grounded estimates of future biodiversity loss. Limitations on the reliability of this method include the difficulty in estimating the proportion of contemporary biota in Singapore that has not yet reached relaxation (that is, presently surviving, but committed to future extinction)[13,25], the unknown extent to which supplemental migration from mainland Malaysia may have buffered local populations in Singapore from extinction, the uncertainties in estimating the true pristine biodiversity of the island, given the likelihood of past habitat-loss-related extinctions in Peninsular Malaysia, and the uneven geographical distribution of endemic biodiversity 'hotspots'[11], which currently suffer from higher rates of deforestation and degradation than the average of the entire region[10]. Collectively, these potential biases suggest that our projected regional losses are likely to be conservative.

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Productivity–biodiversity relationships depend on the history of community assembly

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Identification of the causes of productivity–species diversity relationships remains a central topic of ecological research[1,2]. Different relations have been attributed to the influence of disturbance[3,4], consumers[5,6], niche specialization[7] and spatial scale[8–14]. One unexplored cause is the history of community assembly, the partly stochastic sequential arrival of species from a regional pool of potential community members. The sequence of species arrival can greatly affect community structure[15–19]. If assembly sequence interacts with productivity to influence diversity, different sequences can contribute to variation in productivity–diversity relationships. Here we report a test of this hypothesis by assembling aquatic microbial communities at five productivity levels using four assembly sequences. About 30 generations after assembly, productivity–diversity relationships took various forms, including a positive, a hump-shaped, a U-shaped and a non-significant pattern, depending on assembly sequence. This variation resulted from idiosyncratic joint effects of assembly sequence, productivity and species identity on species abundances. We suggest that the history of community assembly should be added to the growing list of factors that influence productivity–biodiversity patterns.

Productivity, the amount of energy available for ecosystem development in a given location, has a major effect on species diversity[20–22]. Until recently, hump-shaped relationships, in which diversity peaks at intermediate productivity levels, were the most widely observed pattern[23–25]. We now know that the relationship takes many forms, including hump-shaped, U-shaped, positive, negative and flat (non-significant) patterns, and that none of these patterns predominates[1]. Possible causes of variation include the influence of disturbance[3,4], consumers[5,6], niche specialization[7] and spatial scale[8–14], which can create variation between taxonomic groups and habitat types[1,13]. A few studies suggest that productivity might control the probability that alternative community states are produced through assembly[14,26–28].

Table 1 **Introduction sequences used to assemble communities**

	Sequence			
	A	B	C	D
First introduction	Set 1	Set 1	Set 2	Set 2
Second introduction	Set 2	Set 3	Set 1	Set 3
Third introduction	Set 3	Set 2	Set 3	Set 1

Set 1	Set 2	Set 3
*Blepharisma americanum**‡	*Colpidium striatum**	*Aspidisca* sp.*
Chilomonas sp.*	*Colpoda cucullus**	*Holosticha* sp.*
*Colpoda inflata**	*Euplotes* sp.*†‡	*Lepadella* sp.* (r)
Loxocephalus sp.*	*Paramecium tetraurelia**†	*Rotaria* sp.* (r)
*Paramecium caudatum**†	*Tetrahymena vorax**‡	*Spirostomum* sp.*
*Tetrahymena thermophila**	*Uronema* sp.*	*Tillina magna**

The natural history of these rotifers (marked with (r)) and protozoans (all others) indicates that they consume bacteria and/or microflagellates (*), algae (†), and/or small ciliates (‡). Regardless of their diets, all the species can sustain their population solely on bacteria and/or microflagellates and thus potentially compete with one another.

