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Sequentially assembled food webs and extremum principles in ecosystem ecology

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Summary

1. Successional changes during sequential assembly of food webs were examined. This was carried out by numerical methods, drawing one species at a time from a species pool and obtaining the permanent (persistent) community emerging at each step. Interactions among species were based on some simple rules about body sizes of consumers and their prey, and community dynamics were described in terms of flows of biomass density.
2. Sequential assembly acted as a sieve on the communities, assembled communities having many properties different on average from those of feasible, stable communities taken at random from the species pools.
3. Time-series of community development were consistent with certain functions thought to go to an extremum (maximum or minimum) in ecosystem ecology, including a rapid early increase in net primary productivity and ascendency, although a clear trend in total biomass density was not evident and resilience decreased rather than increased.
4. In addition, more gradual changes in food web structure took place during succession to which the ecosystem goal functions were relatively insensitive. These changes included gradual increases in the number of species, invasion resistance, number of loops of length > 2 and number of prey species per consumer species.
5. We therefore argue that ecosystem and community dynamics can offer complementary insights into the process of ecological succession. The extremum principles of ecosystem ecology highlight some of the major properties of succession, whereas the community ecology sheds light on some more subtle changes taking place within the networks.

Key-words: ascendency, goal function, invasion resistance, permanence, succession.

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Introduction

Species rarely, if ever, arrive simultaneously at a given site; they are much more likely to appear sequentially from a regional pool of species, either one at a time or in small groups. When new species arrive, they may or may not become established. If they do establish themselves, they may then lead to extinction of resident species, so that a gradual change in species composition takes place as time goes on. This turnover of species, referred to here as assembly dynamics (Law 1999), is the stuff of succession, a subject as old as ecology itself (McIntosh 1985: 79 *et seq*.), and at the heart both of community ecology and of ecosystem ecology.

Well-established though the subject of succession is, it is surprising how little is known about the changing internal structure of communities during succession. From assembly dynamics, it is known that invasion resistance tends to increase on average (Post & Pimm 1983; Drake 1990; Luh & Pimm 1993; Law & Morton 1996; Lockwood *et al*. 1997). From ecosystem ecology there are several measures, sometimes called goal functions, thought to go towards extrema (maxima or minima) as ecosystems develop (Jørgensen 1994; Fath, Patten & Choi 2001). Some of these ecosystem measures have arisen as empirical generalizations; for instance, the tendency for biomass and primary production to increase during succession (Margalef 1968: 30; Odum 1969). Others have been motivated by thermodynamic and informational considerations, such as maximizing the flux of energy during evolution, and increasing ascendency (Lotka 1922; Ulanowicz 1980). A review and extension of thermodynamic considerations during ecosystem development is given

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by Fath *et al*. (2004). However, it is not known whether the paths towards extrema emerge as a natural consequence of the turnover of species during succession. The ecosystem processes would have to be built on a platform of assembly dynamics to gain this knowledge, because it is the assembly dynamics that determine the turnover of species.

Here a model of ecosystem dynamics, driven explicitly by turnover of species, is analysed. The approach is to construct permanent (*sensu* Hofbauer & Sigmund 1988: 97, 160) communities of consumers and their prey, drawing species one at a time from a species pool, at each step allowing the dynamics of the introduced species coupled to the resident species to determine the new species composition (see Law & Morton 1996). The species have different body sizes, and their interactions are informed by some simple ecological properties of body sizes of consumers and prey (Peters 1983; Yodzis & Innes 1992; Emmerson & Raffaelli 2004). Two tests are carried out on the model. First, some spot checks are made to test whether communities after some species turnover (succession) are statistically different from communities with the same number of species drawn simultaneously at random from the species pool. Secondly, time-series of community assembly are examined to see what, if any, successional trends in food web structure are evident.

The transformation from flux of population density to the flux of biomass density used in ecosystem ecology is straightforward in this model because species' body sizes are known. This direct link between ecosystem and assembly dynamics has two useful consequences. First, it provides an ecosystem model explicitly in terms of the assembly dynamics responsible for the turnover of species. Secondly, it provides a model of assembly dynamics in which the flows of biomass between species are explicit, accounted for fully and energetically reasonable. This link between communities and ecosystems allows, for the first time, an evaluation of whether directional change in ecosystem-level properties such as biomass, productivity and ascendency emerges consistently and naturally from the turnover of species that occurs during community assembly.

Methods

SPECIES POOL

Food-web structure arising from interactions among consumers and their prey was investigated. To ensure that this was not confounded by effects of direct competition, analyses were confined to food webs supported by a single basal species, indexed 1 below.

Constructing a species pool began by assigning a body mass w_i to each of 100 consumer species $i = 2, \ldots, 101$. (The body size of the basal species was taken as 1; those of the consumer species can be thought of as multiples of the size of the basal species.) The $\log_{10}(w_i)$ was drawn uniformly at random from a range 0–6, i.e. over six orders of magnitude. This was intended to reflect the wide range of body sizes of consumers available in real species pools (Leaper & Raffaelli 1999), and was broad enough to ensure that communities drawn from the species pool were constrained by the community dynamics rather than the range of body sizes available. With the body sizes in place, a transformation was made from state variables of community dynamics to those used for mass transfer in ecosystem dynamics: for species i, this is $y_i = w_i x_i$, where y_i is biomass density and x_i is population density; both biomass density and population density are state variables which may change over time.

