Community assembly, stability and signatures of dynamical constraints on food web structure

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ABSTRACT

To understand the dynamics of natural species communities, a major challenge is to quantify the relationship between their assembly, stability, and underlying food web structure. To this end, two complementary aspects of food web structure can be related to community stability: sign structure, which refers to the distributions of trophic links irrespective of interaction strengths, and interaction strength structure, which refers to the distributions of interaction strengths with or without consideration of sign structure. In this paper, using data from a set of relatively well documented community food webs, I show that natural communities generally exhibit a sign structure that renders their stability sensitive to interaction strengths. Using a Lotka–Volterra type population dynamical model, I then show that in such communities, individual consumer species with high values of a measure of their total biomass acquisition rate, which I term "weighted generality", tend to undermine community stability. Thus consumer species' trophic modules (a species and all its resource links) should be "selected" through repeated immigrations and extinctions during assembly into configurations that increase the probability of stable coexistence within the constraints of the community's trophic sign structure. The presence of such constraints can be detected by the incidence and strength of certain non-random structural characteristics. These structural signatures of dynamical constraints are readily measurable, and can be used to gauge the importance of interaction-driven dynamical constraints on communities during and after assembly in natural communities.

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1. Introduction

Food webs, which are networks of interspecific "who-eats-whom" trophic interactions, are crucial for understanding the survival of species in natural communities. Certain structural features of food webs, such as trophic degrees (number of trophic interactions of each species) and chains may reflect constraints of multi-species coexistence, and are key to linking the dynamics of single populations to that of the community as a whole (May, 2006; Levins, 1975). Moreover, the empirical study of multiple species within the context of their community is generally intractable, and any known relationship between food web structure and dynamics can help understand the assembly and persistence of species rich communities from snapshots of interaction patterns (May, 1974; Pimm, 1982).

The relationship between food web structure and dynamical stability of the component species' populations is essentially a feedback between different levels of community organization (May, 2006; Proulx et al., 2005). In order to understand this feedback, an explicit mapping between food web structure and dynamics is needed (Dunne et al., 2005; Pascual et al., 2006). Such mappings were first established mathematically by Levins (1974) and May (1974). For example, May (1974) showed that for a given species richness n, mean of the absolute magnitudes of interaction strengths c and connectance C_T (fraction of potential links that are realized), community "complexity", $c\sqrt{nC_T}$, is a measure of interaction network structure that undermines the probability of stable species coexistence. May's and Levins' results carried the largely implicit assumption that communities undergo a "selection" process that favors network structural configurations that enhance multi-species coexistence stability. In May's (1974, pp. 3–4) words,

> In nature we deal not with arbitrary complex systems, but rather with ones selected by a long and intricate process. The emergent moral is that theoretical work should not try to prove any general theorem that "complexity implies stability", but instead should focus on elucidating the very special sorts of complexity, the singular strategies, which may promote such mathematically atypical stability

In principle, the overall process that leads to the emergence of such stabilizing network structures due to dynamical

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constraints is simple: during community assembly, less stable structural configurations of the food web are weeded out through a combination of adaptive changes, extinctions, and recolonizations of species' populations, until a stable state is achieved. By definition this state either does not change anymore, or as fast. The network structure of this stable system is therefore a non-random subset of all possible ones for a given biotic and abiotic setting. However, a quantification of this process is far from simple, and must simultaneously address three issues:

(i) *Assembly*: How does food web network structure change during community assembly, how important is the pattern of species' immigration?
(ii) *Relationships between network structure and stability*: What features of food web network structure have relatively strong effects on stability?
(iii) *Mechanisms of structural change*: What mechanisms result in the emergence of specific food web network structural configurations, and at what level do they act (e.g., individuals, populations, or groups of populations (subcommunities))?

Past studies have addressed these issues to various degrees, but very few have included all in a single theoretical framework. Community assembly dynamics have been the focus of a set of studies that began with theoretical and empirical work in the 1980s (e.g., Law and Morton, 1996; Post and Pimm, 1983; Robinson and Dickerson, 1987; Virgo et al., 2006). However, other than the traditional measures of connectance and species richness, these studies have not related food web structure and stability to assembly until recently (Bastolla et al., 2005; Kristensen, 2008; Neutel et al., 2007). May's (1974) and Levins' (1974, 1975) seminal contribution mainly addressed the second issue, i.e., of the relationship between food web structure and stability. Subsequent studies sought to further elucidate the effects of different types of trophic structural features on community stability, such as modules consisting of a prey and two shared predators (Yodzis, 1981), trophic chains (Pimm and Lawton, 1977), trophic loops (Neutel et al., 2002) and omnivory (Neutel et al., 2007). However, there is still very little consensus about which food web structural features (modules) play an important part in determining community stability. The third issue, i.e., of the mechanisms of structural change, has received very little attention in the past. However, a series of theoretical studies have recently begun to consider the role of behavioral and evolutionary processes in stabilization of communities (Drossel et al., 2004; Loeuille and Loreau, 2005; Uchida et al., 2007).

Thus on the whole, major gaps currently remain in our understanding of relationship between community assembly, stability, and food web structure. The current paper seeks to make a contribution by simultaneously addressing the above three issues using a relatively simple mathematical model. This paper is organized as follows. Section 2 introduces the mathematical model, describes how food web structure changes dynamically during community assembly, defines community stability (stable species coexistence), and establishes a key relationship between food web structure and community stability. Section 3 then builds upon these preliminaries to show how certain stabilizing food web structural configurations are favored during community assembly, resulting in specific signatures on food web structure that are indicative of dynamically constrained assembly. Section 4 evaluates the robustness of these analyses through numerical simulations under different community assembly scenarios. Section 5 concludes with a discussion of the results.

2. Community assembly, stability, and changes in food web structure

2.1. The model

Let $\mathfrak{N}$ denote the set of unique species indices $1, 2, \ldots, n$ in an n-species community. I will use a Lotka–Volterra (LV) type model of community population dynamics:

$$\frac{dx_i}{dt} = x_i \left(b_i - d_i + \sum_{j=1}^{n} \alpha_{ij} x_j \right), \quad \forall i \in \mathfrak{N} \tag{1a}$$

Here, x_i is the total biomass of the ith species' population, b_i its autonomous biomass production (including reproduction) rate (0 for all consumers) and d_i its intrinsic density—independent biomass loss (including mortality) rate. The constant coefficient α_{ii} represents biomass loss rate due to direct intraspecific interference of the ith species, while α_{ij} represents its biomass loss or gain rate from interaction with the jth species. If the jth species is a consumer of the ith one, biomass gain rate of the former (α_{ji}) and loss of the latter (α_{ij}) are related such that

$$\alpha_{ji} = -e_j \alpha_{ij} \quad (\text{when } j \text{ consumes } i) \tag{1b}$$

e_j is the fraction of biomass lost due to assimilation and production inefficiency of the jth consumer. I assume that all interactions result in a net flow of biomass from one species to another. Thus in the case where two species are capable of consuming each other (e.g., at different life history stages), it is assumed that the interaction, when integrated across all life stages, results in a net flow from one species to another. This also implies that the indices in expression (1b) cannot be reversed for a given species pair. For analytical tractability, I follow previous studies (Hofbauer and Sigmund, 1998; Logofet, 1993; May, 1974; Levins, 1974) in assuming that α_{ij} is a linear, simplified representation of encounter and consumption rates. The effects of more complex interaction coefficients, such as those resulting from the functional response of consumers to increasing availability of resource species' biomass abundance, will be considered in a subsequent paper.

