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Permanence Does Not Predict the Commonly Measured Food Web Structural Attributes

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ABSTRACT: Food web assembly algorithms show great promise for investigating issues involving the dynamics of whole webs, such as succession, rehabilitation, and invasibility. Permanence, which requires that all species densities remain positive and finite, has been suggested as a good stability constraint. This study tests the validity of the permanence constraint by comparing real webs and model webs from the literature to the predictions of three assembly algorithms: one constrained by permanence and feasibility, one constrained by feasibility alone, and one with no dynamical constraint. It is found that the addition of the permanence constraint does not improve the predictive ability of the algorithm. Its main effect is to increase the efficiency of species selected for the web. Dynamically constrained webs have lower connectance and indistinct trophic levels compared to real webs and webs from other models, which is a consequence of omitting species' physiology. Although webs are less likely to be permanent if they have high omnivory and cycling, the web-building process circumvents this constraint. The challenges of testing and justifying system-level hypotheses, including isolating and detecting their effects, are discussed.

Keywords: food webs, stability, permanence, feasibility, niche model, nested-hierarchy model.

A food web-building algorithm is a series of repeating steps by which model food webs can be created. Starting with one or a few species, the algorithm permits new species to invade and some species to be lost at each time

step, according to some prespecified rules. There is already a large body of food web assembly literature (Tregonning and Roberts 1979; Post and Pimm 1983; Mithen and Lawton 1986; Taylor 1988; Drake 1990; Law and Blackford 1992; Luh and Pimm 1993; Law and Morton 1996; Lockwood et al. 1997; Drossel et al. 2001; Bastolla et al. 2005; Virgo et al. 2006) and a complimentary literature testing the predictions of the algorithms in experimental systems such as microcosms (Dickerson and Robinson 1986; Robinson and Dickerson 1987; Drake 1991; Wardle et al. 1995; Moyle and Light 1996; Weatherby et al. 1998; Chase 2003; Fukami 2004). Because assembly algorithms simulate invasion and extinction in a whole food web, they hold great promise for answering questions about succession, rehabilitation, and invasibility.

The rules governing which food webs survive intact to the next time step are often based on dynamical constraints (though not always; e.g., Luh and Pimm 1993). For example, food webs may be constrained to be feasible (i.e., all species have a positive steady state biomass [e.g., Tregonning and Roberts 1979]) or locally stable (e.g., Post and Pimm 1983). This article focuses on a dynamical constraint called permanence. A food web is permanent if the densities of all species remain positive and finite and it can recover after those densities are brought arbitrarily close to 0 (Hofbauer and Sigmund 1988). Permanence has the advantage over local stability in that it does not presuppose the existence of a single steady state but does allow for complex trajectories within the phase space, such as limit cycles (Jansen and Sigmund 1998). Indeed, it does not identify what dynamical behavior the system undergoes, and such behavior remains unknown without further analysis. Therefore, permanence is the mathematical condition closest to what theoreticians mean when they say "stable" (cf. Grimm et al. 1992) and is more consistent with ecologists' experience of real food webs (Hastings 1988; Paine 1988; Hall and Raffaelli 1993).

The concept of invasion and reinvasion is intrinsic to how permanence is tested (Kirlinger 1986), making it a natural candidate for food web assembly. Indeed, a few permanent food web-building algorithms have already ap-

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peared in the literature (Law and Morton 1996; Virgo et al. 2006). However, before it can be considered a reliable tool for quantitatively researching the questions mentioned above, for which it holds much promise, we must have some assurance that it provides a reasonable estimation of how real food webs behave. Ideally, the decrease in parsimony incurred by assuming that food webs are permanent will be offset by some increase in predictive ability. Otherwise, it would be sufficient to use more minimal constraints, such as a feasible numerical solution (e.g., Taylor 1988), or even no dynamics at all (e.g., Luh and Pimm 1993) and to keep permanence for use as a qualitative, conceptual model.

One way to test this is to start by assuming that the patterns in food web structure are a consequence of the processes underlying them. Then we can use the ability to predict food web structure as a method of evaluating the permanent food web–building algorithm against more minimal models. There is a growing literature documenting the structure of large, high-quality empirical webs that can be used for this task (e.g., citations in Williams and Martinez 2000). While no documented food web is a perfect representation, these webs are the product of 20 years of generalizations about food web structure and critiques of the same. Many have been collated specifically to address the criticisms leveled at earlier webs (Briand and Cohen 1984, 1987; Cohen 1989*a*), such as incompleteness (Hall and Raffaelli 1991, 1993; Goldwasser and Roughgarden 1997), the practice of lumping species together (Lawton and Warren 1988; Paine 1988; Pimm and Kitching 1988; Sugihara et al. 1989; 1997; Warren 1989; Hall and Raffaelli 1991; Pimm et al. 1991; Martinez 1993; Martinez et al. 1999), and taxonomic bias (May 1983; Paine 1988; Sugihara et al. 1997). Therefore, these webs represent the best information that is available to us about food web structure.