Communities drawn from the species pool were assumed to be sufficiently well mixed for the dynamics to be unaffected by spatial structure. For simplicity, and to enable a global test of persistence known as permanence (Jansen 1987; Hofbauer & Sigmund 1988: 97, 160), it was assumed that the dynamics of speices i in a community comprising a set S of species indices had the form:

$$\dot{y}_i = y_i f_i(y) = y_i\left(r_i + \sum_{j \in S} c_{ij} y_j\right) \qquad \text{eqn 1}$$

The parameter r_i is an intrinsic rate at which the biomass density of i changes. The parameter c_{ij} describes the effect of a unit biomass of species j on a unit biomass of i per unit time; c_{ij} has a simple relationship to the more familiar parameter a_{ij} of the generalized Lotka–Volterra equations of community dynamics: $c_{ij} = a_{ij}/w_j$ (in a three-dimensional space the dimensions are: length^3 mass^{-1} time^{-1}). Values of these parameters were set by some simple considerations about body size, as described below.

Body size of species coexisting within communities can obviously vary over several orders of magnitude, and the ecological parameters should scale with body size in an appropriate way. The observation that generation time scales approximately as the fourth root of body mass was used as a guiding principle (Peters 1983: 132), or equivalently that the rate terms in eqn 1 scale approximately as $w_i^{-0\cdot25}$ (Yodzis & Innes 1992; Brown *et al*. 2004). The intrinsic rates of consumer species were thus written as

$$r_i = -\rho w_i^{-0\cdot25} \qquad \text{eqn 2}$$

where ρ is a positive parameter that scales from body size to rate, set relative to the intrinsic rate of the basal species (see below).

Effects of consumers on prey deal first with the probability that the prey form part of the consumer diet. On the basis that consumers are typically substantially larger than their prey (Peters 1983: 111), species i was assigned to the diet of j according to a random variable z_{ij} with a Gaussian distribution:

$$z_{ij} = 1 \quad \text{with probability} = \alpha \exp[-(\log_{10}(\beta w_i/w_j)/\gamma)^2]$$
$$\text{given } w_j > w_i$$

$$z_{ij} = 0 \quad \text{otherwise.} \qquad \text{eqn 3}$$

Here α is a parameter in the range $0 < \alpha \leq 1$ describing how likely the consumer is to take the prey with the most preferred body size ratio; a value $\alpha = 1$ was used. Parameter β defines the most preferred ratio of consumer size to prey size; a value in the range 10–100 is of an appropriate order for data given by Peters (1983: 111); the lowest value $\beta = 10$ was used, as this would potentially give most trophic levels within range of body sizes allowed. Parameter γ defines the range of body sizes consumed, and can be thought of as diet breadth, similar to the measure of generality in the niche model (Williams & Martinez 2000); a value of approximately 0·2 is in the range given by Peters (1983 : 111). Prey body size was constrained always to be less than consumer body size. The effect of consumer *j* on prey *i* is then:

$$c_{ij} = -\delta_j \, w^{-0{\cdot}25} z_{ij}, \qquad \text{eqn 4}$$

where δ is a further positive parameter; in the absence of any information, it was assumed that $\delta = 1$.

Effects of prey on consumer biomass density need to account for flow of mass from prey to consumer, allowing for the ecological efficiency *e*; this transfer is known to be low in nature and was set for simplicity at 0·1 across all trophic levels. The following balance between the gain to consumer *i* and the loss to prey *j*, over a short period of time δt was used:

$$\begin{aligned} \textit{i.e.} \quad \underbrace{c_{ij} y_i y_j \delta t}_{\text{gain}} &= \underbrace{e c_{ji} y_j y_i \delta t}_{\text{loss}} \qquad \text{eqn 5} \\ c_{ij} &= -e c_{ji} \end{aligned}$$

Effects of consumers on their own biomass densities were assumed to scale with body size:

$$c_{ii} = -\varepsilon w_i^{-0{\cdot}25}. \qquad \text{eqn 6}$$

The parameter ε weighs the intraspecific interactions relative to the interspecific ones and affects how many species a sequentially assembled community supports. The larger the value of ε, the closer the interaction matrix is to diagonal dominance (eqn A11; see Hofbauer & Sigmund 1988: 193), and the more likely a community is to persist. A value $\varepsilon = 0{\cdot}01$ was chosen as a compromise between communities that would be too simple to show significant structure and too complex to permit numerical tests of permanence.

There remain two parameters to specify for the basal species, r_1 and c_{11}; these determine the rate at which resource flows from the basal species and, in effect, constrain the rate at which energy becomes available to consumers (and hence determine the number of trophic levels). We set $r_1 = 1{\cdot}0$, and scaled the intrinsic rates of consumers relative to this by putting $\rho = 0{\cdot}05$ in eqn 2; a value $c_{11} = -0{\cdot}1$ was used. These values were chosen to give communities usually with three or four trophic levels, as observed often in nature; higher rates of resource flow gave more trophic levels, and much more complicated paths of assembly.