2.2. The dynamics of community assembly, stability and changes in food web structure

Consider community assembly starting with the establishment of at least one basal species (indexed by 1), which we will assume was able to grow in the absence of consumers to a positive equilibrium biomass density, $\hat{x}_1 = -(b_1 - d_1)/\alpha_{11}$. During assembly, the ith immigrant arriving at a community already consisting of m residents ($m \geqslant 1$) will grow in biomass density when rare (invade) if the condition

$$\sum_{j \in \mathfrak{G}_i} |\alpha_{ij}| e_i \hat{x}_j > \sum_{k \in \mathfrak{B}_i} |\alpha_{ik}| \hat{x}_k + d_i, \quad j, k = 1, 2, \ldots, m \tag{2}$$

is satisfied (Roughgarden, 1996; Strobeck, 1973), where $\mathfrak{G}_i$ and $\mathfrak{B}_i$ denote the index sets of the immigrant's resource and consumer species, respectively. Eq. (2) states that the biomass gain rate must be greater than loss rate, measured when all resident species are at equilibrium. If the immigrant can invade, and if subsequently all $m+1$ ($= n$) populations converge on a vector of equilibrium sizes $\hat{\boldsymbol{x}}$ that is a point within the positive orthant $\mathbb{R}^n_+$ of the n-dimensional Euclidean state space (i.e., no population goes extinct), the system is (at least) Hurwitz stable (or locally asymptotically stable) if the $n \times n$ Jacobian $\boldsymbol{C}$ (the familiar "community matrix"; May, 1974) with

elements (e.g., see Logofet, 1993),

$$c_{ij} = \frac{\partial(dx_i/dt)}{\partial x_j}\bigg|_{x=\hat{x}} = \alpha_{ij}\hat{x}_i, \quad \forall i,j \in \mathfrak{R} \qquad (3)$$

has all its eigenvalues $\lambda_i(\boldsymbol{C})$, $i \in \mathfrak{R}$ lying in the negative half of the complex plane i.e., given $\lambda_{\max}(\boldsymbol{C}) \equiv \max\{\text{Re}(\lambda_i(\boldsymbol{C}))\} \forall i \in \mathfrak{R}$, the inequality

$$\lambda_{\max}(\boldsymbol{C}) < 0, \qquad (4)$$

must hold. The element c_{ij} ($i \neq j$) of $\boldsymbol{C}$ represents the population-level effect of a change in the jth species' biomass density on the ith one, or the dependence of the ith species on its own density (if $i = j$), at biomass equilibrium. Note that it is possible for one or more populations under in the LV model to actually settle into periodic or chaotic trajectories. In this case, the system actually converges to the vicinity of a periodic or chaotic attractor (e.g., see Gilpin, 1979), and criterion 4 does not hold. However, as will be seen below, the assumption of a point equilibrium allows the use of the Jacobian matrix and Hurwitz stability criterion, which in turn allows food web structure to be explicitly linked to community stability. Whether predictions about the relationships between food web structure and community stability based upon this assumption are valid will be tested with numerical simulations (Section 4). Note also that an additional condition to satisfy $\lambda_{\max}(\boldsymbol{C}) < 0$ is that there be no disconnected subcommunities in the "community" (the community's graph should be irreducible; Logofet, 1993). But this need not concern us here because the above criteria and all the subsequent results of this paper can be applied to subcommunities separately.

Now, using criterions 2 and 4 together, changes in food web structure during assembly can be understood from the following alternative scenarios after an immigrant's arrival (again, ignoring periodic or chaotic dynamics):

- *Inequality* 2 *is not satisfied*. The immigrant cannot invade and there is no impact on food web structure.
- *Inequalities* 2 and 4 *are both satisfied*. The community grows and food web structure changes by addition of a species and its trophic links. I will call this a "stable invasion".
- *Inequality* 2 *is satisfied, but* 4 *is not*. The immigrant invades but one or more populations eventually go extinct, which may or may not include the immigrant. Hence community size either shrinks or remains the same and food web structure changes by the loss of at least one species and its trophic links. I will call this a "species sorting" event.

Stable invasions result in gradual changes in food web structure during assembly, whereas species sorting events can cause greater structural upheavals. Thus the probability of an invaded community satisfying inequality 4 and being Hurwitz stable (PHS) is crucial for understanding changes in food web structure. PHS is the probability of a randomly chosen community matrix from the space of all possible matrices with the same n, sign structure (the distribution of trophic links across species), and statistical properties of the intra- and interspecific interaction strengths. Before considering assembly dynamics in greater detail, I will show how particular food web structural features can be explicitly linked to community stability.

2.3. Interlinking food web structural features and community stability

In order to relate food web structure to PHS, we need to consider structural measures that directly determine the sign of the real part of the leading eigenvalue (inequality 4). To this end,

two approaches have been used in the past: the consideration of sign structure irrespective of interaction strengths, and the consideration of interaction strength structure (distributions of interaction strengths across trophic links), with or without consideration of the strength structure (Logofet, 1993; May, 1974). The first approach requires the concept of sign stability. Sign stable communities have a pattern of trophic linking between species that guarantees Hurwitz stability irrespective of the magnitudes of the interaction strengths α_{ij} (or c_{ij}) (Logofet, 1993; May, 1974). Thus food web structural configurations that lead to sign stability can be determined. The problem with this approach is that one of the necessary conditions for sign stability precludes the presence of omnivory (because no cycles of length greater than three should be present; Logofet, 1993; May, 1974), even though it is prevalent in empirical food webs (Williams and Martinez, 2004). Here I will focus on the second approach for relating food web structure to stability: consideration of interaction strength structure. May's (1974) complexity measure is an example of this approach because it links PHS to average interaction strength for a given level of connectance (C_T), community size (n), and negative intraspecific density dependence. However, this measure and its refinements (Cohen and Newman, 1985; Geman, 1986; Hastings, 1982) do not show how species-level strategies and small-world food web structural features (involving the interactions between a few species) are related to stability. I address this problem in the current paper; in Appendix A I show that for communities with certain sign structures, and some level of intraspecific density dependence across species (the c_{ii}'s), $\lambda_{\max}(\boldsymbol{C})$ monotonically increases with $\rho(\underline{\boldsymbol{C}})$ (crossing the critical boundary beyond some value), where

$$\rho(\underline{\boldsymbol{C}}) \equiv \max\{|\text{Re}(\lambda_i(\underline{\boldsymbol{C}}))|\}, \quad \forall i \in \mathfrak{R} \qquad (5)$$

and $\underline{\boldsymbol{C}}$ is a matrix with elements defined as

$$\forall i,j \in \mathfrak{R}, \quad \underline{c}_{ij} = \begin{cases} |c_{ij}| & \text{if } i \neq j \\ 0 & \text{if } i = j \end{cases} \qquad (6)$$

In such communities, PHS is inversely related to $\rho(\underline{\boldsymbol{C}})$; hence any food web structural feature that determines $\rho(\underline{\boldsymbol{C}})$ also affects stability, and interaction strength configurations of such a feature that result in a relative decrease of $\rho(\underline{\boldsymbol{C}})$ should be favored during community assembly. Biologically, $\rho(\underline{\boldsymbol{C}})$ can be interpreted as a single measure of the overall interaction strength structure of the community. I call the tendency for $\lambda_{\max}(\boldsymbol{C})$ to increase with $\rho(\underline{\boldsymbol{C}})$ "interaction-strength sensitivity" (ISS), and can be estimated from the correlation coefficient between them (r_{ISS}) over a sufficiently large number of interaction strength randomizations (IS-randomizations; the simulation methodology is described in Appendix A). Thus ISS is essentially a measure of the lack of quasi-sign stability (QSS) proposed by Allesina and Pascual (2008).

To gauge the prevalence of ISS in real-world communities, I examined 17 relatively well documented community food webs from a variety of terrestrial and aquatic habitats (see Supplementary Appendix 1 for data description). Table 1 indicates that all of them show some degree of ISS (r_{ISS} ranging from 0.08 to 0.83). Fig. 1 shows the actual relationship between $\lambda_{\max}(\boldsymbol{C})$ and $\rho(\underline{\boldsymbol{C}})$ for two contrasting examples from these communities.

Note that only the relationship between $\lambda_{\max}(\boldsymbol{C})$ and $\rho(\underline{\boldsymbol{C}})$ matters here; the fact that signs of $\lambda_{\max}(\boldsymbol{C})$'s of IS-randomizations of both communities are all negative does not necessarily indicate that they are inherently stable. $\lambda_{\max}(\boldsymbol{C})$'s can always be guaranteed to be negative if the c_{ii}'s are sufficiently negative; it so happens that the particular choice of the c_{ii}'s for IS-randomizations (see Appendix A) have resulted in all negative eigenvalues for these two communities.

Table 1
The ISS of 17 empirical communities (shown in order of decreasing r_{ISS}), estimated from 2000 IS randomizations.