Concurrent with the accumulation of documented food webs, there has been an effort to provide simple explanations for generalizations that have been made about them. Starting with the cascade model (Cohen and Newman 1985), these models have shown how simple heuristics governing the trophic interactions between individual species can predict whole-web structure. The cascade model assumed that there was a one-dimensional niche ordering, such as body size (Cohen 1989*b*), which meant that no species could prey on another species with a niche value higher than its own. The niche model built on this by introducing a contiguous feeding range and relaxing the feeding hierarchy of the cascade model (Williams and Martinez 2000). The nested-hierarchy model made explicit the heuristic that predators who share one prey are also likely to share others, by merit of similar physiology (Cattin et al. 2004). Stouffer et al. (2005) found that there were two key

properties in these models: first, that species' niche values formed a totally ordered set, and second, that each species has a specific, exponentially decaying probability of preying on a given fraction of species with lower niche values. The niche and nested-hierarchy models share both properties, and the cascade shares the first. Therefore, in this article, we refer to the niche, nested-hierarchy, and generalized cascade models collectively as “ordered-niche models.”

The success of these ordered-niche models presents an additional challenge to permanence. For although permanence is conceptually appealing, it is similar to other higher-level selection theories in that justifying it for quantitative work requires more than just demonstrating that it can predict food web structure (Williams 1966, pp. 101–109). Even when a clear relationship between a dynamical constraint and a food web attribute is determined, if it can also be explained in terms of niche models, then they take precedence as an explanation for web structure because they provide a more parsimonious explanation.

This study attempts to assess the predictive value of permanence, taking into account the issues discussed above. To isolate the effect of permanence from the more minimal assumptions that underlie it, three food web–building algorithms are created: one with feasibility and permanence as constraints, one with only feasibility as a constraint, and one with no dynamical constraint at all. The predictions of these algorithms are then compared to real empirical webs, and their predictive success is contrasted with that of the ordered-niche models.

To date, all published food web–building algorithms using permanence as a constraint have also included physiological considerations (Law and Morton 1996; Virgo et al. 2006), as one would expect when the objective is to make the model as realistic as possible. However, given that the objective in this article is to isolate the predictive value of permanence, no physiological considerations are included. This work also complements previous permanent-assembly algorithms by increasing the set of food web attributes for which the effect of permanence is known. Virgo et al. (2006) measured the value of thermodynamic goal functions arising from permanence, whereas in this work, the structural attributes that are commonly used to verify the ordered-niche models are investigated instead.

Methods

Measuring Food Web Attributes

The algorithms described below were run for 500 successful invasions, and this was repeated as many times as needed to provide a large collection of webs for testing. The collection of webs was chosen such that no two webs have a single species in common.

The food web attributes measured were number of species (n); top (T), intermediate (I), and basal (B) trophic fractions (Cohen 1989a); mean maximum similarity (s_{\max} ; Williams and Martinez 2000); fraction of omnivores (O); interactive connectance ($L/[n(n-1)/2]$, where L is the number of links and n is the number of species; Martinez 1991); directed connectance ($C = L/n^2$; Martinez 1991); fraction of cycles, which are trophic relationships of the form “A eats B, B eats C, ... eats A,” excluding cannibalism (“A eats A”) and mutual predation (“A eats B, B eats A”; Cattin et al. 2004); short-weighted trophic level (Levine 1980; Williams and Martinez 2004); omnivory degree (Williams and Martinez 2000); generality (G) and vulnerability (V ; Schoener 1989); normalized standard deviations of generality ($SD(G)$) and vulnerability ($SD(V)$; Williams and Martinez 2000); and motifs and antimotifs (Milo et al. 2002). A detailed description of these measures can be found in “Detailed Description of Food Web Attributes” in the online edition of the *American Naturalist*. Since a skewed interaction strength distribution is associated with local stability (McCann et al. 1998; Emmerson and Raffaelli 2004), both the interaction strength distributions and local stability (May 1972) were also measured.

Food Web–Building Algorithms

Model Formulation. For dynamically constrained algorithms, the interactions between species were of the Lotka–Volterra form,

$$\frac{dx_i}{dt} = x_i \left(d_i + \sum_{j=1}^n a_{i,j} x_j \right), \quad (1)$$

where x_i is the biomass of species i , d_i represents the intrinsic rate of increase of species i , $a_{i,j}$ represents the interactions between a species i and another species j , and n is the total number of species. The fixed coefficients in the relationships between predator and prey are a simplification, and there are other models in which this is not the case (e.g., Drossel et al. 2001; Kondoh 2003).

If species i was an autotroph, then $d_i > 0$, $a_{i,i} < 0$, and $a_{i,j} \leq 0$. If species i was a heterotroph, then $d_i < 0$, $a_{i,i} = 0$, and $a_{i,j}$ could take either sign. The system was scaled with both $|d_i|$ and $|a_{i,j}| < 1$. These coefficient values are similar those that have been used in other assembly algorithms (e.g., Lockwood et al. 1997).

Using biomass as the state variable is common in the modeling literature (e.g., Laws et al. 2000). Its dimensions, concentration of a nutrient per unit space or volume, permit simplification of the coefficient value choices. If species i is the predator and j the prey (i.e., $a_{i,j}$ is positive and $a_{j,i}$ is negative), then conservation of matter dictates that

the flow out of the prey species must be greater than or equal to the flow into the predator species. Consequently, $|a_{i,j}| \leq |a_{j,i}|$. It should be noted that species abundance is also a common choice for the state variable in theoretical ecology. Choosing one or the other provides a contrast with ordered-niche models, because relationships between abundance, body size, and biomass have been observed and have consequences for food web structure (Cohen et al. 2003).