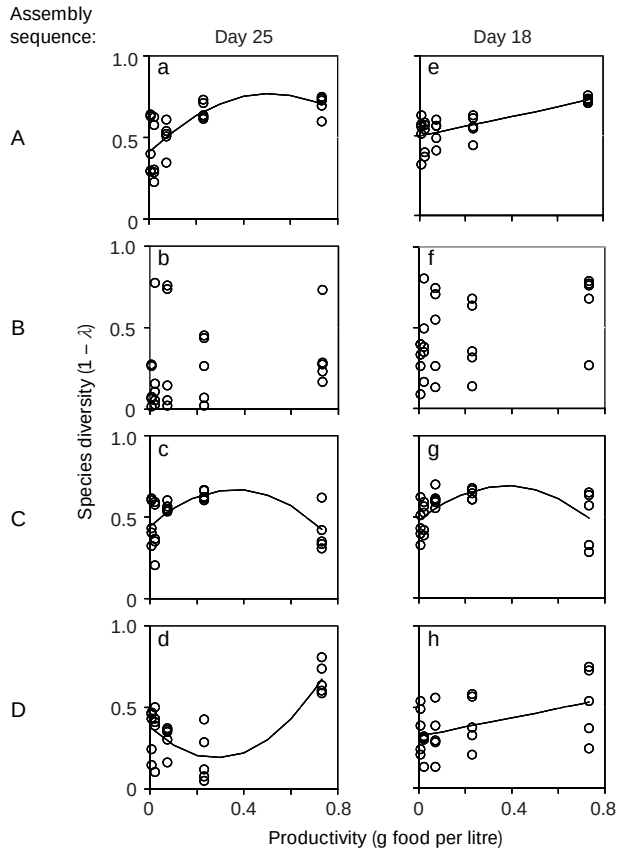

Figure 1 Response of species diversity to productivity. Data are fitted to the best regression models. Productivity refers to protozoan pellet concentration. Some data points are slightly moved vertically (no greater than ±0.005) from their original points so that they can be distinguished more clearly from one another.

Table 2 **Response of species to productivity and assembly sequence**

Species	Productivity 1 (highest)	2	3	4	5 (lowest)
Aspidisca sp.	D C B A	B D C A	D B C A	C B A D	C A B D
	(2.89)	(1.98)	(1.82)	(0.88)	(9.22**)
Blepharisma americanum	A B D C	A C D B	C D A B	A D C B	A D C B
	(13.83***)	(1.69)	(0.67)	(3.30)	(6.65**)
Chilomonas sp.	D C A B	D A C B	D A C B	D A C B	–
	(37.54***)	(1.00)	(1.00)	(1.00)	–
Colpoda cucullus	A B C D	A B C D	A B C D	A B D C	A D C B
	(1.00)	(0.83)	(1.92)	(2.63)	(5.92**)
Euplotes sp.	A C B D	C A B D	C D B A	C A B D	C A B D
	(12.13***)	(6.78**)	(4.21*)	(19.50***)	(5.11*)
Holosticha sp.	C A D B	C A D B	A B D C	D B C A	B D C A
	(3.86)	(24.19***)	(4.07)	(1.09)	(0.28)
Lepadella sp.	A B C D	B A D C	B D C A	A B D C	D C A B
	(4.98)	(7.42**)	(2.20)	(0.86)	(1.79)
Paramecium tetraurelia	C D B A	B A D C	A D C B	A C D B	A B D C
	(7.75**)	(4.25)	(0.42)	(0.82)	(3.58)
Rotaria sp.	B A C D	B A D C	B A D C	B D A C	D B A C
	(160.78***)	(11.13***)	(13.21***)	(6.98**)	(2.96)
Spirostomum sp.	C A B D	C A B D	–	–	–
	(1.03)	(1.57)	–	–	–
Uronema sp.	C B D A	D B A C	B D A C	B D A C	B D C A
	(16.69***)	(12.90***)	(0.33)	(2.37)	(8.04**)

For each species and productivity level, assembly sequences (A, B, C and D) are listed in order of decreasing abundance on day 25. Underlined groups cannot be distinguished statistically with Tukey's studentized range tests. Numbers in parentheses indicate *F*-ratio (ANOVA). *$P < 0.05$; **$P < 0.005$; ***$P < 0.0005$ (only those found to be significant after a sequential Bonferroni correction to preserve a Type 1 error rate of 0.05 are asterisked). Dashes indicate that the species went extinct in all replicates at the corresponding productivity level. Species not listed here went extinct in all replicates at all productivity levels.

We conducted a laboratory experiment using freshwater microbial communities as a model system to test for interactive effects of assembly and productivity on diversity. We manipulated productivity by changing the nutrient concentration of the medium. At each of the five productivity levels used, we first inoculated the medium with bacteria, microflagellates and algae. After allowing them to become abundant, we assembled communities by using four different introduction sequences of 18 protozoan and rotifer species, which consumed bacteria, microflagellates and algae, and thus potentially competed for these shared resources (Table 1). We used a total of 100 microcosms, namely 5 productivity levels × 4 assembly sequences × 5 replicates for each treatment.

