

TWO DEGREES OF SEPARATION IN COMPLEX FOOD WEBS

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ABSTRACT:

Feeding relationships can cause invasions, extirpations, and population fluctuations of a species to dramatically affect other species within a variety of natural habitats.¹⁻¹¹ Such strong effects rarely propagate through food webs more than three links away from the initial perturbation.¹⁻⁴ However, in large food webs the number of species within these spheres of potential influence are generally unknown. Here we show that the vast majority of species within habitats are three or fewer links from each other. Specifically, food webs from widely different ecosystems are shown to be surprisingly small worlds^{12,13} in which species are only two links from each other on average. Contrary to expectations¹⁴, species are drawn even closer as network complexity and species richness increase. Our findings are based on seven of the largest and most complex food webs available¹⁵⁻²¹ as well as a food-web model²² that extends the generality of the empirical results. These results indicate that the dynamics of species within ecosystems may be more highly interconnected¹² and that biodiversity loss and species invasions potentially affect more species than previously thought.

I. INTRODUCTION

The mean distance between all nodes in a web (D) is perhaps the most familiar property of complex networks. For example, the “small world” phenomenon in large social networks is popularly termed “six degrees of separation”.¹² Known as the characteristic path length, D quantifies the average number of links necessary for information or an effect to propagate along the shortest paths between nodes in a network. Networks previously examined for D include film actor guilds, electrical power grids, neural networks, and the Internet,^{12,13} as well as relatively simple food webs with 3 to 33 species¹⁴.

A food web consists of L directed trophic links between S nodes or “trophic species.” Trophic links occur between consumer species (i.e., predators, parasites, etc.) and the resource species (i.e., prey, hosts, etc.) that they eat. Trophic species are functional groups of taxa that share the same consumers and resources within a food web. These groups are a widely accepted and sometimes criticized convention within structural food-web studies that reduces methodological biases in the data and highlights the functionally distinct aspects of food-web networks.²² Connectance (C) is the fraction of all possible links that are realized (L/S^2) and represents a standard measure of food web complexity thought to be independent of S .^{25,26} The distance (d) between every species pair in a web is averaged to compute D .¹² Paths are treated as undirected because effects can propagate through the network in either direction. Species one link from a focal species ($d=1$) are those that are a direct consumer or resource of the focal species. A species two links ($d=2$) from a focal species lacks a direct trophic interaction with the focal species and either 1) shares at least one resource species, 2) shares at least one

consumer species, or 3) consumes a consumer, or 4) is a resource of a resource of the focal species. Having multiple species falling into one or more categories does not alter d . A node in a graph is usually defined as being distance zero from itself¹². Instead of using this convention, we define d for the self-self species pair the same as for any other species pair. In the self-self case, this is simply the shortest path from the species back to itself. This allows us to distinguish cannibals, which have $d=1$, from other species, which have $d=2$. Our method increases D among our webs an average of only 2.5% compared to employing the more standard convention.

II. RESULTS

While there are many food webs in the literature, the vast majority have been criticized for being incomplete, having too few species, and lacking a rigorous empirical base^{14,16,20,24,27}. Therefore, we focused our analyses on seven of the largest, most comprehensive, and highest quality empirical food webs in the primary literature (Tab. 1).²² Three are from freshwater habitats, Skipwith Pond¹⁵, Little Rock Lake¹⁶, and Bridge Brook Lake¹⁷. Two are from habitats at freshwater-marine interfaces, Chesapeake Bay¹⁸ and Ythan Estuary¹⁹. Two are from terrestrial habitats, Coachella Valley²⁰ and the island of St. Martin²¹. Among these webs, D ranges between 1.40 and 2.71 and decreases with increasing connectance (Tab. 1, Fig. 1). Distances between species pairs (d) are closely clustered around the mean with very few widely separated species pairs ($d>3$, Fig. 2). Across the seven webs, an average of 26.1% of species pairs interact directly ($d = 1$), and 80.2% and 96.9% of the species pairs are respectively within two and three links of each other.