Generating the New Species. The algorithm began with a set of five autotrophs, which is comparable to the number of basal species in several large, well-documented webs (Huxham et al. 1995; Opitz 1996) and consistent with previous food web–modeling work (Brose et al. 2006). At each time step, a new species was created to attempt an invasion. The number of autotrophs in the system was restricted to the initial value of five. This means that the new species was always a heterotroph unless there were fewer than five autotrophs in the system. All coefficient values were chosen from a random standard uniform distribution. For each interaction between the new species and the existing species, if i was the predator and j the prey, then $-a_{i,j}$ and $\gamma_{i,j}$ were chosen from a random standard uniform distribution, where the efficiency $\gamma_{i,j} = -a_{i,j}/a_{j,i}$ was used to determine $a_{i,j}$.

Each new species i had a probability f of interacting with each existing species in the system, with equal chance of being its predator or its prey (provided that this did not result in autotrophs “preying” on other species). Values of $f = 0.2$ or $f = 0.8$ were used, as indicated in “Results.”

Can the New Species Invade? After a new species was created, the algorithm tested whether it could invade the food web. The rules for successful invasion depended on which algorithm was used. For the control algorithm, every new species was a successful invader. For the feasible algorithm, a new species could invade only if its steady state biomass was greater than 0. For the permanence algorithm, the new species could invade if it had a positive growth rate at low concentrations, that is, if

$$d_i + \sum_{j=1}^n a_{i,j} x_j^* > 0, \quad (2)$$

where x_j^* is the steady state biomass evaluated in the system where the biomass of the new species approaches 0 (Dieckmann et al. 1995; Metz et al. 1995; Dieckmann 1996; Dieckmann and Law 1996).

If the new species could not invade, another invader was randomly generated, and the process was repeated. If it could invade the system, it was permitted to, and the

dynamical constraints on the web were applied to determine how the system responded to the invasion.

How Does the System Respond to the Invasion? When a new species invades a food web, it can cause other species, including itself, to become extinct. In the algorithms, which species becomes extinct (if any) was determined by the type of dynamical constraint applied to the web. For the control algorithm, no species would become extinct after an invasion.

For the feasible algorithm, species were removed until all species in the web had a positive steady state concentration. Species were removed one at a time, with the most negative species removed first. In some cases, the removal of a species resulted in a singular web. In that case, a singular value decomposition was used to find the generalized inverse of the interaction matrix, which was then used to find the species with the lowest biomass, which was removed.

For the permanence algorithm, species were removed until the entire system satisfied the sufficient condition for permanence (Cantrell and Cosner 2003, chap. 4). This was achieved by combining an analytical proof that all feasible food chains are permanent with the method described by Kirlinger (1986). Details of this may be found in “Motifs in Algorithm Webs” and “Kirlinger’s Method” in the online edition of the *American Naturalist*. In rare cases, this algorithm was not able to find a permanent subsystem (for similar cases, see Law and Morton 1996; Virgo et al. 2006). In such cases, the algorithm simply removed the invader.

Trophic Constraints

In the algorithms above, a heterotroph was permitted to feed on any species, regardless of its trophic level. This was done to ensure that the algorithms were as minimal as possible. However, as shown in “Results,” some food web attributes are strongly dependent on the degree of omnivory in the web. These attributes’ values in real webs reflect the fact that those real webs have relatively well-defined trophic levels and few cycles. Therefore, a very simple set of trophic constraints was created that could be imposed on the algorithms where needed, to demonstrate the importance of distinct trophic levels for those attributes.

A trophic level t_i was randomly assigned to each species. The trophic level constrained the species’ feeding such that it could be fed on by or feed on only species that were within a range w (set to 0.5) of one level above or below it. So, for example, given $w = 0.5$, a species with $t_i = 2.7$ can feed only on prey with t_j in $[1.2, 2.2]$ and be fed on only by predators with t_j in $[3.2, 4.2]$. This ensured that trophic levels were relatively well defined but still permitted a small degree of omnivory.

Results

Webs Often Had a Higher Level of Constraint than Was Imposed on Them

The overwhelming majority of control webs were neither feasible nor stable nor permanent (2,420 of 2,500 webs), and of those that were feasible and stable, most consisted of a single autotroph and a heterotroph (52 of 80), and very few had more than two trophic levels (2 of 80). In contrast, food webs produced by the algorithms often had a higher level of dynamical constraint than had been imposed on them. Of the webs produced by the feasible algorithm, 2,465 of 2,500 webs were permanent, and 2,426 of those were both locally stable and permanent. Similarly, 2,382 of 2,500 webs produced by the permanence algorithm were locally stable. Therefore, to isolate the effect of permanence on food web structure, only the subset of feasible webs that was impermanent was used for the comparisons.