This completes the specification of community dynamics, with the exception that each parameter of eqn 1 was multiplied by a small, normally distributed, random number with mean 1 and standard deviation 0·01. This variation was included on the grounds that uncontrolled factors other than body size would still have some effect on the intrinsic rates and interactions.

To ensure that the results were not attributable to special properties of particular species pools, nine independent pools were constructed using the protocol above. Of these, one pool had to be discarded because it lacked sufficient communities of the correct size for comparison of random vs. assembled communities below, leaving eight pools for analysis. All numerical computations were performed in MATLAB.

PERMANENCE AND SEQUENTIAL ASSEMBLY OF COMMUNITIES

To establish whether a set of species drawn from a species pool could persist, a criterion of permanence was used (Hofbauer & Sigmund 1988: 97, 160; Law 1999). This is a global criterion that ensures no orbits tend to the boundary of the phase space. Permanence makes no assumptions about the kind of attractor the community has; it was used here because it was not known, a priori, whether the communities would have equilibrium points with global asymptotic stability. A test for permanence amounts to testing for the existence of a Lyapunov function, and a sufficient condition for this can be obtained by a linear programming method (Jansen 1987). [See Appendix G of Ebenman, Law & Borrvall (2004) for a detailed worked example of the test.]

Assembly dynamics entailed stepping from the asymptotic biomass densities of one community to those of the next, each step being initiated by arrival of a new species (see Law & Morton 1996). Jumping from one asymptotic state to the next carries an assumption that the short time-scale of community dynamics is separated from the long time-scale of assembly dynamics. The new species was chosen at random from the species pool, and was tested for its ability to invade the asymptotic state of the resident community (Inequality A9a). If invasion occurred, the community augmented by the new species was tested for permanence; if the augmented community was permanent, this became the new community. If the augmented community was not permanent, its subsystems were checked for the existence of one subsystem that was permanent in its own right and uninvadable by any other species from the augmented community; this subsystem then became the new community (orbits would move from the interior of the space into this subsystem). The algorithm could fail to find an outcome if there were no uninvadable subsystems, or more than one. In these circumstances the algorithm switched to numerical integration to find the new community (MATLAB function ode15s, a variable order solver); this procedure was needed in much less than 1% of the assembly steps.

RANDOM VS. ASSEMBLED COMMUNITIES

To compare the effect of random and sequential assembly, communities of eight species were constructed from each species pool. Using the same number of species throughout facilitates comparison of the communities. The number of species was chosen to be eight on the grounds that this was near the median size of assembled communities, and not too big to prohibit calculation of computation-intensive food-web measures.

To obtain random, permanent communities, we picked at random simultaneously and uniformly seven species from the pool (the basal species was always present). This was repeated until 100 permanent communities had been obtained from each species pool. Permanent, eight-species communities were sparse in the space of species and approximately 2×10^6 to 4×10^6 iterations were required to find a permanent one. Although sparse, this still implies 4000–8000 such communities in a pool of 100 species.

To obtain communities by sequential assembly, 100 independent replicate assembly sequences were generated, in each case allowing the assembly to proceed until an uninvadable state was reached, or until 1000 iterations had taken place (whichever happened first). An iteration here means successful invasion by a new species, together with any extinctions that might follow from the invasion. For each assembly sequence, a search was then made for the first occurrence of an eight-species community. To allow a substantial period of assembly to occur prior to picking an assembled community, the search for eight-species communities commenced at the mid point of each assembly sequence. If no eight-species community was found, or if the community had already been used in a previous replicate, the community was discarded; to ensure sufficient eight-species communities, 150 replicate assembly sequences were generated.

The sampling above leads to a complete cross-classification of two assembly methods × eight species pools with 100 replicate communities in each combination, giving 1600 eight-species food webs for analysis. A number of measures of the food webs were computed (Appendix I). Two-way analysis of variance was carried out on each measure to explore formally the effects of assembly method, effects of species pool, and any interaction between them. Because much of the data showed departures from normality (e.g. bimodal distributions, outliers), a non-parametric method, the Scheirer–Ray–Hare test, was used (Sokal & Rolf 1995: 446; Dytham 1999: 131).

TIME-SERIES OF COMMUNITY ASSEMBLY

The assembly sequences used to obtain the assembled eight-species communities also served a second purpose of providing 150 replicate time-series of assembly from each of the eight species pools. Food web measures were calculated on the communities that occurred over the first 50 time steps of each of these time-series ($50 \times 150 \times 8$ communities in total) to examine trends in the food web measures during succession.

Results

Biomass densities in communities at equilibrium were not themselves imposed directly as assumptions of the model, and thus give an indication as to whether reasonable trophic structures emerge from the assumptions about the rate terms in eqn 1. With the species-pool parameters in Table 1, biomass densities usually declined substantially from one trophic level to the next although, in a relatively small number of cases, biomass density at level 2 was greater than at level 1. Figure 1, which shows the uninvadable web to which all assembly sequences in species pool 1 converged, provides an illustrative example of this general trend. In this instance biomass density at equilibrium declined by about two orders of magnitude from bottom to top; because of increasing body size with trophic level, population density declined much faster, by about five orders of magnitude.