This result may be most surprising in Little Rock Lake due to its many species and the strong representation of both benthic and pelagic habitats. D had been expected to increase well beyond 2 in large food webs¹⁴, and boundaries between habitats may be expected to result in food-web compartments²⁴ that would increase D well beyond that in the other webs that contain less representation of different habitats. Consistent with small-world network structure,¹² even though the Little Rock Lake food web is more compartmentalized or clustered than expected at random, the clusters are linked such that significant increases in D are prevented. This finding is supported by a null model that randomly arranges trophic links while maintaining empirically observed S and C and normalizes the model's error with its standard deviation²². The null model underestimates Little Rock Lake's clustering coefficient¹² by over 28 model standard deviations.

With only seven food webs examined, insight into the sensitivity of D to diversity (S) and complexity (C) is limited by the simultaneous variation and few combinations of S and C . We used a model that generates food webs to explore this sensitivity. This "niche model" accepts S and C as input parameters and successfully predicts a dozen food-web properties²² but was untested against D . We compared D of the seven empirical webs to that of webs generated by the niche model²². The niche model constructs webs with the same S and C as the empirical webs by randomly arranging S species on a one-dimensional community niche. Each species eats all species within one contiguous section of the niche. The center of the section has a randomly chosen lower niche value than the consuming species and the width of the section is randomly varied within the constraint that the synthesized web has the

proper C . The niche model accurately and precisely predicts D for all seven empirical food webs (Fig. 1, Table 1). Given the success of the model, we used it to characterize the sensitivity of D to both S and C . Model results indicate that D is moderately sensitive to C and less sensitive to S (Figs. 1, 3). For webs with constant S , D decreases a factor of two with an order-of-magnitude increase of C in an approximate power law relationship whose slope is greater for smaller webs (Fig. 1). For webs with constant C , D decreases weakly with increasing S (Fig. 3), contrary to earlier expectations¹⁴. As S increases 2 orders of magnitude, D decreases roughly 5% in more complex webs ($C > 0.20$) and between 15-50% in less complex webs ($0.05 < C < 0.10$). The variation of D with S does not appear to follow a power law or other mathematically simple relationship (Fig 3).

These findings show that species are generally linked by short chains in food webs, with 80% of species connected by one or two links, resulting in an average shortest path between species of approximately 2. Thus, most species in a food web can be thought of as "local" to each other and existing in surprisingly "small worlds" where species can potentially interact with other species through at least one short trophic chain. Empirical studies show that short-chain indirect effects ($d=2,3$) can be as important as direct effects ($d=1$) and become evident nearly as quickly.^{7,9} Combined with our results, this suggests that the effects of adding, removing, or altering species have the potential to propagate both widely and rapidly throughout large complex communities.

These findings should be tempered by the possibilities of either over- or underestimating D . Food webs may underestimate both the trophic and functional connectance of organisms in complex communities and thus overestimate

the effective D and underestimate the potential for propagation of effects. This may be partly due to scientists underreporting the actual number of trophic links present among species²⁷. More significantly, food webs depict only one of many types of interactions among species. Other non-trophic interactions include ecosystem engineering, facilitation, behavioral modification, and interference competition.^{6,11,28,29} If multiple types of interactions are accounted for, the functional connectance among species should be higher than the trophic connectance we report. Thus, species may be ecologically closer than our results suggest because D decreases with increasing C . On the other hand, our results may overestimate the potential for propagation of effects because many food-web links may be “weak” and therefore unimportant in determining species dynamics and community structure and function^{8,27}. This suggests that food webs that include all trophic links overestimate functional connectance of species. However, recent theoretical and experimental studies show that many purportedly weak links are dynamically important.^{23,29} Even if food webs overestimate functional connectance, empirical and model webs with low connectance ($C < 0.08$) still display short characteristic path lengths ($D < 3$) for all but the smallest and simplest webs (Fig. 1). Small empirical webs rarely have this combination of few species and low connectance¹⁴. These considerations show that our general conclusion of an average of two degrees of separation in complex food webs is theoretically robust and consistent with the best available data. However, two degrees may slightly overestimate of the size of ecological “worlds” when other interspecific interactions are taken into account.