Name	r_{ISS}	n	L_D (0.26*)	C_T (0.30*)	$\bar{G}$ (0.32*)	$\bar{V}$ (0.15)	$\bar{T}_c$ (0.65**)	O_{deg} (0.54**)
Carpinteria Salt Marsh	0.83	125	14.4	0.23	16.6	14.8	7.4	2.7
Skipwith Pond	0.82	33	9.7	0.61	17.8	10.4	4.2	0.6
Broadstone Stream	0.78	28	4.9	0.37	15.3	5.1	4.6	0.8
Company Bay Mudflat	0.77	76	6.8	0.18	7.5	7.8	6.9	1.5
Scotch Broom	0.72	153	2.4	0.03	10.2	77.0	3.2	0.1
Grand Caricaie Marsh	0.71	163	12.8	0.16	24.0	12.9	4.8	1.1
Caribbean Sea	0.59	248	13.1	0.11	13.5	13.1	4.6	0.5
Bridge Brook Lake	0.57	73	7.3	0.20	15.8	7.5	3.4	0.2
Ythan Estuary	0.56	121	3.3	0.05	6.1	63.5	3.1	0.6
Eastern Weddell Sea	0.49	391	4.3	0.02	9.5	196.0	2.9	0.2
Tuesday Lake	0.48	72	5.4	0.15	12.3	5.7	3.8	0.2
Martins Stream	0.45	96	2.7	0.06	5.4	3.7	2.9	0.2
UK Grassland	0.36	75	1.5	0.04	1.7	2.6	2.5	0.1
Little Rock Lake	0.32	117	4.3	0.07	5.6	7.2	3.9	0.3
Dempster's Tussock Stream	0.28	107	9.0	0.17	16.9	10.3	3.1	0.3
Mill Stream	0.17	74	5.0	0.14	8.2	10.5	1.2	0.0
North Carolina Pine Logs	0.08	90	1.7	0.04	1.7	4.0	1.7	0.0

All correlation coefficients are highly significant (two-tailed $p<0.0005$). Various food web characteristics and their correlation with r_{ISS} (r^2 values in parentheses) (Spearman's rank correlation) are also shown: species richness (n), link density (L_D), connectance (C_T), average generality of consumers ($\bar{G}$), average vulnerability of resources ($\bar{V}$), average trophic chain length ($\bar{T}_c$), and omnivory degree (O_{deg}). Correlations with $p<0.05$ and <0.005 are flagged with a single and double asterisk, respectively. $\bar{T}_c$ was estimated from a sample of all paths (to all consumers) arising from basal species (obtained using the path search algorithm described in Supplementary Appendix 2). O_{deg} is the mean of the standard deviations of each consumer species' trophic height (standard deviation of the lengths all the paths to the species from all its basal species (Goldwasser and Roughgarden, 1993)).
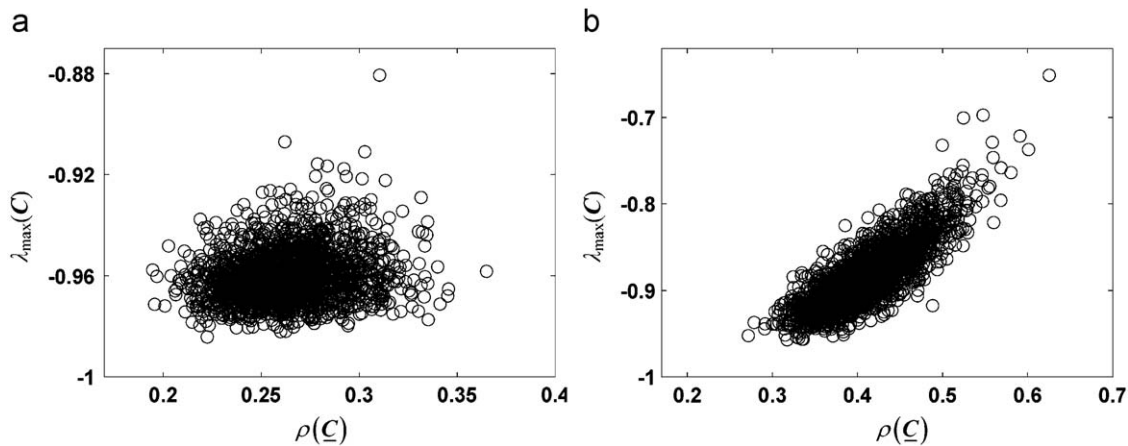

Fig. 1. The relationship between $\lambda_{max}(\mathbf{C})$ and $\rho(\underline{\mathbf{C}})$ across 2000 IS-randomizations in two empirical community food webs: (a) Mill Stream ($r_{ISS} = 0.08$) and (b) Skipwith Pond ($r_{ISS} = 0.83$). The IS-randomization method is described in Appendix A.

Given this wide variation in ISS of the 17 communities, can a general conclusion be drawn about the prevalence and strength of ISS in nature? Table 1 also presents the correlation of r_{ISS} with a suite of commonly measured features of food web sign structure (Pascual and Dunne, 2005). Except mean vulnerability, r_{ISS} is significantly correlated with all of them, suggesting that multiple sign structural features tend to influence ISS. Note that these correlations need to be interpreted with the knowledge that these structural features are not mutually independent (for example, connectance and link density tend to be positively correlated). However, because all these sign structural measures are known to be sensitive to inadequate sampling of interactions (Goldwasser and Roughgarden, 1997) , these correlations also suggest that ISS may be underestimated across the communities. In this context, that r_{ISS} is most strongly correlated with mean trophic chain length and omnivory degree is particularly noteworthy because recent studies indicate that these features have been underestimated in the past due to the omission of host-parasite links (Lafferty et al., 2008). In fact, of the seventeen empirical food

webs, five of the six that that include parasites and parasitoids (Carpinteria Salt Marsh, Company Bay Mudflat, Scotch Broom, Grand Caricaie Marsh, and Ythan Estuary) all show relatively high ISS. The sixth, UK Grassland, shows relatively low ISS, which can be explained by the fact that mainly host-parasitoid interactions were quantified in this community, thus also resulting in a sign structure biased in the opposite direction (too few predator–prey interactions) (Supplementary Appendix 2). Below I will show that model communities resulting from fairly general assembly algorithms also show consistently high ISS.

Hence I concentrate on ISS in this paper, and consider food web structural properties that determine $\rho(\underline{\mathbf{C}})$ (and hence PHS) during assembly. To this end, in Appendix B I establish the following relationship between food web structure and $\rho(\underline{\mathbf{C}})$. First define the quantity,

$$\bar{c}_{ij} = \sqrt{c_{ij}c_{ji}}, \quad \forall i,j \in \mathfrak{R} \tag{7}$$

i.e., geometric mean of the absolute magnitudes of each pair of interaction coefficients constituting a trophic link. The $\bar{c}_{ij}$'s will
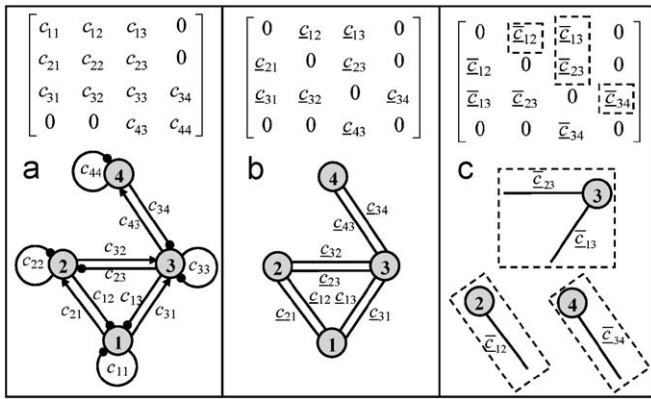
Fig. 2. The analytical steps involved in interrelating food web structure and Hurwitz stability illustrated using a hypothetical four-species community: (a) the community matrix $\mathbf{C}$ (as defined in expression (3)) and associated network representation. The interaction sign structure is represented using Levins (1974)'s scheme: edges ending in arrows represent positive effects (and direction of biomass flow) and those ending in circles, negative ones, (b) the simplified matrix $\underline{\mathbf{C}}$ (with elements defined in expression (6)) and associated network representation, and (c) the symmetrized matrix $S(\underline{\mathbf{C}})$ (with elements $\bar{\underline{c}}_{ji} = \bar{\underline{c}}_{ij} = \sqrt{\underline{c}_{ij}\underline{c}_{ji}}$; see Appendix B) and the associated network representation into species' trophic generality modules (these modules and their corresponding interaction coefficients are enclosed in dashed boxes).

henceforth be called "trophic link strengths" to differentiate them from the interaction strengths α_{ij}'s as well as the elements of $\mathbf{C}$. Now consider each species' "weighted generality", which is defined for the ith species to be

$$G_i^w = \sum_{j \in \mathfrak{G}_i} \bar{\underline{c}}_{ij}, \quad \forall i \in \mathfrak{R}, \tag{8}$$

where $\mathfrak{G}_i$ is the set of its resource species. Thus the total weighted generality of all species in the community is

$$G_{tot}^w \equiv \sum_n G_i^w = \sum_n \sum_{j \in \mathfrak{G}_i} \bar{\underline{c}}_{ij}$$

Then, Appendix B shows that the following relationship holds:

$$\frac{2G_{tot}^w}{n} \leqslant \rho(\underline{\mathbf{C}}), \tag{9}$$

Expression (9) says that $\rho(\underline{\mathbf{C}})$ (and hence PHS in ISS communities) is limited by species' weighted generalities. Fig. 2 gives a graphic overview of the analytical steps that allow species trophic generality modules to be thus related to PHS.