RANDOM VS. ASSEMBLED COMMUNITIES

Sample sizes were large enough for there always to be an effect ($P < 0{\cdot}001$) on the food web measures of: (1) species pool and (2) species pool × assembly method interaction, except for invasion resistance (Inequality

Table 1. Species-pool parameters and their interpretation

Parameter	Value	Interpretation
α	1	Probability with which a consumer takes prey of most preferred size ratio
β	10	Most preferred size ratio of consumer to prey
γ	0·2	Diet breadth
δ	1	Scaling factor from body size to per unit biomass effect of consumer on prey
ε	0·01	Scaling factor from body size of consumer to per unit biomass effect on itself (density dependence)
e	0·1	Ecological efficiency
ρ	0·05	Scaling factor from body weight to intrinsic death rates of consumers
r_1	1	Intrinsic rate of increase of basal species
c_{11}	−0·1	Strength of density dependence of basal species

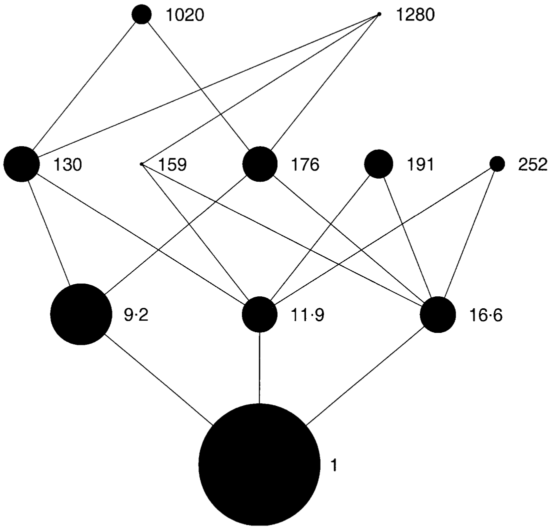

Fig. 1. Uninvadable food web at end-point of assembly of communities from species pool 1. Each row corresponds to a trophic level, with the basal species at the bottom. Circles represent species and lines are feeding links. Circle area is proportional to equilibrium biomass density; the number beside each circle is body mass.

A9b) and return time (eqn A10), where the interaction was relatively weak. Differences between random and assembled communities were also usually significant ($P < 0{\cdot}001$) (Table 2). All communities had the property of local asymptotic stability; this is not a necessary feature of permanence – non-equilibrium attractors are entirely consistent with permanent communities. Omnivory was absent in all but three of the 1600 communities. Species could therefore be assigned to integer trophic levels, and some of the analyses below were therefore performed separately for each trophic level (the trophic level of the rare omnivores was taken to be the maximum path length to the basal species + 1).

Sequential assembly had the effect of increasing the proportion of species at trophic level 2 at the expense of higher trophic levels, and of selecting species of slightly smaller body sizes than random communities (Table 2). The overall biomass density at equilibrium of sequentially assembled communities was a little lower than that of random communities, due mainly to a substantial reduction in biomass at trophic level 1, and countered by slightly higher values at even-numbered trophic levels. The equilibrium flow rate of biomass density out of trophic level 1, due to consumers at level 2 (eqn A2), was not affected systematically by assembly, although the flow rate per unit total biomass density (eqn A4) was greater in sequentially assembled communities. Sequentially assembled communities had lower flow rates into higher trophic levels than did random communities.

Network structure of communities was affected by assembly method (Table 2). The average number of prey species per consumer species, connectance (eqn A5), average interaction strength (eqn A6) and the number of subsystems with feasible equilibria were all slightly increased by sequential assembly. However, measures of the information content in the flow of biomass density were changed relatively little by sequential assembly; community development capacity (eqn A7) (Ulanowicz 1980) was slightly greater following sequential assembly, and ascendency (eqn A8), a more complex measure of shared flows (Ulanowicz 1980), was unchanged.

Some of the largest differences between random and assembled communities were in their stability properties (Table 2). Sequentially assembled communities were more invasion-resistant than random ones (see Inequality A9). It was also striking that there were more than twice as many loops (sometimes referred to as cycles) of length > 2 following assembly and that the maximum weight on such loops was increased by assembly. Curiously, however, return times to equilibrium following a small displacement (eqn A10) were similar, and assembled communities were only slightly further than random communities from diagonal dominance (Inequality A11).

TIME-SERIES OF COMMUNITY ASSEMBLY

Figure 2 shows time-series of several food web measures, obtained from sequential assembly, giving information on the path of community development. The graphs start at time 1 following establishment of the basal species. Results from the different species pools are shown separately because of the somewhat different results of assembly in different species pools noted above.

