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LETTER

The dynamics of assembling food webs

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Abstract

Community assembly is central to ecology, yet ecologists have amassed little quantitative information about how food webs assemble. Theory holds that colonisation rate is a primary driver of community assembly. We present new data from a mesocosm experiment to test the hypothesis that colonisation rate also determines the assembly dynamics of food webs. By manipulating colonisation rate and measuring webs through time, we show how colonisation rate governs structural changes during assembly. Webs experiencing different colonisation rates had stable topologies despite significant species turnover, suggesting that some features of network architecture emerge early and change little through assembly. But webs experiencing low colonisation rates showed less variation in the magnitudes of trophic fluxes, and were less likely to develop coupled fast and slow resource channels – a common feature of published webs. Our results reveal that food web structure develops according to repeatable trajectories that are strongly influenced by colonisation rate.

Keywords

Colonisation, community assembly, food webs, information theory, interaction strengths.

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INTRODUCTION

Food webs in nature develop through a dynamic assembly process; new trophic interactions begin as colonists enter communities, and the arrangement and magnitudes of energy and material fluxes change as populations grow and shrink. Understanding how biotic and abiotic conditions cause food webs to change through time is a goal of both fundamental and applied ecology (Dobson *et al*. 2009; May 2009). Yet, even the most basic empirical questions about temporal variation in food web structure remain unanswered (May 2009). This is due to a paucity of quantitative food web data. Time series data of who eats whom and at what rates do not exist (Olesen *et al*. 2010; Emmerson 2011) and replicated food web experiments are scant.

In contrast to empirical studies, theoretical work has dealt explicitly with food web dynamics, and the dynamics of web assembly in particular. Theory suggests that the emergence of structural features in assembling webs should be strongly driven by colonisation rate – the rate at which new individuals enter a community (Yodzis 1981; Post & Pimm 1983). Subsequent models have extended this prediction, positing that colonisation rate influences the formation of web topology (Pillai *et al*. 2011), distributions of species' per capita interaction strengths (Pawar 2009) and species' abundance distributions (Sole *et al*. 2002). In conjunction with the arrangement of interactions (i.e. the way in which links of different magnitudes are arranged in a web), these properties collectively determine the quantitative structure of a web at a particular point in time (Ulanowicz 2004). Unfortunately, because of a lack of data, it has been difficult to test existing theory (Emmerson 2011). Moreover, it is not clear what empirical patterns new models must explain. There is a pressing need for a more thorough dialogue between food web assembly theory and data (Dobson *et al*. 2009).

Here, we describe results of an aquatic mesocosm experiment designed to determine how colonisation processes affect the trajectory of food web structure through assembly (data set provided in Appendix S1 in supporting information and as electronic supplementary data). Specifically, our goal was to manipulate colonisation rate in an array of field mesocosms, and to study the development of three major structural features of the webs that formed in these mesocosms: (1) web topology, (2) variation in the magnitudes of trophic fluxes, and (3) the arrangement of trophic fluxes. These features are discussed in detail in Materials and Methods and Appendices S2 and S3. We report that variation in colonisation rate among food webs causes consistent differences in the emergence of web structure during assembly. Our results reveal that food web structure develops according to repeatable trajectories that are determined by colonisation rate on timescales that are relevant to the dynamics of real ecological systems.

MATERIALS AND METHODS

In June 2008, Hein & Gillooly (2011) established an array of six 1-m diameter aquatic mesocosms around each of seven permanent lakes at the Ordway-Swisher Biological Station in Melrose, FL, USA (42 mesocosms total). Mesocosms were studied from 11 June 2008 to 6 August 2008. In this study system, natural temporary ponds are seasonally filled with water and colonised by aquatic species (e.g. wind and animal-dispersed phytoplankton and zooplankton, oviposited aquatic insect and amphibian larvae and flying aquatic insects) that immigrate from nearby permanent lakes.

Manipulating colonisation

Hein & Gillooly (2011) showed that increasing the distance between mesocosms and the nearest permanent lake reduces

the colonisation rate of all species (isolated mesocosms are colonised at lower rates than proximate ones). Thus, through this *isolation* treatment, we created high, intermediate and low colonisation rate webs by placing mesocosms 10, 100, or 400 m from a permanent lake colonisation source respectively. As a second manipulation, we inoculated half of the mesocosms in each isolation treatment with species from source lakes. We did this by collecting water from source lakes (see below), removing top predators and adding an inoculum to one of the two mesocosms at each distance. In contrast to the isolation manipulation, this *inoculation* treatment ensured that mesocosms at all distances began assembly with a similar suite of species. This served two purposes: first, because a web at each distance received the same inoculum of species, inoculated webs at all distances began with the same substrate of species thereby eliminating any potential effects of stochastic arrival order of these species on the assembly process (i.e. historical contingencies, Fukami 2010). Second, by adding mid-trophic level species, we provided prey for top predator colonists, which allowed them to overcome the resource limitation that would result from an absence of prey (i.e. sequential dependencies, Holt *et al.* 1999; Hein & Gillooly 2011).