The advantage of converting the c_{ij}'s into $\bar{\underline{c}}_{ij}$'s is apparent; the pair of interaction coefficients associated with each trophic link (effect of consumer on resource and *vice versa*) are reduced to a measure of the overall interaction strength. Moreover, from expressions (1b) and (3), $\bar{\underline{c}}_{ij} = |\alpha_{ij}|\sqrt{e_i\hat{x}_i\hat{x}_j}$ (when i consumes j) and hence

$$G_i^w = \sqrt{e_i\hat{x}_i}\sum_{j \in \mathfrak{G}_i} |\alpha_{ij}|\sqrt{\hat{x}_j}, \quad \forall i \in \mathfrak{R} \tag{10}$$

which shows that G_i^w is essentially a measure of the total biomass acquisition rate of the ith species population at equilibrium. Thus expression (9) further implies that species with relatively high biomass acquisition rates tend to undermine community stability (decrease PHS). I will now show that due to the dynamical stability constraints indicated by expression (9), the emergence of certain stabilizing configurations of species' weighted generality modules should be favored during community assembly.

3. Community assembly, stability, and signatures of dynamical constraints on food web network structure

During assembly, because the number of trophic links per species (link density, or L_D) typically increases with n (Martinez, 1992; because at least some residents acquire additional links at every immigration event; e.g., Piechnik et al., 2008), G_{tot}^w tends to increase, and hence PHS decreases. As assembly proceeds, PHS eventually decreases to the extent that stable invasions are approximately balanced by species sorting events (as defined in Section 2.2), resulting in invasion-extinction quasi-equilibrium (IEE). At this stage, intermittent immigrations prevent the community from reaching a fixed equilibrium in the sense of expression (4), but on average, n remains constant over time (with variance proportional to immigration rate; see Bastolla et al., 2005). Thus as indicated by expression (9), during assembly, food web structural configurations that mitigate species' weighted generalities (relative to increasing L_D) will be favored by successive stable invasions and species sorting events. Furthermore, because G^w is a measure of the ith species' total biomass acquisition rate (see expression (10)), a reexamination of inequality 2 indicates a tradeoff between the invasibility of an immigrant and PHS of the augmented community; the immigrant's G^w should be sufficient to satisfy 2, but not so much as to destabilize the augmented community by increasing $\rho(\underline{\mathbf{C}})$ too much.

Thus the modulation of species' trophic generality characteristics such that G_{tot}^w is mitigated, will allow stable invasions and community growth during assembly, and maintenance of species richness at IEE. This means that species' generality-averaged weighted generality,

$$\bar{G}_i^w \equiv \frac{G_i^w}{G_i} = \frac{\sqrt{\hat{x}_i}\sum_{j \in \mathfrak{G}_i} |\alpha_{ij}|\sqrt{e_i\hat{x}_j}}{G_i}, \quad \forall i \in \mathfrak{R} \tag{11}$$

should be mitigated (or constrained). Thus a species' $\bar{G}^w$ is the average of the strengths of trophic links it has with its resource species (or alternatively, a measure of its link-averaged biomass acquisition rate). From expression (11), it is clear that assuming that efficiencies are similar across taxa, G_{tot}^w mitigation can happen by a modulation of either the interaction coefficients (α_{ij}'s), or equilibrium biomass sizes ($\hat{x}$'s). The contribution of changes in species' consumption strategies alone (without the effects of the $\hat{x}$'s) can be gauged by the degree to which link-averaged interaction strengths,

$$\bar{\alpha}_{G,i} \equiv \frac{\sum_{j \in \mathfrak{G}_i} |\alpha_{ij}|}{G_i}, \quad \forall i \in \mathfrak{R} \tag{12}$$

are constrained. Apart from stable invasions and species sorting, this can also happen by behavioral or evolutionary changes in species' consumption characteristics (although not within the confines of LVM model, where the coefficients α_{ij} are assumed to be constant) (e.g., Drossel et al., 2004; Loeuille and Loreau, 2005; Uchida et al., 2007). On the other hand, changes in equilibrium biomasses ($\hat{x}$) can happen through trophic cascades (Pace et al., 1999; Polis et al., 2000). For example, some populations may equilibrate at lower biomass densities due to density effects propagated along trophic chains upon the successful invasion of a new species (Neutel et al., 2007, 2002). Thus, by considering the dynamics of food web structural changes during community assembly, it can be inferred that repeated stable invasion and species sorting events (see Section 2.2) should favor emergence of the following two signatures of dynamical constraints on food web structure at IEE:

(i) *A negative correlation between species' generality and $\bar{G}^w$.* Because G^w's should be mitigated during assembly due to

stability constraints, increasing generality of a species should be offset by a decrease in its $\bar{G}^w$. This relationship can be measured by a correlation coefficient (see below), and will henceforth be denoted by $r(G, \bar{G}^w)$.

(ii) *A negative correlation between species' trophic level and $\bar{G}^w$*. Later immigrants arrive at a community that is progressively being saturated (approaching IEE). Hence, if community assembly is such that later immigrants tend to occupy successively higher trophic levels (*TL*'s) (i.e., are more likely to occupy the role of consumers rather than resources), community augmentation will be facilitated if species at higher trophic levels have relatively lower $\bar{G}^w$'s. This signature will henceforth be denoted by $r(TL, \bar{G}^w)$.

I now perform numerical simulations to evaluate the robustness of the above analyses by studying study assembly dynamics and food web structural changes in model communities.

4. Signatures of dynamical constraints in model communities

4.1. Community assembly simulations

The community assembly algorithm consisted of three steps based upon the LV model (Eq. (1)):

- *Immigration.* Beginning with the establishment at least one basal species, at 1000 time step intervals, a species population was introduced at an extinction threshold biomass abundance x_e. Each immigrant species was generated by randomly sampling death rate d_i, interspecific interaction coefficients α_{ij}, and intraspecific density-dependence coefficient α_{ii} from the half-normal probability distribution (distribution of the absolute value of a normally distributed random variable with mean 0 and variance σ^2; see "*Numerical method for IS-randomization*" in Appendix A) with fixed means (denoted by μ_d, $\mu_{\alpha,ij}$ and $\mu_{\alpha,ii}$, respectively). The efficiency of all consumers was fixed at some value e.
- *Trophic linking.* Upon colonization, the jth immigrant established a trophic link to the ith pre-existing one with a connectance probability p_c. For each assembly simulation, conditional upon p_c, I also set a "vulnerability probability" p_v ranging between 0.5 and 1; $p_v = 0.5$ meant that the jth immigrant was equally likely to be a resource or a consumer of the ith resident species (provided it was not basal), while $p_v = 1$ meant that the jth immigrant could only be a consumer. p_v replaces the more strict trophic linking rules of static food web structural models such as "cascade" (immigrants can only feed on resident species below them in a undimensional niche ranking; Cohen et al., 1990) and "niche" (immigrants can only feed on resident species that lie within some interval representing a undimensional niche; Williams and Martinez, 2000), because recent studies that include parasites suggest that all consumers do not necessarily feed according to such rules (Lafferty et al., 2008). Instead, depending upon the choice of p_v, trophic structures lying on a continuum ranging from relatively non-hierarchical with cycles (such as that resulting from the niche model; Williams and Martinez, 2000) at $p_v = 0.5$, to hierarchical and acyclic (such as that imposed by the cascade model; Cohen et al., 1990) at $p_v = 1$, can be assembled.
- *Interaction driven extinction.* After immigration, the augmented system was integrated forward for 1000 time steps, during which most populations either reached a nonzero equilibrium size or went extinct. A species was considered extinct and

Table 2
Simulation parameters and their values used for assembling model communities.