Poor Predictions: Low Connectance and Indistinct Trophic Levels

The trophic fractions predicted by the algorithms (fig. 1A–1C) compare best with those in phytotelmata webs, which also had the web size range most similar to that produced by the algorithms. Significant slopes produced by the algorithms were negative for the top fraction, positive for the intermediate fraction, and negative for the basal fraction. This agrees not only with Murtaugh and Kollath’s (1997) reanalysis of Schoenly et al.’s (1991) data, as shown in figure 1, but also with trends found in other compilations of empirical webs (Schoener 1989; Sugihara et al. 1989; Winemiller 1990; Schoenly et al. 1991; Havens 1992; Martinez and Lawton 1995) and trends observed when empirical webs are aggregated on the basis of species’ trophic similarity (Hall and Raffaelli 1991; Goldwasser and Roughgarden 1997; Martinez et al. 1999).

The interactive connectance predicted by the algorithms has a negative relationship with web size (fig. 1D), in agreement with the Schoenly et al. (1991) data. Further, this negative relationship asserts itself even when the algorithm underlying the dynamical constraints would produce a positive relationship. For example, when the probability of a new species interacting with the natives was increased to $f = 0.8$, the control predicted that the interactive connectance would increase with web size ($\text{logit } \hat{p} = -0.309 + 0.01925n$, $P = .013$); however, both the permanent webs and the impermanent feasible webs maintained their negative slope (permanent: $\text{logit } \hat{p} = 0.303 - 0.0759n$, $P < .001$; impermanent: $\text{logit } \hat{p} = 0.429 - 0.0770n$, $P < .001$).

The algorithm performed poorly at predicting empirical food web attributes, in particular by underpredicting mean

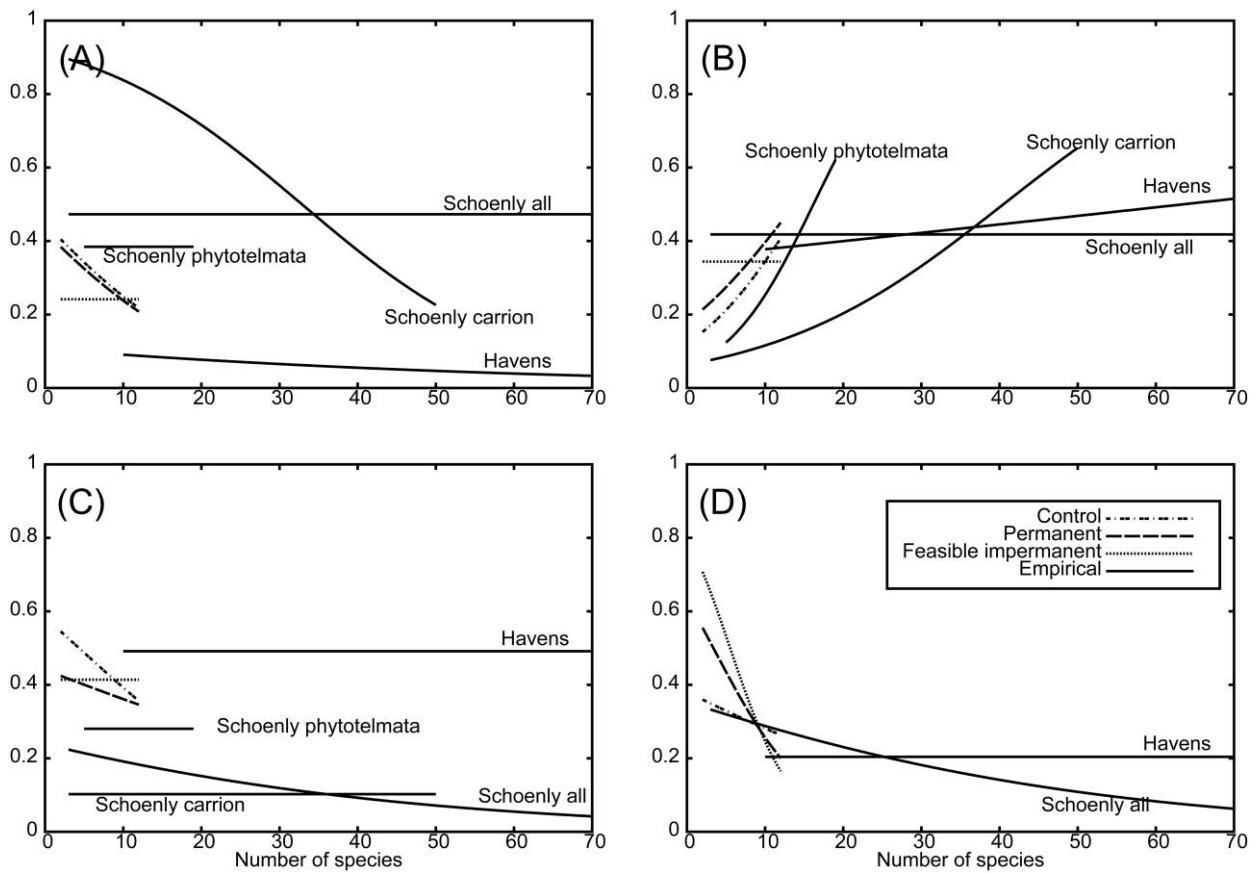


Figure 1: Fraction of top (A), intermediate (B), and basal (C) species and interactive connectance versus the number of species in the web (D), summarized with multinomial regressions (Murtaugh 1994; Murtaugh and Kollath 1997). Dashed and dash-dotted lines represent food web-building algorithms, and solid lines represent empirical webs (details in table A3 in the online edition of the *American Naturalist*). Algorithm webs compare best with phytotelmata webs, but connectance decreases more quickly in dynamically constrained algorithms than in real webs.