III. DISCUSSION

Quantifying the shortest path between species pairs, rather than the more numerous longer chains that can connect the same pairs of species, has important ecological implications because empirical evidence suggests that the strength of species effects on each other attenuates rapidly as chains grow longer than three⁴⁻⁷. Even though theoretical studies suggest longer chains of effects can sometimes be stronger than shorter chains⁷, empirical studies⁵⁻⁷ find the opposite. The most comprehensive review of experimentally demonstrated indirect effects suggests that both direct ($d=1$) and short indirect ($d=2,3$) effects each account for ~40% of the change in community structure due to a species manipulation⁶, with the remaining 20% of the variance unexplained. Strength of indirect effects decrease with increasing chain length in two studies that considered chains of $d > 2$.⁵ Percent of variance explained due to direct and indirect effects appears independent of species richness⁶ which is consistent with our result that D is insensitive to S . With increasing web size, the number of significant short-chain indirect effects per species increases, while the number of significant long-chain indirect effects remains small even as the number of longer paths grows rapidly⁶.

Other empirical studies have demonstrated strong “trophic cascades” in a variety of terrestrial and aquatic ecosystems¹⁻³, where significant effects often propagate two and sometimes three links from manipulated species. These studies confirm that $d < 3$ chains are frequently dynamically important. However, the paucity of demonstrated trophic cascades at long distances ($d > 3$) is consistent with other empirical studies that suggest that species more than 3 links away from each other are functionally (or

dynamically) disconnected. The niche model suggests that d is greater than 3 for more than 5% of species pairs only in the few empirical webs with relatively few species or larger webs with unusually low connectance (i.e., those webs with approximately $C < -0.001S + 0.15$; see supplemental material). The lack of empirical studies showing effects that propagate more than three links thus may be partly due to the difficulty of finding systems with significant fractions of species pairs with $d > 3$. Such difficulty may also be due to aggregation of species¹⁶ in these studies into trophic levels, which could conceal such effects.³ For example, manipulating the density of consumers of secondary carnivores could cause a positively responding plant species to compensate for a negatively responding plant species. More attention on disaggregated species within trophic levels could illuminate such possibilities.³

Together, the empirical studies of species manipulation effects suggest that ‘distant’ ($d > 3$) species do not strongly influence each other, which poses a challenge to the popular ecological adage that “everything is connected to everything else”. Had we found a D larger than three, as in other complex, small-world networks^{12,30}, the adage would have been undermined by the suggestion that substantial fractions of species are functionally isolated from one another. Our findings appear to make this possibility unlikely. Overall, the robustness of short characteristic path length D in food webs to changes in size, complexity, and habitat suggests that the “small world” potential for widespread and rapid dispersion of effects throughout a community of interacting organisms¹² is a general ecological property. Larger D may be found in food webs that span more distinct habitat boundaries (e.g., those between terrestrial and aquatic

ecosystems), which could significantly increase D .

Mechanisms potentially responsible for small D among food webs are currently unknown and deserve further investigation. Our findings suggest that such mechanisms are related to observed levels of connectance^{25,26} and other factors that generate web topology²². Mechanisms associated with population dynamics may also be responsible as suggested by findings that increasing the number of weak interactions may increase dynamic stability^{23,26,29}. Similarities among two very different biological networks suggest mechanisms associated with biological evolution may also be responsible. Both food webs and metabolic networks exhibit minimal sensitivity of D to the number of network nodes and increasing individual node connectivity with node richness.^{25,26,30} As chemical substrate nodes in biochemical networks increase, the links that occur between chemicals involved in the same reactions increase node connectivity.³⁰ Similarly, L/S increases as S increases among food webs.^{25,26} Such topological features in metabolic networks may result from evolutionary processes that maximize efficient substrate distribution and transport and rapid response to internal defects or environmental fluctuations.³⁰ Evolution of feeding capabilities may be responsible for the increase of L/S with S that results in observed levels of C .²⁵

Within habitats as well as among habitats, d can be used to identify which species are more or less likely to affect each other directly or indirectly. Such information could be useful for managing biodiversity. More generally, the variance of d may predict the relative frequencies of strong effects in complex food webs, an important property which has never been rigorously tested in large, complex food webs. Our results specify how biodiversity loss, species

invasions, and changes in populations have the topologically and dynamically demonstrated potential to affect many more co-occurring species than is often appreciated⁴. The degree to which this potential is realized deserves much additional research.

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Table 1. Properties of empirical and niche model food webs.