A primary goal of this study was to determine whether webs subject to different rates of colonisation followed different assembly trajectories. We define a *trajectory* as the path a web follows through the space defined by the metrics described below. If webs in two different isolation treatments (e.g. 10 m and 400 m) have different values of a food web metric at a particular point in time (main effect of *isolation*), or if the value of a food web metric changes at different rates in different isolation treatments (*isolation* × *time* interaction), we say that webs in the two treatments follow different trajectories. As a secondary goal, we wished to determine the causes of any differences in assembly at different isolation distances. We did this using the inoculation treatment. If webs at different distances follow different trajectories despite inoculation, we could conclude that persistent differences in colonisation rate affect assembly by means other than species arrival order (Fukami 2010) and predator resource limitation alone (Hein & Gillooly 2011; e.g. if colonisation continues to significantly augment populations in proximate habitats but not in isolated ones). If on the other hand inoculation removes the effect of isolation on assembly, we can conclude that processes like the timing of species arrivals (e.g. good dispersers arrive first), and predator resource limitation are involved in governing the effect of colonisation rate on assembly.

Experimental design and data collection

The full experimental setup and sampling protocol is described in Hein & Gillooly (2011). Briefly, we scrubbed and rinsed mesocosms and added a thin layer of sand, 70 L of filtered well water and 50 g of rabbit food (Small World, Manna Pro, St. Louis, Missouri, USA) to each mesocosm to provide an initial source of detritus. We deployed six mesocosms (three distance treatments × two inoculation treatments) in an array around each of seven source lakes. To perform inoculations, we collected algae and invertebrates by towing a plankton net through 800 L of water in the littoral zone of each source lake and removed top predators (predatory beetles, dragonflies, Chaoborid larvae). An aliquot of inoculum was added to one mesocosm at each distance (10, 100, or 400 m). Each inoculum contained organisms from *c.* 200 L of lake water, providing relatively dense initial populations in the 70L mesocosm habitats.

We sampled mesocosms 2, 4, 6 and 8 weeks after they were established. Eight weeks exceed the average length of time for which natural temporary ponds continuously contain water in this system during the summer wet season, and is sufficient to capture 2–10 generations of the primary species that colonise small ponds. During each sampling event we counted macroinvertebrates (> 1 mm in length) and amphibians, removed and measured the body lengths of the first 10–25 individuals of each species and returned them to the mesocosm. We then took three 500-mL plankton samples using an integrated depth sampler. All phytoplankton, zooplankton, macroinvertebrates and amphibians were identified to the highest possible taxonomic resolution (species or genus in most cases), populations were enumerated, and body sizes were estimated from measured lengths and published taxon-specific length-mass conversions (Appendix S1).

Diet information

We assigned feeding links among species using a combination of gut content analyses, field observations of trophic interactions, literature sources and discussion with experts (Appendix S1). Occasionally, we detected taxa during censuses that lacked trophic links with the other species that were present. We omitted such species from our analyses. These taxa were almost exclusively haematophagous leeches or moss mites (Appendix S1), and accounted for < 0.42 species per food web, on average. In addition, 24 of the 168 total food web censuses had to be omitted, either because plankton samples were damaged after collection (18 webs from week 2 census), or because fewer than three species were present (six webs in the 400 m treatment from week 2). To ensure our protocol accurately sampled webs, we destroyed each community following the week 8 census, and verified that the results of our samples were statistically indistinguishable from those obtained by counting every individual from destroyed and preserved communities (Hein & Gillooly 2011).