maximum similarity (s_{\max}), overpredicting omnivory degree measures (O_{sw}), and underpredicting directed connectance (C ; table 1). The former two mispredictions result because webs produced by the algorithms have relatively indistinct trophic levels, compared to the empirical webs (see below). The underprediction of directed connectance is also reflected in figure 1D, which shows that the algorithms constrain the interactive connectance with size more strongly than in real webs. The low connectance measures are also reflected in the mean generality and vulnerability, which is at the lower end of the range reported for early, highly aggregated data (Schoener 1989) and well below the values into the tens that can be observed in detailed parasitoid webs (Memmott et al. 2000).

Webs produced by the niche model have lower similarity and higher omnivory degree than small empirical webs, which indicates that obtaining a contiguous web with lower connectance makes the trophic levels less distinct.

However, the algorithm webs still have a lower similarity and higher omnivory degree than those produced by the niche model.

The most noticeable effect of the permanence constraint was to increase the mean and maximum short-weighted trophic levels compared to those in impermanent webs. This was consistently true across the range of web sizes and remained true when impermanent webs were collapsed back into their permanent subset (fig. A5 in the online edition of the *American Naturalist*). As the trophic level has a positive relationship with omnivory degree, permanence also increased the latter; however, permanent webs had fewer omnivores than the impermanent webs, on average (fig. A6 in the online edition of the *American Naturalist*), partly because some taller permanent webs contained no omnivores at all.

The trophic levels in algorithm webs were also made less distinct by frequently containing cycles (fig. 2). Gen-

Table 1: Commonly reported food web attributes as predicted by the algorithms and the niche model of Williams and Martinez (2000), averaged over small empirical EcoWEB webs, and measured in large empirical webs

Attribute	Food web–building algorithms ^a				Empirical webs ^b							
	Control	Permanent	Impermanent	Niche	Small	SP	LRL	BBL	CB	YE	CD	SMI
n	11–13	11–13	10–12	11	8–14	25	92	25	31	83	29	42
T	.22	.21	.25	.25	.40	.04	0	0	.28	.38	0	.17
I	.41	.43	.32	.32	.36	.92	.87	.68	.62	.53	.9	.69
B	.36	.36	.43	.43	.23	.04	.13	.32	.1	.09	.1	.14
s_{\max}	.33	.32	.34	.50	.62	.76	.76	.71	.34	.5	.72	.54
O/n	.34	.33	.3	.23	.20	.636	.38	.53	.79	.6
\overline{O}_{sw}	.72	.88	.74	.67	.43	$\leq .8^c$	$\leq .8^c$	$\leq .8^c$	$\leq .8^c$	$\leq .8^c$	$\leq .8^c$	$\leq .8^c$
$\max(O_{sw})$.97	1.16	.91	.78	.45	$\leq 1.8^d$	$\leq 1.8^d$	$\leq 1.8^d$	$\leq 1.8^d$	$\leq 1.8^d$	$\leq 1.8^d$	$\leq 1.8^d$
C	.1	.1	.11	.11	.14	.32	.12	.17	.07	.06	.31	.12
\overline{TL}	1.88	1.95	1.72	1.75	1.97	2.57	1.95	1.59	2.4	2.44	3.09	2.42
TL_{\max}	3.07	3.3	2.81	2.87	2.88	3.36	3.65	3.43	3.42	4.06	4.29	4.28
$SD(G)$.96	.95	1.09	1.29	.86	.92	1.4	1.09	.71	1.16	.73	1.02
$SD(V)$.86	.75	.82	.81	1.28	.54	.57	.61	1.03	1.4	.6	.78
G	1.99	1.91	1.2	2.16	1.90	1–4 ^e	1–4 ^e	1–4 ^e	1–4 ^e	1–4 ^e	1–4 ^e	1–4 ^e
V	1.68	1.55	1.54	1.64	2.91	1–5 ^e	1–5 ^e	1–5 ^e	1–5 ^e	1–5 ^e	1–5 ^e	1–5 ^e

Note: For definitions of most attributes, see “Measuring Food Web Attributes”; see “Poor Predictions: Low Connectance and Indistinct Trophic Levels” for the definition of C and “Detailed Description of Food Web Attributes,” in the online edition of the *American Naturalist*, for definitions of \overline{TL} and TL_{\max} . All attributes were calculated by Cattin et al. (2004), except mean and maximum trophic levels (TL), which are from Williams and Martinez (2004).

^a Only larger food webs from the algorithms were included, so mean values were taken from 21 control, 21 permanent, and 22 impermanent webs. Niche-model attributes were averaged over 100 randomly generated webs constrained so that they contained no cannibalism or mutual predation.