Food Web	Taxa	<i>S</i>	<i>C</i> (<i>L/S</i> ²)	Observed <i>D</i>	Model <i>D</i>	Error (Model SD)
Skipwith Pond	35	25	0.32	1.40	1.44	1.10
Little Rock Lake	181	92	0.12	1.90	1.88	-0.94
Bridge Brook Lake	75	25	0.17	1.92	1.80	-1.68
Chesapeake Bay	33	31	0.072	2.71	2.55	-0.99
Ythan Estuary	92	78	0.061	2.20	2.32	2.06
Coachella Valley	30	29	0.31	1.47	1.45	-0.68
St. Martin Island	44	42	0.12	1.92	1.98	0.99

“Taxa” refers to the original names for groups of organisms found in the primary reference. “*S*” refers to trophic species. The 7 food webs address 1) primarily invertebrates in Skipwith Pond¹⁵, 2) pelagic and benthic species in Little Rock Lake¹⁶, the largest food web in the primary literature, 3) Bridge Brook Lake, the largest among a recent set of 50 Adirondak lake pelagic food webs¹⁷, 4) the pelagic portion of Chesapeake Bay emphasizing larger fishes¹⁸, 5) mostly birds and fishes among invertebrates and primary producers in the Ythan Estuary¹⁹, 6) a wide range of highly aggregated taxa in the Coachella desert²⁰, and 7) trophic interactions emphasizing *Anolis* lizards on the Caribbean island of St. Martin²¹. Model *D* is the mean of 1000 niche model trials. Errors between the niche model *D* and observed *D* are normalized by dividing the difference by the standard deviation (SD) of the trial results. 95% of normalized errors should be within 2 SD if the model is accurate.²²