Fig. 2a–d shows the time-series of total biomass density, net primary productivity, ascendency and return time, respectively, all of which are ecosystem measures that have been suggested as tending towards a maximum or minimum during succession. In our analyses, they share the feature of changing rapidly at the start of succession and of showing relatively little change beyond about the 20th time step. Total biomass density at equilibrium (Fig. 2a), which started at the carrying capacity of the basal species, was much reduced by arrival of the first consumer of the basal species, but after this its path was less predictable. Net primary productivity flowing to consumers (eqn A2) rose from a value of zero at the start of each assembly sequence when only the basal species was present to a maximum average of about 2·2 units (Fig. 2b). The maximum primary productivity that could flow to consumers would be approximately 2·5 units; evidently consumers tended to overexploit the basal species, resulting in a system kept well below this maximum yield. Time-series of ascendency (eqn A8) were similar to those of primary productivity (Fig. 2c), although a slight tendency to increase remained at later times. Log of return time from small displacements (eqn A10), proportional to the reciprocal of resilience, also increased rapidly at first, and relatively little at later stages (Fig. 2d).

Fig. 2e–h shows evidence of more gradual, continuing changes to food web structure, largely undetected by ecosystem measures. Most obvious was the increasing number of species (Fig. 2e). There was also increasing

Table 2. Results of two-way analysis of variance on food-web measures to compare random and sequentially assembled communities of eight species. *P* is the probability of incorrectly rejecting the null hypothesis of no difference between random and sequentially assembled communities. Details of the food-web measures are given in Appendix I

Food-web measure	*P*	Random	Assembled
Number of species			
Trophic level 2	< 0·001	2·00	2·36
Trophic level 3	< 0·01	3·52	3·39
Trophic level 4	< 0·01	1·47	1·25
Body weight			
Mean of $\log_{10}$ body weight over all trophic levels	< 0·001	1·73	1·67
Mean of $\log_{10}$ body weight at trophic level 2	< 0·001	1·06	1·01
Mean of $\log_{10}$ body weight at trophic level 3	< 0·01	2·05	2·01
Mean of $\log_{10}$ body weight at trophic level 4	< 0·01	3·04	3·02
Equilibrium properties			
Total biomass density	< 0·001	6·38	5·72
Biomass density at trophic level 1	< 0·001	4·37	3·76
Biomass density at trophic level 2	< 0·01	1·02	1·10
Biomass density at trophic level 3*	< 0·001	0·94	0·80
Biomass density at trophic level 4*	< 0·001	0·035	0·054
Net primary productivity	NS	2·18	2·19
Net primary productivity per unit total biomass density	< 0·001	0·35	0·39
Flow rate of biomass density into level 3 from 2	< 0·001	0·019	0·018
Flow rate of biomass density into level 4 from 3	< 0·001	0·00048	0·00030
Network properties			
Average number of prey species per consumer	< 0·001	1·23	1·35
Connectance	< 0·001	0·309	0·337
Average interaction strength	< 0·001	0·180	0·191
Number of equilibria in subsets of community	< 0·001	39·6	42·7
Community development capacity	< 0·01	6·22	6·29
Ascendency	NS	1·29	1·37
Stability properties			
Invasion resistance	< 0·001	0·850	0·899
Log return time	NS	3·75	3·72
Distance from diagonal dominance	< 0·001	0·349	0·358
Number of loops of length > 2	< 0·001	6·93	16·4
Maximum weight of loops of length > 2*	< 0·001	0·037	0·070

*Measures for which statistical analysis was carried out on a reduced data set. This arose when a measure could not be obtained from a replicate, e.g. no species at trophic level 3 (a maximum of 4 per treatment) or trophic level 4 (a maximum of 38 per treatment). The Sheirer–Ray–Hare test requires constant replication across treatments, so the number of replicates was reduced randomly in all treatments down to the minimum level of replication (96 replicates at level 3 and 62 at level 4).

invasion resistance after an initial decline due to arrival of the first consumers (Fig. 2f). It is interesting that an eigenvalue measure of asymptotic stability of the equilibrium points of the communities (return time, Fig. 2d) showed little sign of these later changes, and nor did the distance from diagonal dominance (results not shown). The changes seem to be a consequence of more subtle reconfiguration of the networks. For instance, loops of length > 2 tended to accumulate in number from time 4 onwards (Fig. 2g) (except for a later decrease in one species pool), as did the mean number of prey species per consumer species (Fig. 2h).

Discussion

RANDOM VS. ASSEMBLED COMMUNITIES

There were clear differences between random and assembled communities that transcended particular species pools, despite the large assembly method × species-pool interactions. Species selected by sequential assembly were more likely to be at lower trophic levels, smaller in body size, more strongly coupled to other species through connectance and interactions, more resistant to invasions, having many more long loops and greater maximum weights on these loops.