^b Small empirical webs are nine webs taken from Schoenly et al. (1991): Madagascar pitcher plant (Beaver 1985), Hong Kong pitcher plant (Corker 1984), England tree holes (Kitching 1983), two Australia tree holes (Kitching 1983), Costa Rica *Heliconia* (Seifert and Seifert 1976), Alabama stump hole (Kitching and Pimm 1988), German tree hole (Kitching and Pimm 1988), and Texas rabbit carrion (Schoenly and Reid 1983). Large empirical webs: SP = Skipwith Pond (Warren 1989; Williams and Martinez 2000), LRL = Little Rock Lake (Martinez 1991), BBL = Bridge Brook Lake (Havens 1992), CB = Chesapeake Bay (Baird and Ulanowicz 1989), YE = Ythan Estuary (Hall and Raffaelli 1991), CD = Coachella Desert (Polis 1991), and SMI = St. Martin Island (Goldwasser and Roughgarden 1993).

^c Maximum of approximately 0.8 (Williams and Martinez 2004).

^d Maximum of approximately 1.8 (Williams and Martinez 2004).

^e Schoener 1989.

erally, as the size of the food web increases, the percentage of webs with cycles increases. However, the fraction of webs with cycles tends to be higher and to increase faster for dynamically constrained webs than for the control.

The number of cycles and the number of species involved in cycles was also high compared to those in real webs. Many large, well-documented empirical webs contain no cycles (e.g., Bridge Brook Lake [Havens 1992], Ythan Estuary [Hall and Raffaelli 1991], the Coachella Desert [Polis 1991], St. Martin Island [Goldwasser and Roughgarden 1993]), and those that do have only a low proportion of species involved in the cycle (e.g., 0.12 for Skipwith Pond [Warren 1989] and 0.24 for Chesapeake Bay [Baird and Ulanowicz 1989]). In contrast, the proportion of species in a cycle in permanent webs with $f = 0.2$ ranged from 0.3 to 0.5, that in permanent webs with $f = 0.8$ ranged from 0.33 to 0.75, that in impermanent webs with $f = 0.2$ ranged from 0.27 to 0.8, and that in impermanent webs with $f = 0.8$ ranged from 0.25 to 0.63. In some cases, all heterotrophs were involved in at least one cycle. This was true for 14 out of 24 permanent

webs containing cycles and for 16 of 31 impermanent webs, for $f = 0.8$.

The motifs predicted by algorithms without trophic constraints (see “Trophic Constraints”) did not agree well with the empirical webs (fig. 3). For all three-species patterns and most four-species patterns, the algorithm predicted either no tendency or motifs where there were antimotifs, and vice versa. However, when simple trophic constraints were imposed on the algorithms, agreement improved substantially, and only one motif was incorrectly predicted.

A Skewed Interaction Strength Distribution Was Not Peculiar to Stable Webs

A skewed interaction strength distribution is associated with local stability (McCann et al. 1998; Emmerson and Raffaelli 2004), yet the algorithms produced similar patterns under other pairings of the stable/unstable and permanent/impermanent web characteristics. Analyzing per-biomass effects on predators (positive) and per-biomass effects on prey (negative), skewness values over all food

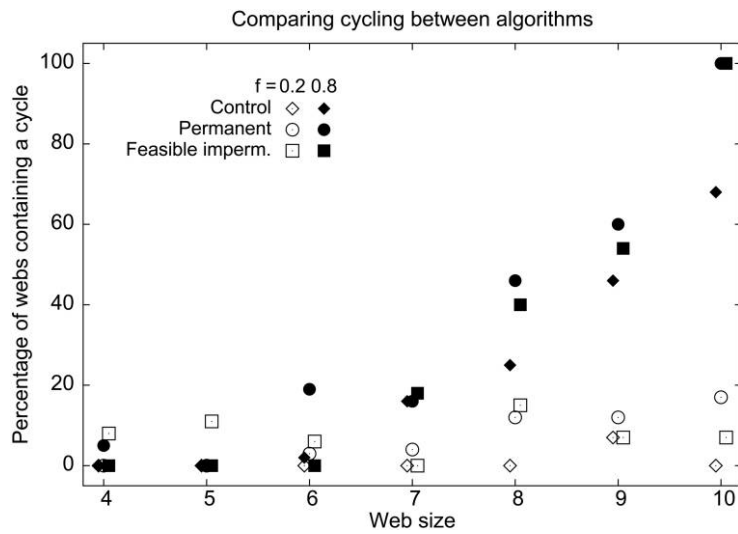


Figure 2: Percentage of food webs that contained at least one cycle for each size class. Cycles are trophic relationships of the form “A eats B, B eats C, ... eats A,” excluding cannibalism and mutual predation.

webs with flow-based trophic height greater than three ($f = 0.2$) were as follows: permanent-stable, 2.3 and -1.6 (from 69 webs totaling 578 interactions); permanent-unstable, 2.3 and -1.4 (from 53 webs totaling 589 interactions); impermanent-unstable, 2.7 and -1.2 (from 54 webs totaling 507 interactions). The impermanent-stable set was too small to measure skew on. For all of the classes, the log-transformed interaction strengths were significantly different (Lilliefors test: all $P < .001$) from a normal distribution (cf. Wootton 1997).