Estimating trophic fluxes

We sampled each experimental community in a matter of minutes, providing something close to an instantaneous estimate of the species composition, abundances and body masses of the organisms present. Unlike the methods typically used to construct webs, this approach does not time-aggregate species that do not co-occur. We used census data to construct a weighted food web matrix T for each community, with elements T_{ij} representing the estimated energetic flux (milliwatts) from resource i to consumer j. We first estimated the individual-level metabolic demand d_j (milliwatts) of each consumer species as

$$d_j = aM_{j,}^{b} \quad (1)$$

where M_j is the average body size (mg) of the consumer, and a and b are a scaling coefficient and scaling exponent, respectively, from published taxon-specific scaling equations for metabolic rate (Peters 1983; pp. 239–248). It would be preferable to estimate demands of all individuals of a particular species and then average these, but we were not able to measure all individuals and therefore used the metabolic demand of an average sized individual as a reasonable estimate (Savage 2004). We estimated instantaneous total flux from resource i to consumer j, assuming

$$T_{ij} = \frac{d_j B_i}{\sum_k B_k} N_j, \quad (2)$$

where $B_i = M_i \times N_i$ is the biomass of resource i (M_i and N_i are the masses and abundances of individuals of species i respectively), N_j is the abundance of consumer j and the sum in the denominator is taken over all k resources in consumer j's diet.

The fact that the communities studied here were not at equilibrium prevented us from using flux estimation techniques that make equilibrium assumptions. These include weighting schemes that assume population production balances losses from mortality (Hunt *et al*. 1987; de Ruiter *et al*. 1995) and balancing algorithms that assume inflows of energy to all species equal outflows (Allesina & Bondavalli 2003). Indeed, our webs were characterised by frequent extinctions that likely resulted from resource deficits or overexploitation by consumers. For this reason, we did not require that the instantaneous rate of flux from resource i to consumer j (T_{ij}) equal the rate of production of resource i. We assumed only that each consumer attempts to satisfy its metabolic demand, and that consumers apportion this demand among their resource species in proportion to the relative biomass of those resources.

Measuring temporal changes in food web structure

As described above, we wished to measure three properties of developing food webs – topology, variation in the relative magnitudes of trophic fluxes and the arrangement of trophic fluxes – and to track how these properties change through time and depended on colonisation rate. We measured web topology using directed connectance C (Martinez 1992). C is calculated as L/S^2 where L is the number of links and S^2 is the maximum number of links in a food web of S species. Although there are many measures of food web topology, most are derived from a small set of variables (L and S) and therefore convey redundant information (Vermaat *et al*. 2009). C has been shown to provide a good overall measure of topology and is more robust to variation in data quality than other metrics (Martinez 1992; Vermaat *et al*. 2009).

To measure changes in the relative magnitudes of trophic fluxes, we used an information theoretic analogue of connectance, herein called quantitative connectance, C_q (the calculation of C_q is described in Appendix S2, and by Ulanowicz & Wolff 1991 and Bersier *et al*. 2002). C_q is based on Shannon entropy and weighs nodes based on the number and magnitude of links between them and other nodes. This metric incorporates both the distribution of per capita interaction strengths (*sensu* McCann *et al*. 1998; Appendix S2) among species in the web and the distribution of species' abundances (Sole *et al*. 2002). The way in which C_q captures variation in trophic fluxes is clear from the following analogy. Suppose one thinks of a food web as a network through which energy and materials flow. Furthermore, suppose that when a quantum of energy reaches an arbitrary node in the network, its probability of following one of the links that connects that node to others is proportional to the flux associated with that link. Nodes that have many incoming and outgoing links with similar fluxes can be described as 'high entropy,' because they contribute much uncertainty to the path that a quantum of energy will follow through the web (Ulanowicz 2004). Conversely, nodes with few incoming or outgoing links, or nodes with few strong links and many weak links contribute less uncertainty because most of the energy passing through the node enters along one of a few strong links and exits through one of only a few strong links. C_q puts greater weight on high entropy nodes than those with low entropy. A node has maximum entropy when all of its ingoing and outgoing links have the same weight, as in the unweighted topological network used to compute C; C_q is equal to C when all links have the same weight, and less than C otherwise. The difference, $C-C_q$, provides a measure of the degree to which the flux through a web is dominated by a fraction of all possible paths. This difference is large if flows through the food web are dominated by major fluxes through simpler substructures embedded within the network. By studying the difference between C and C_q through assembly, we can determine whether the relative strengths of trophic flows within the web become more or less similar. We refer to the difference, $C-C_q$, as C_{diff}.