Parameter	Description	Values
p_c	Connectance probability	0.3
p_v	Vulnerability probability	0.5–1
$\mu_{\alpha,ij}$	Mean of half-normal probability distribution to sample interspecific interaction coefficients	1–10
$\mu_{\alpha,ii}$	Mean of half-normal probability distribution to sample intraspecific interaction coefficients	Dependent upon $\mu_{\alpha,ij}$ and target community size
x_e	Extinction threshold	10^{-32}–10^{-3}
e_j	Assimilation and conversion efficiency of jth consumer	0.1–1
b_i	Intrinsic birth rate of ith basal species	1–10^{10}
μ_d	Mean of half-normal probability distribution to sample intrinsic death rates	0–10^{-3}

deleted from the system if its density dropped below x_e, or decreased during this period.

This algorithm was iterated till the system reached IEE. Simulations were performed in MATLAB using the Runge–Kutta *one-step* solver ode45. During each assembly simulation run, changes in key community characteristics were measured at 1000 time-step intervals (coinciding with the interval for numerical integration).

Simulation parameters and their numerical ranges are listed in Table 2. A 150 replicated assembly simulations were executed, with a total number of time steps sufficient to reach IEE given a particular combination of parameter values. In the LV model, the main factors determining species richness at IEE are the strength of intraspecific density dependence relative to interspecific interactions, and connectance. Hence, for a given p_C and $\mu_{\alpha,ij}$, $\mu_{\alpha,ii}$ was chosen according to a target mean species richness at IEE. For example, for $p_C = 0.3$ and $\mu_{\alpha,ij} = 1$, to obtain webs that reached 50 species on average at IEE, $\mu_{\alpha,ii}$ had to be set to 4. Across all simulations, μ_d was chosen to be orders of magnitude smaller than $\mu_{\alpha,ij}$ and b_i in keeping with the patterns observed in empirical data (cf. Peters, 1983). For all the results shown below, communities were assembled on a single basal species with autonomous biomass production rate of 1. This forces all consumers to be connected to the same energy source, and eliminates the possibility of disconnected subcommunities. The conversion efficiency for all species was chosen to be 0.5. Simulations with greater variation in number of basal species, connectance probability, intrinsic biomass loss rates, efficiency, or extinction threshold (parameter ranges given in Table 2) only affect the size of communities at IEE, not the main results. The use of a uniform instead of the half-normal probability distribution also did not alter the main results. Furthermore, similar results were obtained using discrete time assembly simulations (using the recursive form of Eq. (1)).

4.2. Simulation results

ISS of model communities. Because we are interested in modeling the dynamics and structure of interaction strength sensitive communities, it is first necessary to gauge the ISS of sign structures resulting from the above assembly algorithm. Fig. 3 compares the r_{ISS} for communities assembled from the trophic linking rules of the dynamical assembly algorithm with those of the cascade (Cohen et al., 1990) and niche (Williams and Martinez, 2000) models (for a detailed description of the assembly rule sets of the latter two models, see Stouffer et al., 2005). For each model, I generated sets of 50 communities across different values of n for

the same expected value of connectance. Fig. 3 shows that in all community types, r_{ISS} increases asymptotically with n, reaching values comparable with those of empirical communities with high ISS (Table 1). Within communities assembled using the dynamical assembly rules, for a given n, r_{ISS} increases with p_v (i.e., non-hierarchical communities show more ISS). This is consistent with patterns of ISS in empirical communities, where relatively non-hierarchical communities with higher omnivory degrees tend to have higher r_{ISS} than the others (see Table 1 and Section 2.3). Note that on the other hand, the association between n and r_{ISS} in model communities need not necessarily be seen in the empirical ones because the latter have variable connectance (Table 1), resulting at least partly from uneven sampling of interactions (see Section 2.3). The r_{ISS} curves for the cascade and niche models are comparable to those of the dynamical model, especially for $p_v = 1$. Thus at least as far as ISS of the sign structure is concerned, the simpler trophic linking rules of the dynamical assembly algorithm are able to produce communities comparable to those assembled from static structure models.

Signatures of dynamical constraints *on the structure of model food webs*. Fig. 4 shows the two predicted signatures of dynamical constraints observed at IEE in a typical model community assembled with an intermediate p_v value (0.75). Because of the nonlinear change of $\bar{G}_i^w$ in both signatures, their strengths were measured using the Spearman rank correlation coefficient. Table 3 compares the incidences and strengths of signatures for communities assembled at different levels of trophic hierarchy.
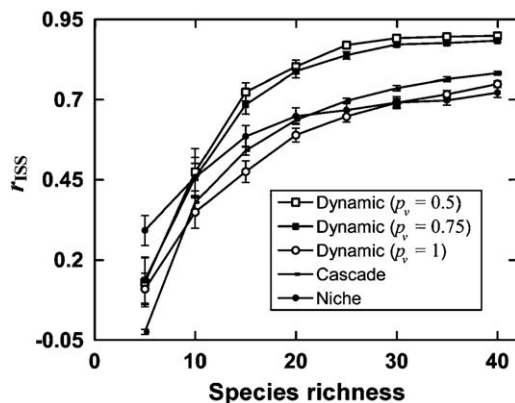

Fig. 3. Change in ISS with increasing species richness in communities assembled using the trophic linking rules of the dynamical assembly algorithm (Section 4.1), as well as two static food web structural models (niche and cascade). For each species richness value in each community type (a specific assembly algorithm), the mean ISS across 50 communities is shown with 99% confidence intervals. ISS was estimated from 2000 IS-randomizations. All assembly algorithm runs had the same connectance probability ($p_c = 0.3$).
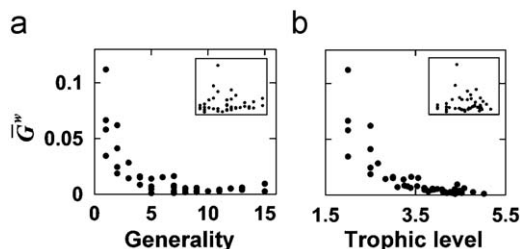

Fig. 4. Signatures of dynamical constraints on food web structure in a 45-species community at IEE: the correlation of $\bar{G}^w$ with species': (a) generality (G) and (b) trophic level (TL). The same measures in a typical community assembled with weaker constraints ($\mu_{\alpha,ii} = 100$; see Fig. 6) are shown in the inset figures. This community was assembled with $p_v = 0.75$; changes in the incidence and strengths of these signatures with variation in p_v are summarized in Table 2.

Table 3
Signatures of dynamical constraints in model food webs at IEE: correlation (Spearman's rank correlation coefficient) between species' generality and link-averaged weighted generality ($r(G, \bar{G}^w)$), and trophic level ($r(TL, \bar{G}^w)$).

Assembly type (p_v)	Species richness at IEE	Signatures of dynamical constraints	
		$r(G, \bar{G}^w)$	$r(TL, \bar{G}^w)$
1	39.7 (± 5.5)	100 (-0.78 ± 0.07)	100 (-0.82 ± 0.08)
0.75	46.4 (± 9.6)	100 (-0.65 ± 0.08)	52 (-0.67 ± 0.10)
0.5	50.1 (± 10.8)	100 (-0.63 ± 0.08)	18 (-0.34 ± 0.12)

Tabulated values give the percentage of 150 model food webs that showed the expected negative correlation (Spearman's rank correlation coefficient) with a p-value <0.01 (two-tailed), along with the mean value ($\pm$SD) of corresponding correlation coefficients in parentheses. Features in columns 2 and 3 correspond to those in Fig. 4a and b. The mean species richness ($\pm$SD) values at IEE for each assembly type are also shown.

Both signatures are seen across assembly types, but as expected (Section 3), the decrease in weighted generality with trophic level ($r(TL, \bar{G}^w)$) was the weakest with lowest incidence in relatively non-hierarchical communities ($p_v < 1$). Surprisingly, the decline in $\bar{G}^w$ with generality also became less pronounced as $p_v \to 0.5$ even though ISS increases in the same direction (see "*ISS of model communities*" above), suggesting that relaxation of hierarchical assembly decreases stability limitations on communities. This conclusion is supported by the fact that average n at IEE increased as $p_v \to 0.5$ (Table 3).