Using the same sizes, number of links, and number of basal species as found for impermanent webs generated by the feasible algorithm, 141 feasible webs with trophic height greater than three were generated using random-matrix methods (e.g., Gardner and Ashby 1970). Coefficients were drawn from a random standard uniform dis-

tribution. The skewness values of the interaction strength were comparable to those above. For all unstable webs, skewness was 2.8 and -1.6 (from 25 webs totaling 193 interactions), and webs that were both unstable and impermanent had skewness of 3.0 and -1.2 (from seven webs totaling 65 interactions).

Discussion

Making Valid Comparisons

The food web-building algorithms produced webs with low connectance and relatively indistinct trophic levels, compared to real webs. However, directly comparing the algorithm webs to the empirical webs is difficult, as algorithm webs were much smaller than the large, well-

Small empirical webs	+	+	+	-	+	-	-	+	+	+
Large empirical webs		+							+	
Permanence no constraints	-	-	-	+	+		-		-	-
Permanence trophic constraints	+	+	+	-	+	-	-	+	+	-/+

Figure 3: Trophic patterns that appeared as a motif (*plus sign*) or antimotif (*minus sign*) in at least one web from each set. Small empirical webs were taken from Schoenly et al. (1991): Madagascar pitcher plant (Beaver 1985), Hong Kong pitcher plant (Corker 1984), two Australia tree holes (Kitching 1983), and Texas rabbit carrion (Schoenly and Reid 1983). Large-empirical-web results were taken from Milo et al. (2002). Full algorithm results can be found in “Supplementary Tables and Figures” in the online edition of the *American Naturalist*.

documented empirical webs and had lower connectance than the similar-sized, small empirical webs. It is known that both size and connectance influence web attributes, which are used as tunable parameters in ordered-niche models.

The web size was constrained by the amount of biomass the five autotrophs could provide. Further, larger webs could not be created using the permanence algorithm by simply increasing the number of autotrophs, because the algorithm required the identification of subsets of the web, and the number of these increases exponentially with web size. This difficulty is peculiar to permanence, and readers interested in creating larger webs may do so with relative ease if some other dynamical constraint is chosen (e.g., numerical integration through time; Taylor 1988; Lockwood et al. 1997).

To address this mismatch of size and connectance, the algorithm webs can be compared to the mean attributes of webs of similar size and connectance produced by the niche model (Williams and Martinez 2000). Comparing the niche model and the small empirical webs suggests that obtaining a contiguous web with lower connectance does cause the trophic levels to become less distinct. However, the algorithm webs still had less distinct trophic levels than those created by the niche model.

The Algorithms Produced Low-Connectance Webs with Indistinct Trophic Levels

The likelihood of obtaining a stable web decreases with increasing size and connectance (May 1972; Chen and Cohen 2001). Although food web-building algorithms can go some way to circumventing the connectance constraint (Post and Pimm 1983; Taylor 1988; Drake 1990), the algorithms in this article were not able to match the behavior of real webs. Consequently, in order to obtain webs with realistic connectance, dynamical algorithms will have to be supplemented with additional stabilizing assumptions, such as taking into account the body mass of the species (Brose et al. 2006). Alternatively, connectance may be better explained by the behavioral and morphological characteristics of the species, such as foraging traits (Beckerman et al. 2006), rather than dynamical constraints alone.

Because no trophic constraints were imposed on the species in the web, it is unsurprising that they did not form into distinct trophic levels. However, what is interesting is that many of the mispredicted attributes of real food webs can be related to this property: the underprediction of mean maximum similarity and the overprediction of omnivory degree and cycling. Similarly, the motifs and antimotifs predicted by the algorithms were almost the opposite of those observed in real webs, and this was corrected when a simple trophic hierarchy was imposed

on the webs. This implies that food web motifs are primarily the result of trophic levels rather than the flow of energy up the web, as previously suggested (Milo et al. 2002). Taken together, these results suggest that relatively distinct trophic levels are an important aspect of what we know about food web attributes and that dynamically constrained algorithms that do not include trophic constraints will perform poorly at predicting web attributes (cf. Williams and Martinez 2004).

One explanation for the distinct trophic levels in food webs is the physiology of the species. For example, body size may restrict heterotrophs so that they can feed only on species that are smaller and within a certain size range (Cohen 1989b). The niche model performs better than the dynamically constrained algorithms because, like other ordered-niche models (cascade, nested hierarchy), it presupposes that some trophic hierarchy exists and expresses it in the form of a heuristic niche ordering on the species (Stouffer et al. 2005). I know of only one dynamically based model that can produce distinct trophic levels as an emergent property—that is, without imposing them explicitly—and that is the Webworld algorithm (Drossel et al. 2001).

The Effects of Different Dynamical Constraints

Of theoretical interest is the effect that the addition of each dynamical constraint had on food web structure. For the most part, the addition of permanence to feasibility did not change the attributes much; however, it did increase the trophic height of the webs. The reason for this was that both the feasible and the permanent webs selected heterotrophs with higher feeding efficiency (“Building the Proof” in the online edition of the *American Naturalist*), but the selection was stronger in permanent webs because of the invasion process. Under the permanence constraint, a successful invader i is one that satisfies $\sum -a_{j,i} \gamma_{i,j} x_j^* + d_i > 0$. In the preceding relationship, having a high efficiency γ increases the likelihood that a new species is a successful invader. Thus, efficiency determines not only which species can obtain enough biomass to stay feasible but also which can enter the system in the first place. Therefore, when less energy is dissipated in the trophic interactions, as in permanent webs, then more species can be maintained on the energy available, and the web can be taller.