Finally, by keeping track of the arrangement of links, we were able to characterise the development of two functional substructures within webs: fast resource channels (i.e. channels through which the flux of energy and materials is relatively rapid), and the coupling between these fast resource channels and slow resource channels (i.e. channels through which flux is relatively slow) by predators. Time-aggregated data sets from aquatic, marine and terrestrial systems suggest that these are common features of web architecture (Rooney *et al*. 2006). We wished to study the emergence of these features through assembly, given their ubiquity in published food webs and their implications for population dynamics (Rooney *et al*. 2006; Rip *et al*. 2010). To accomplish this, we first identified fast resource channels by identifying the minimum fraction of links needed to account for 75% of total system flux, F_{75}. We did this separately for each web by ranking T_{ij} values for that web, counting the smallest number of links needed to account for at least 75% of the web's total throughput, and dividing this number by L. We chose a cut-off of 75% based on the average flux through fast channels in a collection of eight published food webs (Table 1 and Table S1 in Rooney *et al*. 2006). However, the qualitative conclusions presented below are unchanged by the choice of cut-off (51, 60, 75, or 95% yield the same qualitative results). After identifying F_{75}, we determined the proportion of total food webs in each treatment that exhibited coupled fast and slow resource channels using graph-theoretic techniques (Appendix S3).

Table 1 Results from analysis of food web properties through time

		Not-inoculated			Inoculated		
Analysis	Treatment	Sign	*F*(*df*)	*P*-value	Sign	*F*(*df*)	*P*-value
C	Time	NS	1.4 (3,41)	0.25	NS	2.1 (3,49)	0.11
	Isolation	NS	0.012 (1,13)	0.91	NS	0.82 (1,13)	0.38
	Isolation × Time	NS	0.023 (3,41)	0.96	NS	0.45 (3,49)	0.72
C_{diff}	Time	+	6.2 (3,41)	**0.0015**	+	11 (3,49)	**< 0.0001**
	Isolation	−	9.0 (1,13)	**0.01**	NS	1.4 (1,13)	0.26
	Isolation × Time	NS	0.15 (3,41)	0.93	NS	0.19 (3,49)	0.9
F_{75}	Time	−	7.7 (3,41)	**0.0004**	−	13 (3,49)	**< 0.0001**
	Isolation	+	9.3 (1,13)	**0.0094**	NS	0.0018 (1,13)	0.97
	Isolation × Time	NS	0.22 (3,41)	0.88	NS	1.7 (3,49)	0.18
Coupled channels	Time	+	NA	**0.024 (week 4)** 0.086(week 6) **< 0.0001(week 8)**	+	NA	**< 0.0001**
	Isolation	−	NA	**0.003**	NS	NA	0.49

'Analysis' column indicates the food web property to which statistics refer. Data are divided into non-inoculated and inoculated treatments. 'Sign' column indicates whether the treatment variable resulted in an increase (+) or decrease (−) in the value of the food web property. Significant effects ($P < 0.05$) are listed in bold. Note that isolation and time have a significant effect on C_{diff} F_{75}, and fraction of coupled channels in non-inoculated webs, indicating that isolation affected the trajectory of assembly. Isolation did not significantly affect any food web property in inoculated webs. *Isolation* × *time* interaction is omitted for coupled channels analysis (see Materials and Methods). F-values are not given for coupled channels because *P*-values were calculated using a robust parametric bootstrap method, rather than using a standard reference distribution (see Appendix S3).

Statistical analyses

We used a series of linear and generalised linear mixed model analyses to determine how food web properties depended on covariates. For each metric (C, C_{diff}, F_{75}), we fit a model of the form $Y = B_1(time) + B_2(isolation) + B_3(time \times isolation) + G + H + E$, where Y is the food web property, B_1–B_3 are regression coefficients, G and H are random effects of mesocosm identity (to account for the fact that repeated measurements were made on each mesocosm) nested within spatial block (the source lake identity) and E is a vector of errors (a similar application of random effects models is described by Hein & Gillooly 2011). We analysed non-inoculated and inoculated webs separately. This allowed us to formally test the hypothesis that inoculated food webs in all isolation treatments followed the same trajectories. To improve normality of residuals, we square-root transformed C_{diff} and fourth-root transformed F_{75} prior to analyses. Normality of residuals was confirmed in all models using quantile–quantile plots. All models were fitted using the *nlme* package in the statistical programming environment, R (R Development Core Team 2013). To determine how the frequency of food webs with coupled fast and slow resource channels changed through assembly, we used a generalised linear mixed model to describe the proportion of webs with coupled fast and slow resource channels as a function of the same covariates and random effects used in models described above (Appendix S3), except that we omitted the *time* × *isolation* interaction because statistical fits were unstable when this interaction was included.

RESULTS

Food webs grew in size through time, from an average of 5.1 species in week 2 (range = 3–11 spp.) to 12 species in week 8 (range = 3–26 spp.). The number of links between species was 7.6 in week 2, on average (range = 2–24 links), and increased to an average of 42 (range = 3–137 links) in week 8. Throughout the experiment, the rate of species turnover (calculated as the number of species at time t absent at $t + 1$, over the number of species present at time t) was high, with an average of 53% of species turning over between time periods.