Figure 1

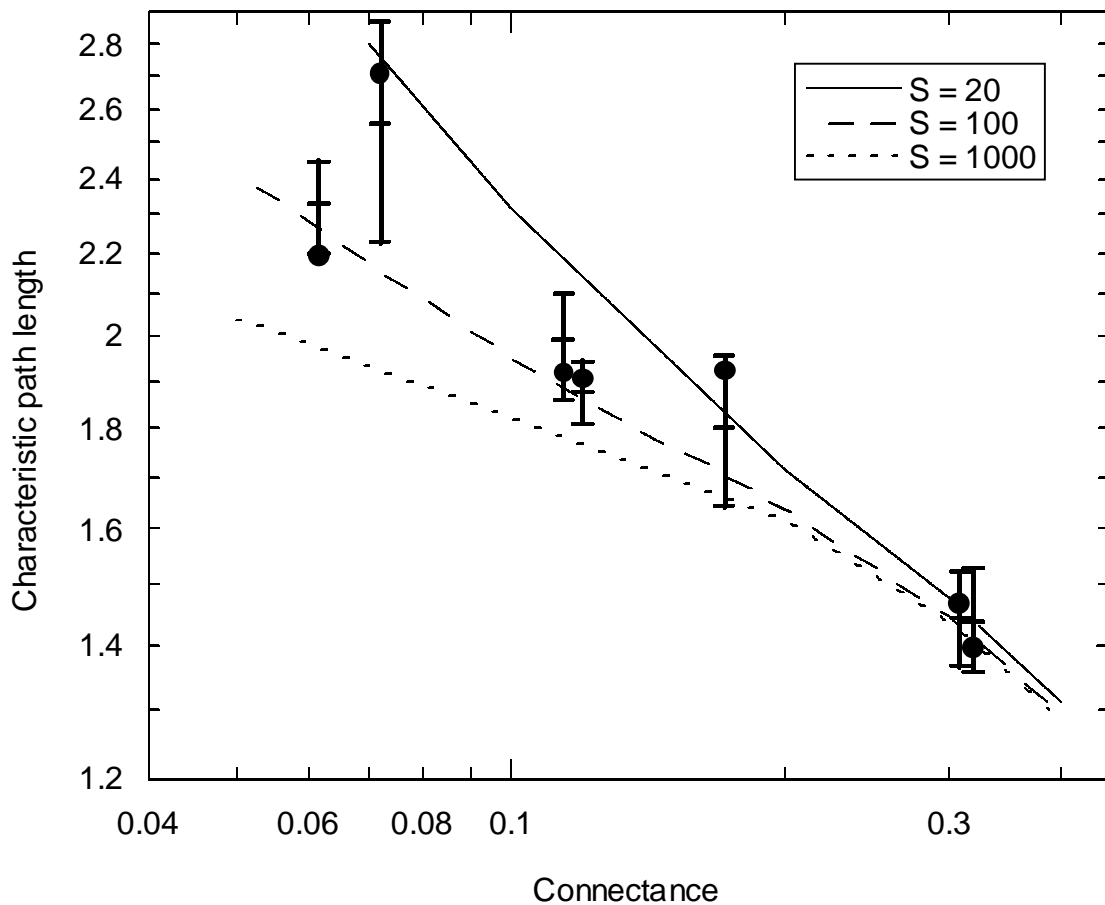


Figure 1. Characteristic path length D of the seven empirical webs listed in table 1 (\bullet), error bars showing mean ± 2 standard deviations for niche model webs with the same S and C as the empirical webs, and curves showing mean D vs. C for niche model webs with $S = 20, 100$ and 1000 . Log-log plot shows the approximate power-law relationship between mean D of niche model webs and C for all S . The seven empirical webs are, from left to right, Ythan Estuary ($S = 78$), Chesapeake Bay ($S = 31$), St Martin Island ($S = 42$), Little Rock Lake ($S = 92$), Bridge Brook Lake ($S = 25$), Coachella Valley ($S = 29$) and Skipwith Pond ($S = 25$). Since the niche model is a stochastic model, previously described Monte Carlo techniques²¹ were used to measure the mean and standard deviation of the niche model predictions, and errors are normalized by the standard deviation of the model prediction (Tab. 1). The mean normalized error is -0.02 model standard deviations which is very close to zero as expected when the model fits the data. The standard deviation of the errors is 1.4 , showing slightly greater variability of normalized error than the theoretically expected SD of 1 .²¹ A null model that randomly arranges trophic links while maintaining empirically observed S and C ²¹ fits the data much worse as indicated by a normalized error mean of -2.6 and SD of 5.4 .