Fig. 5 shows actual changes in community characteristics during assembly (for $p_v = 0.75$) that culminate in the structural signatures seen in Fig. 4 and Table 3. As link density (L_D) increases with n during assembly (Fig. 5a and b), so do G_{tot}^w and $\rho(\underline{\mathbf{C}})$ (Fig. 5c and d). As expected, G_{tot}^w increases linearly with L_D (Fig. 5c inset), and $\rho(\underline{\mathbf{C}})$ with G_{tot}^w/n (Fig. 5d inset) (the latter as indicated by expression (9)). The numbers of extinctions, which include both failed invasions and species sorting events (counted in epochs of 1000 time steps) also increase and then equilibrate, resulting in IEE. Again as expected, the numbers of extinctions increase linearly with G_{tot}^w/n (because it increases $\rho(\underline{\mathbf{C}})$). Finally, Fig. 5f shows changes in the most fundamental of the two signatures ($r(G, \bar{G}^w)$), and the contribution of changes in species' trophic generality characteristics ($\bar{\alpha}_i$) alone to it ($r(G, \bar{\alpha})$). For both, an increasingly negative correlation is seen as assembly proceeds, indicating the increasing level of dynamical constraints (decreasing PHS) with assembly. As Table 1 indicates, patterns similar to those in Fig. 4 were seen in communities assembled at $p_v = 1$ and 0.5, but with a more gradual decline in $r(G, \bar{G}^w)$ and $r(G, \bar{\alpha})$ (result not shown).

Signatures of dynamical constraints *on the structure of model food webs*. In order to compare communities assembled under dynamical constraints with those assembled under relatively weaker constraints ("relaxed assembly"), I increased the value of $\mu_{\alpha,ii}$ while keeping all other parameter values the same. This imposed higher intraspecific density dependence across species, which increased the PHS, and hence decreased the number of extinctions due to species sorting events. Because increasing $\mu_{\alpha,ii}$ results in larger feasible communities, assembly was terminated when n reached the average IEE species richness value of dynamically constrained communities assembled using the same parameter values. Fig. 6a shows that during relaxed assembly, the number of epochal extinctions decreases as expected (reflecting a decrease in the number of species sorting events). Fig. 6b and c show that as a result, the decline in $r(G, \bar{G}^w)$ and $r(G, \bar{\alpha})$ becomes
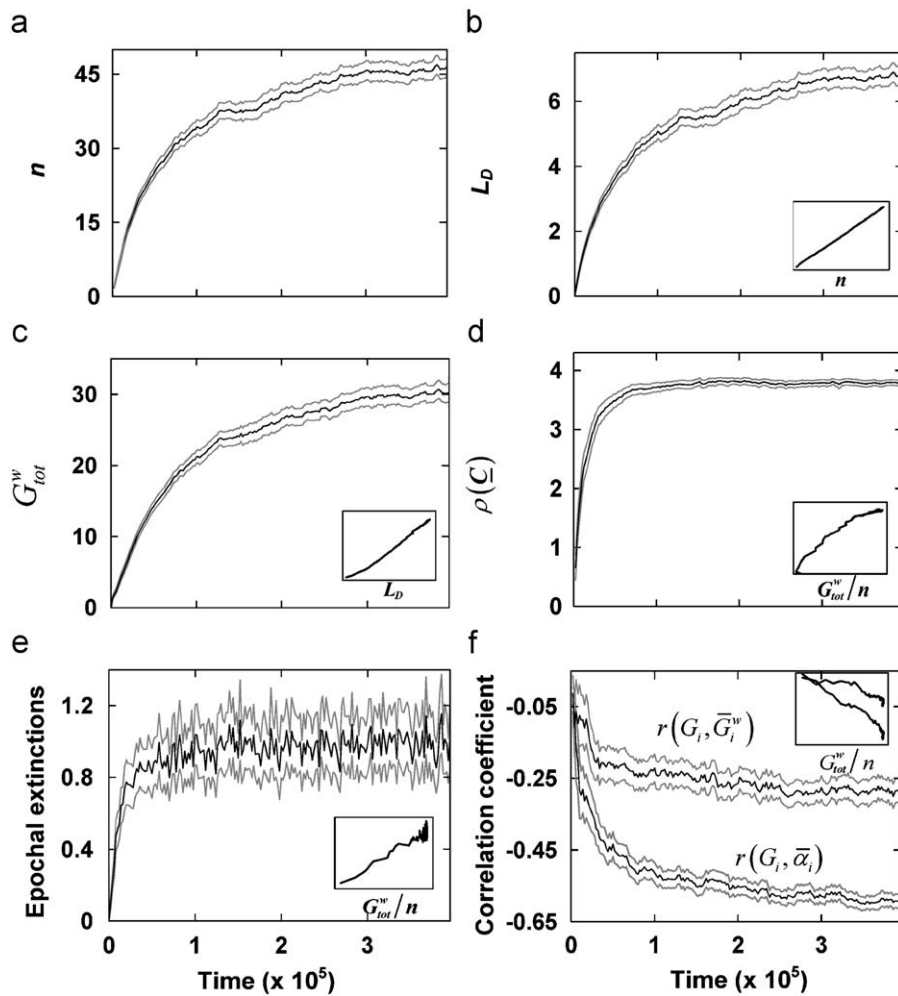
Fig. 5. Changes in key food web properties of model communities during assembly. Mean values with 99% confidence intervals (gray lines) across 150 simulation runs over 350 000 time steps are shown for: (a) species richness (n), (b) link density ($L_D = L/n$), (c) total weighted generality (G_{tot}^w), (d) spectral radius of $\underline{\mathbf{C}}$ ($\rho(\underline{\mathbf{C}})$), (e) the total number of extinctions in 1000 time step epochs, and (f) Spearman rank correlation coefficient between generality and $\bar{G}^w(r(G, \bar{G}^w))$ (lower lines) and $\bar{\alpha}(r(G, \bar{\alpha}))$ (upper lines). The relationships of features b–f with those that directly determine them are shown in the inset figures. These assembly trends are for $p_v = 0.75$ communities; similar trends are seen across the range $0.5 \leqslant p_v \leqslant 1$. For a given p_v, these assembly patterns remain essentially the same across a wide range of parameter values (see Table 2).

weaker (the structural signatures of dynamical constraints emerge more slowly).

5. Conclusion

This study is a step towards bridging the gaps in our understanding of the interrelationship between community assembly, stability, and food web structure. I have shown that natural communities typically show a sign structure that renders their Hurwitz stability sensitive to the distribution of interaction strengths (ISS, estimated using r_{ISS}). In such communities, consumer species with a high weighted generality (a measure of their total biomass acquisition rate) tend to undermine community stability. As a result, species associated with trophic modules carrying high weighted generality are eliminated through a process of repeated colonization and extinction (species sorting) events during community assembly. This ultimately results in the emergence of a non-random food web structure wherein weighted generality has been constrained across species. This can be detected using two food web structural signatures (Section 3 and Fig. 4), the incidences and strengths of which can allow a measurement of the importance of dynamical constraints during assembly. The overall picture that emerges is fascinating, wherein

communities assemble and persist through dynamic feedbacks between food web structure and stability, resulting in certain non-random structural configurations. The predicted existence of signatures of dynamical constraints is an interesting and important result because it means that the influence of dynamical constraints imposed by the requirement of multi-species stable coexistence can be inferred from snapshots of community food web structure in nature.

To the best of my knowledge, this is the first study to explicitly show how interaction strength properties of food web structural modules consisting of consumer species and their trophic links affect community stability. Previous such studies have focused on the effects of trophic chains (Pimm and Lawton, 1977), loops (Neutel et al., 2002) and omnivory (Neutel et al., 2007). Further studies are needed to compare the importance of these different structural features to community stability. Insofar that trophic generality is a small-world property of food web networks, the results of this study are in agreement with those of Allesina and Pascual (2008), who used a different theoretical technique to show that small predator–prey modules consisting of groups of a few connected species) have strong effects on community stability.