Effects of *time*, *isolation* and *inoculation* on food web topology

The results of our analyses are summarised in Table 1. In all food webs, directed connectance, C, remained constant through time (non-significant time effect in non-inoculated webs: $F_{3,41} = 1.4$, $P = 0.25$, Fig. 1a; non-significant time effect in inoculated webs: $F_{3,49} = 2.1$, $P = 0.72$, Fig. 1b), despite an increase in species richness (Hein & Gillooly 2011). Although not statistically significant, the apparent decline in C between weeks 2 and 4 (Fig. 1b) was driven by four small food webs that contained a large fraction of cannibalistic species, leading to high connectance values. On average, species in all food webs were connected to 23% of the other species present through assembly. When we analysed data from non-inoculated webs only, isolation did not have an effect on C (non-significant isolation effect: $F_{1,13} = 0.12$, $P = 0.91$, Fig. 1a), or the manner in which C changed through time (non-significant time × isolation interaction: $F_{3,41} = 0.023$, $P = 0.96$). Likewise, we did not detect an isolation effect ($F_{1,13} = 0.82$, $P = 0.38$, Fig. 1b), or a time by isolation effect ($F_{3,49} = 0.45$, $P = 0.72$) on C in inoculated webs. In short, constant mean connectance was conserved over time and across colonisation treatments.

Effects of *time*, *isolation* and *inoculation* on relative magnitudes of trophic fluxes

In contrast to constant connectance, our analysis revealed major changes in the relative magnitudes of trophic fluxes through time; C_{diff} increased through time in all webs (positive

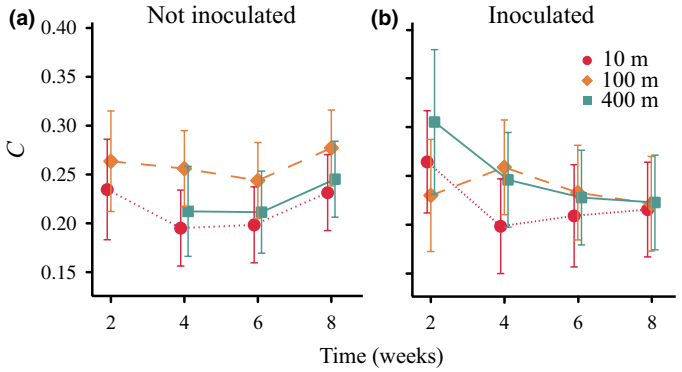

Figure 1 Directed connectance through time in experimental mesocosm food webs (± 2 SEM) subjected to different *isolation* and *inoculation* (i.e. species addition) treatments: (a) = non-inoculated food webs, (b) = inoculated food webs. Red circles (dotted line), yellow diamonds (dashed line) and teal squares (solid line) correspond to 10, 100 and 400 m isolation treatments respectively. In this figure and Figs 2, 4 and 5, no value is reported for the non-inoculated 400-m treatment in week 2 because these communities consisted of fewer than three species. Colours online only.

time effect in non-inoculated webs: $F_{3,41} = 6.2$, $P < 0.0015$, Fig. 2a; positive time effect in inoculated webs: $F_{3,49} = 0.45$, $P < 0.0001$, Fig. 2b). C_{diff} decreased with isolation in non-inoculated habitats (negative isolation effect: $F_{3,41} = 0.023$, $P = 0.01$, Fig. 2a). Critically, when we analysed only data from inoculated mesocosms, distance did not have a significant effect on C_{diff}, ($F_{1,13} = 1.4$, $P = 0.26$; Fig. 2b), indicating that inoculated food webs followed the same trajectories in C_{diff}, regardless of their distances from colonisation sources. There was no significant interaction between time and isolation in either inoculated or non-inoculated webs, indicating that C_{diff} of food webs at all distances changed at a similar rate within their respective inoculation treatments (Table 1).