Species diversity was expressed as the complement of Simpson's index[29], $1 - \lambda = 1 - \sum p_i(1 - p_i)$, where p_i is the relative frequency of species i, using data obtained 18 and 25 days after the last introduction. We examined the relationship between productivity and species diversity by fitting data to the following models:

model 1: $d = b_0 + b_1 p$
model 2: $d = b_0 + b_1 p + b_2 p^2$
model 3: $d = b_0 + b_1 \log_{10} p$
model 4: $d = b_0 + b_1 \log_{10} p + b_2 (\log_{10} p)^2$

where d is species diversity $(1 - \lambda)$, p is productivity (grams protozoan pellet per litre), and b_0, b_1 and b_2 are regression parameters. Models 1 and 3 linearly relate species diversity to productivity and to log-transformed productivity, respectively. A quadratic term is added to models 1 and 3 to form models 2 and 4, respectively, to test for curvilinearity.

The use of microcosms permitted rigorous control over assembly history, productivity and other environmental conditions. It also enabled us to observe patterns resulting from long-term community dynamics. Use of an experimental duration spanning tens of generations limited the possibility that observed patterns were trivial over ecologically important timescales. It would have been impossible to ensure this level of experimental control in most other natural or laboratory settings. Because all of our microcosms ultimately received the same set of species, any differences in productivity–diversity relations could be attributed to different assembly sequences.

The specific assembly sequence used to create communities generated striking differences in productivity–diversity relationships. Statistical analysis (see Methods) revealed positive ($F = 11.23$, $P = 0.0004$, adjusted $R^2 = 0.4601$ for the best model (model 2); Fig. 1a), non-significant (flat; $F < 1.45$, $P > 0.2425$, adjusted $R^2 < 0.0181$ for all the models; Fig. 1b), hump-shaped ($F = 6.31$, $P = 0.0068$, adjusted $R^2 = 0.3066$ for the best model (model 2) and $P < 0.05$ for Mitchell-Olds & Shaw's test[30]; Fig. 1c) and U-shaped ($F = 19.96$, $P < 0.0001$, adjusted $R^2 = 0.124$ for the best model (model 2) and $P < 0.05$ for Mitchell-Olds & Shaw's test[30]; Fig. 1d) patterns under sequences A, B, C and D, respectively, 25 days after introduction of the last species (see also Supplementary Information). This endpoint corresponded to about 30 complete generations of the organisms involved in community dynamics.

These results also qualitatively hold for data collected 18 days after the last introduction (Fig. 1e–h), confirming that the patterns were temporally consistent and long-lived over ecologically important timescales (see also population dynamics in Supplementary Information). On both days, the relationship was positive, flat (non-significant) and hump-shaped under sequences A, B and C, respectively. Under sequence D, the best model was positive linear for day 18 (Fig. 1h), whereas it was U-shaped for day 25 (Fig. 1d). However, model selection was relatively indecisive for this sequence on day 18, and a U-shaped model (adjusted $R^2 = 0.181$, model 4) explained data almost as well as the positive linear model selected did (adjusted $R^2 = 0.184$, model 1).

We examined how each species responded to productivity and

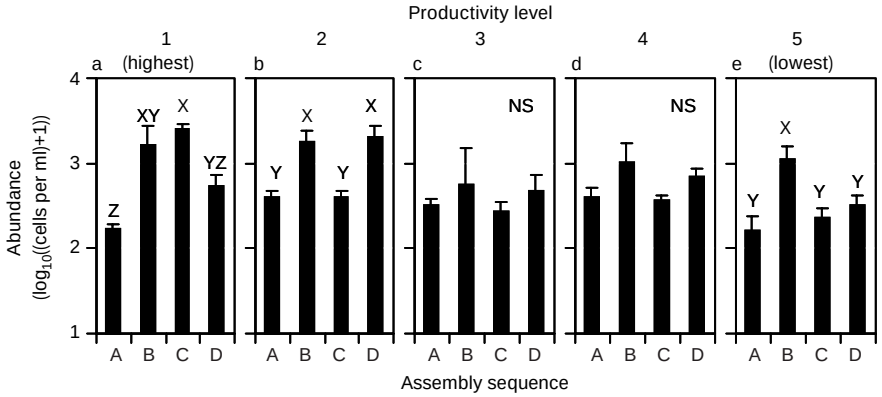

Figure 2 Response of the abundance of *Uronema* sp. to productivity and assembly sequence on day 25. Bars with the same letter above them did not differ in Tukey's studentized range tests. We applied a sequential Bonferroni correction to preserve a Type I error rate of 0.05. NS, not significant (see Table 2). Error bars are s.e.m.