Figure 2

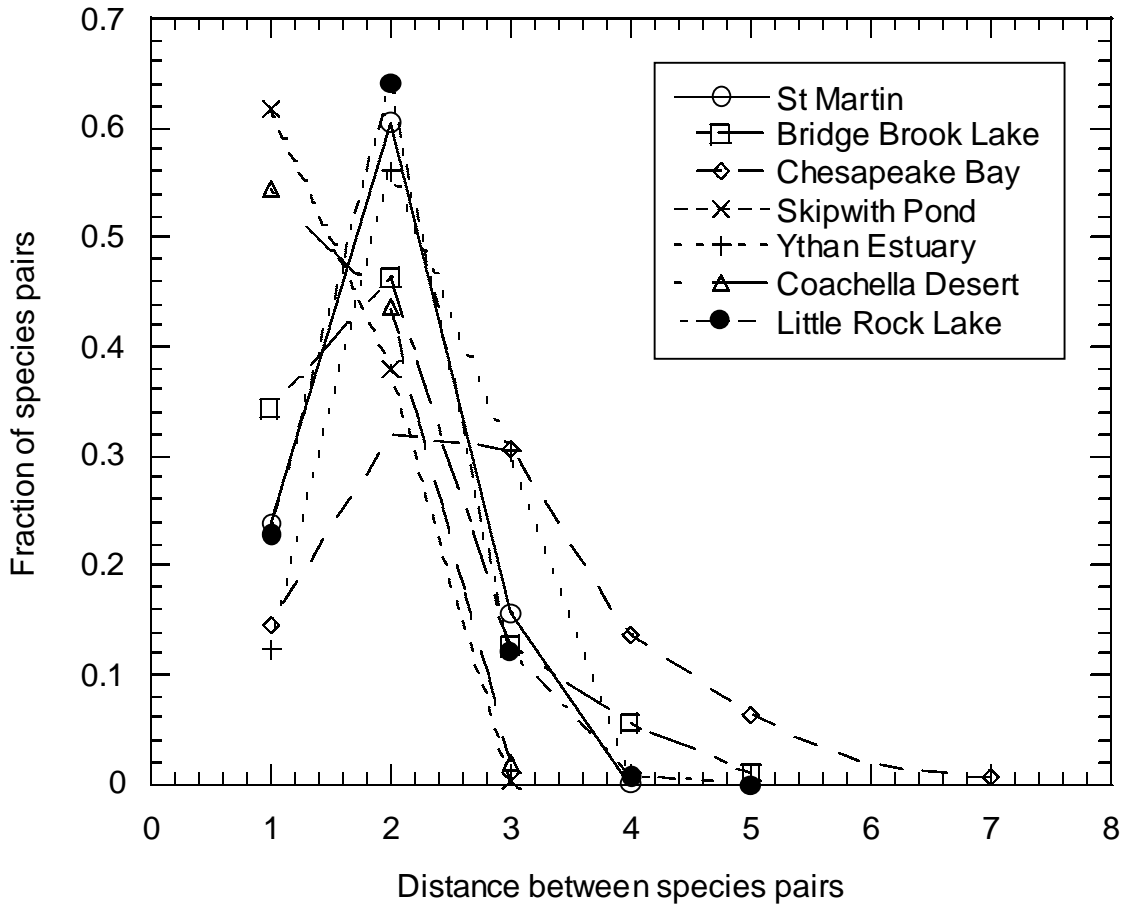


Figure 2. Distributions of distances (d) between species pairs for the seven webs listed in table 1. The histograms are normalized to show the fraction of species pairs at each distance.