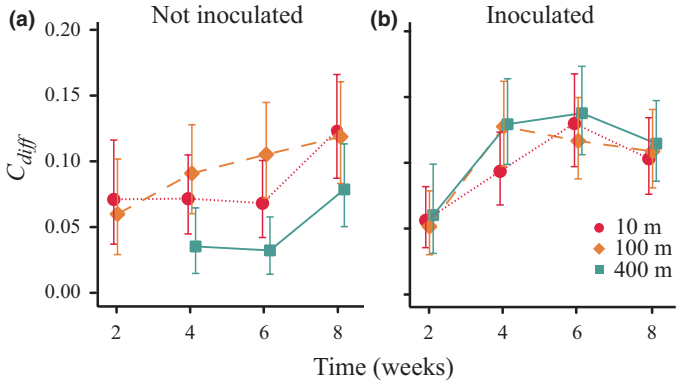

Figure 2 The difference between directed connectance and quantitative connectance, C_{diff}, through time in experimental mesocosm food webs (± 2 SEM) subjected to different *isolation* and *inoculation* treatments. Panels, colours, line type and symbols as in Fig. 1. A C_{diff} value of zero indicates that all species feed on each of their resources, and are fed upon by each of their consumers at the same rate. $C_{diff} > 0$ indicates that some fluxes are unequal in magnitude. C_{diff} increases as magnitudes of trophic fluxes become more dissimilar.

Effects of *time*, *isolation* and *inoculation* on the arrangement of trophic fluxes

To visualise changes in food webs that could account for the observed change in the relative magnitudes of trophic fluxes (i.e. C_{diff}), we calculated the fraction of all food web links needed to account for 75% of each web's total flux, F_{75} (Figs 3b and 4). F_{75} decreased strongly through time in all food webs (negative time effect in non-inoculated webs: $F_{3,41} = 7.7$, $P = 0.0004$, Fig. 4a; negative time effect in inoculated webs: $F_{3,49} = 1.7$, $P < 0.0001$, Fig. 4b). When we analysed only non-inoculated webs, there was a significant positive effect of isolation ($F_{1,13} = 9.3$, $P = 0.0094$, Fig. 4a), indicating the fraction of total links needed to account for 75% of the systems' flux was higher in more isolated habitats. When we inoculated webs, there was no significant effect of isolation ($F_{3,49} = 1.7$, $P = 0.18$), demonstrating that inoculation was sufficient to remove the effect of isolation on the fraction of links required to account for 75% of total flux. We could not distinguish a difference in the rate of decrease of F_{75} through time in inoculated or non-inoculated webs (*isolation* × *time* interaction not significant, Table 1).

We used the links that constituted F_{75} to reconstruct the substructure in each web through which most of the energy and materials fluxed (compare Figs 3a and 3b). These links comprised a single connected substructure of two to six species in 95% of communities, regardless of total food web size. We refer to this substructure as a *fast resource channel*. Of the webs with a single connected fast resource channel, 51% consisted of species in a linear arrangement (linear sequences of two, three, or four species), 28% consisted of 'fan' webs of two to four species competing for a shared resource, 3% consisted of 'bottleneck' webs of one to two resources leading to a consumer that is consumed by multiple predators and 18% consisted of a single connected combination of the aforementioned substructures.

Effects of *time*, *isolation* and *inoculation* on coupled resource channels

We identified the presence of coupled fast and slow resource channels as described in Appendix S3. The proportion of all food webs that exhibited coupled fast and slow channels increased through time (positive time effect in non-inoculated webs: $P = 0.0055$ in week 8, Fig. 5a; positive time effect in inoculated webs: $P = 0.0082$, Fig. 5b). Increasing isolation reduced the likelihood of observing this feature when mesocosms were not inoculated (negative isolation effect: $P = 0.029$, Fig. 5a), but had no effect when mesocosms were inoculated (non-significant isolation effect: $P = 0.65$, Fig. 5b), again suggesting that inoculation was sufficient to remove the effect of isolation on the rate at which fast and slow resource channels become coupled to one another.

DISCUSSION

Our results show that food web structure changes through assembly in a way that depends strongly on colonisation processes. When assembly begins from a state in which all species are absent, the trajectory of developing webs is governed by