assembly sequence to search for processes that might have created different patterns. For many species, the effect of assembly sequence on abundance depended on productivity. For example, the assembly sequence significantly influenced the abundance of *Uronema* sp. at three out of five productivity levels (Fig. 2). When significant, the effect of assembly sequence on abundance also depended on productivity. *Uronema* was more abundant in sequence C than in sequence D at one productivity level (Fig. 2a), but the difference was reversed at another level (Fig. 2b) and became non-significant at the other levels (Fig. 2c–e). Thus, productivity determined whether a certain sequence either facilitated or inhibited population growth. Furthermore, the effect of sequence also depended on species identity (Table 2). Joint effects of assembly sequence, productivity and species identity were highly idiosyncratic, with no discernible general trends across species (Table 2).

Our results show that community assembly potentially interacts with productivity to create a remarkable variety of productivity–diversity patterns. We emphasize that different assembly sequences alone produced various productivity–diversity patterns, without experimental imposition of variation in disturbance[3,4], consumers[5,6], niche specialization[7] or spatial scale[8–14]. We suspect that assembly sequence might have influenced the operation of these unmanipulated proximate mechanisms[17]. For example, some sequences might have caused consumers and niche specialization, realized by diet differences between species (Table 1), to exert a strong effect on productivity–diversity patterns, whereas other sequences might have minimized their influence. The next step in understanding this phenomenon would be to uncover general mechanisms that explain how assembly produces such diverse patterns. Our results caution against assuming that a single explanatory mechanism at the community level exists, because interactions between species apparently depend in a complex way on assembly sequence, productivity and species identity (Table 2).

Our interpretation of these data assumes that the spatial scale of productivity variation is smaller than that for assembly sequences. Some natural systems meet this assumption. Examples include situations where regular seasonal phenology of species arrival drives assembly or where species invade a region through biogeographic events and spread before the next species invade. Other systems contain local sites that vary in both productivity and assembly sequence. However, we note that assembly has important implications even for these systems: it can make patterns sensitive to the scale of observation[14]. We found that the productivity–diversity relationship was positive linear at a local scale ($P = 0.0017$ and adjusted $R^2 = 0.3255$ for model 1, which was the best model), whereas it was non-significant at a regional scale ($P > 0.02$ for all models; note that $\alpha = 0.0125$ with Bonferroni correction; see Supplementary Information for how we calculated local and regional diversity).

We studied only four of the many possible assembly sequences that could have been used with our species pool. This small sample of assembly sequences makes it impossible to say whether any one of the specific patterns that we observed might predominate in a larger sample. Nevertheless, it is possible that the variety of productivity–biodiversity relationships seen in nature reflects differences in assembly as well as other factors. We suggest that the history of community assembly should be added to the growing list of factors that influence productivity–biodiversity patterns. Assembly history does not preclude the importance of other factors. However, because the detailed assembly history of natural communities is seldom known, it might be difficult to deduce the proximal causes of natural productivity–diversity patterns unambiguously. For this reason, manipulative experiments remain an essential tool for exploring the possible causes of productivity–diversity relationships within the historical context of community assembly. □

Methods

Microcosms

Microcosms were covered sterile 118-ml polypropylene containers. These containers were filled with 30 ml of medium (made from Carolina Biological Supply protozoan pellet, Herpetivite powdered vitamin supplement, and soil in well water) and kept at 22 °C with 14 h light/10 h dark cycles. The medium was autoclaved before use and inoculated with bacteria (*Bacillus subtilis*, *Bacillus cereus*, *Proteus vulgaris*, *Serratia marcescens* and other unidentified bacteria filtered from the stock cultures of all the protozoan and rotifer species used in the experiment), microflagellates and algae (*Chlamydomonas* spp.). These inoculations were done before the medium was distributed to microcosms.

Manipulating productivity

We used five levels of productivity, evenly spaced on a logarithmic scale. The medium for the lowest productivity level consisted of 0.007 g of the protozoan pellet, 0.033 g of the soil and 0.001 g of the vitamins in each litre of well water. The media for the other productivity levels consisted of 0.023, 0.073, 0.232 and 0.733 g of the pellet, 0.106, 0.334, 1.055 and 3.335 g of the soil, and 0.004, 0.013, 0.042 and 0.133 g of the vitamins per litre, respectively, from the second lowest to the highest levels. Removal and replacement of 3 ml (that is, 10%) of the medium of the corresponding nutrient concentration once a week renewed nutrients.