Because the above structural signatures involve a measure of foraging characteristics of consumers, they provide deeper
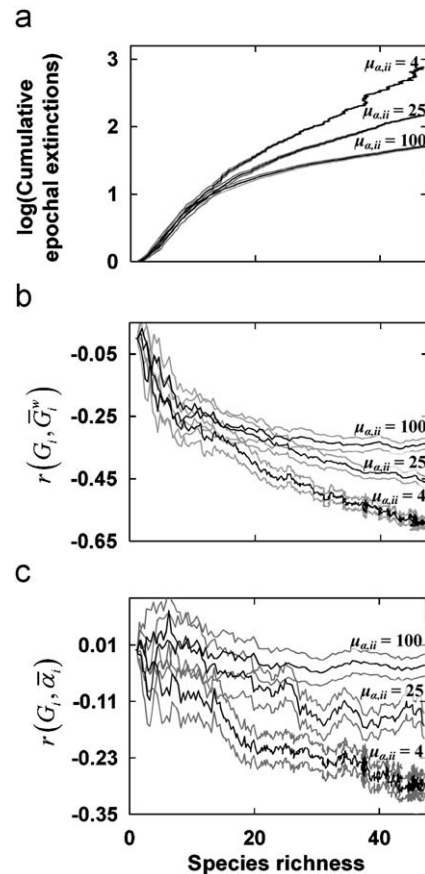
Fig. 6. The effect of relaxation of dynamical constraints (increasing $\mu_{\alpha,ii}$) on changes in key structural signatures during assembly of model communities, for $p_v = 0.75$. Mean values with 99% confidence intervals (gray lines) of 150 assembly simulation runs over 350 000 time steps for: (a) logarithm of the cumulative number of extinctions in 1000 time-step epochs, (b) $r(G_i, \bar{G}_i^w)$, and (c) $r(G, \bar{\alpha}_G)$. Each variable is plotted against n to allow comparison between different types of assembly. In contrast to Fig. 5e, extinction trends are shown as a logarithm of cumulative numbers to allow visual comparison of the three different assembly types, which have large differences in extinction numbers. Also note that the assembly trends for $\mu_{\alpha,ii} = 4$ are from the same simulations shown in Fig. 5. These differences between communities assembled under different $\mu_{\alpha,ii}$'s were similar across wide ranges of values of other model parameters (see Table 2). The greater fluctuations in all lines representing $\mu_{\alpha,ii} = 4$ (dynamically constrained assembly) towards the later assembly stages is a result of the fact that the communities are at IEE on average.

insights into the feedback between community-level dynamics of multi-species coexistence and individual species' survival strategies. Thus the frequently observed pattern that interaction strength distributions are skewed towards weaker values, presumably due to stability constraints (Berlow et al., 2004; Drossel et al., 2004; McCann et al., 1998), can now be linked to changes in trophic properties of single species or small groups of species. This is important because treating each trophic link as an entity that can be somehow modulated independent of other links is inconsistent with the fact that biological mechanisms either affect aggregate properties of trophic modules consisting of multiple species (e.g., as seen in species sorting), or individual species' trophic characteristics as a whole (e.g., behavioral or adaptive changes in a species' foraging strategies simultaneously affect all its trophic links).

In terms of food web structural changes during assembly, the above results complement those of a recent study by Neutel et al. (2007, 2002), who find evidence for directional changes in distributions of interactions along trophic loops and 3-species

omnivorous trophic modules in soil community food webs, also driven by dynamical constraints. Apart from their focus on different structural features, there are two key differences between the results of this study and those of Neutel et al. First, they only consider dynamical constraints on species' equilibrium biomasses ($\hat{x}$'s; one of the two components of each interaction strength at equilibrium; see expression (3)), and the stabilizing effects of trophic cascades (as defined in Section 3 of this paper). However, here I have shown that dynamical constraints can also force interaction strengths (α_{ij}'s) to decrease through modification of species' trophic characteristics such that the $\bar{\alpha}$'s (expression (12)) are constrained across species (see Fig. 5f). This also means that in contrast to the conclusions of some recent papers (Beckerman et al., 2006; Petchey et al., 2008), species' foraging strategies are expected to be determined not just by their energetic requirements, but also by their impact on community stability. Second, Neutel et al. (2007, 2002), stress upon the importance of asymmetry in top-down and bottom-up effects (the pairs of coefficients c_{ij} and c_{ji}, respectively, when j eats i) on stability, whereas I have shown here that a measure that combines these effects (the trophic link strengths $\underline{c}_{ij}$; expression (7)) can provide simpler insights into the relationship between food web structure and stability.

Because ISS is essentially a measure of the lack of quasi-sign stability (as defined by Allesina and Pascual, 2008), it is interesting to compare the results of this study with theirs. A problem that precludes a direct comparison is that only three communities are common between the two studies. This is because I imposed certain criteria for selecting datasets (see Supplementary Appendix 1) and used additional datasets apparently not considered by them. Nevertheless, the levels of r_{ISS} observed across the communities in this study clearly indicate that QSS may not be as prevalent as suggested by Allesina and Pascual (2008). Moreover, I also found some evidence that ISS might be underestimated in natural communities because of inadequate sampling of trophic interactions (see Section 2.3). In particular, community food web datasets that include host-parasite links tend to show stronger ISS, suggesting that the inclusion of such interactions has non-trivial effects on the elucidation of population dynamical properties of communities, and their effects on food web structure, as has been suggested by recent studies (Lafferty et al., 2008; Marcogliese, 2003; Marcogliese and Cone, 1997).

Caveats. In deriving the relationship between interaction strength structure and community stability (Section 2.3), I have largely ignored the role of the diagonal elements of C by assuming them to be fixed (or lying within a fixed range). However, a community can also be stabilized by increasing the diagonal elements c_{ii} (i.e., the negative intraspecific density dependences). The importance of this issue depends upon how strong intraspecific density dependence is in nature (and how it is regulated). There is some direct evidence for such effects in real systems (e.g., Agrawal et al., 2004; Schmitt and Holbrook, 2007), and more empirical studies are needed on the feedback between intra-population interactions and community stability, or the relationship between inter- and intraspecific interactions (e.g., Bystrom and Garcia-Berthou, 1999; Kratina et al., 2009; Wahlstrom et al., 2000).

Further studies are needed to understand the mechanisms by which mitigation of total weighted generality actually occurs. This will lead to the development of more detailed hypotheses about the signatures of dynamical constraints of food web structural features. To this end, we need to look well beyond basic Lotka–Volterra type models for a comprehensive understanding of stabilizing mechanisms. These mechanisms include adaptive foraging behavior and physiological changes (e.g., consumer

functional response) and coevolution. In particular, consumer functional responses (wherein the α_{ij}'s change in response to increasing availability of resource species' biomass abundance) are relevant at ecological time scales, and their effects of food web structural changes will be evaluated in a subsequent paper.

Only one of many different definitions of stability (Grimm and Wissel, 1997; Ives and Carpenter, 2007) has been used in this study. Some of these definitions are more general than Hurwitz stability, either because they guarantee global stability of the multi-species point equilibrium ($\hat{\mathbf{x}}$), or do not require a point equilibrium (e.g., permanence; see Hofbauer and Sigmund, 1998; Law and Morton, 1996). This is an important consideration because in Lotka–Volterra type models, populations may actually converge to the vicinity of a periodic or chaotic attractor instead of a point equilibrium (e.g., see Gilpin, 1979). I have ignored this in the above analysis by using the Jacobian matrix and the Hurwitz stability criterion, because it allows food web structure to be explicitly linked to community stability (also see May, 1974). The numerical simulations of Section 4 show that the predictions about the relationships between food web structure and stability based upon this assumption are well supported, indicating either or both, that periodic or chaotic population trajectories are not dominant, and that they not substantially alter the predicted relationship between food web structure and stability. Another reason why other definitions of stability need to be explored is that some of them quantify the speed of return to equilibrium following external perturbations (e.g., resilience; Harrison, 1979). For example, in addition to Hurwitz stability, the distribution of interaction strengths in the community matrix $\mathbf{C}$ also determines short- and long-term population dynamics following external perturbations (Neubert et al., 2004). Further work will show how food web structure is related to such measures of stability.

Finally, though I have only considered trophic interactions in this study, population dynamics in real communities are also partly governed by interspecific competitive and mutualistic interactions. Hence it is worth noting that the fundamental results of this study do not change even upon the inclusion of these interaction types, because we will still only need to consider the nonnegative matrix $\underline{\mathbf{C}}$.