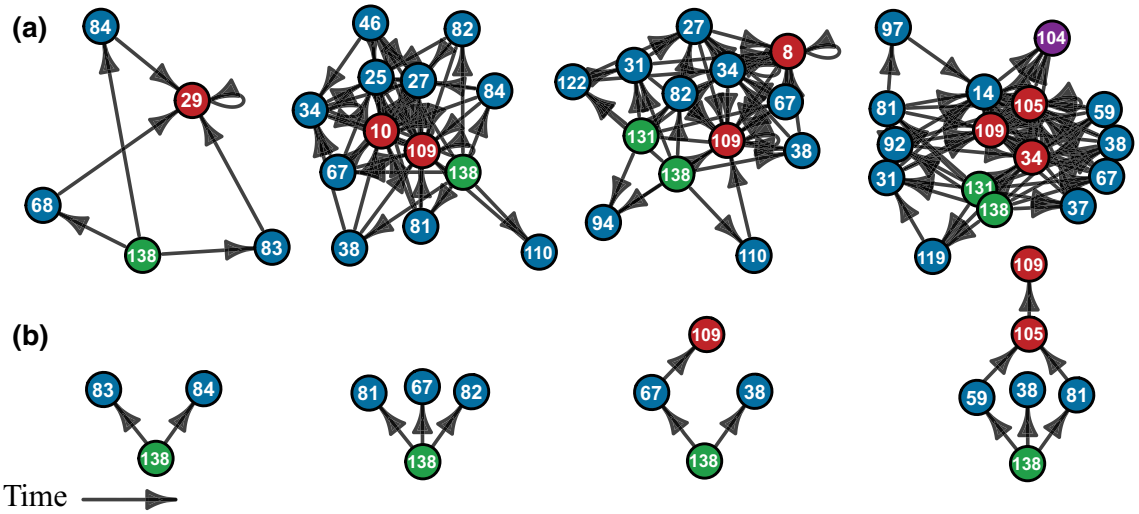

Figure 3 Dynamics of a typical high colonisation rate food web over the course of our study. Panel (a) shows the change in web topology through time (from left to right) and includes all species (nodes) and the links (edges) among them, regardless of flux rate. Panel (b) shows only the fast resource channel from the same web. Fast channels were detected by ranking fluxes, and selecting the smallest number of links needed to account for 75% of total system activity (F_{75}). These links comprised a single structure of two to six species in 95% of communities, regardless of total food web size. Nodes are numbered based on species' identities in Appendix S1, and coloured based on loose trophic classifications: green = resource; blue = consumer; red = predator; purple = parasite.

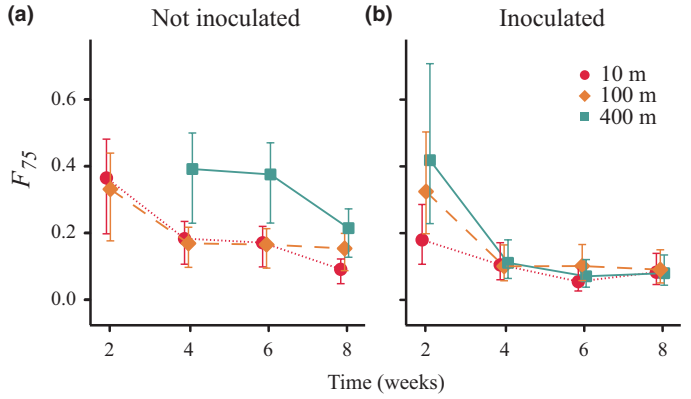

Figure 4 The fraction of total links needed to account for 75% of total system flux, F_{75}, through time in experimental mesocosm food webs (± 2 SEM) subjected to different *isolation* and *inoculation* treatments. Panels, colours, line type and symbols as in Fig. 1

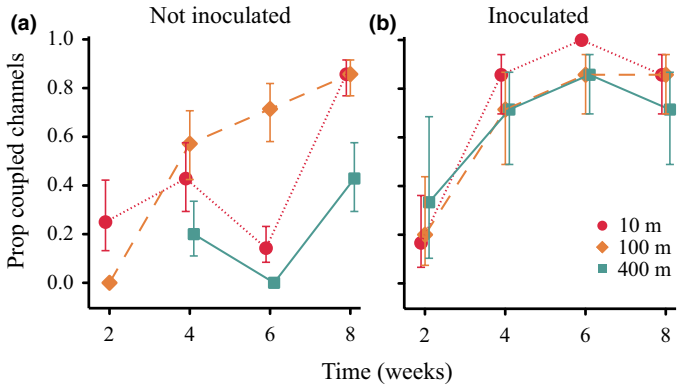

Figure 5 The fraction food webs exhibiting coupled fast and slow resource channels through time in experimental mesocosm food webs (± 2 SEM) subjected to different *isolation* and *inoculation* treatments. Panels, colours, line type and symbols as in Fig. 1

colonisation rate. This is evident from the distinct developmental trajectories followed by non-inoculated webs at different distances from source lakes (Figs 2a, 4a, and 5a). By demonstrating these patterns using replicate experimental webs, we show that this appears to be a general feature of assembly.