Manipulating assembly sequence

Protozoan and rotifer species were introduced to the microcosms sequentially in accordance with predetermined schedules (Table 1). Stock cultures of six species were used for each introduction. First species were introduced 3 days after the algal inoculation. Subsequent introductions had 14-day intervals. Microcosms received a very small number of individuals, namely less than 0.7% of carrying capacity, but at least 20 individuals per species to preclude trivial extinction by chance at initial stages. To standardize the number of individuals introduced across introduction occasions, population densities in stock cultures were estimated and, if necessary, diluted before introductions. The age of the stock cultures at the time of species introductions was also standardized to minimize variation in physiological conditions of species between different introduction occasions. Microcosms also contained three additional algal species. Because these algae were most probably from cultures of a particular species (*Euplotes* sp.), they did not confound the effect of assembly sequence.

Measuring population abundances

The population abundance of each species in each microcosm was measured once a week until 25 days after the last introduction. Twenty-five days corresponds to roughly 30 generations of the protozoa and rotifer species. Densities were estimated by counting protozoa and rotifers in samples of known volume, typically 0.3 ml, from the 3 ml of medium removed for nutrient replacement. When species were too abundant to count reliably, the sample was diluted. When one or more species were absent from the 0.3-ml sample, the entire 3 ml of medium (and the entire microcosm on the last sampling occasion) was scanned and protozoa and rotifers were counted.

Productivity–diversity relationships

When $P > 0.0125$ (that is, 0.05/4, using a Bonferroni correction to retain a Type I error rate of 0.05) for all models (see model description in text), we concluded that the relationship between productivity and diversity was not significant. When $P < 0.0125$ for more than one model, we selected as the best model the one that had the highest value of adjusted R^2. Adjusted R^2 values are adjusted for the number of parameters in the models. When model 2 or 4 was selected, we determined whether the relationship was hump-shaped or U-shaped by using Mitchell-Olds & Shaw's test[30] (see Supplementary Information). We focused on the diversity of protozoan and rotifer species; our diversity index does not include bacteria, microflagellates or algae. Productivity–diversity relationships depended on assembly history when species richness (number of species per unit volume), rather than the complement of Simpson's index, was also used to express species diversity (see Supplementary Information).

Response of species

We conducted analyses of variance to test for effects of introduction sequence on species abundance at each productivity level. Abundance was transformed as $\log_{10}$((individuals per ml) + 1) before analysis to minimize heteroscedasticity. For each species we used a sequential Bonferroni correction for the five tests corresponding to the five productivity levels to preserve a Type I error rate of 0.05. When analyses of variance found a significant effect of sequence, Tukey's studentized range tests were used to identify which treatments differed.

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The role of neuronal identity in synaptic competition

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In developing mammalian muscle, axon branches of several motor neurons co-innervate the same muscle fibre. Competition among them results in the strengthening of one and the withdrawal of the rest[1,2]. It is not known why one particular axon branch survives or why some competitions resolve sooner than others[3]. Here we show that the fate of axonal branches is strictly related to the identity of the axons with which they compete. When two neurons co-innervate multiple target cells, the losing axon branches in each contest belong to the same neuron and are at nearly the same stage of withdrawal. The axonal arbor of one neuron engages in multiple sets of competitions simultaneously. Each set proceeds at a different rate and heads towards a common outcome based on the identity of the competitor. Competitive vigour at each of these sets of local competitions depends on a globally distributed resource: neurons with larger arborizations are at a competitive disadvantage when confronting neurons with smaller arborizations. An accompanying paper tests the idea that the amount of neurotransmitter released is this global resource[4].

A central feature of mammalian neural development is the reapportionment of synaptic contacts such that neurons progressively innervate fewer postsynaptic cells but with more synapses[5–7]. Synapse elimination at the skeletal neuromuscular junction is currently the best studied of all such rearrangements and viewed by some as a model for changes that occur in the developing brain. In the neuromuscular system of neonatal rodents, the number of muscle fibres contacted by one motor neuron decreases during the first two postnatal weeks until each muscle fibre is innervated by only one axon[8]. Within the arbor of a single motor axon, this branch withdrawal is protracted and asynchronous; after some terminal branches have definitively won or lost at some neuromuscular junctions, other branches of the same neuron still share synaptic sites with other innervating axons[3]. Several lines of evidence suggest that competitions between axon branches underlie this process[9,10]. It is not known, however, what properties of an axonal branch or its environment determine its destiny in these competitions. Here, we ask whether the competitive vigour of each axon branch is determined by local factors or rather is set by a global property of the parent neuron. If axonal branches were acting as agents of their