Acknowledgments

Appendix A. The relationship between $\rho(\underline{C})$ and probability of Hurwitz stability

Here I will show that $\rho(\underline{\mathbf{C}})$ (as defined in expression (5)) is related to PHS in communities with certain interaction sign structures. For this, it needs to be established that $\lambda_{\max}(\mathbf{C})$ can increase monotonically with $\rho(\underline{\mathbf{C}})$ for a given set of diagonal elements of $\mathbf{C}$. A strict pre-condition for this is that $\rho(\underline{\mathbf{C}}) > 0$, which is of course guaranteed for biologically relevant systems because each row of $\underline{\mathbf{C}}$ is bound to have at least one interaction coefficient (all species have at least one trophic interaction) (e.g., see corollary

8.1.25 in Horn and Johnson, 1985). Now, I begin by noting that the very existence of sign stable (Logofet, 1993; May, 1974) and "quasi-sign stable" (in the sense of Allesina and Pascual, 2008) communities precludes the possibility of a general, monotonically increasing relationship between $\lambda_{\max}(\mathbf{C})$ and $\rho(\underline{\mathbf{C}})$. In such communities, $\lambda_{\max}(\mathbf{C})$ either does not increase and cross the critical boundary even if $\rho(\underline{\mathbf{C}})$ increases infinitely (strictly sign-stable), or is relatively insensitive to changes in it (quasi-sign stable). Nevertheless, for a given n it is always possible to find a non-trivial sign structure that renders $\lambda_{\max}(\mathbf{C})$ sensitive to $\rho(\underline{\mathbf{C}})$. To show this, the following example is sufficient. Consider the community matrix

$$\mathbf{C} = \begin{bmatrix} -1 & 0 & -1 \\ 0 & -1 & c \\ c & -1 & -1 \end{bmatrix}, \text{ which means that } \underline{\mathbf{C}} = \begin{bmatrix} 0 & 0 & 1 \\ 0 & 0 & c \\ c & 1 & 0 \end{bmatrix}$$

The eigenvalues of $\mathbf{C}$ are -1, $-1 + \sqrt{-2c}$, and $-1 - \sqrt{-2c}$, and $\rho(\underline{\mathbf{C}}) = \sqrt{2c}$. Thus while $\rho(\underline{\mathbf{C}})$ increases with c, $\lambda_{\max}(\mathbf{C})$ remains constant (-1), and the system remains Hurwitz stable. Now let us make a change to the sign structure of $\mathbf{C}$ by adding one more trophic link such that

$$\mathbf{C} = \begin{bmatrix} -1 & c & -1 \\ -1 & -1 & c \\ c & -1 & -1 \end{bmatrix}, \text{ and } \underline{\mathbf{C}} = \begin{bmatrix} 0 & c & 1 \\ 1 & 0 & c \\ c & 1 & 0 \end{bmatrix}$$

Now the eigenvalues of $\mathbf{C}$ are $c-2$, $0.5(-1 + \sqrt{3}i)(c + 1)$, and $-0.5(1 + \sqrt{3}i)(c + 1)$, while $\rho(\underline{\mathbf{C}}) = c + 1$. Now, as $\rho(\underline{\mathbf{C}})$ increases (with c), so does $\lambda_{\max}(\mathbf{C})$. This shows that in certain trophic sign structured communities, given some level of negative density dependence across species in the community, $\lambda_{\max}(\mathbf{C})$ is bound to become positive (and Hurwitz stability lost) as $\rho(\underline{\mathbf{C}})$ increases. In other words, PHS is inversely related to $\rho(\underline{\mathbf{C}})$. I call this property of community sign structure "interaction strength sensitivity", which can be gauged from the correlation coefficient between $\lambda_{\max}(\mathbf{C})$ and $\rho(\underline{\mathbf{C}})$ (r_{ISS}) across randomly generated food webs that have the same sign structure, but random interaction strength configurations (IS-randomized; see below for numerical methods) (two contrasting empirical examples of this measure are shown in Fig. 1). In Table 1, the ISS of seventeen empirical communities is shown. Fig. 3 shows that model communities assembled using fairly general rules too have consistently high ISS.

I note that the use of $\rho(\underline{\mathbf{C}})$ to interlink food web structure and stability is similar to Neutel et al.'s (2002) approach. Neutel et al. base their analysis on the conjecture that $\rho(\underline{\mathbf{C}})$ limits global stability (instead of Hurwitz stability as shown above). However, I do not use this approach because a combination of invasibility criteria and Hurwitz stability alone is sufficient to explain changes in food web structure driven by stability constraints (see Section 2.2 of the main text).

Numerical method for IS-randomization: To generate each IS-randomized version of a given community, I generated the off-diagonal elements of the community matrix $\mathbf{C}$ by sampling the element c_{ij} (if j eats i) from a half-normal probability distribution (distribution of the absolute value of a normally distributed random variable with mean 0 and variance σ^2), which has a cumulative density function,

$$F_Y(y; \sigma) = \int_0^y \frac{1}{\sigma} \sqrt{\frac{2}{\pi}} \exp\left(-\frac{z^2}{2\sigma^2}\right) dz$$

and expectation and variance that scale with σ as $\sigma\sqrt{2/\pi}$ and $\sigma^2(1 - (2/\pi))$, respectively. The corresponding element c_{ji} was also sampled from the half-normal distribution, and then multiplied by 10^κ, with κ sampled from a uniform distribution over the interval $[a, b]$. Thus the choice of $[a, b]$ determines the degree of asymmetry of the interactions in each trophic link (effect of consumer on resource (c_{ij}) vs. resource on consumer (c_{ji})), and the

right-skewness of the interaction strength distribution. Empirical data show that this asymmetry is typically high (e.g., Jonsson and Ebenman, 1998; Neutel et al., 2002; Ruiter et al., 1995), with a strongly right-skewed interaction strength distribution (Wootton and Emmerson, 2005). The diagonal elements of C (all negative) were sampled from a uniform distribution with range C_{ii}. The results for ISS in Table 1, Figs. 1 and 2 are for $\sigma = 1$, $[a, b] = [-2, 2]$, and $C_{ii} = [0, 1]$. Using other combinations of parameter values, or different distributions for sampling parameters (such as uniform or log-normal) alters the strengths of the estimated ISS of communities, but not the differences between them.

Appendix B. The relationship between species' weighted generality and $\rho(\underline{C})$

Here I will establish the relationship 9 of the main text. We begin by defining the symmetric matrix $S(\underline{C})$ with elements,

$$\bar{c}_{ij}(= \bar{c}_{ji}) = \sqrt{c_{ij}c_{ji}}, \quad \forall i, j \in \mathfrak{N} \tag{B.1}$$

and the symmetry measure on $\underline{C}$:

$$S_{\underline{C}} \equiv \sum_{i,j=}^{n} |c_{ij} - \bar{c}_{ij}|$$

Then, from the main result of Schwenk (1986) it follows that:

$$\lim_{S_{\underline{C}} \to 0} (\rho(\underline{C}) - \rho(S(\underline{C}))) = 0 \tag{B.2}$$

i.e., $\rho(S(\underline{C}))$ approaches $\rho(\underline{C})$ from below as $\underline{C}$ increases in symmetry (also see Kolotilina, 1993). Converting $\underline{C}$ to the symmetric matrix $S(\underline{C})$ makes it easier to interlink food web structure and community stability because the coefficients c_{ij} and c_{ji} of each trophic interaction are reduced to a single entity $\bar{c}_{ij}$ that contributes to the overall biomass transfer rate between species (see expression (10) in the main text). Expression (B.2) implies that $\rho(\underline{C}) \cong \rho(S(\underline{C}))$ if the pairs of the off-diagonal elements c_{ji} and c_{ij} are sufficiently close to each other in magnitude such that species' biomasses are somewhat balanced, i.e., $\hat{x}_i \cong e_j \hat{x}_j, \quad \forall i, j \in \mathfrak{N}$ (using expression (1b) from the main text). In fact, it can be shown that even if $S_{\underline{C}}$ is low (interactions are typically very asymmetric), the structural symmetry of $\underline{C}$ (i.e., $c_{ji} \neq 0$ iff $c_{ij} \neq 0$) is in itself sufficient to guarantee that $\rho(S(\underline{C}))$ is a tight lower bound of $\rho(\underline{C})$ (Schwenk, 1986). Now, because $S(\underline{C})$ is symmetric, $\rho(S(\underline{C}))$ is itself bounded below by the Rayleigh quotient (Horn and Johnson, 1985, p. 176),

$$\frac{z^t S(\underline{C}) z}{z^t z} \leqslant \rho(S(\underline{C}))$$

where $z = (1, 1, \ldots, 1)^t$. And because

$$\frac{z^t S(\underline{C}) z}{z^t z} = \frac{1}{n} \sum_{i,j=1}^{n} \bar{c}_{ij},$$

we have

$$\frac{1}{n} \sum_{i,j=1}^{n} \bar{c}_{ij} \leqslant \rho(S(\underline{C})) \tag{B.3}$$

which from expression (B.2) means that

$$\frac{1}{n} \sum_{i,j=1}^{n} \bar{c}_{ij} \leqslant \rho(\underline{C}) \tag{B.4}$$

Now, the sum in expression (B.4) can be partitioned into species' weighted generalities (as defined in expression (8) of the main text),

$$\sum_{i,j=1}^{n} \bar{c}_{ij} = 2 \sum_{n} G_i^w = 2 G_{tot}^w$$

and hence bound (9) of the main text follows.

Appendix C. Supplementary material

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.jtbi.2009.04.006.

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