetic acid (IAA)] appears to activate cellular responses, such as the promotion of cell elongation, by binding to specific receptor proteins. Evidence for auxin binding to both membrane-bound and soluble proteins has been reported (1). However, no direct experimental connection has been made between any plasma membrane auxin-binding protein and a known molecular or cellular response to auxin (2). Obtaining such evidence in conjunction with the isolation of the receptor would be important in elucidating the molecular mechanism of auxin action.

One way to investigate the physiological relevance of putative auxin receptors is through the use of mutant plants that are insensitive to auxin or which exhibit abnormalities likely to be influenced by IAA. The *diageotropica* (*dgt*) mutant of tomato (*Lycopersicon*

esculentum, Mill.) is a recessive mutant of the parental variety, VFN8, and appears to have arisen spontaneously at a single locus. Tomato plants homozygous for the *dgt* mutation have diageotropic shoot growth, abnormal vascular tissue, altered leaf morphology, and no lateral root branching (3, 4). Although the endogenous levels of auxin are the same in *dgt* and VFN8 shoot apices (5), *dgt* mutants are insensitive to exogenously applied auxin in ethylene production (4, 6) and stem elongation (7). The morphological abnormalities exhibited by *dgt* plants, in addition to their inability to elongate in response to auxin, suggest that the *dgt* lesion is associated with a primary site of auxin perception or action. We report here on experiments that were designed to test the hypothesis that the mutated *dgt* gene codes for a receptor protein which is present at abnormally low levels or has a greatly

reduced ability to bind auxin.

To label and identify potential auxin receptors, we used a radioactively labeled photoaffinity auxin analog, [³H]5N₃-IAA (azido-IAA). Azido-IAA is an active auxin in several different bioassays and its uptake and transport characteristics in stems are similar to those of auxin (8). Thus, one would expect azido-IAA to bind to auxin receptors with an affinity similar to that of auxin. In an earlier study on the binding of the azido-IAA to plasma membrane proteins from zucchini hypocotyls, the vesicles were exposed to azido-IAA and photolyzed with ultraviolet light (300 nm) at -196°C (9). Subsequent SDS-polyacrylamide gel electrophoresis (SDS-PAGE) followed by fluorography revealed that azido-IAA was associated at high specific activity with a polypeptide doublet of 40 and 42 kD. These polypeptides are of low abundance, as they cannot be visualized in silver-stained gels until they have been electroeluted and concentrated approximately tenfold. Competition experiments with various auxin analogs suggest that this doublet binds auxin specifically (9).

We have now performed a similar experiment with microsomal membrane preparations from the hypocotyls (stems) or roots

G. R. Hicks and T. L. Lomax, Department of Botany and Plant Pathology, and Center for Gene Research and Biotechnology, Oregon State University, Corvallis, OR 97331-2902.

D. L. Rayle, Department of Biology and Molecular Biology Institute, San Diego State University, San Diego, CA 92182.

*To whom correspondence should be addressed.