A possible reason for several of the properties of assembled communities is the development of greater diet breadth during the turnover of species, leading to greater cross-linking of the webs. During sequential assembly of communities, consumer species with wider diets would have an inherent advantage immediately on entering communities, because there would be more food for them. Whether their diets would remain broad after establishment is less clear, because there is no guarantee that all their prey species would continue to exist as the consumer's density increased. However, we conjecture that, even the initial advantage that comes

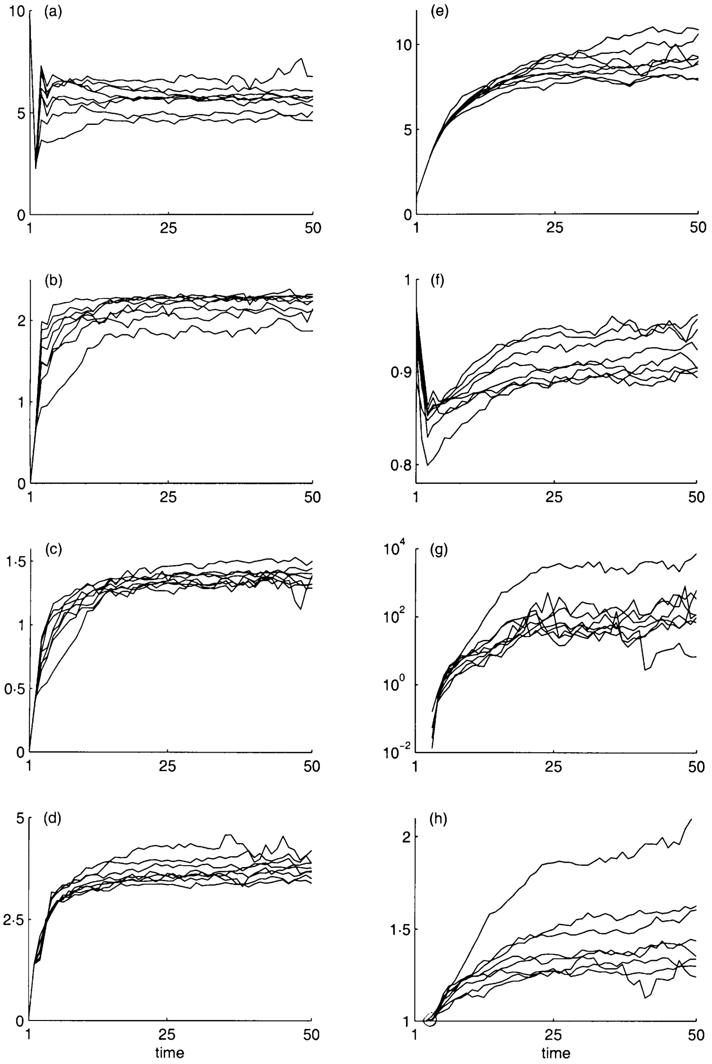

Fig. 2. Time-series of food-web measures during assembly. Time is measured as the number of successful invasions by new species. Each line refers to a separate species pool, and is an average of replicate assembly paths; communities were removed when they reached the end-point of assembly so the number of replicates decreases from a starting value of 150. (a) Total biomass density; (b) net primary productivity; (c) ascendency; (d) $\log_{10}$ return time (there were 16 communities with unstable equilibria excluded from these results); (e) number of species; (f) invasion resistance; (g) number of loops of length > 2; (h) mean number of prey species per consumer species.

from a consumer having more prey, gives an advantage to such species and makes it increasingly difficult for other species to gain a foothold, thereby contributing to increased invasion resistance of the community.

It would, in fact, be surprising if communities obtained by sequential assembly and random sampling were not different. Almost inevitably, some communities have more assembly paths leading to them than others, and are reached more easily through the gradual arrival of species than others. Assembly graphs of persistent protist microcosms are known to have this property, with some communities that are difficult to attain at all (Warren, Law & Weatherby 2003). Luh & Pimm (1993) also found unreachable states likely to exist in simulation models with simple ecological assumptions. The need for assembly paths to exist and the number of such paths are extra constraints on the likelihood of finding a community, over and above the requirement that it should persist.

Our results thus indicate that an understanding of the kinds of community to be expected in nature needs to go beyond the properties of random stable communities (May 1972). The turnover of species leads assembled communities to differ from random stable communities in repeatable ways, suggesting that succession is accompanied by directional change in community structure.

TIME-SERIES OF COMMUNITY ASSEMBLY

Our results show that, at a statistical level (averaging over many assembly paths) certain ecosystem functions do increase rapidly at first, with relatively little change later on (Fig. 2, column 1). This is evident for net primary productivity flowing to consumers, and is in keeping with Margalef's (1968: 30) suggestion. However, a trend in total biomass density was not so evident (cf. Margalef 1968: 30; maximum storage principle: Jørgensen

& Mejer 1979; Fath *et al.* 2001). Our time-series of ascendency, an information-theoretical measure on flows through food webs, also increased rapidly near the start of succession, as argued by Ulanowicz (1980); these time-series were similar to those of net primary productivity, in keeping with the suggestion that ascendency is dominated by the magnitude of flows through communities (Fath *et al.* 2001). Return time, proportional to the inverse of resilience – a recent addition to the goal functions – also increased rapidly, with relatively little systematic change later; this increase corresponds to a loss in resilience, the reverse of the direction suggested by Cropp & Gabric (2002).