When webs at each distance were inoculated with the same suite of lower and mid trophic level species, isolation had no effect on web structure, or the trajectories webs followed through assembly (Figs 2b, 4b, and 5b). If persistent differences in colonisation rate had been important, we would have expected webs in different isolation treatments to differ, despite inoculation. But this was not the case. The observation that inoculating pools removed the isolation effect suggests that two processes are responsible for the effects of isolation. First, mesocosms that were inoculated simultaneously received the same suite of species from source lakes, which relaxed the effect of variation in species arrival order (i.e. historical contingencies, Fukami 2010). Prior experiments have demonstrated that the effect of species arrival order on community structure is more pronounced when communities experience low colonisation rates (Robinson & Edgemon 1988). Thus, removing variation in species arrival order between mesocosms at different distances likely eliminated this effect, contributing to the similar trajectories observed in all inoculated habitats. A second reason for the relative insensitivity of inoculated webs to isolation is that all inoculated webs began with a base of mid-trophic level species upon which top predators could feed. Hein & Gillooly (2011) showed that the abundances and richness of ephemeral pond top predators depend strongly on the abundances of their prey. By adding these prey species to inoculated ponds, we relaxed limits on predator populations set by a lack of

available resources. The arrival and establishment of top predators was at least partially responsible for the changes in inoculated webs between weeks 2 and 4 (contrast week 2 and week 4 in Figs 2b, 4b, and 5b). A goal for future studies will be to separate the effects of historical contingencies and predators' resource limitation on web dynamics, although this may prove challenging because the two processes can be conflated in assembling webs.

Average connectance of experimental webs in all treatments was constant through time, indicating that the number of links, L, in assembling webs increased quadratically with the number of species, S ($C = L/S^2 = zS^2/S^2$, where z is a constant, so $L = zS^2$). Constant C after an initial decline during assembly has also been observed in Simberloff & Wilson's (1969) mangrove experiments (Piechnik *et al*. 2008). Yet, in our experiment, stable connectance masked major changes in the relative magnitudes and arrangement of trophic fluxes. Webs were characterised by a relatively static fast resource channel consisting of two to six species, and a relatively dynamic slow channel comprising the remaining species in the web. The disparity between the static fast resource channels, and the growing dissimilarity in the magnitudes of trophic fluxes indicated by increasing C_{diff} and decreasing F_{75} (Figs 2 and 4) can be explained by the observation that most new species that entered communities contributed relatively little to total system flux. These species formed slow resource channels that became coupled to fast channels by predators later in assembly. It is interesting that webs maintain constant connectance and simple fast resource channels, despite major changes in web size (as few as three species early in the experiment to up to 26 species late in the experiment) and substantial species turnover. On average, roughly half of species present in a given web during one sample period were gone by the next sample period. Thus, some features of network architecture such as C and F_{75} are relatively conserved despite major changes in the identity of species. This is explained in part by the fact that species turnover rates are much lower in fast channels compared to slow channels (only 21% of species in fast channels turnover on average between periods). Theoretical studies of assembly suggest that food webs receiving immigrants from external colonisation sources go through cycles (e.g. Steiner & Leibold 2004; Pawar 2009; also called community churning, Holt 2010), where systems continuously experience species extinctions and recolonisations as they develop. Our experiment reveals that most of this 'churning' occurs among species in slow resource channels. The reasons for this may simply be that these species are rarer and more susceptible to stochastic extinction. However, this phenomenon warrants further empirical and theoretical investigation.

Although we use a model system to study the dynamics of food web assembly, we expect many of the qualitative features observed in this study to apply to other ecological systems. The major features of our study system include periodic disturbances that lead to regular disassembly and assembly events, colonisation of local habitats by individuals from outside systems, population and colonisation dynamics that occur on similar timescales and trophic dependencies that make arrival order and resource limitation important in governing food web structure. These conditions certainly apply to habitats with regular system-wide disturbances and well-defined borders (e.g. oceanic islands, phytotelmata communities). But they also apply, at least at some spatial scale, to many if not most ecosystems studied to date (Levin 1992; Holt 2010).

The challenge of understanding how ecological networks are formed and change through time has been severely hampered by a lack of observational data and replicated experiments. Static depictions of webs from many systems show that webs exhibit structural regularities, like a limited range of connectance values (usually 0.03–0.3, Dunne *et al*. 2002), skewed distributions of interaction strengths (McCann *et al*. 1998) and abundances (Sole *et al*. 2002) leading to strong variation in the relative magnitudes of trophic fluxes (Ulanowicz & Wolff 1991) and characteristic substructures, such as coupled fast and slow resource channels (Rooney *et al*. 2006). Our experiment reveals how these features develop in real food webs. We show that food webs follow a repeatable assembly process, and demonstrate how colonisation influences this process. These results should encourage researchers to measure the dynamics of food webs in other ecological systems.

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AUTHORSHIP

AMH designed experiment, AKF and AMH collected data, AKF and AMH performed analyses, AKF and AMH wrote the manuscript.

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