Figure 3

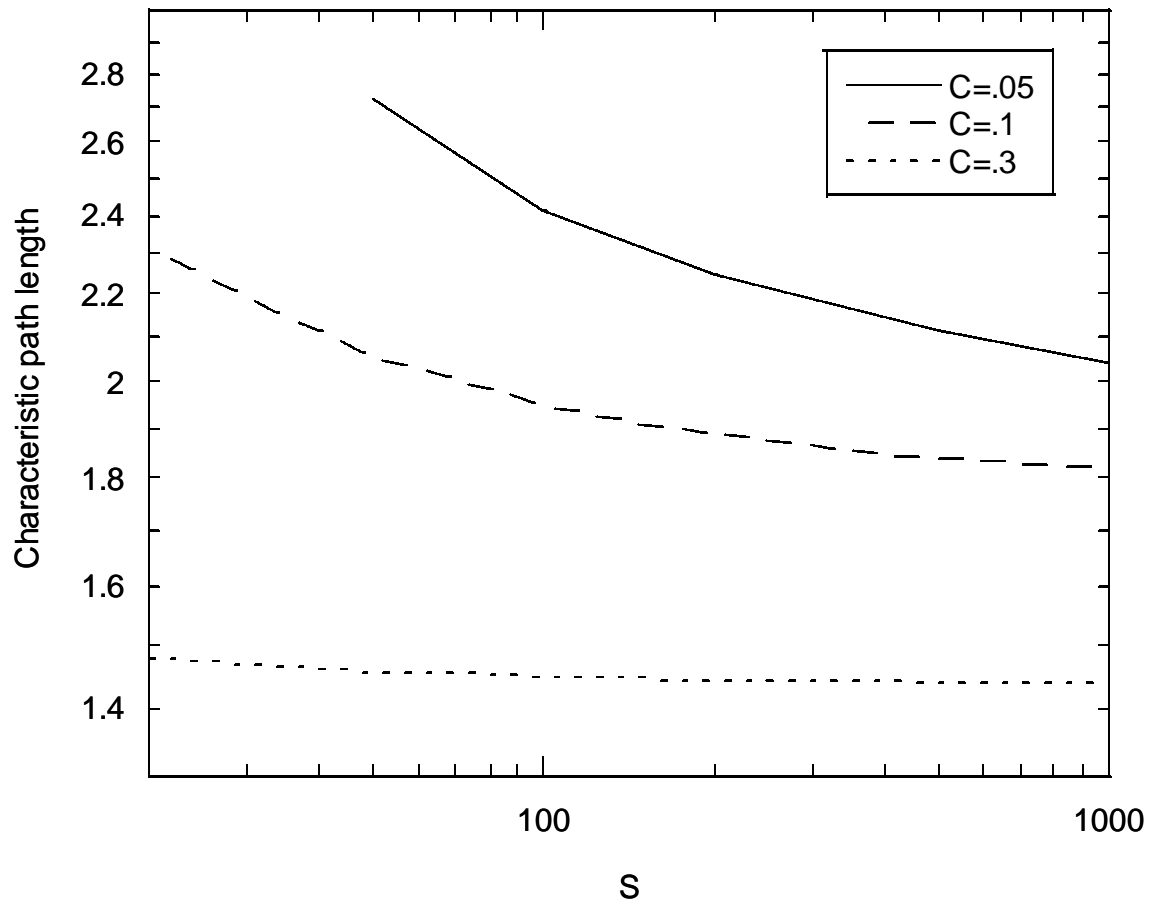


Figure 3. Sensitivity of D among niche model webs to S . Lines connect the means from 1000 iterations for each level of S and C .

Figure 4

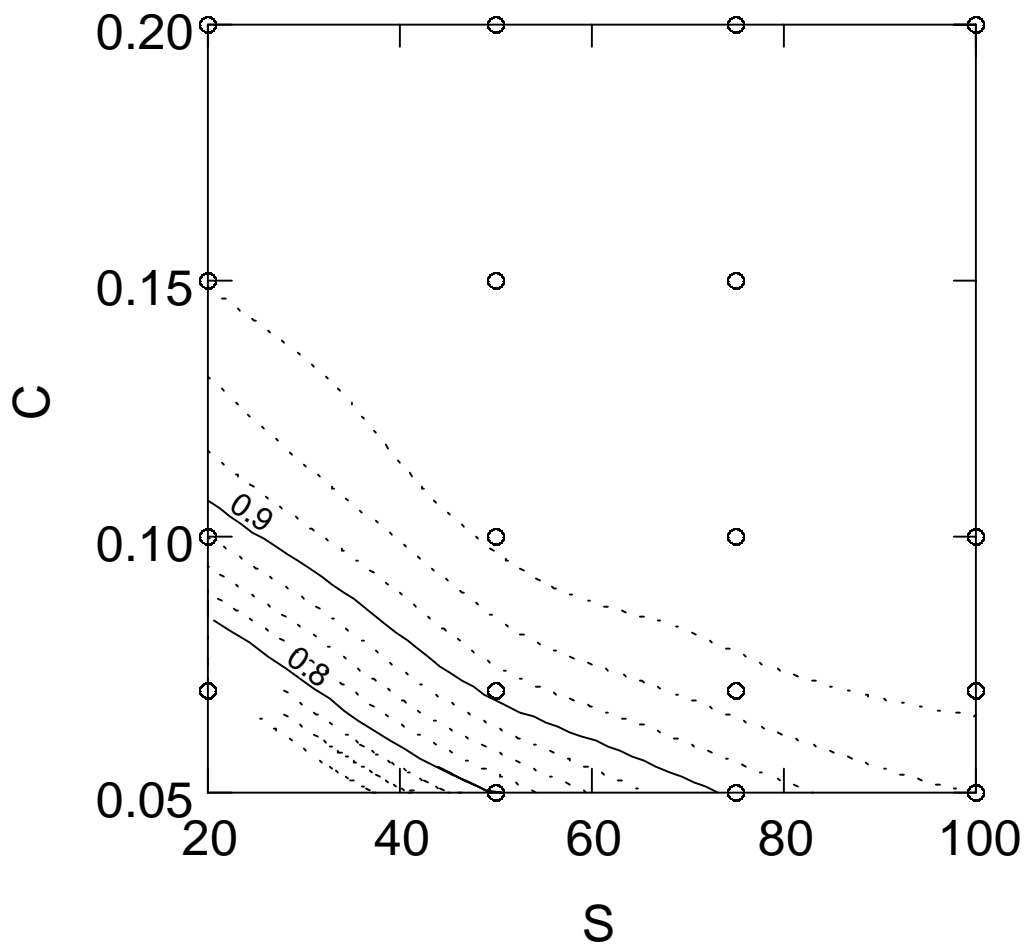


Figure 4. Fraction of species pairs 3 or fewer links apart in niche model webs. Adjacent lines designate isopleths that are 0.025 apart.