However, there are also properties of food webs that ecosystem goal functions do not detect so readily. It is notable that primary productivity, ascendency and return time were the only three measures that did not register a significant difference between random and assembled communities. In the time-series of community assembly, there were gradual continuing changes in the network measures in the right-hand column of Fig. 2 much less evident in the ecosystem measures of the left-hand column. Most visible of the network properties was the number of species, which continued to grow in some species pools at a time when of relatively little change in the ecosystem goal functions. Also striking was the tendency for invasion resistance to continue to increase. In keeping with the results on random and assembled communities, the number of long loops continued to increase at these later stages, as did the breadth of diet of consumer species. These later changes took place with little alteration to the overall web connectance (results not shown), suggesting reorganization of the webs towards greater cross-linking of their parts. We conjecture that the build-up of opportunistic cross-linking could contribute to the lack of clustering which often applies to other kinds of networks (Dunne, Williams & Martinez 2002).

CAVEATS AND CONCLUSIONS

It is as well to understand that our species pools had their own simplifying assumptions, and that other assumptions could well give different types of assembly behaviour. For instance, larger values of parameters r_1 and c_{11}, which determined the primary productivity flowing to consumers (eqn A2), could potentially give much more complex assembly paths and eventually would have probably resulted in communities of much greater species richness and variability in species composition over time and space (Steiner & Leibold 2004). However, the communities usually developed roughly pyramidal trophic structures at equilibrium with the parameter values used. That these pyramids emerged without being directly imposed suggests that the assumptions are sufficient to capture some basic structural properties of communities. We conjecture that the key to achieving this is an energetic constraint to community dynamics (Yodzis & Innes 1992), and an appropriate scaling from body size to rates of change in biomass density (because of the many orders of magnitude of variation in body size within species pools).

Important though the simplifications are, we have no reason to suppose that they affect the three main results of the study. First, sequential assembly acts as a sieve, selecting non-random subsets of communities from species pools. Secondly, extremum principles of ecosystem dynamics capture some major changes in communities at early stages of succession. Thirdly, there are also more subtle aspects of network structure that change gradually during succession that need to be understood within the context of community assembly.

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Appendix I: Measures of food-web structure

Biomass densities and flow rates at Equilibrium.

In almost all cases communities had the property of local asymptotic stability of the equilibrium point at which all species had positive densities (as well as the property of permanence); these equilibria thus give useful information on local asymptotic states. The equilibrium biomass densities $\hat{y}_i$ and flow rates become, respectively, the compartments and flows of a steady-state, ecosystem model; in making the switch to ecosystem dynamics, we add an extra term (a) to the community model:

$$0=\hat{y}_i\left(r_i+c_{ii}\hat{y}_i\underbrace{-\sum_{j\in S_i^+}c_{ji}\hat{y}_j}_{\text{(a)}}\underbrace{+\sum_{j\in S_i^+}(c_{ji}+c_{ij})\hat{y}_j}_{\text{(b)}}+\sum_{j\in S_i^-}c_{ij}\hat{y}_j\right); \qquad \text{eqn A1}$$

where S_i^+ (respectively S_i^-) is the set of species that are prey (respectively consumers) of i. Expression (a) is positive (c_{ji} is negative) and describes the total flow rate of biomass density into species i; it cancels out in expression (b) and has no effect on the dynamics or equilibrium biomass densities, but is called for by the bookkeeping of biomass density in the ecosystem model. Expression (b) is negative because ecological efficiency is low (eqn 5); adding this to the loss due to the intrinsic death rate and intraspecific density dependence gives the overall rate at which species i dissipates biomass density accumulated from prey species.

Net primary productivity.

P_1 was measured as the net flow of biomass density into the basal species at equilibrium

$$P_1=\hat{y}_1(r_1+c_{11}\hat{y}_1);$$
$$\text{(dimensions: mass length}^{-3}\text{ time}^{-1}) \qquad \text{eqn A2}$$

this is also the rate of flow of biomass density from the basal to consumer species (no attempt is made to keep track of other losses of biomass density in the basal species). Note that summing eqn A1 over all species, gives:

$$\hat{y}_1(r_1+c_{11}\hat{y}_1)=-\sum_{i>1}\hat{y}_i\left(r_i+c_{ii}\hat{y}_i+\sum_{j\in S_i^-}(c_{ji}+c_{ij})\hat{y}_j\right) \qquad \text{eqn A3}$$

i.e. the net primary productivity is exactly balanced by the total rate at which consumers dissipate biomass density from the ecosystem at equilibrium. Thus the ecosystem model is properly constrained by the primary productivity and, by inference, so is the community model. The ratio of *net primary productivity to total biomass density* at equilibrium is:

$$P_1/\hat{Y}=\hat{y}_1(r_1+c_{11}\hat{y}_1)\Big/\sum_i\hat{y}_i \quad \text{(dimensions: time}^{-1}) \qquad \text{eqn A4}$$

where $\hat{Y}$ is the total biomass density of the ecosystem at equilibrium.