Both dynamically constrained algorithms produced a greater proportion of webs containing cycles than the control. Cycling reuses energy that would otherwise be dissipated, allowing more species to be maintained on the same amount of autotroph-supplied energy. This suggests that the cycling is being promoted by dynamically constrained food webs for energetic reasons. In contrast, well-

documented empirical webs that are much larger than this often contain no cycles (Hall and Raffaelli 1991; Havens 1992; Goldwasser and Roughgarden 1993), and this is true even in webs that have high omnivory (Sprules and Bowerman 1988; Schmid-Araya et al. 2002), suggesting that physiological constraints precede the energetic benefits of cycling. In this article, imposing simple trophic constraints that excluded cycles and limited omnivory posed no barrier to satisfying feasibility or permanence, and previous authors (Law and Morton 1996; Virgo et al. 2006) reported no difficulties in obtaining permanent webs, given the physiological constraints used in their algorithms.

Randomly generated food webs can have attributes significantly different from those obtained via a food web-building algorithm (Virgo et al. 2006). Consequently, generalizations made about webs produced under certain constraints may no longer apply. For example, both cycling and omnivory (Pimm 1982; Pimm and Rice 1987) are thought to be destabilizing (but see Fagan 1997; McCann and Hastings 1997), yet the dynamically constrained algorithms produced webs with high values of both. This is because the adaptive power of the assembly process allows it to obtain atypical webs (cf. Post and Pimm 1983; Taylor 1988; Drake 1990). Therefore, if real food webs do behave like a food web-building algorithm, this may make detecting indicators of a dynamical constraint difficult.

Real food webs have a skewed distribution of interaction strengths, with a few strong links embedded in a majority of weak links (Paine 1992; Fagan and Hurd 1994; Wootton 1997; Neutel et al. 2002; Sala and Graham 2002; Emmerson and Raffaelli 2004; Wootton and Emmerson 2005). Further, it can be demonstrated that using a skewed distribution of interaction strengths increases the probability of a stable model food web (McCann et al. 1998; Emmerson and Raffaelli 2004; Emmerson and Yearsley 2004), which has led some authors to interpret the observed skew as evidence of stability constraints acting on real webs (Emmerson and Raffaelli 2004). Yet in this study, a similarly skewed distribution of interaction strengths was obtained for all dynamically constrained webs, including those that were locally unstable and impermanent. Therefore, although local stability may favor a skewed distribution, the former is not a necessary condition for the latter, and a skewed distribution can arise through other means (cf. Kokkoris et al. 1999).

Conclusion

In closing their review of food web attributes, Hall and Raffaelli (1993) suggested that simulated food web assembly and the permanence constraint were promising avenues for investigating the cause of patterns observed in real food webs. However, in this work, it was found that

permanent webs lacked the key properties of real webs and that adding permanence as a constraint did not improve the predictive ability over feasibility alone. While disappointing, this result provides a counterweight to any potential "publication bias," whereby the predictive successes of stability constraints are widely known but the areas in which they fail are not.

In contrast, the ordered-niche models used by other authors have been very successful at predicting the structure of real food webs (e.g., Williams and Martinez 2000; Cattin et al. 2004). As a heuristic based on the physiology of species is a more parsimonious explanation for food web pattern than dynamical constraints, this implies that the former is the best explanation we have for what is currently known about food web structure.

The literature suggests that, provided that some assembly algorithm is used, dynamical constraints are fairly amenable to being satisfied regardless of other structural constraints imposed. Taken together with this study's main result, this suggests that it is physiology that determines the coarse structure of food webs and that dynamics will augment only the finer details within those constraints. This, in turn, suggests that detecting the effects of dynamics on structure will be difficult.

Nevertheless, there is evidence that real food webs have a structure peculiarly suited to promoting stability, particularly when interaction strengths are accounted for (Yodzis 1981; de Ruiter et al. 1995; Neutel et al. 2002). However, it is difficult to summarize these idiosyncratic high-stability states in one simple measure. Slight changes in food web topology can greatly change the stability of a web (Fox 2006). Where such measures are known, they often require detailed information on species interactions (e.g., those identified by Chen and Cohen [2001]). In contrast, the easily measured attributes that have been used, which are those for which the most empirical data exist, are relatively insensitive to small changes in food web topology (cf. Fox 2006). So while physiological constraints may be the best current explanation of web structure, this should be qualified by noting that what we know about food web structure may well be restricted to those aspects that are determined by physiological constraints to begin with.

Despite the inadequacy of the dynamically constrained food web-building algorithms, they do have one compelling advantage over the ordered-niche algorithms: in order for the cascade model, niche model, or nested hierarchy to be used, one must provide it with the desired number of species and links in the web. In contrast, the dynamically constrained food web produces these as emergent properties—a consequence of the energy flow and stability constraints on it. Consequently, hybrid models where minimal dynamical constraints are combined with

physiological constraints, such as Webworld (Drossel et al. 2001), show much promise.

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