Connectance c of a community was measured as for a directed acyclic graph as:

$$c=2l/(s(s-1)) \qquad \text{eqn A5}$$

where l is the number of links and s is the number of species. *Average interaction strength* was measured as the average absolute value of the non-zero off-diagonal c_{ji} s

$$\bar{c}=\frac{1}{n}\sum_{i\neq j}|c_{ij}| \qquad \text{eqn A6}$$

where n is the number of non-zero off-diagonal c_{ij} s.

Community development capacity C measures the information content of a food web. Here it was calculated from the total flow T_i of biomass density through each species i at equilibrium; expression (a) in eqn A1 was used for consumers and, in the absence of more detailed information, the net primary productivity P_1 (eqn A2) for the basal species, writing the proportion of the flow passing through species i as $Q_i = T_i/T$, where $T = \sum_i T_i$. C was measured as:

$$C = -T\sum_i Q_i \log_e Q_i \qquad \text{eqn A7}$$

(Ulanowicz 1980: eqn 1).

Ascendency A was measured as in eqn 2 of Ulanowicz (1980):

$$A = T\sum_k \sum_j f_{kj}Q_k \log_e\left[f_{kj}\Big/\sum_i f_{ij}Q_i\right] \qquad \text{eqn A8}$$

where f_{ij} is the proportion of biomass density flowing out of species i per unit time, that goes to species j. Eqn 5 does not make explicit whether the loss in biomass density attributable to the ecological efficiency is accounted to the prey or the consumer. The biomass density was subtracted from the consumer here; the assumption makes little difference to the overall results.

Invasion resistance of a community is the proportion of species in the species pool that are: (1) absent from the community and (2) unable to establish themselves in the community. The resident community can be thought of as being at an equilibrium point with biomass densities given by a vector $\hat{\mathbf{y}}$; the rate of increase $f_i(\hat{\mathbf{y}},0)$ of another species j (per unit biomass of j), absent from the community is measured at the equilibrium point of the resident community, giving the following result:

(a) $f_j(\hat{\mathbf{y}},0) > 0 \Rightarrow$ species j invades Inequality A9
(b) $f_j(\hat{\mathbf{y}},0) \leq 0 \Rightarrow$ species j does not invade

(Law 1999: 162). For a community with Lotka–Volterra dynamics, it is remarkable that this result applies even if the resident community has an attractor which is not an equilibrium point. Obtaining the invasion resistance amounts to counting the proportion of the species absent from the community that have property (b); if invasion resistance reaches a value 1, the community is invulnerable to further invasions and at an endpoint of assembly (Morton & Law 1997).

Return time R for a small displacement from equilibrium was computed from the eigenvalues λ of the Jacobian matrix of the community evaluated at the interior equilibrium point as:

$$R = -1/\max(\mathrm{real}(\lambda)). \qquad \text{eqn A10}$$

Distance from diagonal dominance

A Jacobian matrix of a system with Lotka–Volterra dynamics has negative diagonal dominance if there exists a vector of positive constants π_i that satisfy:

$$0 > c_{ii}\pi_i + \sum_{j\neq i} |c_{ij}|\,\pi_j \qquad \text{Inequality A11}$$

(Hofbauer & Sigmund 1988: 193); here the parameters c_{ij} are as defined in eqn 1. Diagonal dominance is useful to know about, because it follows from diagonal dominance that the interior equilibrium must have the property of global asymptotic stability (Hofbauer & Sigmund 1988: 193). It is possible to measure how far from diagonal dominance the Jacobian is using a matrix in which: (1) each off-diagonal element c_{ij} is replaced by its absolute value and (2) the diagonal elements are set to zero. The dominant eigenvalue $\bar{\lambda}_{\max}$ of this new matrix is real and positive, and is the smallest quantity which must be subtracted from the diagonal to achieve diagonal dominance (Neutel, Heesterbeek & de Ruiter 2002). A community in which interactions between species are strongly destabilizing would have a dominant eigenvalue of relatively large positive value. This eigenvalue was therefore used as a measure of the distance from diagonal dominance.

Loop weights carry information about the internal structure of a food web. (The term 'loop' is used interchangably with 'cycle' in different parts of the literature.) The weight W_{kl} of the lth distinct loop of length k is defined as a geometric mean of k non-zero interaction terms $W_{kl} = |c_{i_1i_2}c_{i_2i_3} \dots c_{i_ki_1}|^{1/k}$ and has the property:

$$\bar{\lambda}_{\max} > \max_{k>2,l}(W_{kl}) \qquad \text{Inequality A12}$$

(Krasnosel'skij, Lifshits & Sobolev 1989: 174; Neutel *et al.* 2002); this means that the larger the maximum loop weight, the greater the distance the Jacobian is from diagonal dominance. [The check on loop weights is confined to loops of length > 2 because consumer–prey communities with: (1) density dependence in each species; (2) no loops of length > 2; and (3) dynamics of the type in eqn 1 have a globally stable interior equilibrium point (Hofbauer & Sigmund 1988: 205).] The number of loops of length > 2 was used as an indicator of the extent of cross-linking among consumers in the food web. The maximum weight of loops > 2 in length was used as an indicator of whether loop structure generated by sequential assembly makes diagonal dominance harder to achieve than the loop structure of random communities.